Growth Responses Of Three Coexisting Conifer Species To Climate Variables Across A Range Of Climate Conditions

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ABSTRACT

Tree-ring analyses and an interpolated climate model (ClimateBC) were used to compare radial growth responses to climate variables among three coexisting, ecologically distinct conifer species, including interior spruce (*Picea glauca x Picea Engelmannii*), lodgepole pine (*Pinus contorta* var. *latifolia*) and subalpine fir (*Abies lasiocarpa*) across a range of climate conditions in western Canada, and altitudinal treelines in the Engelmann Spruce-Subalpine Fir forests in central British Columbia (BC). Ring-width chronologies were developed and correlated with site-specific climate data in the past 50 years from 1953-2002. Spruce ring-width chronologies were mainly correlated with June-July temperatures across the sample sites, while pine and fir chronologies from in BC were correlated with October-March temperatures. Given the species- and site-specific growth responses to climate, future climate change will likely alter interactions among coexisting tree species, potentially leading to changes in species dominance, compositions and distributions of forest communities.

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Chapter 1. Introduction

1.1. Tree responses to climate change

Instrumental records indicate that global surface air temperature increased approximately 0.6 °C in the past 150 years, with nine out of the 10 warmest years on record after 1997 (Jones et al. 1999, Brohan et al. 2006). Based on climate records, higher latitudes warmed more than lower latitudes in the Northern Hemisphere and general circulation models project continued warming in mean annual temperature and slight increase or little change in precipitation in the northern continents (Jones et al. 1999). These changes could significantly affect the distribution and growth of tree species (Woodward 1987). Changes in temperature, precipitation and their interactions will likely alter many factors regulating tree growth, including growing season temperature, heat-sum accumulation, the duration of growing season, chilling requirement and soil moisture availability. Changes in humidity, evapotranspiration and the amount of spring runoff (that is associated with winter snowpack) can also influence moisture availability in soils.

Trees have the ability to adapt to both short- and long-term changes in climate (Linhart and Grant 1996, Ackerly et al. 2000, Gray 2005). Many temperate and boreal tree species tend to show a high degree of intraspecific genetic diversity due to outcrossing, wind pollination, high fecundity and long generation times (Aitken and Hannerz 2001, Hamrick 2004). A high degree of plasticity in trees has been demonstrated in provenance studies, whereby seeds from a single population are planted in different environmental conditions (Rehfeldt et al. 1999). High genetic variation and phenotypic plasticity may allow trees to respond to a greater range of year-to-year environmental variability and extreme events over their long life spans, compared with annuals or short-lived herbaceous perennials (Loehle and LeBlanc 1996, Cordell et al. 1998, Ackerly et al. 2000, Hamrick 2004).

Tree responses to climate may vary by site conditions and species, due to the considerable variations in environmental characteristics (e.g., elevation and topography) and in adaptive traits in trees (e.g., physiology, morphology) (Spittlehouse 1997, 2005, Walther 2003, Gray 2005). For example, high-elevation trees are thought to be more sensitive to temperature variability while the low-elevation trees of the same species may be more sensitive to precipitation variability (Loehle 2000). It has been suggested that the warming in the past 60 years led to the enhanced growth and upward migration of European tree species at altitudinal treelines in the Alps (Kullman 2002), but the warming possibly induced moisture stresses on trees at northern treelines and caused the southward recession of white spruce ranges in Alaska and Yukon (Barber et al. 2000, D'Arrigo et al. 2004). Green (2005) reported that phenological responses, such as advancement or delay of growth initiation and cessation, differed among species and along elevation in northwestern conifers in Canada.

Species-specific responses to climate change may affect competitive ability, with potentially significant impacts on forest ecosystem functioning (Hansen et al. 2001, Walther et al. 2002). Species interactions, dominance, and compositions may change if future climate conditions favour one species over the others. Dullinger et al. (2005), for example, reported that the increases in abundance of Mugo pine (*Pinus mugo* Turra) negatively affected the recruitment and growth of Norway spruce (*Picea abies* [L.] Karst.) and European larch (*Larix decidua* Mill.) seedlings under warming conditions at altitudinal treelines in Austria. They suggest that this could affect the species compositions and geographical distributions of the three coexisting species in the long run.

1.2. Management perspectives

Several authors have suggested that forest managers need to develop adaptive management strategies to minimize risks and maximize benefits that can result from climate change (Spittlehouse 1997, 2005, Stewart et al. 1998, Chuine and Beaubien 2001, Thuiller 2003, Hamrick 2004). From wood-production perspectives, changes in wood supply may pose economic impacts to some extent if future climate alters tree growth rate, reproductive capacity and susceptibility to disturbances (Rehfeldt et al. 1999, Nigh et al. 2004, Wang et al. 2006). For example, Wang et al. (2006) projected that the productivity of interior lodgepole pine in BC will likely increase if mean annual temperature increases to certain thresholds (values are site-specific), but will likely decrease if the warming continues beyond the thresholds. This warming may also change wood strength by changing the proportion of thick cell-walled, dense latewood and thin cell-walled earlywood (Denne 1976, Telewski et al. 1999).

Forest managers should ensure that planted genotypes or species are suited to the current and future environments (Nigh et al. 2004, Spittlehouse 2005). A detailed understanding of site- and species-specific growth responses and potential adaptive patterns may help in refining seed transfer zones and species selection guidelines for reforestation (Spittlehouse 1997, Johnson et al. 2004). A facilitated migration, for example, is a transfer of species or genotypes to regions where productivity may be increased under anticipated future climate conditions (Hamann and Wang 2006, Wang et al. 2006). Wang et al. (2006), for example, projected that the overall productivity of interior lodgepole pine increases 14-36 % if optimal seeds sources, compared with local seed sources, are used for reforestation under a scenario in which mean annual temperature increases by 2 °C in the next 50-100 years. In the absence of additional information, however, genotype redistribution within a species range may have an advantage over the introduction of a species to the regions outside of its current ranges, in terms of minimizing the risk of unexpected decline in the productivity and ecosystem health (Natural Resources Canada 2002).

1.3. Study objectives

This study was conducted to compare radial growth-climate relationships among three coexisting, ecologically distinct northern conifer species. The study species included shade-intolerant, early-successional interior lodgepole pine, shade-tolerant, late-successional subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) and intermediate-shade-tolerant, mid-successional interior spruce (*Picea glauca* (Moench) Voss *x Picea Engelmannii* Parry ex Engelm.). Interior spruce included white spruce (*Picea glauca* [Moench] Voss), Engelmann spruce and their hybrids (*P. glauca* x *P. engelmannii*). These three spruce are treated as the same species in British Columbia (BC) for management purposes (Nigh et al. 2004) and we used this practice in this study. Tree-ring analyses were used to identify important climate variable(s) that were correlated with annual ring-widths in the past 50 years. These important correlations (i.e., growth response) and the strength and direction of the correlations (i.e., growth sensitivity) were compared among and within species at different spatial scales.

Chapter two focused on populations sampled from wide geographic and climate ranges, extending from the southern interior of BC to central Yukon. Changes in growth sensitivities were characterized along climate gradients for each species. Species-specific growth responses to climate were evaluated in relation to the shade-tolerance and successional positions of species.

Chapter three focused on populations at altitudinal treelines, where climate changes are expected to be large (Millar et al. 2004, Christensen et al. 2007). We examined populations at three climatically and geographically distinct treelines in the Engelmann Spruce-Subalpine Fir forests in central BC. We tested a hypothesis that high-elevation trees are more sensitive to temperature than to precipitation. We also investigated potential associations between tree radial growth and the Pacific Decadal Oscillation, a large-scale interdecadal climate variability that is thought to influence the climate of western North America (Mantua and Hare 2002).

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Chapter 2. Growth responses of three coexisting conifer species to climate variables across wide geographic and climate ranges

Abstract

Tree-ring analyses were used to compare radial growth-climate relationships among three coexisting conifer species across wide geographic and climate ranges extending from southern British Columbia (BC) to central Yukon, Canada. Study species included interior spruce (*Picea glauca x Picea Engelmannii*), lodgepole pine (*Pinus contorta* var. *latifolia*) and subalpine fir (*Abies lasiocarpa*). Interior spruce was positively or negatively correlated with June-July temperatures of the current growth year across the sample sites while lodgepole pine and subalpine fir showed intraspecific variations in growth-climate correlations across the sites. BC pine and fir were predominantly positively correlated with October-March temperatures prior to growth. Our data suggest that 1) the growth-climate relationships of interior spruce may differ distinctively from those of lodgepole pine and subalpine fir, 2) winter temperatures prior to growth may have significant impacts on tree growth and forest communities at some sites, and 3) the shade-tolerance and successional positions of tree species may not contribute to predict growth-climate relationships for mature trees.

2.1. Introduction

Climate plays a fundamental role regulating many physiological and phenological activities of trees (Kramer et al. 2000, Kozlowski 2002, Walther 2003). Climate change may result in changes in the growth, survival and reproductive capacity of trees, leading to altered forest communities, including species interaction, abundance, composition, distribution and susceptibility to disturbances (Hänninen et al. 2001, Kramer et al. 2000, 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 analyses can provide long-term growth-climate relationships (Fritts 1976). A large body of literature on tree-ring analyses suggests that radial growth responses to climate are likely site- and species-specific (Cook and Cole 1991, Graumlich 1993, Peterson and Peterson 1994, Villalba et al. 1994, Hofgaard et al. 1999, Mäkinen et al. 2002, Pederson et al. 2004, Goldblum and Rigg 2005). In western North America, for example, numerous studies reported that the radial growth of white spruce (*Picea glauca* [Moench] Voss) was positively (St. George and Luckman 2001, D'Arrigo et al. 2005) or negatively (D'Arrigo et al. 2004, Wilmking et al. 2004) correlated with summer temperatures of the current growth year depending on site environmental conditions of the study sites. Similarly, Splechtna et al. (2000) reported that the radial growth of subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) was negatively correlated with summer temperatures at low-elevations, but positively correlated at high-elevations in the interior of British Columbia (BC). Species-specific growth responses to climate among coexisting species were also reported in several forest types in North America (Graumlich 1993, Peterson and Peterson 1994, Goldblum and Rigg 2005). For example, Peterson and Peterson (1994) reported that the radial growth of Engelmann spruce was correlated with summer temperatures but subalpine fir was correlated with winter precipitation at high-elevation sites in the North Cascade Mountains. Coexisting tree species probably display unique growth responses to climate because they tend to exhibit somewhat different optima for resource requirements to coexist (May 1972, Bazzaz 1987, He et al. 2005).

Many northern conifers are reported to 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 condition (Linderholm 2001). For example, studies reported that the importance of June-July temperatures on the radial growth of Norway spruce (*Picea abies* [L.] Karst.) increased with elevation (Savva et al. 2006) and with latitude (Mäkinen et al. 2002). Although many tree-ring studies have demonstrated intraspecific variations in the growth-climate relationships for single species across its distribution or multiple species within small spatial scales (Villalba et al. 1994, Peterson et al. 2002), it is not clear how these relationships change within and among species across wide geographic and climate ranges.

Interior spruce (*Picea glauca* [Moench] Voss *x Picea Engelmannii* Parry ex Engelm.), lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) and subalpine fir are three conifer species that often coexist across wide geographic and climate ranges in western North America (Burns and Honkala 1990). Lodgepole pine is a shade-intolerant, early-successional species that colonizes quickly after disturbance. Interior spruce is an intermediate-shade-tolerant, mid-successional species, and subalpine fir is a shade-tolerant, late-successional species that increases in abundance and dominance through time in the absence of disturbance. Green (2005, 2007) suggests that lodgepole pine and subalpine fir may show distinct patterns in the growth-climate relationships while interior spruce may display an intermediate pattern among the three study species because of the dissimilarities in ecological characteristics, such as shade-tolerance and successional positions. Green (2007) reported the potential associations between ecological characteristics and phenological responses to seasonal weather conditions among the three coexisting species based on seedling studies in the central interior of BC. However, a question remains if this association exists for mature trees across wide geographic and climate ranges (Green 2007).

Specific study objectives were 1) to identify and compare climate variables most strongly correlated with tree radial growth within and among the species of lodgepole pine, interior spruce and subalpine fir, 2) to characterize clinal patterns in the growth sensitivities of populations to common predictor climate variables along climate gradients for each species, and compare the patterns among species, and 3) to evaluate these comparisons in relation to the shade-tolerance and successional positions of species.

2.2. Methods

2.2.1. Study sites

Study sites extended from the southern interior of British Columbia (BC) to central Yukon, Canada, covering a wide range in mean annual temperature and precipitation (Table 2.1, Figure 2.1, 2.2, Appendix A). The sample sites in BC ranged from 650 m to an altitudinal treeline at 1800 m in elevation and climate conditions varied considerably among the sites. The sample sites were located within five biogeoclimatic zones, including Interior Douglas-fir (IDF), Montane Spruce (MS), Interior Cedar-Hemlock (ICH), Engelmann

Spruce-Subalpine Fir (ESSF), and Sub-Boreal-Spruce (SBS) zones (Meidinger and Pojar 1991) (Table 2.1). IDF has dry and warm summers with relatively long growing seasons and cool winters. MS has warm, relatively short summers and cold winters. ICH is one of the wettest zones in the interior of BC and has warm dry summers and cool wet winters. ESSF occurs at high-elevations and has cool and short summers and long, cold, and snowy winters. The climate of the SBS is characterized as relatively warm, moist, and short summers and severe, snowy winters. Central Yukon has a continental climate characterized by very cold and long winters, and warm short summers with relatively low precipitation (Figure 2.2).

