Regional, ecological, and temporal patterns in Douglas-fir climate-growth relationships in the British Columbia Interior

Hardy Griesbauer
B.Sc. Augustana University College, 1995

Thesis Submitted In Partial Fulfillment Of

The Requirements For The Degree Of

Master of Science

In

Natural Resources and Environmental Studies

(Forestry)

The University of Northern British Columbia

October 2008

Library and
Archives Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 978-0-494-48778-5
Our file Notre référence
ISBN: 978-0-494-48778-5

NOTICE:
The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:
L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

ABSTRACT

How climate change will affect tree growth across species' ranges remains a critical knowledge gap. Tree-ring data were analyzed from 33 Douglas-fir stands spanning a wide climatic and geographic range in the interior of British Columbia to identify regional and ecological patterns between climate and growth. Populations growing in warm and dry climates had growth patterns correlated mostly to local annual precipitation, whereas populations growing in high-elevation wet and cold climates were more correlated to annual/winter snowfall/winter temperatures and quasi-periodic ocean-atmosphere climate systems. Populations growing near the climatic margins of the species' range had the strongest responses to climate variability. Examining these relationships over different temporal scales revealed that some climate-growth relationships have varied substantially over time. Our results indicate that in the interior of British Columbia, Douglas-fir growth responses to climate change will not be uniform over time and space.

TABLE OF CONTENTS

ABSTRACT ii
TABLE OF CONTENTS iii
LIST OF TABLES vi
LIST OF FIGURES vii
ACKNOWLEDGEMENTS ix

Chapter 1. Introduction

- 1.1 Climate change in western North America and British Columbia 10
- 1.2 Climate change and forests 14
  - 1.2.1 The effects of climate change on forest growth 15
- 1.3 Douglas-fir 17
  - 1.3.1 Douglas-fir climate-growth relationships 19
    - 1.3.1.1 Douglas-fir growth responses to precipitation 19
    - 1.3.1.2 Douglas-fir growth responses to temperature 21
- 1.4 Project objectives 22
- 1.5 Literature cited 24

Chapter 2. Regional and ecological patterns in Douglas-fir climate-growth relationships in the British Columbia Interior

Abstract 32
2.1 Introduction 33
2.2 Materials and methods 36
2.2.1 Sampling 36
2.2.2 Processing and chronology development 37

2.2.3 Data analysis 38
2.2.3.1 Chronology analysis 38
2.2.3.2 Climate-growth relationships 40
2.2.3.2.1 Climate data 40
2.2.3.2.2 Regional climate-growth relationships 44
2.2.3.2.3 Climatic gradient analysis 44
2.3 Results 45
2.3.1 Chronologies 45
2.3.2 Multivariate analysis 46
2.3.2.1 Northern Interior sites 46
2.3.2.2 Southern Interior sites 47
2.3.2.3 Chilcotin Plateau sites 48
2.3.3 Climate-growth relationships 49
2.3.3.1 Regional climate-growth relationships 49
2.3.3.1.1 Northern Interior sites 49
2.3.3.1.2 Southern Interior sites 50
2.3.3.1.3 Chilcotin Plateau sites 51
2.3.3.2 Climatic gradient analysis 51
2.4 Discussion 52
2.4.1 Ecological growth patterns 52
2.4.2 Climate-growth relationships 53
2.4.2.1 Low- to mid-elevation dry sites 53
2.4.2.2 High-elevation sites 57
2.4.2.3 Sites at the northern geographic limits 59
2.4.3 Conclusion 60
2.5 Literature cited 62
Appendix A. Sample site mean annual temperature and precipitation normals. 87
Appendix B. Regional growth chronology time series derived from residual growth chronologies. 88
Appendix C. Example of climate gradient analysis. 89

Chapter 3. Temporal variability in climate-growth relationships at the climatic margins of Douglas-fir in British Columbia

Abstract 90
3.1 Introduction 91
3.2 Materials and methods 93
  3.2.1 Field sampling 93
  3.2.2 Processing and chronology development 94
  3.2.3 Principal components analysis 96
  3.2.4 Climate data 97
  3.2.5 Analysis of climate-growth relationships and inter-regional growth patterns 99
3.3 Results 102
  3.3.1 Temporal variation in high-elevation growth and climate-growth relationships
    3.3.1.1 Inter-regional growth patterns 102
    3.3.1.2 Temperature-growth relationships 102
    3.3.1.3 Snowfall-growth relationships 103
    3.3.1.4 Ocean-atmosphere climate indices-growth relationships 103
  3.3.2 Temporal variation in dry-site inter-regional growth patterns and climate-growth relationships
    3.3.2.1 Inter-regional growth patterns 104
    3.3.2.2 Temperature-growth relationships 104
    3.3.2.3 Precipitation-growth relationships 105
3.4 Discussion 106
  3.4.1 High-elevation sites 107
  3.4.2 Dry sites 111
  3.4.3 Conclusions 114
3.5 Literature cited 116
Appendix A. Time series of October-March precipitation anomalies for Vernon, British Columbia, from 1904 to 2004. 130
Appendix B. Time series of annual (prior July to current June) precipitation anomalies for Vernon, British Columbia, from 1904 to 2004. 130
Appendix C. Time series of annual (prior July to current June) precipitation anomalies for Williams Lake, BC, from 1940 to 2005. 131

Chapter 4. Summary and management implications
4.1 Introduction 132
4.2 Key study results and management implications 132
  4.2.1 Mid- to low-elevation dry-site Douglas-fir populations 133
  4.2.2 High-elevation Douglas-fir populations 137
4.3 Research limitations and future directions 139
4.4 Conclusions 140
4.5 Literature Cited 142

LIST OF TABLES

Table 2.1. Site descriptions and chronology statistics. 70

Table 2.2. Sample site climate normals. 71

Table 2.3. Summary of meteorological records used in Chapter 2. 72

Table 2.4. Missing precipitation data in meteorological records (between 1940 and 2004). 72

Table 2.5. Monthly climate values used to derive annual and seasonal variables used for correlation analysis. 73

Table 2.6. Principal components used for climate-growth analysis. 73

Table 2.7. Principal components analysis summary. 74

Table 2.8. Correlation coefficients between Douglas-fir growth variation and annual/seasonal climatic variables. 75

Table 3.1. Meteorological records used in Chapter 3. 123

Table 3.2. Missing rain, snow, and precipitation data in meteorological records. 124

Table 3.3. Monthly variables used to create seasonal variables for climate-growth analyses. 124

Table 3.4. Correlation coefficients between high-elevation Douglas-fir growth and ocean-atmosphere climate system indices. 124

LIST OF FIGURES

Figure 2.1. Sampling region overview map. 76

Figure 2.2. Sampling site locations in Northern Interior study region. 77

Figure 2.3. Sampling site locations in Chilcotin Plateau study region. 78

Figure 2.4. Sampling site locations in Southern Interior study region. 79

Figure 2.5. Chronology statistics against sample site mean annual climate normals. 80

Figure 2.6. Variation in annual precipitation-growth correlation and regression coefficients over annual heat-moisture index normals. 81

Figure 2.7. Variation in annual precipitation-growth correlation and regression coefficients over summer heat-moisture index normals. 81

Figure 2.8. Variation in annual precipitation-growth correlation and regression coefficients over mean annual precipitation normals. 82

Figure 2.9. Variation in annual precipitation-growth correlation and regression coefficients over (log-transformed) mean annual precipitation normals. 82

Figure 2.10. Variation in winter PNA index-growth correlation and regression coefficients over annual heat-moisture index. 83

Figure 2.11. Variation in winter PDO index-growth correlation and regression coefficients over annual heat-moisture index. 83

Figure 2.12. Northern Interior PC loads against geographic variables and climatic normals. 84

Figure 2.13. Southern Interior PC loads against geographic variables and climate normals. 85

Figure 2.14. Chilcotin Plateau PC loads against geographic variables and climate normals. 86