Site-selection criteria included 1) more than 60-year old stands to provide sufficient ring-width records, 2) stands on zonal sites to represent intermediate topographic and edaphic conditions within an area, 3) the minimal visible evidence of stand-level disturbance events to minimize non-climatic signals in tree ring-widths, and 4) proximity to a local weather station to minimize potential errors in site-specific climate records estimated by the ClimateBC model (described in 2.2.3). Stands were naturally regenerated, mid- to late-successional stage forests. Sampling along an elevational transect was conducted wherever possible to provide climate gradients within narrow geographic locations (E1-E4 and N2-N3). Three species were sampled from one stand when possible (i.e., C1, W), but they were sampled from two or three nearby stands when only single species dominated sample stands (i.e., S, Nn). Low- to mid- elevation stands ($\leq$ 1400 m) were characterized as dense, closed canopy and deciduous-conifer mixed stands. High-elevation stands (1500 - 1800 m) were typically less dense, open canopy and conifer-dominant stands.

2.2.2. Chronology development

One or two tree increment cores were extracted at breast height (1.3 m) from a minimum of 20 trees per species per site in 2005-2006. The coring height of 1.3 m was chosen because it provided sufficient growth ring records of longer than 50 years. Healthy, canopy-dominant trees with little observable damage were selected for coring to minimize non-climatic variation in ring-widths. Standard dendrochronology techniques were applied to develop site- and species-specific tree-ring chronologies (Fritts 1976). Sampled cores were mounted and sanded with increasing grain size (to 600 per inch) to observe annual rings clearly (Stokes and Smiley 1968). Crossdating is a procedure to identify the exact year of ring formation by synchronously matching ring-width patterns among all sampled cores from a given site. Crossdating helps to detect any missing or false rings, because trees may fail to produce an annual ring or may produce two rings in a year. Narrow rings were used as pointer-years during visual crossdating (Yamaguchi 1991). Annual ring-widths were measured to 0.01 mm using the computer program WinDENDRO™ (Regent Instruments Inc. 2005). The Velmex ring-measurement system (Velmex Inc. 1992) interfaced with MeasureJ2X (VoorTech Consulting 2004) with precision 0.001 mm was used to measure small rings. A computer program COFECHA (Grissino-Mayer 2001) was used to statistically detect potential errors and to validate visual crossdating. Cores that did not crossdate (with a critical threshold intercorrelation value of 0.36 based on 40-year segment with 20-year lag) were re-examined under a microscope and remeasured using MeasureJ2X. Those cores that did not crossdate after the re-examination were removed from the final chronology development.

The raw ring-width measurements for each crossdated series were standardized by converting to dimensionless ring-width indices to minimize non-climatic factors and autocorrelations

(Fritts 1976). Non-climatic factors influencing ring-width variation may include tree age, competition, disturbance and random variation (Cook 1985). Younger trees, for instance, generally have higher photosynthetic rates than older trees. This age-dependent biological trend often results in the formation of wider annual rings during the early years of growth and narrower annual rings during the later years regardless of climate condition. Changes in interspecific and intraspecific competitions and below-ground characteristics also influence low-frequency variation in ring-widths. Ring-width series may retain autocorrelation because 1) physiological processes within a tree often cause a lag in growth responses to climate and 2) climate conditions tend to persist from one year to the next.

Each core was standardized by fitting a cubic smoothing spline with a 50% frequency response cutoff of 20 or 40 years using a program ARSTAN (Cook 1985). The ring-width indices of individually standardized cores were then averaged among all crossdated cores in a population to develop a ring-width chronology for each species at each site. The Arstan chronology, autocorrelation removed and pooled autoregression (common persistence) built back in, was developed to maximize climate signal in the ring-width variation (Cook and Holmes 1986). The preliminary results and visual assessment of the standardized chronologies showed that the 40-year smoothing spline reduced unwanted low-frequency variation while maintaining strong common signals for most populations. A more stochastic detrending method with the 20-year smoothing spline was used for populations from dense, closed-canopy and low-elevation stands to minimize low-frequency variation that may have resulted from stand dynamics (Appendix B). Different spline lengths were applied because standardization should maximize the climate signals of each chronology from forests with different stand histories and characteristics. This practice is rare in dendroecology, but has been done to study populations from closed versus open canopy stands (Szeicz 1997).

Mean sensitivity and standard deviation were calculated to evaluate the quality of standardized chronologies. Mean sensitivity is a measure of response to year-to-year climate variation and standard deviation indicates low- to medium-frequency variation in the ring-width chronologies, and higher values indicate that the ring-width chronologies contain common climate signals (Fritts 1976, Villalba et al. 1994). Mean sensitivity is calculated as the absolute difference between adjacent ring-widths divided by the mean of the two ring-widths.

2.2.3. Climate data

Site-specific climate data were estimated using a climate model, ClimateBC version 3.2 (Wang et al. 2006). ClimateBC requires latitude, longitude, and elevation to generate site-specific monthly, seasonal and annual climate variables in western Canada based on PRISM (parameter-elevation regressions on independent slopes model). PRISM is a regression-based model that incorporates geographic influences on climate, including elevation, aspect, coastal effects and orographic influences (Daly et al. 2002, Hamann and Wang 2005). For example, elevation is a strong predictor of temperature because temperature decreases almost linearly with altitude. Based on the topographical features, PRISM adjusts reference weather station data to estimate mean monthly temperature and precipitation for each grid at a resolution of approximately 4 km. Information from each reference weather station is weighted based on a distance from a target grid cell, elevation and other topographic factors to calculate the values of the target cell. On top of the medium resolution climate data of 4 km grid, ClimateBC uses a high-resolution digital elevation model to build a locally and temporary scale-free climate model for finer scale climate estimates (Wang et al. 2006). The verification was conducted by comparing predicted and observed climate data from 191 weather stations that had sufficient climate records included in the 1951-1980 or 1961-1990 normals (Wang et al. 2006).

2.2.4. Growth-climate relationships

Pearson simple correlation coefficients were calculated to identify climate variable(s) associated with variations in the Arstan chronologies ($P < 0.05$). We selected monthly climate variables for 17 months extending from May of the previous growth year to September of the current growth year to include two complete growing seasons (Larsen and McDonald 1995, Brooks et al. 1998). Climate variables used in the correlation analyses included mean, minimum and maximum monthly temperatures, monthly total precipitation, monthly heat-moisture indices and annual derived variables, including degree-days, frost-free days and frost-free period (the number of consecutive frost-free days) (Wang et al. 2006). Heat-moisture index indicates moisture availability in a given month and is calculated as

Heat-moisture index = temperature / (precipitation / 1000)

Because this index considers both precipitation and evapotranspiration (related to temperature), it tends to better reflect moisture availability than precipitation alone (Wang et al. 2006). Degree-days are the amount of heat energy available for plant growth, calculated as the sum of the difference between mean daily temperature and 5 °C (growing degree-days) or 18 °C (heating degree-days) for a year. A 50-year period from 1953 to 2002 was used because this length could minimize errors in climate data estimates related to the small numbers of monitoring stations in existence prior to 1950.

2.2.5. Gradient analyses

When ring-width chronologies showed strong significant correlations with the climate variables of two or more consecutive months, these monthly climate variables were averaged to form a seasonal climate variable. Simple linear regression analyses were used to evaluate the strength and importance of predictor climate variables on variation in ring-width indices. The slope of regression (b1) represented the direction and strength of the relationship and was defined as the growth sensitivity of a population to the climate variable. We considered multiple regression analyses to improve the prediction of annual ring-width indices using multiple climate variables. However, multiple regression results were not reported because the predictor climate variables were seldom consistent across the large number of sampled populations and they would limit comparative investigation across the sites and among species.

The regression coefficients (b1) of populations to the selected predictor climate variables were examined along climate gradients for each species using simple- and multiple regression analyses ($P < 0.05$). Climate gradients used to predict the regression coefficients included mean annual and seasonal temperatures and precipitation during the 1961-1990 period. Normality was tested using the Kolmogorov-Smirnov normality test. The analyses were conducted using the statistical software SPSS (SPSS Inc. 1999).

2.3. Results

2.3.1. Chronology statistics

Forty Arstan ring-width chronologies were developed (Appendix B). Average mean sensitivity was 0.16 ± 0.03, 0.14 ± 0.04 and 0.12 ± 0.02 for lodgepole pine, interior spruce and subalpine fir, respectively. Previous studies suggest that a mean sensitivity range of 0.09-0.16 is sufficient to make growth-climate comparisons for the three species (Villalba et al. 1994, Ettl and Peterson 1995). Standard deviations were 0.77 ± 0.25, 0.58 ± 0.22 and 0.57 ± 0.18 for lodgepole pine, interior spruce and subalpine fir, respectively.

2.3.2. Growth-climate relationships

We focused on correlations established between ring-width chronologies and mean monthly temperatures to examine growth-climate relationships for two reasons. First, ring-width chronologies generally had stronger and more consistent correlations with mean monthly temperatures than with monthly precipitation (Appendix C). Second, ring-width chronologies showed significant correlations with several climate variables that were highly associated with each other. For example, populations that showed positive correlations with mean June-July temperatures generally showed positive correlations with June-July maximum and minimum temperatures and growing and heating degree-days. The objective of this study was the comparative investigation among populations rather than among the related climate variables and thus, we mainly presented the relationships between growth and monthly temperatures, except where there were important precipitation and heat-moisture correlations that might be related to temperature influences.

Our data showed that significant correlations between monthly temperatures and ring-width chronologies varied among the three species (Table 2.2). Eleven out of the 14 interior spruce populations had significant correlations with June and/or July temperatures of the current growth year (Table 2.2a). Interior spruce populations at low-elevation and warmer sites in BC (S, C1, C2, E1, E2) and northern most site in Yukon (Nn) showed either negative or no correlations with June temperatures of the current growth year. However, high-elevation and western populations in BC (E3, E4, W, Ww) and two Yukon populations (N1, N2) were positively correlated with June and July temperatures.

Monthly temperature variables that were significantly correlated with lodgepole pine ring-width chronologies varied among sites, most notably between BC and Yukon. BC populations except for the southern most site (S) were predominantly positively correlated with temperatures from October to March prior to growth, with an exception of no significant correlation in December (Table 2.2b). Seven out of the 10 BC populations also showed weak (Appendix C) positive correlations with July and August temperatures of the current growth year. Yukon populations, however, were primarily negatively correlated with June temperatures of the current growth year and summer temperatures in the previous growth year. In addition, Yukon populations also showed negative correlations with summer heat-moisture conditions, including July and August of the previous growth year and June of the current growth year (Table 2.3).

Monthly temperature variables that were significantly correlated with subalpine fir varied considerably among the sample sites (Table 2.2c). Within BC, high-elevation and western populations (E4, W, Ww) were strongly positively correlated with temperatures from October to March prior to growth (Table 2.2c, Appendix C). During summer months, western populations (W, Ww) were positively correlated with July temperatures of the current growth year, while low- to mid-elevation populations in BC (E1-3, C1, S) were negatively correlated with May and/or June temperatures of the current growth year and July and/or August temperatures of the previous growth year. Yukon populations were negatively correlated with temperatures of the previous or current growing seasons.

2.3.3. Gradient analyses

Based on the correlations (Table 2.2), we selected growing season and October-March temperature variables to analyze how sensitivities of populations to these common predictor variables changed along climate gradients (Table 2.4). Growing season temperature was defined as any month(s) between May and August with which each population showed significant correlations. The regression coefficients (b1) of interior spruce and lodgepole pine to the growing season temperatures changed linearly along gradients in mean summer (June-August) temperature and/or precipitation (Figure 2.3). The regression coefficients of lodgepole pine and subalpine fir to October-March temperatures changed along the mean annual temperature gradient in BC (Figure 2.4). We considered the interactive effects of site temperature and precipitation to predict regression coefficients, but no multiple regressions were significant. Thus, only results from simple linear regression were presented.

2.3.3.1. Growing season temperatures

The regression coefficients of interior spruce ring-width indices regressed on June-July temperatures had an inverse relationship with mean summer temperatures ($P < 0.0004$, Figure 2.3a), but had no significant relationship with mean summer precipitation ($P = 0.51$, Figure 2.3b). The threshold temperature (x-intercept at $y = 0$) where the regression relationships changed from positive to negative was 12.4 °C.

Important growing season temperature variables that predicted the ring-width indices of lodgepole pine varied between BC and Yukon (Table 2.4). In BC, the regression coefficients of lodgepole pine ring-width indices against July-August temperatures had negative relationship with mean summer temperatures ($P = 0.02$, Figure 2.3c). No significant correlation was found between the regression coefficients and mean summer temperatures across the entire study region ($P = 0.09$, Figure 2.3c). However, a non-linear positive relationship was observed between mean summer precipitation and the regression coefficients of the ring-width indices against growing season temperatures (July-August for BC and June for Yukon) across the entire study region ($P < 0.0004$, Figure 2.3d). Further examination of the non-linear relationship revealed that the regression coefficients of pine increased linearly along summer precipitation up to 250 mm ($P < 0.0004$), after which no further increases were observed. The threshold precipitation (x-intercept at $y = 0$) where significant relationships changed from positive to negative was 167 mm.

Although eight out of the 12 subalpine fir ring-width chronologies were significantly correlated with growing season temperatures (either positively to July or negatively to May-June, Table 2.4), the regression coefficients of fir against the predictor growing season temperatures did not change along gradients of mean summer temperatures ($P = 0.07$) or mean summer precipitation ($P = 0.80$). No linear tend was found among BC populations for either summer temperature or precipitation gradients ($P \geq 0.16$).

2.3.3.2. October-March temperatures

Based on the correlations found with lodgepole pine and subalpine fir (Table 2.2), mean monthly temperatures from October to March prior to growing season were averaged. In BC, nine out of the ten lodgepole pine and five out of the nine subalpine fir ring-width chronologies had positive correlations with average October-March temperatures prior to growth (Table 2.4). No such relationship was observed for any Yukon populations or spruce. Within BC, the regression coefficients of ring-width indices against October-March temperatures had a negative relationship with mean annual temperatures for lodgepole pine ($P < 0.0004$) and subalpine fir ($P = 0.009$, Figure 2.4). The regression coefficients of lodgepole pine and subalpine fir against October-March temperatures were not correlated with mean annual precipitation for lodgepole pine ($P = 0.71$) or fir ($P = 0.80$) within BC. Mean annual temperatures were significantly positively correlated with growing degree-days (> 5°C), frost-free days and frost-free period within BC ($P < 0.0004$ for each variable).