Figure 3.1. Correlations between climate and growth for high-elevation Douglas-fir populations in two regions of British Columbia over two sub-periods. 125

Figure 3.2. Moving correlation functions between climate and growth for high-elevation Douglas-fir populations in two regions of British Columbia. 126

Figure 3.3. Correlations between climate and growth for Douglas-fir populations growing in dry climates in two regions of British Columbia over two sub-periods. 127

Figure 3.4. Moving correlation functions between climate and growth for Douglas-fir populations growing in dry climates in two regions of British Columbia. 128

Figure 3.5. Moving correlation functions between temperatures and growth for Douglas-fir populations growing in dry climates in two regions of British Columbia. 129

Figure 4.1. Projected future climate for Douglas-fir sample sites in the three study regions. 145

Figure 4.2. Growth-annual precipitation regression coefficients against site annual heat-moisture index. 146

Figure 4.3. Growth-annual precipitation regression coefficients against site mean annual precipitation. 146

ACKNOWLEDGEMENTS

I would like to thank Dr. Scott Green for his mentorship, support, and guidance throughout this project, Dr. Greg O'Neill and Dr. Stephen Déry for guidance, advice, and suggestions as members of my committee, Emily Muller, Kara Przeczek, Kasia Caputa, and Yumiko Miyamoto for field and lab assistance, Chris Steeves for GIS data and maps, and of course, my wife Gretchen Prystawik for everything!

This projected was funded by the Forest Science Program (British Columbia), Natural Sciences and Engineering Research Council of Canada, and the province of British Columbia.

Chapter 1. Introduction

1.1 Climate change in western North America and British Columbia

Anthropogenic factors have contributed to an increase in global temperatures of approximately 0.6 °C over the last century, with warming occurring from 1910 to 1940 and from 1975 to the present day (Meehl et al. 2005, Christensen et al. 2007, Jones 1988). The rate of temperature increase has been faster in British Columbia (BC), where annual temperatures have increased by 0.5 to 1.7°C over the past century (the strongest increases have been in the northern and interior regions of the province) (BC MWLAP 2002). Seasonally, spring temperatures in BC show the strongest and most consistent trend over the past century, although winter and summer temperatures in some regions also show significant upward trends, especially over the last 50 years (BC MWLAP 2002, BC MoE 2007). Nighttime minimum temperatures have been increasing more rapidly than daytime maximum temperatures, thus lowering the diurnal temperature range, reducing growing season frost events, and lengthening the growing season (Karl et al. 1993, Dai et al. 1999, BC MWLAP 2002, BC MoE 2007). Annual precipitation has also increased significantly over most of western North America (Zhang et al. 2007, Trenberth 1990), although some regions of BC have become drier over the past 50 years (BC MoE 2007). Generally, winters in BC have become drier and the spring and summer seasons have become wetter (BC MoE 2007). The frequency of droughts, severe storms, and other extreme climatic events may also be increasing in association with climate change (Easterling et al. 2000).

Temperatures are projected to increase at possibly unprecedented rates during the 21st century, although future scenarios are uncertain due to a link with future changes in greenhouse gas emissions (Christensen et al. 2007, Moberg et al. 2005). Climate change models project that BC temperatures could increase by 2-5 °C above 1961-1990 averages by the middle of the 21st century, with the fastest rate of increase occurring over the winter, especially in the interior and northern regions of the province (BC MoE 2007, BC MWLAP 2007).

Precipitation trends are also difficult to predict, and model projections vary (Christensen et al. 2007). Annual precipitation over North America is generally expected to increase, although some areas may experience net drying due to increased evaporation and transpiration associated with higher temperatures (Christensen et al. 2007). Although winter precipitation in BC is expected to increase, snowpacks may actually diminish as a result of shorter winters, increased winter rains, and earlier spring snowmelt, particularly at low- to mid-elevations (Christensen et al. 2007, Knowles et al. 2006, Leung et al. 2004, BC MoE 2007, BC MWLAP 2002). Summer precipitation is expected to decrease over most of western North America (Christensen et al. 2007), although some projections for BC show a modest increase over most of the province with a possible slight decrease in southern coastal areas by the mid-21st century (BC MoE 2007).

Embedded in the temperature and precipitation trends over the past century are annual and decadal patterns of climatic variation that reflect the influence of spatially large quasi-periodic ocean-atmosphere systems on local climate (Cayan et al. 1998, Mantua and Hare 2002, BC MoE 2007). In western North America, the El Niño Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO), and Pacific/North American teleconnection index (PNA) are important drivers of local seasonal temperature and precipitation patterns (Mantua et al.

1997, Hare and Mantua 2001, Cayan et al. 1998, Knowles et al. 2006, Leathers et al. 1991, BC WLAP 2002, BC MoE 2007) and therefore may influence ecosystem functioning (e.g., Mantua et al. 1997, Case and Peterson 2005, Fagre et al. 2003, Daniels and Veblen 2004).

ENSO represents a quasi-periodic oscillation in sea surface temperature and atmospheric pressure anomalies in the tropical-subtropical Pacific and Indian Oceans (Allan 2000) that generally alternates between two extreme phases (often termed El Niño and La Niña events) every 2 to 7 years, with individual events lasting anywhere from 8 to 24 months (Allan 2000, Hare and Mantua 2001). ENSO affects climate variability on an almost global scale (Allan 2000) and is the strongest climate signal over most of the Pacific Ocean after the seasonal cycle (Hare and Mantua 2001). El Niño (La Niña) events typically bring warmer (cooler) and drier (wetter) winters to BC (BC MoE 2007, BC MWLAP 2002). Smith and Sardeshmukh (2000) created a monthly ENSO index time series using an average of standardized monthly sea surface temperature and air pressure anomalies (http://www.cdc.noaa.gov/people/cathy.smith/best/enso.ts.1mn.txt).

PDO is a quasi-periodic system of decadal variability in sea surface temperatures, sea level pressure, and wind patterns over the Pacific Ocean (Mantua et al. 1997, Mantua and Hare 2002, Biondi et al. 2001), with "warm" and "cool" phases lasting approximately 15 to 30 years (Mantua and Hare 2002, Gedalov and Mantua 2002), although PDO reconstructions based on tree-rings suggest that phase reversals may have occurred at different frequencies prior to the instrumental record (Gedalov and Smith 2001, Gedalov and Mantua 2002, Biondi et al. 2001). PDO may also have a 50-70 year cycle, although this has not been extensively studied to date (Mantua and Hare 2002, Hare and Mantua 2001). Over the past century, PDO warm phases have occurred from approximately 1925 to 1946, and from 1977 to present day (Mantua et al. 1997, Mantua and Hare 2002, Gedalov and Mantua 2002, Hare and Mantua 2001, Biondi et al. 2001). Cool phases have occurred from approximately 1900 to 1925, and from 1947 to 1976 (Mantua et al. 1997, Mantua and Hare 2002, Gedalov and Mantua 2002, Hare and Mantua 2001, Biondi et al. 2001). In western North America, warm (cool) PDO phases tend to result in warm and dry (cool and wet) anomalous climatic conditions (Hare and Mantua 2001, BC MoE 2007, BC MWLAP 2002). PDO and ENSO can have strong combined impacts on climate variability in western North America (Gershunov et al. 2001, Biondi et al. 2001). A time series of monthly PDO indices, derived from the leading principal component of sea surface temperature anomalies in the North Pacific Ocean, is available online at: http://jisao.washington.edu/pdo/PDO.latest.

PNA describes a connection pattern between mid- to upper-tropospheric air flow anomalies over the North Pacific Ocean and North America, and is a leading mode of atmospheric variability in the Northern Hemisphere winter (Leathers et al. 1991). PNA variability occurs at timescales ranging from weeks to decades (Leathers et al. 1991), and is strongly correlated to surface temperatures and precipitation (mostly winter and early spring) in the United States and Canada (Shabbar et al. 1997, Leathers et al. 1991). A PNA time series derived from a rotated (Varimax) principal components analysis of standardized monthly mean 500-millibar height anomalies over the Northern Hemisphere is available online at: http://www.cdc.noaa.gov/Correlation/pna.data.

1.2 Climate change and forests

Climate change is expected to have profound effects on forested ecosystems through multiple pathways (Millar et al. 2007, Parmesan 2006, Loehle 2000, Gates 1990, Walther 2003) and in conjunction with co-occurring phenomena such as forest fragmentation, exotic species invasions, habitat degradation, increased atmospheric carbon dioxide concentrations, nitrogen deposition, and pollution (Noss 2001, D'Arrigo et al. 2007, Millar et al. 2007). This combination of factors may create historically unprecedented environmental conditions and a highly uncertain situation for forest managers (Millar et al. 2007).

Some effects of climate change will be dramatic. For example, large-scale forest losses may result from a higher frequency of extreme events such as droughts, windstorms, and wildfires (Christensen et al. 2007, Gates 1990, Breshears et al. 2005) as well as climate-change-mediated disease and insect outbreaks (Woods et al. 2005, Carroll et al. 2006). Somewhat more subtle forest adaptation and migration responses to climate change will be associated with changes in growing season length, growing degree-days, soil moisture availability, and other climate-related factors important to plant life cycles (Davis and Shaw 2001, Parmesan 2006).

Adaptation will occur through numerous pathways such as physiological responses, phenological shifts, and evolution that may allow *in situ* individuals and populations to persist under new environmental conditions (Kozlowski and Pallardy 2002, Körner 2003, Davis and Shaw 2001, Walther 2003, Parmesan 2006). Although trees are generally resilient to climatic variation (Kozlowski and Pallardy 2002, Noss 2001), adaptive capacities may vary with factors such as species, region, ecological conditions, age, and genetic diversity, and in some cases, may be challenged by the unprecedented rapid rate of current environmental change (Aitken et al. 2008, Davis and Shaw 2001, Spittlehouse 2005, Noss 2001, Millar et al. 2007).

Over a long period, Northern Hemispheric tree species are generally expected to migrate northwards and upwards in elevation as temperatures increase (Davis and Shaw 2001, Lenoir et al. 2008, Parmesan 2006). Tree migration will be a slow and somewhat random process controlled by seed dispersal, germination, and seedling establishment rates, and may be an insufficient response to current climate change from a species survival perspective due to habitat fragmentation, competition from already established species, topographical barriers such as mountain ranges, and other local factors (Parmesan 2006, Millar et al. 2007, Davis and Shaw 2001, Hoegh-Guldberg et al. 2008, Aitken et al. 2008). Management interventions such as facilitated migration may be applicable where species or populations have low capacity to adapt or migrate in response to climate change, however, many critical knowledge gaps and concerns need to be addressed (Hoegh-Guldberg et al. 2008, Millar et al. 2007, Aitken et al. 2008).

1.2.1 The effects of climate change on forest growth

As climate is a key factor influencing tree growth (Fritts 1976, Kimmins 1997, Nigh et al. 2004), large patterns of forest productivity shifts may occur as a result of climate change (Nigh et al. 2004, Littell 2006, D'Arrigo et al. 2007). Elucidating species-, site-, and time-specific growth responses to climate change using dendroecological techniques (the study of tree-rings and ecology; Fritts 1976) can help address critical knowledge gaps regarding future species adaptation, productivity, abundances, resilience to disturbance, and community associations (Fritts 1976, Littell and Peterson 2005, Littell 2006, Carrer and Urbinati 2006, Zhang and Hebda 2004, Case and Peterson 2005, Pfeifer et al. 2005). Most tree-ring studies have focused on the influence of temperature and precipitation on tree growth, as they are primary climatic influences (Fritts 1976, Kimmins 1997) and historical data for these variables are easily obtained from climate station instrumental records.

Many tree-ring studies have shown that climate-growth relationships vary among species (e.g., Daniels and Watson 2003, Peterson and Peterson 2001, Adams and Kolb 2005), which may reflect unique adaptive capacities, growth strategies, and resource requirements that allow species to coexist (Davis and Shaw 2001, Green 2005, He et al. 2005). Species-specific climate-growth relationships have also been shown to vary along environmental gradients such as elevation (Adams and Kolb 2005, Zhang and Hebda 2004, Case and Peterson 2005), latitude (Watson and Luckman 2002, Feliksek and Wilczyński 2003), and climate regime (Littell 2006, Littell and Peterson 2005), possibly reflecting the dominant climatic limitation in a given environment. For example, growth tends to be limited by temperatures in cooler and wetter environments, and by precipitation in warmer and drier environments (Adams and Kolb 2005, Littell 2006), although interactions between temperature and precipitation are also important regulators of forest growth (Littell and Peterson 2005). Growth responses to a given climatic variable may be especially strong in populations growing near ecotonal boundaries and may provide an indication of future broader species responses (Littell and Peterson 2005, Neilson 1993, Loehle 2000, Walther et al. 2002).

Recent studies have shown that climate-growth relationships can vary over time, possibly as a function of climate change. For example, some historically cold-limited northern forests have shown a decrease in temperature sensitivity and/or developed a new sensitivity to precipitation over recent decades, possibly as a result of temperature-induced drought and/or co-occurring non-climatic anthropogenic forcings such as pollution, increased atmospheric carbon dioxide concentrations, and global dimming (Jacoby and D'Arrigo 1995, Lloyd and Fastie 2002, Barber et al. 2000, and see D'Arrigo et al. 2007 for a review). Similar findings have been reported for many tree species in northern Eurasia and North America (e.g., Pfeifer et al. 2005, Wilmking and Myers-Smith 2008, Carrer and Urbinati 2006), implying that this phenomenon may be widespread. Climate-growth relationships have also been shown to vary during different phases of ocean-atmosphere climate systems such as PDO (e.g., Fagre et al. 2003, Daniels and Veblen 2004). These types of findings challenge assumptions of stable ecosystem responses to climate change (Millar et al. 2007, Millar et al. 2006) and have significant implications for various aspects of forest management such as carbon cycle modeling, growth and yield, the management of climatically sensitive populations, and the use of tree-rings as historical climate proxies (Millar et al. 2006, D'Arrigo et al. 2007, Carrer and Urbinati 2006, Wilson and Elling 2004, Pfeifer et al. 2005).

1.3 Douglas-fir

This project used dendroecological techniques to study the climate-growth relationships of Douglas-fir (*Pseudotsuga menziesii*) in the British Columbia Interior. This species was chosen for study because it typically has a strong growth response to climate, and, in the interior of British Columbia, covers a wide climatic amplitude and occurs at three geographic/climatic limits (high-elevation, dry, and northern). Douglas-fir is a productive and commercial conifer found naturally in western North America from Mexico to BC (Hermann and Lavender 1990), and is also an economically important exotic species in Europe, Australia, New Zealand, and Chile (St. Clair et al. 2005, Hermann 1987). Two main varieties of the species are recognized in BC; the coastal variety (*P. menziesii* (Mirb.) Franco var. *menziesii*), which is generally found proximal to the Pacific Coast, and the interior variety (*P. menziesii* var. *glauca* (Beissn.) Franco), which ranges eastward from the rainshadow of the Coast Mountains. This project focused on the interior variety.

Interior Douglas-fir has a wide ecological amplitude, largely as a function of high intra-specific genetic diversity with a resulting strong capacity to adapt to local conditions (St. Clair et al. 2005, Arno 1991, Anekonda et al. 2002, Rehfeldt 1991). In the BC Interior, the species ranges from dry semi-arid forests in the lee of the Coast Mountains to low- to high-elevation wetbelt forests on the western slopes of the Rocky Mountains (Arno 1991) to cold interior forests near Fort St. James (Jull 1999), and inhabits seven biogeoclimatic zones, including the Interior Douglas-fir, Engelmann Spruce-Subalpine Fir, Sub-Boreal Pine and Spruce, Montane Spruce, Ponderosa Pine, Interior Cedar-Hemlock, and Sub-Boreal Spruce zones (Meidinger and Pojar 1991, Hamann and Wang 2006). This species has a competitive advantage in drier, fire-prone ecosystems, as mature trees have fire-resistant bark and can grow adventitious roots, allowing trees to persist and reproduce after low-intensity groundfires (Hermann and Lavender 1990, Delong 1999).