2.4. Discussion

Our data suggest that 1) the response and sensitivity of trees to seasonal climate variables vary among species and sites, 2) the growth-climate relationships of interior spruce may differ distinctively from those of lodgepole pine and subalpine fir examined across the wide geographic and climate ranges sampled in British Columbia (BC) and Yukon, 3) winter temperatures prior to active growth may be important in assessing the potential impacts of climate change on tree growth and forest communities and 4) the shade-tolerance and successional positions of tree species may not contribute to prediction of the radial growth-climate relationships for mature trees.

2.4.1. Spatial patterns

The three study species showed different spatial variations in growth-climate relationships across the sample sites in BC and Yukon. Our data suggest that interior spruce may exhibit a common ring-width response to summer temperatures over several thousand kilometers in western Canada. Previous studies also found spatially consistent growth responses (positively or negatively) to summer temperatures among the populations of white spruce (Peterson and Peterson 1994), Engelmann spruce (St. George and Luckman 2001) and Norway spruce (*Picea* *abies* [L.] Karst.) (Mäkinen et al. 2000, 2002). For example, St. George and Luckman (2001) studied 17 Engelmann spruce ring-width chronologies across a 500-km-long sample region in the Canadian Rocky Mountains, and they found positive correlations with summer temperatures (most obviously in June-July) of the current growth year for most populations. In Scandinavia, Mäkinen et al. (2000) reported the similar results for 40 Norway spruce populations sampled from five geographic regions, characterized as having different environmental conditions, extending from central Finland to the Arctic timberline.

Our data showed that the growth-climate relationships of lodgepole pine differed distinctively between BC and Yukon. Wheeler and Guries (1982) suggest the genetically distinct subgroups of interior lodgepole pine between BC and Yukon, based on the number and frequency of rare alleles. They suggest that the genetic differentiation of lodgepole pine possibly occurred during the most recent glacial event. Lodgepole pine that is currently distributed in western Canada probably existed in two separate ice-free refugia, including western central Yukon and the southwestern United States. The northern populations of lodgepole pine might have migrated southward as the glacier retreated and met by the lodgepole pine populations moving north, probably around a few kilometers south of the BC-Yukon boarder. Xie and Ying (1995) also suggest distinct lodgepole pine subgroups based on provenance studies. They reported that lodgepole pine populations from southern and central BC showed similar variations in 20-year height growth and volume, but they showed significantly different variations in these growth traits from populations north of 57 °N. Therefore, genetic differentiation within species may explain the distinct growth-climate relationships found between BC and Yukon populations in this study.

Our data and previous studies suggest that the growth-climate relationships of subalpine fir may be spatially variable due 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 data agreed with previous studies that subalpine fir populations at low-elevation were negatively correlated with May and/or June temperatures of the current growth year while populations at high-elevations were positively correlated with July temperatures in the southern and central interior of BC (Splechtna et al. 2000) and on the northwest coast of the United States (Ettl and Peterson 1995, Peterson et al. 2002). Several studies also reported that subalpine fir had strong associations with winter and spring temperatures and snow depth at high-elevations but not at low-elevations (Ettl and Peterson 1995, Peterson et al. 2002, Larocque and Smith 2005).

2.4.2. Gradient analyses

2.4.2.1. Growing season temperatures

Our data suggest that local summer temperatures may be important in predicting the growth responses and sensitivities of interior spruce to June-July temperatures (Figure 2.3a). Warm June-July temperatures enhance tree radial growth at cooler sites for several possible reasons. These include higher day- and night-time temperatures that enhance photosynthesis and carbohydrate allocation to the stem (Körner 1998), higher photosynthetically active radiation available due to more sunny days (Goldblum and Rigg 2005), the extension of the growing season (Danby and Hik 2007) and/or the interaction of these factors. Savva et al. (2006), for example, found that the positive correlation coefficients between the radial growth of Norway spruce and June-July temperatures increased linearly with elevation. They suggest that warm summer temperatures may favour the growth of populations at high-elevation sites, where growing season is generally short. St. George and Luckman (2001) and Wilson and Luckman (2003) also reported similar results for high-elevation Engelmann spruce in BC. By contrast, warm temperatures during the growing season may induce moisture stress and cause reduced growth at warm sites (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). Trees may increase transpiration rates and close a large proportion of stomata on leaves to minimize water losses in response to warm temperatures and moisture stress, which may result in reduced net photosynthesis and growth (Kozlowski 2002). For example, 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 evapotraspiration potentially equals annual precipitation. They found that the negative relationship was associated with reduced CO_2 uptake and higher water vapour loss during photosynthesis.

In contrast with spruce, local precipitation may be more important than temperatures in predicting the growth sensitivities of lodgepole pine to growing season temperatures (Figure 2.3d). All Yukon sites received less than 150 mm of summer precipitation and thus, warm temperatures might have induced moisture stress on tree radial growth as suggested in spruce (Barber et al. 2000, D'Arrigo et al. 2004, 2005, Wilmking et al. 2004). On the other hand, temperature-induced moisture stress was unlikely for lodgepole pine in BC because they occurred at sites moister than 155 mm and had positive correlations with growing season temperatures. Among the three study species, lodgepole pine tends to grow at warmer and drier sites, whereas interior spruce often dominates cooler and moister environments (Burns and

Honkala 1990). Therefore, moisture may be more of a limiting resource for lodgepole pine, and temperature may be more of a limiting resource for interior spruce during the growing season.

2.4.2.2. October-March temperatures

Temperatures prior to active growth may have stronger impact than growing season temperatures on the radial growth of lodgepole pine and subalpine fir in BC. Several studies suggest that the extension of the growing season, associated with early snowmelt and late snowfall, may explain the positive effects of 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) suggest that the timing of snowmelt in the spring may 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), lodgepole pine (Case and Peterson 2007) and mountain hemlock (Graumlich and Brubaker 1986, Peterson and Peterson 2001) at high-elevations in western North America and several *Larix* species in subarctic Russia (Kirdyanov et al. 2003).

Preconditioning may explain the positive influences of warm early winter temperatures on tree growth in the following growing season (Lebourgeois 2000). Although stem growth processes cease in late summer, trees may continue photosynthetic activities under favourable growing conditions that are extended into late fall. Carbohydrates produced at this time can be stored in plant tissues (i.e., roots, twigs, old leaves) in the fall and used for 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 southern European Alps (Oberhuber 2004, Pfeifer et al. 2005, Carrer et al. 2007).

Our data showed that the importance of warm October-March temperatures on radial growth increased as mean annual temperatures decreased. Mean annual temperatures were positively correlated with growing degree-days (> 5 °C), frost-free days and frost-free period within BC, suggesting that growing season conditions were limited at colder sites in BC. In addition, no pine populations had significant correlations with temperatures in December (Table 2.2b), suggesting that temperatures in the early and late winter months might be more important than those in the mid-winter for lodgepole pine.

The potential negative impacts of high snowfall on tree growth (Peterson and Peterson 2001, Larocque and Smith 2005) remained unclear in this study because our data did not show significant relationships between winter precipitation and the ring-width chronologies of lodgepole pine or subalpine fir (Appendix C). However, Knowles et al. (2006) showed that reduced snowfall in the western United States in the past 55 years was unrelated to the changes in the total precipitation. Holding precipitation constant, warm winter temperatures decrease the percentage of precipitation that falls as snow and increase dense, wet snow that is close to melting point (MWLAP 2002, Wang et al. 2006). Therefore, variation in temperature rather than precipitation may have more impacts on the total amounts of snowfall 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.

2.4.3. Growth responses of ecologically distinct species

This study suggests that shade-tolerance or successional positions may not contribute to predict the growth responses of coexisting species to climate variables across their ranges in BC and Yukon, at least for mature trees growing under natural conditions. Interior spruce and subalpine fir are expected to 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). In this study, the growth responses of interior spruce differed distinctively from those of lodgepole pine and subalpine fir. By contrast, Green (2005, 2007) found distinct clinal patterns in phenological responses between lodgepole pine and subalpine fir seedlings along an elevational transect in central BC. These contradictory observations between our data and previous studies may be related to tree age. Tree physiology generally changes with age, which may cause shifts in sensitivities to environmental stresses (Carrer and Urbinati 2004). For example, He et al. (2005) reported that the drought sensitivities of four deciduous tree species were associated with shade-tolerance and successional positions in saplings, but not in mature trees. Van Der Kamp (1990) also reported that the susceptibility of conifer buds to the extreme cold weather differed between young (10-15 years) and mature trees in BC. Differences in growth responses among species with different levels of shade-tolerance and successional positions may be more directly related to changes in competition levels (i.e., light) and the frequency of disturbance (i.e., fire), respectively, than to climate (Johnstone and Chapin 2003, Simard et al. 2004).

Biogeography and genecology of each species may provide possible explanations of the species- and site-specific adaptive responses to climate. For example, lodgepole pine in Yukon and BC exhibited unique responses to climate possibly due to distinct genetic structures and migration routes found between the two subgroups (Wheeler and Guries 1982, Xie and Ying 1995). Similarly, geologic studies suggest that subalpine fir existed in the coastal regions of the southwestern United States (Ettl and Peterson 2001) while white spruce existed in the unglaciated regions in Yukon and Alaska (Cwynar and Spear 1991) during the most recent glacial period. These two species might have been subjected to different selection pressures during their migrations into the current ranges in BC and Yukon from different routes. White spruce was probably more suited for cold continental climate than subalpine fir (Cwynar and Spear 1991). Therefore, evolutionary history might explain the expression of unique growth-climate relationships among species.

2.4.4. Implications

Different growth responses to seasonal climate among coexisting species may alter the species interaction, dominance and composition of forest communities under future climate change (Stohlgren and Bachand 1997, Zolbrod and Peterson 1999, Millar et al. 2004). For example, changes in growing season temperatures may significantly alter competitive relationships between lodgepole pine and interior spruce at warmer sites in BC, because lodgepole pine was positively and interior spruce was negatively correlated with growing season temperatures at sites warmer than 12.4 °C. This study also suggests that changes in winter temperatures can have significant impacts on tree radial growth and forest ecosystems. Instrumental climate records showed that the greatest magnitude of warming in the past 150 years occurred in winter and early spring, rather than summer, at the global scale (Jones et al. 1999, Barber et al. 2000). General circulation models also predict that winter minimum temperatures will increase and more winter precipitation will occur as rain in northwestern North America in the next several decades (Christensen 2007). Warm winter temperatures may favour the growth of lodgepole pine and subalpine fir at cold sites in the interior of BC, potentially resulting in higher survival rates, mechanical stability and reproductive capacity of these species (Givnish 1995, Despland and Houle 1997, Loehle 2000). Consequently, lodgepole pine may increase in abundance and shift its ranges into high-elevation spruce-fir forests (Millar et al. 2004). Winter condition, therefore, should be considered when evaluating the potential impacts of tree growth and forest ecosystems.

2.5. Literature cited

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Table 2.1. Descriptions of the sample sites.

Site	Species	Elevation (m)	Latitude (N)	Longitude (W)	Aspect	BEC in BC	Site Codes
British Columbia							
Vernon							
Silver Star	Pl	1000	50° 19’	119° 08’	S	IDF mw	S
King Eddy	Sx	1165	50° 10’	119° 11’	SE	MS dm	S
King Eddy	Bl	1200	50° 10’	119° 11’	SE	MS dm	S
Prince George							
Cranbrook Hill	Pl/Sx/Bl	753.5	53° 55’	122° 53’	Flat	SBS dw	C1
Domano Blvd.	Pl/Sx	650.4	53° 48’	122° 44’	Flat	SBS mk	C2
McBride							
McBride Peak	Pl/Sx/Bl	1200	53° 19’	120° 09’	SW	ICH mm	E1
McBride Peak	Pl/Sx/Bl	1400	53° 19’	120° 08’	SW	ICH mm	E2
McBride Peak	Pl/Sx/Bl	1600	53° 19’	120° 07’	SW	ESSF mm	E3
McBride Peak*	Pl/Sx/Bl	1800	53° 20’	120° 07’	SW	ESSF mm	E4*
Smithers							
Onion Mnt. *	Pl/Sx/Bl	1550	54° 48’	126° 52’	SW	ESSF mc	Ww1*
Onion Mnt.	Sx/Bl	1360	54° 48’	126° 53’	SW	ESSF mc	Ww2
Hudson Bay Mnt.	Pl	1400	54° 45’	127° 15’	S	ESSF wv	Ww2
South of Fraser Lake							
Top Lake*	Pl/Sx/Bl	1640	53° 16’	125° 10’	SW	ESSF mv	W*
Yukon							
Whitehorse							
Wolf Creek	Pl/Sx/Bl	950	60° 35’	135° 03’	SW	N/A	N1
Grey Mountain	Pl/Sx/Bl	1150	60° 39’	134° 53’	E	N/A	N2
Grey Mountain	Pl	820	60° 41’	134° 58’	E	N/A	N3
Grey Mountain	Sx	845	60° 41’	134° 57’	E	N/A	N3
Mayo, Keno							
Mayo	Sx	520	63° 37’	135° 53’	SW	N/A	Nn
Mayo	Pl	510	63° 29’	136° 16’	Flat	N/A	Nn
Keno Hill	Bl	1300	63° 55’	135° 15’	S	N/A	Nn

Note: Abbreviations for the tree species are lodgepole pine (Pl), interior spruce (Sx) and subalpine fir (Bl). Abbreviations for biogeoclimatic zones are Interior Douglas-fir (IDF), Montane Spruce (MS), Interior Cedar-Hemlock (ICH), Engelmann Spruce-Subalpine Fir (ESSF), and Sub-Boreal-Spruce (SBS); subzones are moist-mild (mm), wet-cool (wk), wet-cold (wc), dry-warm (dw) and moist-cool (mk) (Meidinger and Pojar 1991). * indicate altitudinal treeline sites. Site codes were assigned based on relative NEWS direction from Prince George (Central).