1.3.1 Douglas-fir climate-growth relationships

Many population- and regional-level dendroecological studies have shown Douglas-fir radial growth to be sensitive to climatic (mostly temperature and precipitation) variables (e.g., Adams and Kolb 2005, Daniels and Watson 2003, Case and Peterson 2005, Zhang and Hebda 2004, Littel 2006, Littell and Peterson 2005, Watson and Luckman 2002, Nigh et al. 2004). Growth responses of Douglas-fir to climate have been strong enough to be used in reconstructing historical temporal precipitation (e.g. Daniels and Watson 2003, Watson and Luckman 2001), temperature (Wilson and Luckman 2003, Laroque and Smith 2005), and PDO (D'Arrigo et al. 2001, Biondi et al. 2001) variability.

1.3.1.1 Douglas-fir growth responses to precipitation

Douglas-fir radial growth is generally more sensitive to water deficits than any other environmental variable (Littel 2006, Lopushinksy 1991, Case and Peterson 2005, Zhang and Hebda 2004), although this growth response can vary with local ecological conditions (Littel 2006, Case and Peterson 2005, Zhang and Hebda 2004). In warm and dry environments, Douglas-fir radial growth can be strongly limited by growing season precipitation (Adams and Kolb 2005, Daniels and Watson 2003, Littell 2006, Case and Peterson 2005), reflecting relatively poor stomatal control during droughts and low sapwood water storage capacity (Lopushinksy 1991). In extended droughts, Douglas-fir stomata may remain permanently closed, resulting in limited gas exchange, photosynthesis, (Lassoie and Salo 1981) and reduced transpiration (Lopushinski and Klock 1974).

Although Douglas-fir growth in cold environments (i.e., high-elevation and northern) is often primarily limited by cold temperatures (Feliksek and Wilczyński 2003, Case and Peterson 2005, Zhang and Hebda 2004, Littell 2006, Adams and Kolb 2005), significant positive correlations with growing season precipitation have been found (Case and Peterson 2005, Watson and Luckman 2002, Laroque and Smith 2005, Feliksek and Wilczyński 2003), possibly reflecting a sensitivity to drought events that reduce an already short growing season (Zhang and Hebda 2004). Douglas-fir growth in high-elevation environments can also have negative correlations with snowfall (Littell 2006, Case and Peterson 2005), as deep snowpacks may delay soil thaw and the start of the growing season (Littel 2006, Case and Peterson 2005, Vaganov et al. 1999), decreasing root growth and water uptake (Brubaker 1980).

Douglas-fir annual growth has also been shown to be correlated to precipitation from the previous year's growing season. Specifically, the earlywood portion of the annual ring can be correlated to precipitation from the previous growing season, whereas the latewood portion can be correlated to current summer precipitation (Daniels and Watson 2003, Watson and Luckman 2002). A correlation between earlywood and previous growing season precipitation may be explained in that primordial tissues are formed during the end of the growing season, and water availability during the summer influences carbohydrate allocation to the following year's formative tissues (Fritts 1976, Littel 2006). As well, Douglas-fir needles are fully growing and photosynthesizing early in the season (compared to co-occurring species such as ponderosa pine [*Pinus ponderosa* Douglas ex C. Lawson]), and therefore, may use soil moisture present from the previous year's precipitation (Watson and Luckman 2002).

1.3.1.2 Douglas-fir growth responses to temperature

Douglas-fir radial growth can be positively correlated to growing season and winter temperatures, particularly in cold high-elevation (Case and Peterson 2005, Zhang and Hebda 2004, Laroque and Smith 2005) and continental (Feliksek and Wilczyński 2003) sites. The typically low temperatures found in cold environments limit growth by inhibiting photosynthesis, glucose uptake, and meristematic activities (Körner 2003, Grace et al. 2002) as well as creating limiting site conditions such as low soil temperatures, increased snowpacks, and short growing seasons (Körner 2003, Kimmins 1997, Case and Peterson 2005, Laroque and Smith 2005). Growing season frost events can damage mature Douglas-fir needles, inhibit hormonal system functioning, and delay the activity of formation tissue, resulting in a smaller annual increment the following year (Feliksek and Wilczyński 2003). Although warmer temperatures associated with recent climate change may alleviate cold limitations to growth in these types of environments, they may also result in complex climate interactions and new limitations to tree growth such as drought (Lloyd and Fastie 2002, Barber et al. 2000). As well, winter temperatures may rise above the bud-chilling requirement of Douglas-fir, resulting in a delay of bud burst in the spring and lower growth (McCreary et al. 1990).

Growing season temperatures are often negatively correlated with Douglas-fir radial growth on warm and dry sites at mid- to low-elevations (Case and Peterson 2005, Zhang and Hebda 2004, Laroque and Smith 2005, Feliksek and Wilczyński 2003, Daniels and Watson 2003, Watson and Luckman 2001). An increase in temperature affects respiration and transpiration processes and may reduce growth by increasing water loss, reducing nutrient storage, decreasing foliage efficiency (Laroque and Smith 2005, Kimmins 1997, Balatinecz and

Anderson 1986), or by exceeding a species-specific upper photosynthesis threshold (which can be as low as 20-25°C for Douglas-fir; Salo 1974, Doehlert and Walker 1981).

1.4 Project objectives

A key step in preparing for climate change will be addressing the many knowledge gaps regarding historical and possible future tree species growth responses to climate variability (Littell and Peterson 2005, Littell 2006). The climate-growth relationships of Douglas-fir have been extensively studied, however, many knowledge gaps remain. Although Douglas-fir climate-growth relationships have been quantified across elevation (e.g., Zhang and Hebda 2004, Case and Peterson 2005) and latitude (e.g.,Watson and Luckman 2002) gradients, to our knowledge, there have been no studies examining changes in Douglas-fir climate-growth relationships over a large climatic gradient (as defined by local climate normals) in the British Columbia Interior. As well, we know very little about the climate-growth relationships at the climatic margins of the species in the BC Interior, and how these relationships relate to broader species responses. Further, there appears to be very little knowledge about the temporal stability of Douglas-fir climate-growth relationships. This project addressed these knowledge gaps by describing regional, climatic, and temporal patterns in Douglas-fir climate-growth relationships across a wide climatic range in the BC Interior, including populations growing at the climatic margins of the species' range. When describing site characteristics in this study, the term 'climatic' refers to climate normals (defined as the average from 1961-1990), whereas 'ecological' refers to both climate normals and associated site characteristics such as elevation and topography.

This project focused on the following specific questions:

1) Are there spatially coherent ecological patterns in Interior Douglas-fir climate-growth relationships?
2) How do climate-growth relationships change over a climatic gradient, including populations located in climatically extreme environments?
3) Are climate-growth relationships stable over time?
4) Are there ecological patterns in temporally unstable climate-growth relationships?

These questions were addressed in two research chapters. Regional and ecological patterns in Douglas-fir climate-growth relationships across the BC Interior are described in Chapter 2. In chapter 3, temporal patterns in climate-growth relationships are examined with a focus on populations growing at two climatic limits (cold and wet high-elevation sites and dry climate sites). The management implications of key study results are discussed in Chapter 4.

1.5 Literature cited

Adams, H.D. and T.E. Kolb. 2005. Tree growth response to drought and temperature in a mountain landscape in northern Arizona, USA. Journal of Biogeography 32: 1629-1640.

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

Allan, R.J. 2000. ENSO and climatic variability in the past 150 years, p. 3-56. In El Nino and the Southern Oscillation: multiscale variability and global and regional impacts. Diaz, H. F. and Markgraf, V. (eds). Cambridge University Press, New York.

Anekonda, T.S., M.C. Lomas, W.T. Adams, K.L. Kavanagh, and S.N. Aitken. 2002. Genetic variation in drought hardiness of coastal Douglas-fir seedlings from British Columbia. Canadian Journal of Forest Research 32: 1701-1716.

Arno, S.F. 1991. Ecological relationships of interior Douglas-fir, p. 47-51. In Interior Douglas-fir: The species and its management symposium proceedings. Baumgartner, D. M. (ed). Department of Natural Resource Sciences, Washington State University, Pullman, Washington.

Balatinecz, J.J. and H.W. Anderson. 1986. Effects of climatic factors on the formation of wood and its quality, p. 195-200. In Climate Applications in Forest Renewal and Forest Production, Proceedings of Forest Climate 1986. MacIver, D. C., Street, R. B., and Auclair, A. N. (eds). Canadian Forestry Service, Ottawa, Ontario.

Barber, V., G. Juday, and B. Finney. 2000. Reduced growth of Alaska white spruce in the twentieth century from temperature-induced drought stress. Nature 405: 668-672.

BC MoE. 2007. Environmental Trends in British Columbia: 2007. State of Environment Reporting. BC Ministry of Environment, Victoria, B.C.

BC MWLAP. 2002. Indicators of climate change for British Columbia, 2002. Indicators of climate change for British Columbia, 2002. BC Ministry of Water, Land and Air Protection, Victoria, B.C.

Biondi, F., A. Gershunov, and D. Cayan. 2001. North Pacific decadal climate variability since 1661. Journal of Climate 14: 5-10.

Breshears, D.D., N.S. Cobb, P.M. Rich, K.P. Price, C.D. Allen, R.G. Balice, W.H. Romme, J.H. Kastens, M.L. Floyd, J. Belnap, J.J. Anderson, O.B. Myers, and C.W. Meyer. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences 102: 15144-15148.

Brubaker, L.B. 1980. Spatial patterns of tree growth anomalies in the Pacific Northwest. Ecology 6: 798-807.

Carrer, M. and C. Urbinati. 2006. Long-term change in the sensitivity of tree-ring growth to climate forcing in Larix decidua. New Phytologist 170: 861-872.

Carroll, A.L., J. Régniere, J.A. Logan, S.W. Taylor, B.J. Bentz, and J.A. Powell. 2006. Impacts of climate change on range expansion by the mountain pine beetle. Mountain Pine Beetle Initiative Working Paper 2006-14. Natural Resources Canada, Victoria, B.C.

Case, M.J. and D.L. Peterson. 2005. Fine-scale variability in growth-climate relationships of Douglas-fir, North Cascade Range, Washington. Canadian Journal of Forest Research 35: 2743-2755.

Cayan, D.R., M.D. Dettinger, H.F. Diaz, and N.E. Graham. 1998. Decadal variation of precipitation over Western Northern America. Journal of Climate 11: 3148-3166.

Christensen, J.H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R.K. Kolli, W.-T. Kwon, R. Laprise, V. Magaña Rueda, L. Mearns, C.G. Menéndez, J. Räisänen, A. Rinke, A. Sarr, and P. Whetton. 2007. Regional Climate Projections, p. 848-940. In Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Solomon, S. D., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. M. (eds). Cambridge University Press, New York.

D'Arrigo, R., R. Villalba, and G. Wiles. 2001. Tree-ring estimates of Pacific decadal climate variability. Climate Dynamics 18: 219-224.

D'Arrigo, R., R. Wilson, B. Liepert, and P. Cherubini. 2007. On the 'Divergence Problem' in Northern Forests: A review of the tree-ring evidence and possible causes. Global and Planetary Change 289-305.

Dai, A., K.E. Trenberth, and T.R. Karl. 1999. Effects of clouds, soil moisture, precipitation, and water vapor on diurnal temperature range. Journal of Climate 12: 2451-2473.

Daniels, L.D. and T.T. Veblen. 2004. Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. Ecology 85: 1284-1296.

Daniels, L.D. and E. Watson. 2003. Climate-fire-vegetation interactions in the Cariboo forests: a dendrochronological analysis. Report to Forest Innovation and Investment. Forest Innovation and Investment Research Program, Vancouver, BC.

Davis, M.B. and Shaw. R.G. 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292: 673-679.

Delong, S.C. 1999. Ecology of Douglas-fir at its northern limits, p. 27-28. In Ecology and management of interior Douglas-fir (Pseudotsuga menziesii var glauca) at the northern extreme of its range. Proceedings of a workshop held 7-9 October 1996 in Fort St. James, British Columbia. Lousier, J. D. and Kessler, W. B. (eds). University of Northern British Columbia, Prince George, BC.

Doehlert, D.C. and R.B. Walker. 1981. Photosynthesis and photorespiration in Douglas-fir as influenced by irradiance, CO2 concentration, and temperature. Forest Science 27: 641-650.

Easterling, D.R., G.A. Meehl, C. Parmesan, S.A. Changnon, T.R. Karl, and L.O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. Science 289: 2068-2074.

Fagre, D.B., D.L. Peterson, and A.E. Hessl. 2003. Taking the pulse of mountains: Ecosystem responses to climatic variability. Climatic Change 59: 263-282.

Feliksek, E. and S. Wilczyński. 2003. Dendroecological characterization of Douglas-fir (Pseudotsuga menziesii Franco) in the Wielkopolska region. Electronic Journal of Polish Agricultural Universities 6: Series: Forestry.

Fritts, H.C. 1976. Tree rings and climate. The Blackburn Press, New Jersey.

Gates, D.M. 1990. Climate change and forests. Tree Physiology 7: 1-5.

Gedalov, Z. and N.J. Mantua. 2002. A multi-century perspective of variability in the Pacific Decadal Oscillation: new insights from tree rings and coral. Geophysical Research Letters 29: 1-4.

Gedalov, Z. and D.J. Smith. 2001. Interdecadal climate variability and regime-scale shifts in Pacific North America. Geophysical Research Letters 28: 1515-1518.

Gershunov, A., N. Schneider, and T. Barnett. 2001. Low-frequency modulation of ENSO - Indian Monsoon rainfall relationship: signal or noise? Journal of Climate 14: 2486-2492.

Grace, J., F. Berninger, and N. Laszlo. 2002. Impacts of climate change on the tree line. Annals of Botany 90: 537-544.

Green, D.S. 2005. Adaptive strategies in seedlings of three co-occurring, ecologically distinct northern coniferous tree species across and elevational gradient. Canadian Journal of Forest Research 35: 910-917.

Hamann, A. and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87: 2773-2786.

Hare, S.R. and N.J. Mantua. 2001. An historical narrative on the Pacific Decadal Oscillation, interdecadal climate variability and ecosystem impacts. Report of a talk presented at the 20th NE Pacific Pink and Chum workshop, Seattle, WA, 22 March 2001. http://www.iphc.washington.edu/Staff/hare/html/papers/pcworkshop/pcworkshop.pdf.

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

Hermann, R.K. 1987. North American tree species in Europe. Journal of Forestry 85: 27-32.

Hermann, R.K. and D.P. Lavender.1990. Douglas-fir. In Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. Burns, R. M. and Honkala, B. H. (eds). U.S. Department of Agriculture, Washington, DC. http://www.na.fs.fed.us/spfo/pubs/silvics_manual/Volume_1/pseudotsuga/menziesii.htm.

Hoegh-Guldberg, O., L. Hughes, S. McIntyre, D.B. Lindenmayer, C. Parmesan, H.P. Possingham, and C.D. Thomas. 2008. Assisted colonization and rapid climate change. Science 321: 345-346.

Jacoby, G.C. and R. D'Arrigo. 1995. Tree-ring width and density evidence of climatic and potential forest change in Alaska. Global Biogeochemical Cycles 9: 227-234.

Jones, P.D. 1988. Hemispheric surface air temperature variations: Recent trends and an update to 1987. Journal of Climate 1: 654-660.