Table 2.2. Significant correlation relationships between mean monthly temperatures and ring-width chronologies from May of the previous growth year to September of the current growth year for the period 1953-2002. Only significant relationships are shown ($P < 0.05$).

a) Interior spruce

	Previous year								Current year								
Site	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S
S		-			-												
C1		-												-			
C2														-			
E1		-	-														
E2														-			
E3						-								+	+		
E4			-											+	+		
W														+	+		
Ww1							+						+	+	+		
Ww2				+									+	+	+		
N1										-	-			+	+		
N2		-									-			+	+		
N3										+							
Nn		-	-	-									-	-			
	0	5	3	2	1	1	1	0	0	2	2	0	4	11	7	0	0

Number of significant correlations

b) Lodgepole pine

	Previous year								Current year								
Site	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S
S																	
C1							+			+							-
C2							+		+	+	+						
E1							+		+	+	+				+	+	
E2				-		+	+			+	+				+	+	
E3				-			+		+	+	+					+	
E4			-	-		+	+		+	+							
W		-				+	+		+		+				+	+	
Ww1		+				+			+	+	+				+		-
Ww2	+	+	+			+	+		+		+				+		-
N1				-										-			
N2			-	-	-									-			
N3				-	-									-			
Nn			-					+						-		+	
	1	3	4	6	2	5	8	1	7	7	7	0	0	4	5	5	3

Number of significant correlations

c) Subalpine fir

	Previous year								Current year								
Site	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S
S				-									-			+	
C1													-	-			
E1			-	-			+						-	-			
E2			-	-		+								-			
E3			-										-				
E4			-		+	+	+	+									
W						+	+	+	+		+				+		
Ww1	+	+	+		+	+	+	+	+		+			+	+		-
Ww2						+	+		+	+		-			+		
N1			-	-													
N2			-	-										-			
Nn													-		+		
	1	2	5	4	2	5	5	3	3	1	2	1	4	5	5	1	1

Number of significant correlations

Table 2.3. Correlation relationships between monthly heat-moisture chronologies and the ring-width chronologies of lodgepole pine populations in Yukon from May of the previous growth year to September of the current growth year for the period 1953-2002. Only significant relationships are shown ($P < 0.05$).

	Previous year								Current year								
Site	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S
N1			-											-			
N2			-	-										-			-
N3				-	-						+		-	-			
Nn			-	-				-	+					-			

Table 2.4. The coefficient of determination (R^2) from the simple linear regression analyses between ring-width chronologies and selected predictor climate variables. Only significant relationships are shown ($P < 0.05$).

	Spruce	Lodgepole pine			Subalpine fir	
Sites	Growing season	Growing season	Oct-March	Summer HM	Growing season	Oct-March
S	-	-	-	-	-	-
C1	0.11	-	0.18	-	0.30 ^{d}	-
C2	0.13	-	0.21	-	n/a	n/a
E1	-	0.18 ^{a}	0.16	-	0.23 ^{d}	-
E2	-	0.16 ^{a}	0.25	-	0.15 ^{d}	-
E3	0.17	0.11 ^{a}	0.34	-	0.09 ^{d}	0.10
E4	0.20	0.08 ^{a}	0.23	-	-	0.25
W	0.34	0.11 ^{a}	0.24	-	0.16 ^{b}	0.25
Ww1	0.48	0.09 ^{b}	0.18	-	0.19 ^{b}	0.42
Ww2	0.54	0.14 ^{b}	0.15	-	0.11 ^{b}	0.20
N1	0.19	-	-	0.19	-	-
N2	0.16	0.13 ^{c}	-	0.18	0.14 ^{d}	-
N3	-	0.12 ^{c}	-	0.24	n/a	n/a
Nn	0.18	0.11 ^{c}	-	0.22	-	-

Note: ^{a} growing season = July-August, ^{b} growing season = July, ^{c} growing season = June, ^{d} growing season = May-June. Growing season for all spruce populations are June-July. n/a = no chronologies were established for the sites. Summer heat-moisture (HM) is the average summer heat-moisture from the previous and current growth year. The significance of the regressions are $P < 0.001$ ($R^2 > 0.19$), $P = 0.001$-0.01 ($R^2 = 0.13$-0.19), $P > 0.01$ ($R^2 < 0.13$). Shaded values indicate negative relationships.

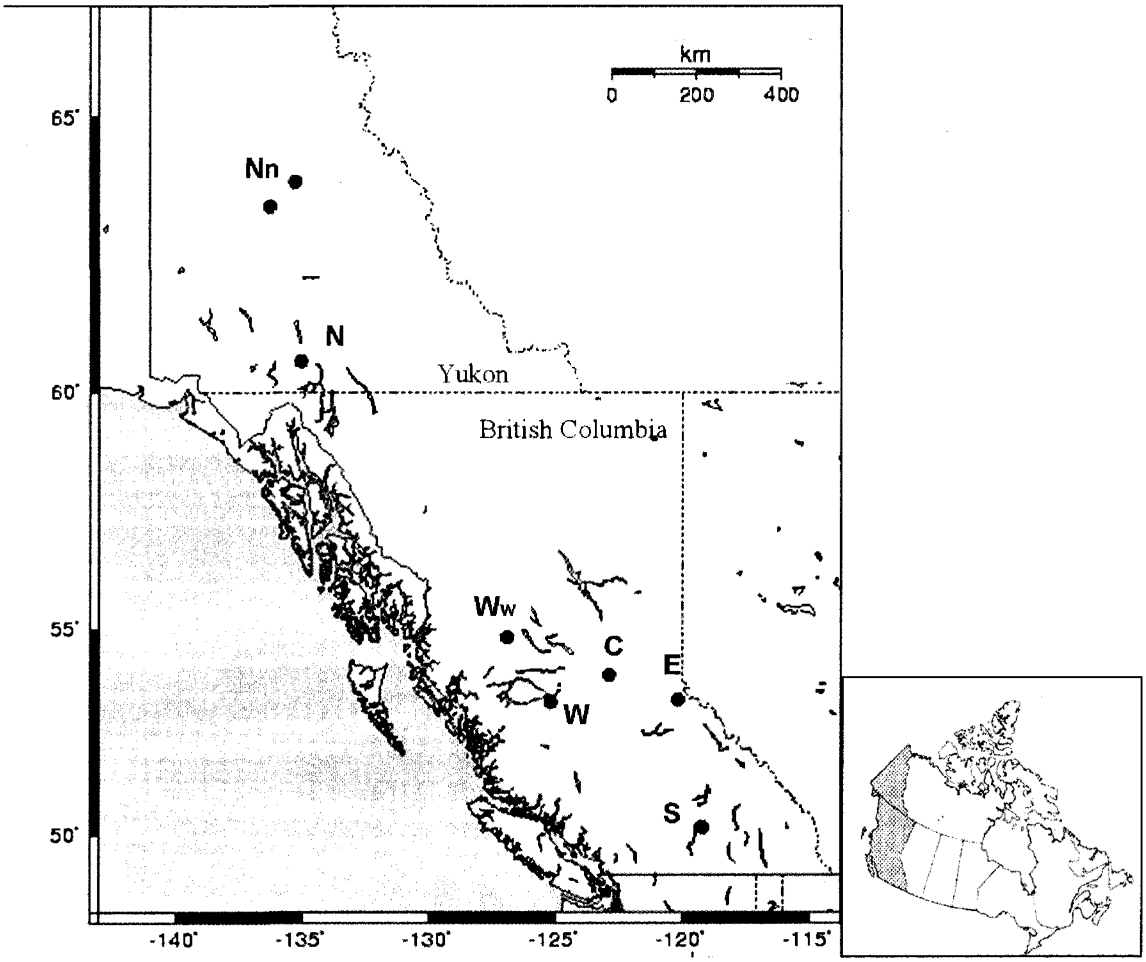


Figure 2.1. Study locations in Yukon and British Columbia, Canada. Site codes were assigned based on relative NEWS direction from Prince George (Central).

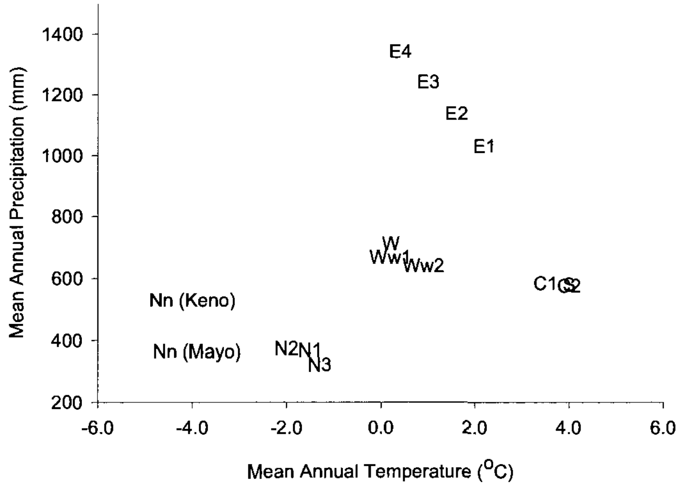


Figure 2.2. The range of climate conditions across the sample sites (ClimateBC version 3.2). Each point represents the mean annual temperature and mean annual precipitation of each sample site for the period 1961-1990.

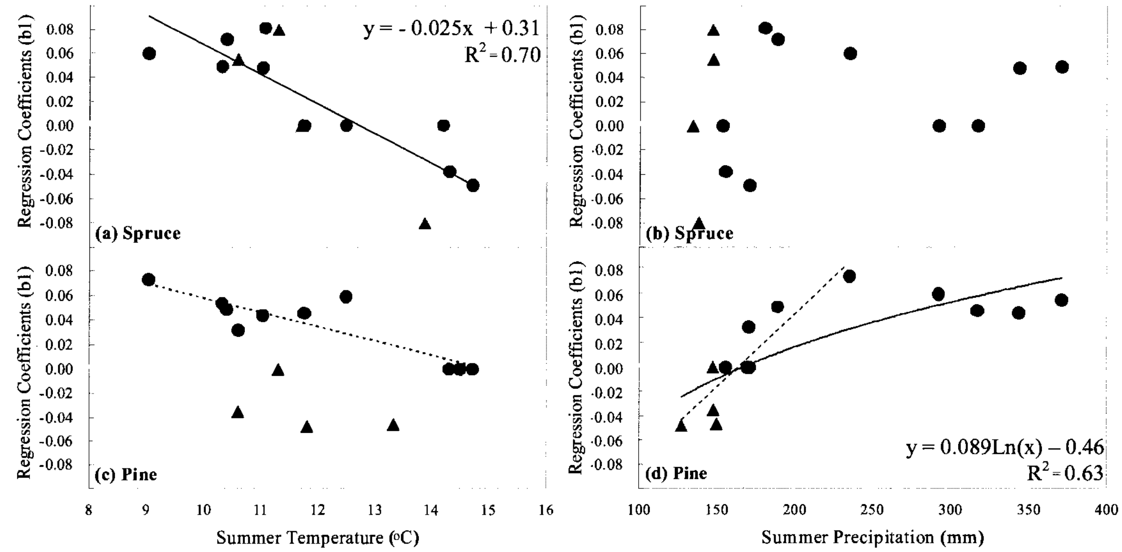


Figure 2.3. The growth sensitivities (regression coefficients: b1) of interior spruce and lodgepole pine to the current growing season temperatures (June-August) along summer temperature and precipitation gradients. The following symbols ● and ▲ represent BC and Yukon chronologies, respectively. Value zero indicates that the standardized chronology had no significant correlations with growing season temperature variables. The solid lines represent the broad trends across the sample sites ($P < 0.05$). The dotted lines represent (c) the regional trend in BC ($y = -0.011x + 0.18$, $R^2 = 0.77$), and (d) the trend across the sites below the precipitation threshold of 250 mm ($y = 0.0012x - 0.20$, $R^2 = 0.80$). Site summer temperature and precipitation were the 1961-1990 normal.

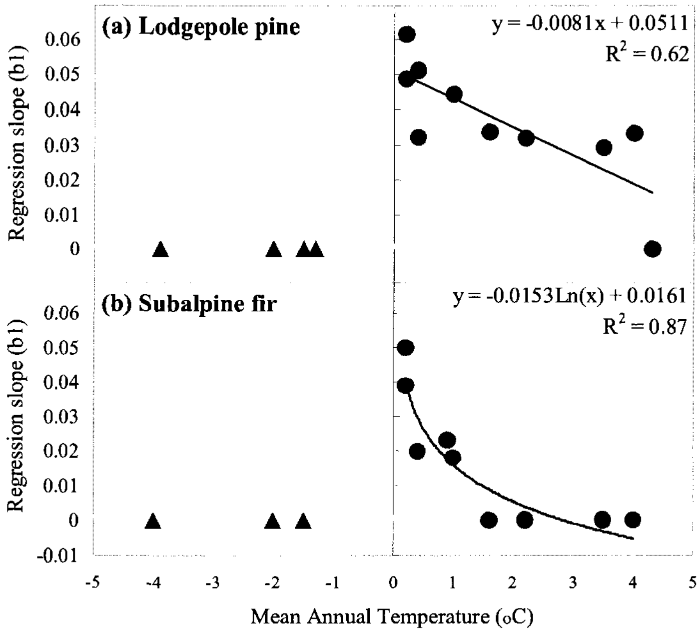


Figure 2.4. The growth sensitivities (regression coefficients: b1) of lodgepole pine (a) and subalpine fir (b) to October- March temperatures prior to growth along the mean annual temperature (°C) gradient. The following symbols ● and ▲ represent BC and Yukon chronologies, respectively. Value zero indicates that the standardized chronology had no significant correlations with October-March temperatures. Linear and natural logarithmic regressions were only applied for BC sites. The mean annual temperature of each site was the 1961-1990 normal.