Jull, M.J. 1999. Douglas-fir silviculture "on the edge": silvicultural systems at the northern range of the species, p. 34-44. In Ecology and management of interior Douglas-fir (Pseudotsuga menziesii var glauca) at the northern extreme of its range. Proceedings of a workshop held 7-9 October 1996 in Fort St. James, British Columbia. Lousier, J. D. and Kessler, W. B. (eds). University of Northern British Columbia, Prince George, BC.

Karl. T.R., Jones. P.D., R.W. Knight, G. Kukla, N. Plummer, V. Razuvayev, K.P. Gallo, J. Lindsaey, R.J. Charlson, and T.C. Peterson. 1993. A new perspective on recent global warming: asymmetric trends of daily maximum and minimum temperature. Bulletin of the American Meteorological Society 74: 1007-1023.

Kimmins, J. P. 1997. Forest Ecology. Prentice-Hall Inc., New Jersey.

Knowles, N., M.D. Dettinger, and D.R. Cayan. 2006. Trends in snowfall versus rainfall in the Western United States. Journal of Climate 19: 4545-4559.

Kozlowski, T.T. and S.G. Pallardy. 2002. Acclimation and adapative responses of woody plants to environmental stresses. The Botanical Review 68: 270-334.

Körner, C. 2003. Alpine plant life. Springer-Verlag, New York.

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

Lassoie, J.P. and D.J. Salo. 1981. Physiological response of large Douglas-fir to natural and induced soil water deficits. Plant physiology and biochemistry 11: 139-144.

Leathers, D.J., B. Yarnal, and M.A. Palecki . 1991. The Pacific/North American Teleconnection Pattern and United State Climate. Part I: Regional Temperature and Precipitation Associations. Journal of Climate 4: 517-528.

Lenoir, J., J.C. Gégout, P.A. Marquet, P. de Huffray, and H. Brisse. 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science 320: 1768-1771.

Leung, L.R., Y. Qian, X. Bian, W.M. Washington, J. Han, and J.O. Roads . 2004. Mid-century ensemble regional climate change scenarios for the western United States. Climatic Change 62: 75-113.

Littell, J. S. 2006. Climate impacts to forest ecosystem processes: Douglas-fir growth in north-western U.S. mountain landscapes and area burned by wildfire in western U.S. eco-provinces. PhD Dissertation. University of Washington. Seattle, WA.

Littell, J.S. and D.L. Peterson. 2005. A method for estimating vulnerability of Douglas-fir growth to climate change in the northwestern U.S. The Forestry Chronicle 81: 369-374.

Lloyd, A.H. and C.L. Fastie. 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. Climatic Change 52: 481-509.

Loehle, C. 2000. Forest ecotone response to climate change: sensitivity to temperature response functional forms. Canadian Journal of Forest Research 30: 1632-1645.

Lopushinksy, W. 1991. Water relations of interior Douglas-fir, p. 35-46. In Interior Douglas-fir: The species and its management symposium proceedings. Baumgartner, D. M. (ed). Department of Natural Resource Sciences, Washington State University, Pullman, Washington.

Lopushinksy, W. and G.O. Klock. 1974. Transpiration of conifer seedlings in relation to soil water potential. Forest Science 20: 181-186.

Mantua, N.J. and S.R. Hare. 2002. The Pacific Decadal Oscillation. Journal of Oceanography 58: 35-44.

Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace, and R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78: 1069-1079.

McCreary D.D., D.P. Lavender, and R.K. Hermann. 1990. Predicted global warming and Douglas-fir chilling requirements. Annals of Forest Science 47: 325-330.

Meehl, G.A., W.M. Washington, W.D. Collins, J.M. Arblaster, A. Hu, L.E. Buja, W.G. Strand, and H. Teng. 2005. How much more global warming and sea level rise? Science 307: 1769-1772.

Meidinger, D. and J. Pojar. 1991. Ecosystems of British Columbia. BC Ministry of Forests, Victoria, B.C.

Millar, C., R. Neilson, D. Bachelet, R. Drapek, and J. Lenihan. 2006. Climate change at multiple scales, p. 30-60. In Forests, carbon and climate change: a synthesis of science findings. Oregon Forest Resources Institute, Portland, Oregon.

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

Moberg, A., D.M. Sonechkin, N.M. Holmgren, N.M. Datsenko, and W. Karlen. 2005. Highly variable Northern Hemisphere temperatures reconstructed from low- and high-resolution proxy data. Nature 433: 613-617.

Neilson, R.P. 1993. Transient ecotone response to climatic change: some conceptual and modelling approaches. Ecological Applications 3: 385-395.

Nigh, G.D., C.C. Ying, and H. Qian. 2004. Climate and productivity of major conifer species in the interior of British Columbia, Canada. Forest Science 50: 659-671.

Noss, R.F. 2001. Beyond Kyoto: forest management in a time of rapid climate change. Conservation Biology 15: 578-590.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37: 637-669.

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

Pfeifer, K., W. Kofler, and W. Oberhuber. 2005. Climate related causes of distinct radial growth reductions in Pinus cembra during the last 200 yr. Vegetation History and Archaeobotany 14: 211-220.

Rehfeldt, J. 1991. The genetic resource of Douglas-fir in the interior northwest, p. 53-62. In Interior Douglas-fir: The species and its management symposium proceedings. Baumgartner, D. M. (ed). Department of Natural Resource Sciences, Washington State University, Pullman, Washington.

Salo, D. J. 1974. Factors affecting photosynthesis in Douglas-fir. PhD Dissertation. University of Washington. Seattle, WA.

Shabbar, A., B. Bonsal, and M. Khandekar. 1997. Canadian Precipitation Patterns Associated with the Southern Oscillation. Journal of Climate 10: 3016-3027.

Smith, C.A. and P. Sardeshmukh. 2000. The effect of ENSO on the intraseasonal variance of surface temperature in winter. International Journal of Climatology 20: 1543-1557.

Spittlehouse, D.L. 2005. Integrating climate change adaptation into forest management. Forestry Chronicle 81: 691-695.

St. Clair, J.B., N.L. Mandel, and K.W. Vance-Borland. 2005. Genecology of Douglas Fir in Western Oregon and Washington. Annals of Botany 96: 1199-1214.

Trenberth, K.E. 1990. Recent observed interdecadal climate changes in the Northern Hemisphere. Bulletin of the American Meteorological Society 71: 988-993.

Vaganov, E.A., M.K. Hughes, A.V. Kirdyanov, F.H. Schweingruber, and P.P. Silkin. 1999. Influence of snowfall and melt timing on tree growth in subarctic Eurasia. Nature 400: 149-151.

Walther, G.-R. 2003. Plants in a warmer world. Perspectives in Plant Ecology, Evolution, and Systematics 6: 169-185.

Walther, G.-R., E. Post, P. Convey, A. Menzei, C. Parmesan, T.J.C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416: 389-395.

Watson, E. and B. Luckman. 2001. Dendroclimatic reconstruction of precipitation for sites in the southern Canadian Rockies. The Holocene 11: 203-213.

Watson, E. and B.H. Luckman. 2002. The dendroclimatic signal in Douglas-fir and ponderosa pine tree-ring chronologies from the southern Canadian Cordillera. Canadian Journal of Forest Research 32: 1858-1874.

Wilmking M. and I. Myers-Smith. 2008. Changing climate sensitivity of black spruce (Picea mariana Mill.) in a peatland-forest landscape in Interior Alaska. Dendrochronologia 25: 167-175.

Wilson, R. and W. Elling. 2004. Temporal instability in tree growth/climate response in the Lower Bavarian Forest region: implications for dendroclimatic reconstruction. Trees 18: 19-28.

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

Woods, A., K.D. Coates, and A. Hamann. 2005. Is an unprecedented Dothistroma needle blight epidemic related to climate change? BioScience 55: 761-769.

Zhang, Q.-B. and R.J. Hebda. 2004. Variation in radial growth patterns of Pseudotsuga menziesii on the central coast of British Columbia, Canada. Canadian Journal of Forest Research 34: 1946-1954.