Appendix A. Mean annual temperature and mean annual precipitation of each sample site for the period 1961-1990. SD stands for standard deviation.

Site	Site code	Annual Temperature		Annual Precipitation	
		Mean	SD	Mean	SD
Vernon	S	4.1	0.85	552	84.58
Prince George	C1	3.6	0.94	583	72.35
	C2	4.1	0.93	576	68.70
McBride	E1	2.3	0.89	1000	118.87
	E2	1.7	0.89	1103	131.15
	E3	1.1	0.88	1203	143.10
	E4	0.5	0.88	1301	155.04
Smithers	Ww1	0.3	0.89	657	87.49
	Ww2	1.0	0.89	630	83.76
Top Lake	W	0.2	0.88	722	107.35
Whitehorse	N1	-1.1	1.26	353	53.60
	N2	-1.7	1.27	359	54.42
	N3	-1.0	1.27	310	46.87
Mayo	Nn	-3.6	1.41	353	48.71
Keno	Nn	-3.7	1.40	513	76.16

Appendix B. Summary characteristics of the Arstan chronology of each population.

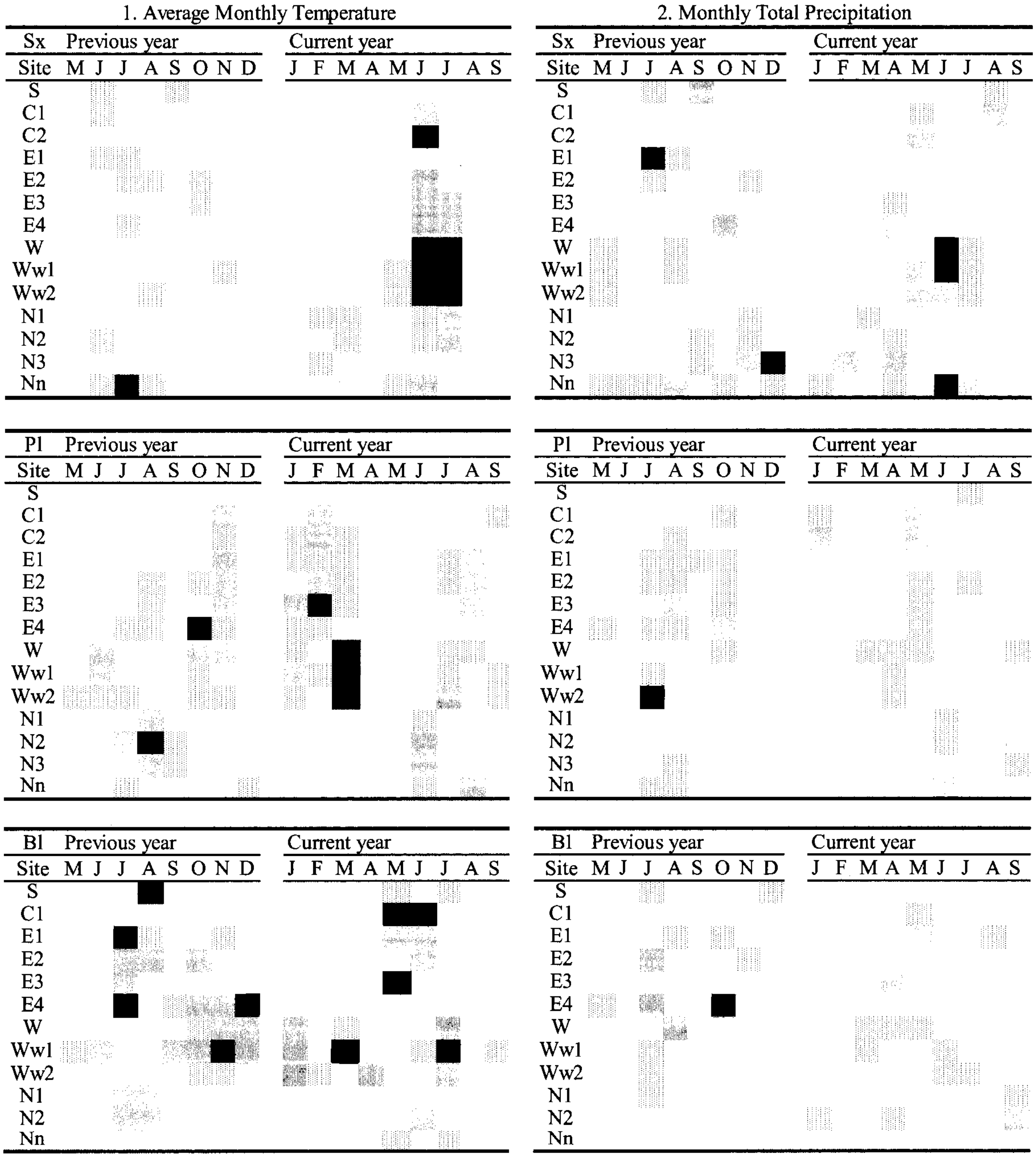
Species	Site	Site Code	No. radii	No. Trees	Start- End	Mean No. years	Mean Sensitivity	Standard Deviation	Series Intercorrelation	AC(1)	Spline
Pl	Silver Star	S	38	23	1917-2005	79.1	0.150	0.168	0.614	0.318	20
	Cranbrook Hill	C1	16	16	1901-2004	82.3	0.131	0.120	0.533	0.338	40
	Domano Blvd.	C2	20	20	1904-2004	76.3	0.133	0.149	0.581	0.251	20
	McBride Peak 1200m	E1	21	20	1901-2004	89.6	0.123	0.121	0.556	0.149	20
	McBride Peak 1400m	E2	21	21	1928-2004	69.5	0.142	0.111	0.562	-0.244	20
	McBride Peak 1600m	E3	20	20	1911-2004	79.3	0.131	0.121	0.552	-	40
	McBride Peak 1800m	E4	20	20	1904-2004	79.6	0.163	0.194	0.615	0.349	40
	Onion Mountain 1550m	Ww1	24	16	1899-2005	84	0.201	0.226	0.635	0.174	40
	Hudson Bay Mnt.	Ww2	30	20	1858-2005	94.9	0.157	0.151	0.588	0.143	40
	Top Lake	W	27	18	1870-2005	86.6	0.241	0.256	0.685	0.254	40
	Wolf Creek	N1	26	15	1937-2004	63.3	0.160	0.177	0.693	0.407	40
	Grey Mountain 1150m	N2	17	13	1919-2004	65.7	0.157	0.152	0.595	0.173	40
	Grey Mountain 820m	N3	27	20	1887-2004	109.7	0.140	0.165	0.674	0.453	40
	Mayo	Nn	19	14	1905-2004	61.7	0.176	0.183	0.596	0.333	40
Sx	King Eddy	S	38	21	1876-2005	107.1	0.146	0.154	0.664	0.332	20
	Cranbrook Hill	C1	21	18	1868-2004	85.2	0.107	0.121	0.525	0.289	40
	Domano Blvd.	C2	26	22	1912-2004	71.2	0.133	0.136	0.613	0.224	20
	McBride Peak 1200m	E1	17	17	1910-2004	79.1	0.099	0.098	0.590	0.212	20
	McBride Peak 1400m	E2	12	12	1927-2004	69.1	0.083	0.094	0.547	0.368	40
	McBride Peak 1600m	E3	22	22	1920-2004	74.6	0.106	0.107	0.539	0.252	40
	McBride Peak 1800m	E4	23	23	1920-2004	73	0.104	0.099	0.547	0.191	40
	Onion Mountain 1550m	Ww1	25	17	1907-2005	81.4	0.151	0.152	0.582	0.182	40
	Onion Mountain 1360m	Ww2	27	18	1810-2005	154	0.142	0.147	0.640	0.123	40
	Top Lake	W	30	22	1843-2005	96.9	0.160	0.160	0.634	0.147	40
	Wolf Creek	N1	20	14	1919-2004	72.5	0.130	0.137	0.691	0.328	40
	Grey Mountain 1150 m	N2	38	24	1888-2004	88.3	0.147	0.132	0.671	-	40
	Grey Mountain 845 m	N3	25	15	1795-2004	114.6	0.186	0.206	0.754	0.285	40
	Mayo	Nn	37	21	1895-2004	107.4	0.233	0.270	0.786	0.365	40
Bl	King Eddy	S	28	18	1880-2005	99.5	0.119	0.115	0.573	0.181	20
	Cranbrook Hill	C1	20	20	1882-2004	82.6	0.117	0.138	0.596	0.365	40
	McBride Peak 1200m	E1	22	20	1914-2004	68.6	0.129	0.135	0.558	0.339	40
	McBride Peak 1400m	E2	20	20	1927-2004	65.6	0.112	0.101	0.610	-	40

Appendix B. Continued.

Species	Site	Site Code	No. radii	No. Trees	Start- End	Mean No. years	Mean Sens.	Std. Dev.	Series Intercorrelation	AC(1)	Spline
Bl	McBride Peak 1600m	E3	25	25	1920-2004	74.7	0.090	0.096	0.593	-	40
	McBride Peak 1800m	E4	18	18	1923-2004	72.8	0.106	0.108	0.597	-	40
	Onion Mountain 1550m	Ww1	31	17	1870-2005	82.6	0.175	0.168	0.673	0.207	40
	Onion Mountain 1360m	Ww2	26	15	1811-2005	138.8	0.102	0.115	0.577	0.210	40
	Top Lake	W	31	20	1888-2005	90.7	0.144	0.170	0.666	0.182	40
	Wolf Creek	N1	29	19	1928-2004	66.9	0.123	0.128	0.668	0.343	40
	Grey Mountain 1150m	N2	22	14	1926-2004	69.5	0.116	0.140	0.658	0.453	40
	Keno Hill	Nn	63	40	1890-2004	81.8	0.136	0.136	0.627	0.248	40

Note: Species are lodgepole pine (Pl), interior spruce (Sx) and subalpine fir (Bl). Mean sens., Std, Dev. and AC(1) are mean sensitivity, standard deviation and first-order autocorrelation, respectively, after standardization. Spline indicates 20- or 40-year cubic smoothing spline length used to standardize the raw ring-widths. One core per tree was taken in June 2005 and two cores per tree were taken during the later samplings to improve crossdating.

Appendix C. Pearson correlation significance of ring-width chronologies against mean monthly temperatures (1) and precipitation (2) from May of the previous growth year to September of the current growth year for the three species.



Note: Species are interior spruce (Sx), lodgepole pine (Pl) and subalpine fir (Bl). Significance are ■ $P < 0.001$, ▒ $0.001 \leq P \leq 0.01$, ░ $0.01 < P < 0.05$

Chapter 3. Growth responses of three coexisting conifer species at altitudinal treelines in the central interior of British Columbia.

Abstract

Tree-ring analyses were used to compare radial growth-climate relationships among three coexisting, ecologically distinct conifer species at altitudinal treelines in the Engelmann Spruce-Subalpine Fir forests in the central interior of British Columbia, Canada. Study species included lodgepole pine (*Pinus contorta* var. *latifolia*), Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Our data showed that Engelmann spruce were positively correlated with June and July temperatures, whereas lodgepole pine and subalpine fir were positively correlated with October-March temperatures and Pacific Decadal Oscillation (PDO) prior to growth. Temperature, more than precipitation, also appeared to have a stronger influence on the tree growth. Our data suggest that the populations of the same species growing at geographically different sites may show more similar growth-climate correlations than different species coexisting in a community. The high values of October-March PDO are often associated with reduced snowpack in western North America, which may extend the duration of the growing season and consequently enhance tree radial growth at altitudinal treelines. Winter warming may lead to increase in the abundance of lodgepole pine in the spruce-fir forests at high-elevations in the interior of British Columbia.

3.1. Introduction

Trees at altitudinal treelines in the extratropical regions often experience severe environmental conditions, including cool summer temperatures, short growing seasons, deep snowpack, mechanical injuries due to wind-blown snow crystals, winter desiccation, low soil temperatures, shallow soils and limited nutrients due to slow decomposition rates (Stevens and Fox 1991, Körner 2003). Studies suggest that cold air and soil temperatures are probably the primary factors determining altitudinal treeline positions globally (Körner 1998, 2003, Körner and Pausen 2004). Cold temperatures often limit meristematic activities (i.e., cellular division, cell elongations), photosynthesis and carbon allocation that may result in reduced growth rate, reproduction and seedling establishment at high-elevations (Körner 1998, Loehle 2000a, Jobbágy and Jackson 2000, Smith et al. 2003, Körner and Pausen 2004). Consequently changes in temperature may affect tree productivity and vigour. Studies suggest that increases in global annual temperatures in the future may result in changes in interactions between tree species, reorganizations of community structures and shifts in tree species' ranges to higher elevations (Hansen et al. 2001, Grace et al. 2002, Walther 2003).

The high-elevation Engelmann Spruce-Subalpine Fir (ESSF) forests in British Columbia (BC), Canada, may experience significant changes in community structures under projected warming (Hamann and Wang 2006). Predicting the potential impacts of climate change on altitudinal treelines may require a better understanding of species-specific growth responses (Zolbrod and Peterson 1999, Davis and Shaw 2001, Thuiller 2003). In BC three ecologically distinct conifer species can coexist at altitudinal treelines. These include an early-successional, shade-intolerant lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.), a mid-successional, intermediate shade-tolerant Engelmann spruce (*Picea engelmannii* Parry ex

Engelm.), and a late-successional, shade-tolerant subalpine fir (*Abies lasiocarpa* [Hook.]) Nutt.) (Burns and Honkala 1990). Niche theory suggests that coexisting species should exhibit different resource requirements and optima to coexist (Bazzaz 1987, He et al. 2005) and thus, growth responses to climate change may differ among species. For example, Green (2005, 2007) reported that height growth responses to late growing season temperatures varied among coexisting lodgepole pine, Engelmann spruce and subalpine fir in the central interior of BC. Green (2005) suggests that future climate change may have more impact on the growth of lodgepole pine than that of subalpine fir because high-elevation lodgepole pine showed the strongest sensitivity while subalpine fir showed the weakest sensitivity to the extended growing season conditions into fall. Coexisting species grow under the same or similar environmental conditions and thus, they may provide insight into species-specific growth responses to climate and underlying mechanisms.

Tree-ring analyses often provide information on the long-term impacts of climate on tree radial growth due to the strong associations found between annual rings and climate records in the temperate regions (Fritts 1976). Tree radial growth may be a good indicator of vigour and competitiveness because larger radial growth is often associated with higher mechanical stability, larger height and volume (Givnish 1995) and higher reproductive and dispersal abilities (Despland and Houle 1997, Loehle 2000b).

Radial growth-climate relationships may be site- and species-specific because of the considerable variations in environmental conditions (i.e., elevation, latitude) and adaptive traits (i.e., physiology, morphology) found among species. Graumlich (1993), for example, suggests that deciduous and coniferous trees respond to climate differently due to the different size and arrangement of xylem cells, water relations and photosynthetic capacities. Villalba et al. (1994) also reported that correlations between radial growth and monthly temperatures and precipitation varied among lodgepole pine, Engelmann spruce and subalpine fir at mesic high-elevation sites in the Colorado Front Range. They also found that important monthly climate variables differed within species between mesic and xeric sites. Given the considerable variation in topographic features, habitats, and local climate in high-elevation mountain landscapes, the growth-climate relationships of trees may not be uniform across sites. Thus, differences in local climate conditions may need to be considered.

Regional climate can also have significant impacts on tree growth as well as local climate (Millar et al. 2004, Holman and Peterson 2006). The Pacific Decadal Oscillation (PDO) is a large-scale interdecadal climate variability that influences the local climate of the Pacific Northwest including BC (Mantua and Hare 2002, Biondi et al. 2001, MWLAP 2002). PDO, often expressed as index series, has positive and negative phases that alternate every 20-30 years. The negative values of PDO index are generally associated with cold and wet winters and the positive values are generally associated with warm and dry winters. Studies reported that the radial growth of subalpine fir (Ettl and Peterson 1995, Peterson et al. 2002), lodgepole pine (Case and Peterson 2007) and mountain hemlock (Peterson and Peterson 2001) at high-elevations showed positive correlations with winter PDO in the Cascade and Olympic Mountains in Washington. The potential influences of PDO on conifer growth were mainly reported for coastal populations but rarely for interior populations in western North America. Detecting a signal in tree growth may help clarify the existence and geographic extent of PDO and its impacts on high-elevation ecosystems in BC.

In this study, we compared the growth responses and sensitivities of coexisting lodgepole pine, Engelmann spruce and subalpine fir to climate variables at altitudinal treelines in the ESSF zone in the central interior of BC. Growth response is defined as the significant relationship between tree growth and climate variables, and growth sensitivity is defined as the direction and strength of the relationships. Three hypotheses included: 1) temperature has stronger influence on limiting tree radial growth than precipitation, 2) the growth responses of tree populations to climate vary among species more than among sites, and 3) the large-scale decadal oscillation, PDO, influences the radial growth of interior tree populations at altitudinal treelines in central BC.

3.2. Methods

3.2.1. Study sites

Engelmann Spruce-Subalpine Fir (ESSF) forests occur in mountainous terrain and form uppermost elevation forests in central British Columbia (BC) (Meidinger and Pojar 1991). The climate of ESSF is characterized as long cold winters and short cool summers. Mean monthly temperatures remain below 0 °C for 5 to 7 months and exceed 10 °C for 0 to 2 months each year. Precipitation varies considerably within the zone, and 50-70 % of precipitation occurs as snow and maximum snowpack depth ranges between 1-4 m. Three sample sites were located on the southwest facing slopes in the moist interior subzones of ESSF (Table 3.1, Figure 3.1). Onion Mountain is located in the lee side of the Coast Mountains where dry air from the mountains results in relatively low annual precipitation. McBride Peak is located on the windward side of the Canadian Rocky Mountains and receives the highest amounts of rainfall and snowfall among the three sites (Table 3.1). The distance between Onion Mountain and McBride Peak is approximately 600 km (Figure 3.1). Top Lake is located between the two sites and shows similar climate conditions to Onion Mountain.

It is difficult to define altitudinal treelines because they often lack distinct lines in mountainous regions. Treelines in this study were defined as transition zones between the upper limit of continuous canopy forest and the highest patches of upright trees (Körner 1998). The sample stands were more than 70 years old, naturally regenerated, and mid- to late-successional stages. We selected healthy stands with the minimal visible evidence of stand level disturbance to minimize non-climatic influences on tree radial growth. Subalpine fir and Engelmann spruce co-dominated and lodgepole pine occurred in low abundance at the three sites.

3.2.2. Chronology development

One or two tree increment cores were extracted at breast height (1.3 m) from a minimum of 20 trees per species per site in 2005-2006. A conventional coring height of 1.3 m was chosen because it provided sufficient growth ring records of longer than 50 years. Healthy, canopy-dominant trees with little observable damage were selected for coring to minimize non-climatic variation in ring-widths. Standard dendrochronology techniques were applied to develop site- and species-specific tree-ring chronologies (Fritts 1976). Sampled cores were mounted and sanded with increasing grain size (to 600 per inch) to observe annual rings clearly (Stokes and Smiley 1968). Crossdating is a procedure to identify the exact year of ring formation by synchronously matching ring-width patterns among all sampled cores from a given site. Crossdating helps to detect any missing or false rings, because trees may fail to produce an annual ring or may produce two rings in a year. Narrow rings were used as pointer-years during visual crossdating (Yamaguchi 1991). Annual ring-widths were measured to 0.01 mm using the computer program WinDENDRO™ (Regent Instruments Inc.

2005). The Velmex ring-measurement system (Velmex Inc. 1992) interfaced with MeasureJ2X (VoorTech Consulting 2004) with precision 0.001 mm was used to measure small rings. A computer program COFECHA (Grissino-Mayer 2001) was used to statistically detect potential errors and to validate visual crossdating. Cores that did not crossdate (with a critical threshold intercorrelation value of 0.36 based on 40-year segment with 20-year lag) were re-examined under a microscope and remeasured using MeasureJ2X. Those cores that did not crossdate after the re-examination were removed from the final chronology development.

The raw ring-width measurements for each crossdated series were standardized by converting to dimensionless ring-width indices to minimize non-climatic factors and autocorrelations (Fritts 1976). Non-climatic factors influencing ring-width variation may include tree age, competition, disturbance and random variation (Cook 1985). Younger trees, for instance, generally have higher photosynthetic rates than older trees. This age-dependent biological trend often results in the formation of wider annual rings during the early years of growth and narrower annual rings during the later years regardless of climate condition. Changes in interspecific and intraspecific competitions and below-ground characteristics also influence low-frequency variation in ring-widths. Ring-width series may retain autocorrelation because 1) physiological processes within a tree often cause a lag in growth responses to climate and 2) climate conditions tend to persist from one year to the next.

Each core was standardized by fitting a cubic smoothing spline with a 50% frequency response cutoff of 40 years using a program ARSTAN (Cook 1985). The ring-width indices of individually standardized cores were then averaged among all crossdated cores in a population to develop a ring-width chronology for each species at each site. The Arstan chronology, autocorrelation removed and pooled autoregression (common persistence) built back in, was developed to maximize climate signal in the ring-width variation (Cook and Holmes 1986).

Mean sensitivity and standard deviation were calculated to evaluate the quality of standardized chronologies. Mean sensitivity is a measure of response to year-to-year climate variation and standard deviation indicates low- to medium-frequency variation in the ring-width chronologies, and higher values indicate that the ring-width chronologies contain common climate signals (Fritts 1976, Villalba et al. 1994). Mean sensitivity is calculated as the absolute difference between adjacent ring-widths divided by the mean of the two ring-widths.

3.2.3. Data analyses

3.2.3.1. Principal component analysis

A principal component analysis (PCA) was used to identify populations that had similar patterns in ring-width variations in the past 50 years (1953-2002) (Graumlich 1993, Peterson and Peterson 1994). PCA is a data clustering technique that transforms a large number of variables into a new set of variables, called principal components (PCs), which are weighted linear combinations of the original variables. The PCs are uncorrelated with each other and the first few PCs account for most of the variability in the original variables. The factor loadings of ring-width chronologies are based on the correlation matrix and provide information on similarities and differences among populations. Ring-width chronologies with positive factor loadings are positively correlated with the resulting PC. The extracted PCs were subjected to an orthogonal Varimax rotation to increase interpretability by maximizing the factor loadings of loaded variables (Tabachnick and Fidell 1989). Only those PCs with eigenvalues larger than

1.0 were retained for further analyses. Scatter plots of the factor loadings for the PCs were used to display the group of ring-width chronologies with similar growth patterns.

3.2.3.2. Climate model

Site-specific climate data were estimated using a climate model, ClimateBC version 3.2 (Wang et al. 2006). ClimateBC requires latitude, longitude, and elevation to generate site-specific monthly, seasonal and annual climate variables in western Canada based on PRISM (parameter-elevation regressions on independent slopes model). PRISM is a regression-based model that incorporates geographic influences on climate, including elevation, aspect, coastal effects and orographic influences (Daly et al. 2002, Hamann and Wang 2005). For example, elevation is a strong predictor of temperature because temperature decreases almost linearly with altitude. Based on the topographical features, PRISM adjusts reference weather station data to estimate mean monthly temperature and precipitation for each grid at the resolution of approximately 4 km (Daly et al. 2002). Each reference weather station is weighted based on a distance from a target grid cell, elevation and other topographic factors, and the value of the target is calculated. On top of the medium resolution climate data of 4 km grid, ClimateBC uses a high-resolution digital elevation model to build a locally and temporary scale-free climate model for finer scale climate estimates (Wang et al. 2006). The verification was conducted by comparing predicted and observed climate data from 191 weather stations that had sufficient climate records included in the 1951-1980 or 1961-1990 normals (Wang et al. 2006).

3.2.3.3. Growth-climate relationships

We used a 50-year period of climate data from 1953 to 2002 in the analyses due to the reliability of the climate records and the increased number of climate stations in North America after 1950 (Wang et al. 2006). The climate variables used in the analyses included mean monthly temperatures and monthly total precipitation generated by ClimateBC, and the monthly Pacific Decadal Oscillation indices (PDO) obtained from the National Oceanic and Atmospheric Administration (NOAA 2006). Seventeen months extending from May of the previous growth year to September of the current growth year were used because this period included two complete growing seasons (Larsen and McDonald 1995, Brooks et al. 1998).

We used response function analyses (PRECON version 5.11, Fritts 1996) to compare the importance of temperature and precipitation on ring-width indices. The response function transforms monthly climate variables into orthogonal eigenvectors using PCA and calculates the multiple correlation R^2, the percentage of the ring-width variance explained by the 17-months of monthly temperature and precipitation, respectively (Fritts 1976). R^2 were compared between temperature and precipitation.

Pearson simple linear correlation coefficients were calculated to identify climate variables significantly correlated with the ring-width indices ($P < 0.05$). Based on the correlations, we selected predictor climate variables, which had strong correlations and were common across the sample populations. The direction and strength of the regression relationships (b1) between the ring-width indices and predictor climate variables were determined using simple linear regression analyses and then compared among species and sites using separate slopes analyses ($P < 0.05$). Normality was tested using the Kolmogorov-Smirnov normality test. The analyses were conducted using the statistical software SPSS (SPSS Inc. 1999).

3.3. Results

3.3.1. Chronology statistics

At each site, lodgepole pine had the highest mean sensitivity and standard deviation compared with Engelmann spruce and subalpine fir (Table 3.2). Within species, the ring-width chronologies at Onion Mountain and Top Lake had higher mean sensitivities and standard deviations than those at McBride Peak. Previous studies suggest that a mean sensitivity range of 0.095-0.166 is sufficient to make growth-climate comparison for the three species (Villalba et al. 1994, Ettl and Peterson 1995).

3.3.2. Ring-width variation explained by temperature versus precipitation

Temperature had higher percentages in explaining the ring-width variation than precipitation for eight out of the nine populations (Table 3.3). The simple correlation analyses also identified stronger and more significant relationships between the ring-width chronologies and mean monthly temperatures compared with monthly precipitation (Figure 3.2).

3.3.3. Similarity among ring-width chronologies

The first three principal components (PCs) together accounted for 76.8 % of the total variance in the nine ring-width chronologies for the period 1953-2002 (Table 3.4). The scatter plots of the factor loadings for the PCs showed the clustering of populations with similar growth patterns if the loadings were greater than 0.5 (Kaiser 1974) (Figure 3.3). The first component (PC1) showed the greatest dissimilarity in loadings between Engelmann spruce and lodgepole pine. All pine populations had higher loadings on the PC1 than subsequent components. Subalpine fir at Onion Mountain and Top Lake also loaded on the PC1. The principal component 2 contained spruce at Onion Mountain and Top Lake, and the principal component

3 contained spruce and fir at McBride Peak. The scatter plots showed that all pine populations clustered together whereas fir and spruce at McBride Peak did not cluster with other populations within species (Figure 3.3).