Zhang, X., F.W. Zwiers, G.C. Hegerl, F.H. Lambert, N.P. Gillett, S. Solomon, P.A. Stott, and T. Nozawa. 2007. Detection of human influence on twentieth-century precipitation trends. Nature 448: 461-465.

Chapter 2. Regional and ecological patterns in Douglas-fir climate-growth relationships in the British Columbia Interior

Abstract

How climate change will affect tree growth across species' ranges remains a critical knowledge gap. Tree-ring data were analyzed from 33 Douglas-fir stands spanning a wide climatic and geographic range in the interior of British Columbia to identify regional and ecological patterns between climate and growth. Populations growing in warm and dry climates had growth patterns correlated mostly to local annual precipitation, whereas populations growing in high-elevation wet and cold climates were more correlated to annual/winter snowfall/winter temperatures and quasi-periodic ocean-atmosphere climate systems. Site annual/summer heat-moisture index and precipitation regime were able to predict the strength of population growth responses to annual precipitation and PNA/PDO index, and the strongest responses to both variables were found in populations growing at the climatic extremes. Across most of its range, Douglas-fir growth appears to be limited by annual moisture, likely reflecting a high sensitivity to available soil moisture. Future temperature-induced drought conditions in BC could result in widespread heightened sensitivity to precipitation and productivity declines.

2.1 Introduction

In British Columbia (BC), annual temperatures have increased by 0.5 to 1.7°C over the past century and are projected to increase by 2 to 5°C above 1961-1990 averages by the middle of the 21st century, depending on future greenhouse emissions (BC MWLAP 2002, BC MoE 2007, Christensen et al. 2007, Meehl et al. 2005). Nighttime minimum temperatures have increased more rapidly than daytime maximum temperatures, thus lowering the diurnal temperature range, reducing growing season frost events, and lengthening the growing season (Karl et al. 1993, Dai et al. 1999, BC MWLAP 2002, BC MoE 2007). Annual precipitation has also increased significantly over most of western North America (Zhang et al. 2007, Trenberth 1990), although some regions of BC have become drier over the past 50 years (BC MoE 2007). Projections show a modest precipitation increase over most of BC, with wetter summers and more winter rains at low- to mid-elevations (BC MoE 2007), however, some areas may experience net drying as a result of increased temperatures and lower snowpacks (Christensen et al. 2007, Leung et al. 2004, Knowles et al. 2006). The frequency of droughts, severe storms, and other extreme climatic events may also increase in association with climate change (Easterling et al. 2000). In western North America, oscillatory interactions between the Pacific Ocean and the atmosphere are important sources of low-frequency climate variation that will additionally influence future regional climate regimes (Mantua et al. 1997, Hare and Mantua 2001, Cayan et al. 1998, Knowles et al. 2006, Leathers et al. 1991).

Temperature-precipitation changes are expected to significantly affect forests by influencing growing season length, growing degree-days, soil moisture availability, and other climate-related factors important to plant life cycles (Kimmins 1997, Fritts 1976, Davis and Shaw 2001). Tree responses to climate change will be expressed through changes in reproductive, physiological, and phenological processes (Aitken et al. 2008, Walther 2003, Walther et al. 2002, Aber et al. 2001, Hansen et al. 2001, Parmesan and Yohe 2003, Gates 1990, Graham et al. 1990), and will reflect species-specific adaptive capacities as well as the influence of local factors such as soil nutrients, competition, forest disturbances, and genetic diversity (Aitken et al. 2008, Hamann and Wang 2006, Graumlich 1991, Spittlehouse and Stewart 2003). Over a long period, species- and site-specific responses to climate change will result in altered forest compositions and new species ranges (Hamann and Wang 2006, Davis and Shaw 2001).

Tree growth and productivity may rapidly shift in response to climate change (Littell 2006, Stephenson and van Mantgem 2005, Hanson and Weltzin 2000) and identifying the climate mechanisms underlying these shifts may provide important information regarding species adaptation, survival, productivity, resilience to disturbance, and long-term range shifts (Peterson and Peterson 2001, D'Arrigo et al. 2007, Carrer and Urbinati 2006, Zhang and Hebda 2004, Littell and Peterson 2005, Case and Peterson 2005). Climate-growth relationships should be quantified across the spectrum of the species' ecological range, including its extremes (Peterson and Peterson 2001, Littell 2006, Littell and Peterson 2005, Case and Peterson 2005, Zhang and Hebda 2004), as climatic growth limitations may vary with local environmental conditions. For example, trees growing in cold environments tend to be limited by low temperatures (Barber et al. 2000, Case and Peterson 2005, Zhang and Hebda 2004), whereas dry ecosystem forests are often more limited by precipitation (Adams and Kolb 2005, Lloyd and Fastie 2002). Stands growing near their ecological margins may be especially sensitive to climate variation due to strong environmental limitations and may provide an indication of future broader species responses (Loehle 2000, Lloyd 2005, Neilson 1993, Case and Peterson 2005).

Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco) is a commercially important conifer that grows over a wide range of ecological conditions and is found at its high-elevation, northern, and dry limits in the interior of British Columbia (Hermann and Lavendar 1990, Jull 1999, Delong 1999, Arno 1991). Numerous studies have shown this species has a high sensitivity to climate (e.g., Daniels and Watson 2003, Watson and Luckman 2002) and that its climate-growth relationships can vary over elevation (e.g., Zhang and Hebda 2004, Case and Peterson 2005, Adams and Kolb 2005), continentality (e.g., Feliksek and Wilczyński 2003), and latitude (e.g.,Watson and Luckman 2002) gradients, however, relatively little is known about Douglas-fir climate-growth relationships along its climatic range (as defined by local mean annual temperature and precipitation) (Littell 2006), particularly in British Columbia (Spittlehouse 2003).

This study used dendroecological methods (Fritts 1976) to quantify radial growth variation and climate-growth relationships of interior Douglas-fir across a wide climatic and geographic range in the British Columbia Interior, encompassing sites near the geographic and climatic margins. The objectives of this study were to: 1) identify climate variables that influence Douglas-fir growth and 2) identify and examine regional and ecological (i.e. site climate normals and associated features such as elevation) patterns of interior Douglas-fir growth variation across its climatic range in the interior of British Columbia.

2.2 Materials and methods

2.2.1 Sampling

We sampled 33 mature stands of Douglas-fir in three geographic regions (Figure 2.1) in the British Columbia Interior: 1) Northern Interior (Figure 2.2), 2) Chilcotin Plateau (2.3), and 3) Southern Interior (Figure 2.4). The 33 sample stands (sites) were strategically chosen to encompass a wide range of climatic regimes, including sites located at the extremes in each region. Potential sampling sites were identified by overlaying spatial mean annual temperature (MAT) and precipitation (MAP) data (1961-1990 climate normal period, Spittlehouse 2006) obtained from ClimateBC (v3.1, Wang et al. 2006) onto mature Douglas-fir coverage obtained from the BC Ministry of Forest and Range's Vegetation Resource Inventory. Sample site MAT ranged from 1.5 to 7.4 °C, and MAP ranged from 335 to 2077 mm (Table 2.2). The elevation range was 370 to 1540 m (Table 2.1). The sampled sites encompassed seven biogeoclimatic (BEC) zones (Meidinger and Pojar 1991), representing a wide diversity of ecosystems (Table 2.2).

Sample sites and trees were chosen to maximize the climate signal in growth variation. Sites without evidence of edaphic limiting factors (e.g., shallow rocky soils, cold air ponding, steep northerly aspects) or recent abiotic or biotic disturbance were selected in order to minimize the growth impacts of non-climatic factors. The influence of inter-tree competition was minimized by sampling trees with a dominant canopy position. We avoided sampling trees with obvious growth defects or evidence of disease, fire scarring, or insect attacks as much as possible. At each site, between 18 and 40 mature trees greater than 100 years old were sampled to build a robust population sample. A single increment core was taken from each sample tree at approximately breast height (1.3m, Josza 1988). Where sampling occurred on slopes, increment cores were taken perpendicular to the slope direction to avoid compression and tension wood (Josza 1988).