3.3.4. Growth-climate relationships

3.3.4.1. Identification of predictor climate variables

We identified four common climate variables most strongly correlated with the ring-width indices during the 1953-2002 period based on the correlation analyses (Figure 3.2, 3.4). They were June and July temperatures of the current growth year and October-March temperatures and October-March PDO prior to growth (Figure 3.5). Seven out of the nine ring-width chronologies had positive correlations with July temperatures of the current growth year. June temperatures appeared to be also important for spruce growth at all sites. The monthly temperatures from October to March prior to growth were averaged to form a seasonal climate variable based on the correlations found for pine and fir (Figure 3.2). Subalpine fir showed strong correlations with the monthly Pacific Decadal Oscillation (PDO) while Engelmann spruce showed a few significant correlations with PDO (Figure 3.4). PDO indices from October to March prior to growth were average and used for the further analyses because 1) this duration corresponded to the October-March temperatures and thus, the impacts of PDO and temperatures on tree growth can be easily associated, 2) PDO generally has the strongest influences on the local climate of western North America from October to March (Biondi et al. 2001), and 3) several studies reported the importance of PDO for tree radial growth in the winter months (i.e., Ettl and Peterson 1995, Gedalof and Smith 2001, Peterson et al. 2002, Larocque and Smith 2005). October-March PDO and temperatures were also positively correlated at each site (Table 3.5).

3.3.4.2. Regression and separate slopes analyses

Engelmann spruce ring-width indices had positive correlations with June and July temperatures of the current growth year at each site (Figure 3.5). Separate slopes analyses showed that the regression coefficients of the spruce ring-width indices to temperatures in June ($P \geq 0.26$) and in July ($P \geq 0.25$) did not differ among sites. Lodgepole pine and subalpine fir had positive correlations with October-March temperatures and PDO prior to growth at each site (Figure 3.5). Separate slopes analyses showed that the regression coefficients of pine ring-width indices to temperatures ($P \geq 0.56$) and to PDO ($P \geq 0.053$) did not differ among sites. Subalpine fir at Onion Mountain had a higher regression coefficient than fir at McBride Peak for temperatures ($P = 0.048$) and for PDO ($P = 0.03$). However, the regression coefficients of subalpine fir did not differ between Onion Mountain and Top Lake ($P = 0.40$ for temperatures, $P = 0.65$ for PDO) or Top Lake and McBride Peak ($P = 0.35$ for temperatures, $P = 0.11$ for PDO). Subalpine fir at Onion Mountain and Top Lake were also positively correlated with July temperatures of the current growth year, and the regression coefficients did not differ between the two sites ($P = 0.93$).

3.4. Discussion

Results from this study suggest that 1) temperature probably affects tree radial growth more than precipitation, 2) the populations of the same species growing on geographically distinct sites may show more similar growth patterns and growth-climate correlations than among different species coexisting in a community, 3) the Pacific Decadal Oscillation (PDO) influences the radial growth of interior populations, but the effects are species-specific.

3.4.1. Importance of temperature versus precipitation

Temperature appeared to influence tree radial growth more strongly than precipitation in this study, probably because sufficient moisture was available for tree growth in the moist ESSF treelines. It is general that the ratio of precipitation-to-evapotranspiration increases with altitude, leading to greater moisture surplus at high-elevation ecosystems (Körner 2003). Adaptive strategies to moisture deficit are rare for high-elevation trees, except for the tolerance to desiccation stress related to cold temperatures (Körner 2003). Contrary, several studies suggest that high-elevation trees have developed adaptive strategies to cold temperatures, such as increased photosynthesis at cool summer temperatures and freezing tolerance in winter (Sakai and Larcher 1987, Grace et al. 2002). Thus, future changes in temperature may be more important than precipitation in predicting tree growth at mesic treelines.

3.4.2. Similarity among ring-width chronologies

Species may be more important than site conditions in predicting tree responses to future climate at altitudinal treelines across a large geographic range in British Columbia (BC). Our data agreed with previous studies (Graumlich 1993, Peterson and Peterson 1994) that the growth-climate relationships were more similar among the populations of the same species growing at geographically different sites than different species coexisting in a site. Peterson and Peterson (1994), for example, reported these patterns among high-elevation Engelmann spruce, subalpine fir and subalpine larch (*Larix lyallii* Parl.) in the North Cascade Mountains in Washington.

Although some species (i.e., Engelmann spruce) may exhibit a common climate signal over large geographical areas (Mäkinen et al. 2000, 2002, St. George and Luckman 2001, Wilson and Luckman 2003), site conditions may be important for other species in predicting growth responses to climate. In this study, subalpine fir at McBride Peak showed different growth responses and sensitivities to the seasonal climate conditions compared with fir populations at Onion Mountain and Top Lake. Subalpine fir may be more sensitive to slight differences in site conditions than Engelmann spruce or lodgepole pine, although the adaptive mechanisms remain unknown.

3.4.3. Important growth-climate relationships

Engelmann spruce had positive correlations with June-July temperatures, which may be due to higher day- and night-time temperatures that enhance photosynthesis and carbohydrate allocation at treelines where growing season temperatures are generally low (Körner 1998). Other possible causes of the positive correlations include higher photosynthetically active radiation due to more sunny days (Goldblum and Rigg 2005), the extension of the growing season (Danby and Hik 2007) and/or the combination of these factors. High June-July precipitation may cause reduced spruce growth due to limited root activities in wet soils (Kramer and Kozlowski 1979), and/or cool, cloudy summer conditions associated with high precipitation (Table 3.5). However, high water content of soils is unlikely to cause growth reduction in mature trees during summer at mesic sites (Körner 2003). Thus, the influence of temperatures may be stronger than that of precipitation in limiting spruce growth in this study.

Subalpine fir and lodgepole pine had strong correlations with October-March temperatures and PDO prior to growth in this study, suggesting that winter PDO can have significant influence on tree radial growth at altitudinal treelines in the interior regions of BC. Several studies reported the positive impacts of winter temperatures and PDO on the radial growth of high-elevation conifers in the Coastal Mountain regions of western North America, probably associated with the snowpack and duration of the growing season (Ettl and Peterson 1995, Gedalof and Smith 2001, Peterson et al. 2002, Larocque and Smith 2005). The negative values of winter PDO are often accompanied by cold temperatures and high precipitation with above average snowpack in the Pacific Northwest including BC (Mantua and Hare 2002, MWLAP 2002). Deep snowpack generally maintains low air and soil temperatures into late spring to early summer, which may lead to delayed bud burst, reduced shoot elongation and radial growth (Graumlich and Brubaker 1986, Ettl and Peterson 1995). For example, Peterson and Peterson (1994) suggest that soil temperatures and the accumulation of growing-days after snowmelt may determine the timing of bud burst and the height growth initiation of subalpine fir. Several tree-ring studies showed that high-elevation subalpine fir (Peterson and Peterson 1994, Ettl and Peterson 1995, Peterson et al. 2002, Larocque and Smith 2005) and lodgepole pine (Case and Peterson 2007) had negative correlations with winter precipitation, spring snowpack and PDO prior to growth in the Pacific Northwest extending from the western Cascade Mountain in Oregon to the Coast Mountains in BC. In the Alps, several authors reported stronger influences of winter temperatures than summer temperatures on the radial growth of stone pine (*P. cembra* L.) at high-elevation sites where snow played important physical roles in the ecosystems (Oberhuber 2004, Pfeifer et al. 2005, Carrer et al. 2007). Although no monthly snowpack data were available in this study, reduced snowpack was expected in the positive PDO years because October-March PDO had positive correlations with temperatures and negative correlations with precipitation at most sites (Table 3.5). Actual snow date may help in clarifying the PDO-snow relationships at each site and in examining correlations between ring-width chronologies and snow variables such as snow depth and timing of snowmelt in spring (Oberhuber 2004, Pfeifer et al. 2005).

3.4.4. Interspecific differences and adaptive mechanisms

Coexisting species experience similar external conditions including photoperiod, local climate and soil properties and thus, interspecific growth-climate relationships may result from species-specific internal factors such as physiological and phenological processes. For example, studies suggest that the sensitivities of trees to cold soils differ among species (Varpaavuori et al. 1992, Landhäusser et al. 2001). Cold soils often limit root growth and water uptake by trees due to high water viscosity and decreased root permeability, which often limit the growth activities of aboveground tissues including photosynthesis and shoot expansion (Day et al. 1989, Landhäusser et al. 2001). However, Day et al. (1989) suggest that spruce is insensitive to cold soil temperatures and may initiate growth under snow cover. They reported that Engelmann spruce seedlings showed higher net photosynthesis and root growth rates than lodgepole pine seedlings at cold soil temperatures based on a field experiment. Growth responses of trees to spring soil temperatures may provide possible mechanisms of unique species-specific growth responses to climate change.

Engelmann spruce showed a unique growth-climate relationship among the three study species possibly because spruce is more adapted to cold continental climate conditions than subalpine fir or lodgepole pine. Geologic and genetic studies suggest that spruce existed in the unglaciated regions in Yukon and Alaska (Cwynar and Spear 1991, Landhausser et al. 2001) while lodgepole pine and subalpine fir existed in the coastal regions of the southwestern United States during the most recent glacial period (Wheeler and Guries 1982, Xie and Ying 1995, Ettl and Peterson 2001). Although the three study species occupied BC after the ice retreated, their migration routes seemed to be different. Spruce might have been subjected to extreme cold and dry conditions while pine and fir were subjected to relatively mild conditions. Past climate conditions that each species experienced may determine the adaptive responses of trees to the current climate conditions. Biogeography of species, therefore, may provide insights into the adaptive mechanisms of unique growth-climate relationships.

3.4.5. Implications and future research

Our data suggest that tree species may respond to future climate differently, resulting in shifts in species dominance, abundance and distribution in the interior ESSF forests in BC. For example, lodgepole pine and subalpine fir may become more competitive than Engelmann spruce under warm winter conditions, resulting in increased abundance of pine and fir in subalpine habitats. Community shifts may occur most noticeably at altitudinal treelines in interior regions where magnitude of climate change, especially during winter time, is expected to be large (Christensen et al. 2007). General circulation models predict that winter temperatures will increase more than summer temperatures and more winter precipitation will occur as rain in high-elevation regions in North America (Christensen et al. 2007). Therefore, changes in winter conditions may need to be considered to assess the potential impacts of climate change on forests at treelines.

Further studies on age-specific growth responses to climate may provide a better prediction of community shifts, because younger trees may show different responses to winter warming from mature trees. Warmer winters may favour growth and establishment of seedlings at high-elevations due to earlier snowmelt and extended growing seasons (Smith et al. 2004). However, warm winters may cause trees to develop weak cold hardiness and break dormancy early in spring, which may increase the risks of cold injuries when extreme cold weather and spring frost occur (Aitken and Hannerz 2001, Bertrand and Castonguay 2003). Trees may also increase respiration and consume large amounts of carbohydrate reserves during warm winter, which may result in lower amounts of carbohydrates for spring flush and growth (Lebourgeois 2000). Younger trees were reported to be more sensitive to extreme cold events (Van Der Kamp and Worrall 1990) and to the loss of carbon reserves through respiration during warm winter (Körner 1998) than mature trees. Tree developmental stages may need to be considered to accurately predict how trees respond to winter warming.

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Table 3.1. Locations and climate conditions of sample sites. Climate data are the 1961-1990 normals estimated from ClimateBC (version 3.2).

Site name	Elevation (m)	Latitude (N)	Longitude (W)	MAT (°C)	MAP (mm)	MST (°C)	MSP (mm)	GDD (>5°C)	NFFD	PAS (mm)
Onion Mountain	1550	54° 48'	126° 52'	0.2	670	10.4	190	624	120	320
Top Lake	1640	53° 16'	125° 10'	0.2	710	9.0	240	507	111	320
McBride Peak	1800	53° 20'	120° 07'	0.4	1340	10.3	370	736	127	620

Note: Mean annual temperature (MAT), mean annual precipitation (MAP), mean summer temperature (MST), mean summer precipitation (MSP), growing degree-days (GDD), the number of frost-free days (NFFD) and precipitation as snow (PAS). Summer is June-August.

Table 3.2. Descriptions of the Arstan chronology statistics.

Site	**Species**	**No. radii**	**Chronology length (mean no. of years)**	**Mean Sensitivity**	**Standard Deviation**	r_{bar}	**AC (1)**
Onion Mountain	Pine	24	1899-2005 (84.0)	0.201	0.226	0.635	0.174
	Spruce	25	1907-2005 (81.4)	0.151	0.152	0.582	0.182
	Fir	31	1870-2005 (82.6)	0.175	0.168	0.673	0.207
Top Lake	Pine	27	1870-2005 (86.6)	0.241	0.256	0.685	0.254
	Spruce	30	1843-2005 (96.9)	0.160	0.160	0.634	0.147
	Fir	31	1888-2005 (90.7)	0.144	0.170	0.666	0.182
McBride	Pine	20	1904-2004 (79.6)	0.163	0.194	0.615	0.349
	Spruce	23	1920-2004 (73.0)	0.104	0.099	0.547	0.191
	Fir	18	1923-2004 (72.8)	0.106	0.108	0.597	-

Note: First-order autocorrelation (AC (1)) and series intercorrelation (r_{bar})

Table 3.3. Percent variance in ring-width chronologies explained by 17 monthly climate variables (PRECON, version 5.11). Climate variables were mean monthly temperatures and precipitation from May of the previous growth year to September of the current growth year for the 1953-2002 period.

Site	**species**	**Temperature**	**Precipitation**	**Interaction**
Onion Mountain	Engelmann spruce	0.597	0.495	0.665
	Lodgepole pine	0.528	0.292	0.496
	Subalpine fir	0.668	0.269	0.703
Top Lake	Engelmann spruce	0.466	0.361	0.658
	Lodgepole pine	0.613	0.384	0.649
	Subalpine fir	0.468	0.378	0.635
McBride Peak	Engelmann spruce	0.345	0.350	0.507
	Lodgepole pine	0.533	0.458	0.574
	Subalpine fir	0.512	0.421	0.608

Note: Interaction (%) represents the ring-width variance explained by 34 monthly variables including both temperature and precipitation.

Table 3.4. Varimax orthogonally rotated factor loadings for the PC1-PC3 of the nine ring-width chronologies for the period 1953-2002.

		Factor loadings		
Species	Site	PC 1	PC 2	PC 3
Spruce	Onion Mountain	0.211	0.878	0.059
	Top Lake	0.281	0.827	0.069
	McBride Peak	-0.14	0.478	0.748
Pine	Onion Mountain	0.798	0.231	-0.158
	Top Lake	0.853	0.168	0.144
	McBride Peak	0.745	0.077	0.492
Fir	Onion Mountain	0.662	0.459	0.284
	Top Lake	0.581	0.458	0.263
	McBride Peak	0.358	-0.085	0.858
	Eigenvalue	3.0	2.2	1.7
	% variance	33.0	24.4	19.4

Table 3.5. Correlations between predictor climate variables for the 1953-2002 period. The correlations are positive (+), negative (-) and not significant (ns) at $P < 0.05$.

Climate variables	Month	Onion Mountain	Top Lake	McBride Peak
Temperature x Precipitation	June-July	-	-	-
PDO x Temperature	October-March	+	+	+
PDO x Precipitation	October-March	ns	-	-

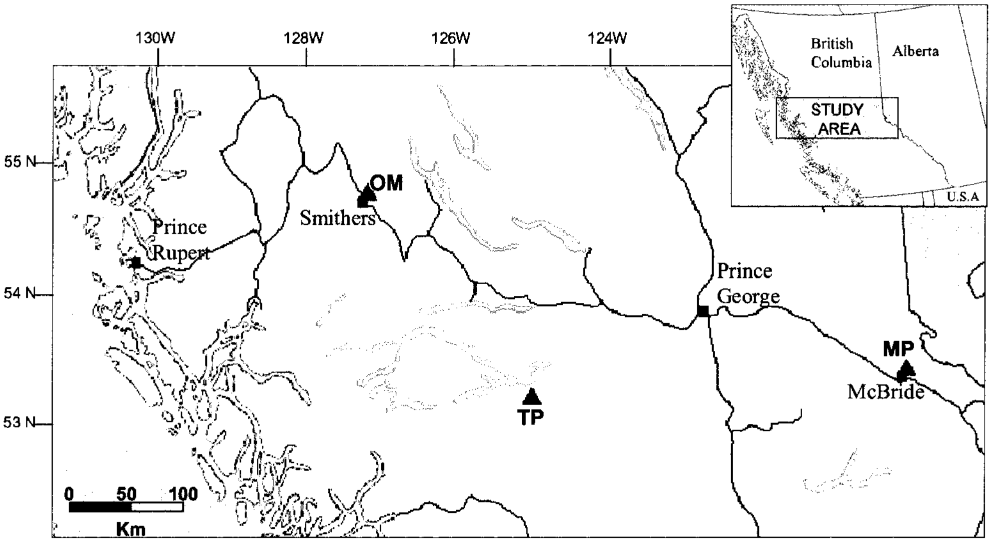

Figure 3.1.Study sites in central British Columbia, Canada. Site codes are Onion Mountain (OM), Top Lake (TP) and McBride Peak (MP).

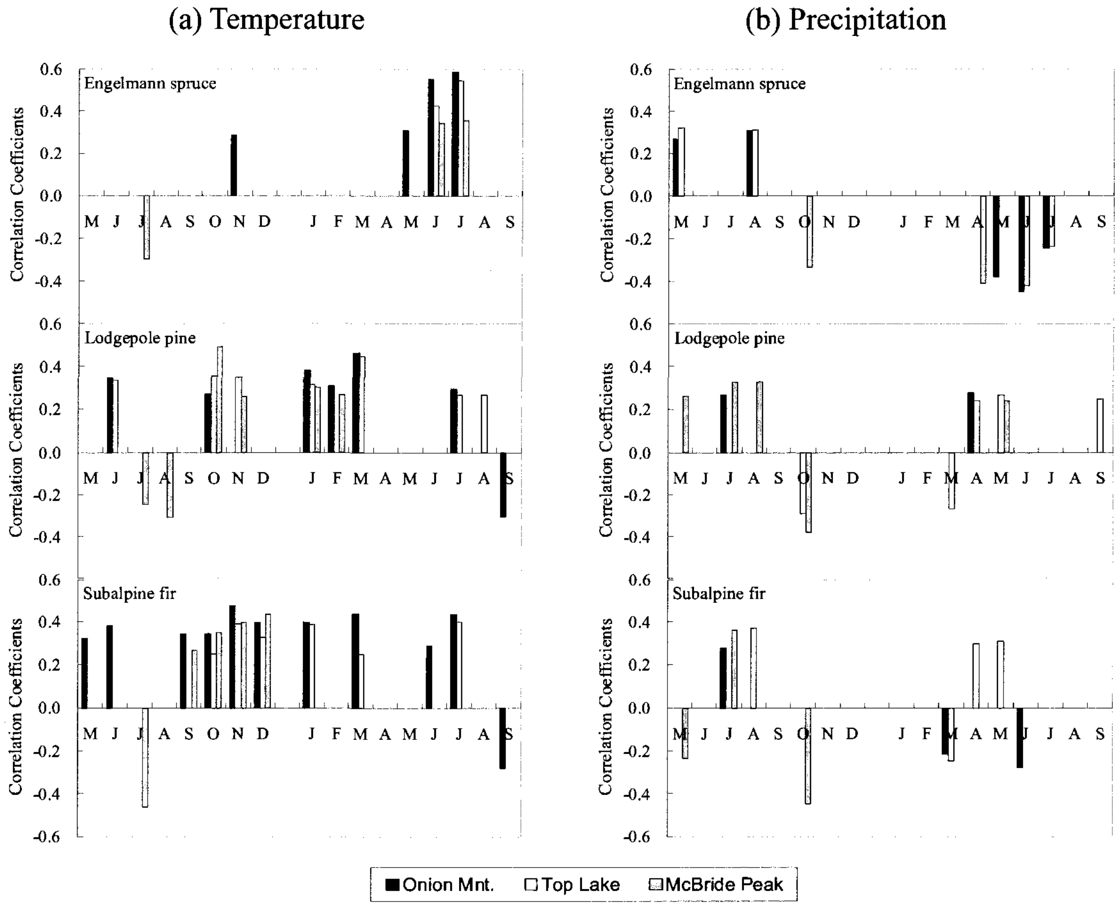

Figure 3.2. Pearson correlation coefficients between ring-width chronologies and mean monthly temperature (a) and precipitation (b) from May of the previous growth year to September of the current growth year (horizontal axes) for the period 1953-2002. Only significant correlations ($P < 0.05$) are shown.

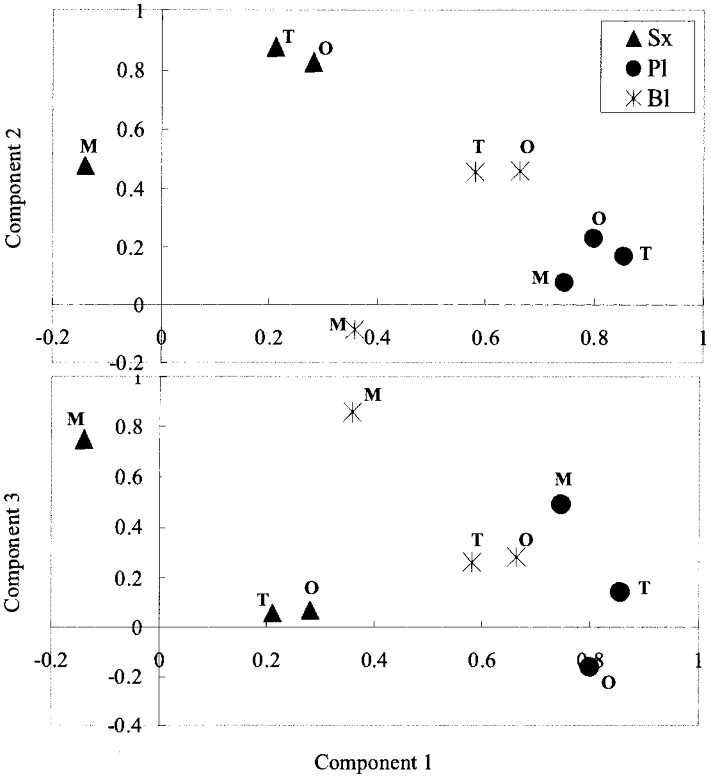

Figure 3.3. Similarity of ring-width variability among the nine ring-width chronologies according to the three axes resulting from a principal component analysis with Varimax rotation. Site codes are Onion Mountain (O), Top Lake (T), and McBride Peak (M).

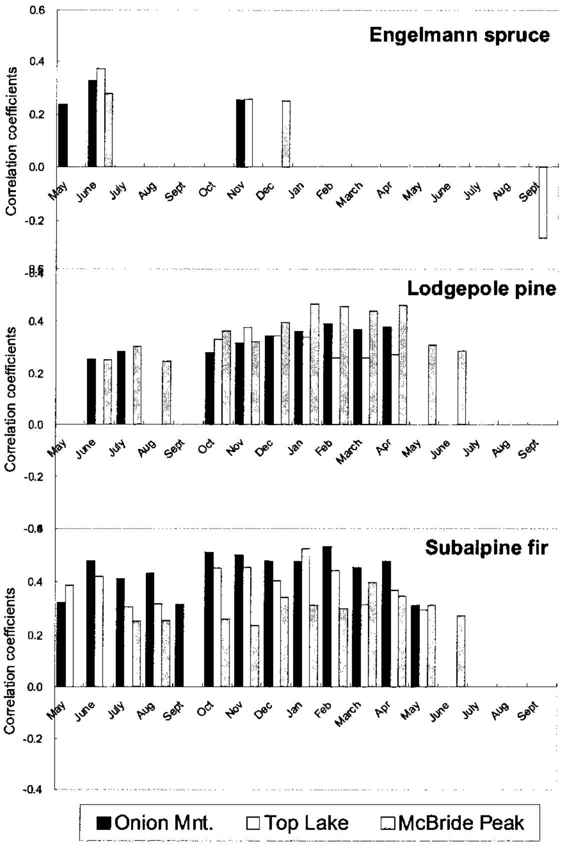

Figure 3.4. Pearson correlation coefficients between ring-width indices and monthly PDO from May of the previous growth year to September of the current growth year (horizontal axes) for the period 1953-2002. Only significant correlations ($P < 0.05$) are shown.

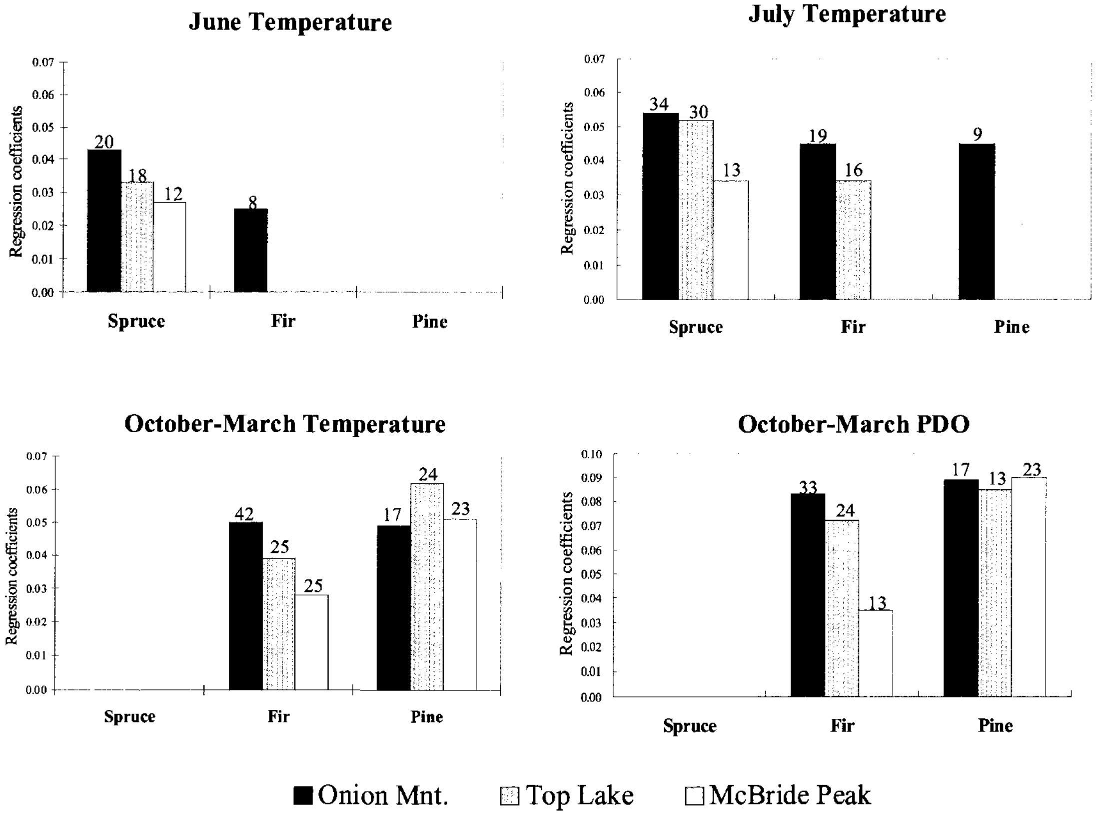

Figure 3.5. Linear regression coefficients (b1) between ring-width indices and selected climate variables for the period 1953-2002 at the three study sites. The number above each bar indicates the coefficients of determination (R^2). Only significant ($P < 0.05$) regression relationships are shown.