2.2.2 Processing and chronology development

Increment cores were mounted and sanded to enhance the contrast of tree ring boundaries. Cores were then visually crossdated to assign calendar years to annual growth rings (Cook and Kairiukstis 1990). Ring widths were measured using WinDendro™ image analysis software (Regent Instruments Inc. 2005) to the nearest 0.01mm. Crossdating was verified using COFECHA software (Holmes 1983). After checking for measurement errors, cores that did not crossdate with the master chronology were excluded from the final chronology (Daniels and Watson 2003).

The ARSTAN software (Cook and Krusic 2005) was used to remove the age-related growth trend from each series, as this trend usually dominates the variance and masks the climate signal (Fritts 1976, Cook and Kairiukstis 1990, Cook 1985). A cubic smoothing spline with a 50% frequency response cutoff of 60 years was used to remove very low-frequency (i.e., age-related trend) variation (Cook 1985, Cook and Kairiukstis 1990). Cubic smoothing splines remove unwanted variation by filtering data in the frequency domain; the spline used in this study removed 50% of the signal amplitude at a frequency of 1 cycle/60 years, and an increasing (decreasing) percentage of the signal amplitude at frequencies lower (higher) than 60 years (Cook 1985, Cook and Kairiukstis 1990).

After detrending, ARSTAN was used to analyze autocorrelation and apply a common autoregressive model to each series for a given site (Cook and Krusic 2005, Cook 1985). Residuals from autoregressive modeling were then averaged together using robust mean calculation to produce a residual growth chronology that represented stand growth variation (Cook and Krusic 2005). Removing autocorrelation from growth chronologies is a common procedure in dendroecological studies (e.g., Chhin et al. 2008, Case and Peterson 2005, Littell 2006, Pfeifer et al. 2005) because autocorrelation has statistical implications (Pfeifer et al. 2005, Littell 2006, Meko 2007) and may be a function of non-climatic processes such as stand-level disturbances and morphological influences on growth (Littell 2006, Cook 1985, Fritts 1976). A preliminary analysis of this dataset revealed that autocorrelation confounded climate-growth relationships (i.e. autocorrelation may have resulted from non-climatic sources, Chhin et al. 2008, Biondi and Swetnam 1987). Robust mean calculation is more resistant to outliers, which may serve to reduce noise from tree-level growth disturbances (Cook 1985, Cook and Kairiukstis 1990).

2.2.3 Data analysis

2.2.3.1 Chronology analysis

Chronology statistics were calculated for each site, including mean sensitivity, standard deviation (both indicate annual ring-width variability, Cook and Kairiukstis 1990, Fritts 1976), and average intrasite correlation (average correlation of all trees within a site to the chronology, analogous to the population signal, Cook and Kairiukstis 1990, Fritts 1976).

The 33 chronologies were analyzed using principal components analysis (PCA, The Mathworks Inc. 2007) to identify common growth patterns and generate composite chronologies for climate-growth analysis. Analysis was restricted to a common time period (1900-2005). This time period was also chosen because it matched the longest climate records in the study and therefore allowed for subsequent analysis of climate-growth relationships over the past century (see Chapter 2). PCA uses eigenvalues and eigenvectors to recombine a dataset into a smaller set of latent variables (often termed 'principal components', hereafter, PCs) that represent the main modes of variability in the original data (Fritts 1976, Biondi and Waikul 2004, Tabachnick and Fidell 1989). In this case, extracted PCs were time series that represented growth variation. PCs with a corresponding eigenvalue greater than 1 were considered significant and retained for analysis (Tabachnick and Fidell 1989). Varimax rotation was used to improve the interpretability of PCA results relative to the original data set (The Mathworks Inc. 2007, Tabachnick and Fidell 1989).

A preliminary PCA on the entire domain (i.e., using all chronologies) revealed that growth patterns were dominated by regional variation that masked underlying ecological patterns. In order to control for regional variation, we treated each sampling region (Northern Interior, Southern Interior, and Chilcotin Plateau) as a separate group for PCA (i.e., a separate PCA was completed for each region). This approach also allowed for a comparison between the main growth patterns in each region and allowed for correlation analysis between PCs and local climate station data (see below for description of local climate station data). Using PCA to compare the main modes of variability between groups is rare in dendroecology, however, this approach has been used in other fields (e.g., ichthyology, Rising and Somers 1989, Douglas 1993, and c.f. Tabachnick and Fidell 1989).

The relationships between the regional PCs and the original chronologies were analyzed using correlation analysis. Correlation coefficients (also referred to as 'loadings') computed between the original chronologies and the PCs were plotted against site-specific climatic normals and geographic variables to determine the ecological conditions and spatial patterns represented by the PCs.

2.2.3.2 Climate-growth relationships

Climate-growth relationships were examined in two separate analyses. The first analysis (termed 'regional climate-growth relationship analysis', see below) correlated regional growth variation (as represented by the PCs) with Environment Canada Climate Station Data and ocean-atmosphere climate system indices to determine the primary climatic limitations in each study region. The second analysis (termed 'climatic gradient analysis') examined how population-level climate-growth relationships varied over a climatic gradient spanning the entire study domain.

Analyses were performed using annual, seasonal, and monthly variables, however, results involving only annual and seasonal variables are presented because they explained more growth variation than monthly variables (e.g., Littell 2006, Watson and Luckman 2002).

2.2.3.2.1 Climate data

Environment Canada climate station temperature and precipitation data were used as predictor variables in the regional climate-growth relationship analysis. Climate stations corresponding to regional PCs were chosen based on spatial and ecological interpretations of the PCA results, proximity to sample sites, and sufficient time series length. Adjusted monthly precipitation records (Mekis and Hogg 1999) and homogenized monthly temperature records (Vincent and Gullett 1999, Vincent et al. 2002) provided by the Climate Research Division of the Meteorological Service of Canada (http://www.cccma.bc.ec.gc.ca/hccd/) for the chosen climate stations were used to account for non-climatic variation in the instrumental records caused by changes in station location, measurement procedures, instrument changes, and other factors (Mekis and Hogg 1999, Vincent and Gullett 1999, Vincent et al. 2002).

We made further adjustments to two data records. The Williams Lake temperature record was not homogenized at the time of this study, therefore we used the observed data. However, the station moved location (and over 300m up in elevation) in 1961, which likely introduced inhomogeneities in the climate record. We accounted for this by using ClimateBC elevation-adjusted and interpolated homogenized historical temperature data (Wang et al. 2006, Mitchell and Jones 2005) from 1939-1960 (see below for a description of the ClimateBC model). A visual comparison of Williams Lake observed temperature data and ClimateBC temperature data from 1939 to 1960 (data not shown) indicated a possible step change in temperatures around 1960, which presumably could be associated with the change in station location and elevation.

At the time of this study, adjusted precipitation, rain, and snow data for the Vernon Coldstream Ranch were only available up to April 1997. To create a time series that matched the other records used in the analysis, we used observed data from a nearby station (Vernon Bella Vista) to extend the record to 2005.

Climate station data are summarized in Table 2.3. Missing precipitation, rain, and snow data in the Tatlayoko, Williams Lake, and Vernon stations over the analysis time period (1940-2004) are listed in Table 2.4. We did not replace missing precipitation data due to a high potential for errors in estimating precipitation (Mekis and Hogg 1999). Missing data were omitted pair-wise from analysis.

For the climatic gradient analysis (see below for details on this analysis), site-specific climate time series data were generated using the ClimateBC model (Wang et al. 2006). ClimateBC combines bi-linear interpolation and elevation adjustment techniques to downscale gridded climate data from the PRISM model (Daly et al. 2002) to produce scale-free spatiotemporal climate data covering western Canada (Spittlehouse 2006). The model produces climate time series and historical/future normals for a specific geographic point, based on user-provided latitude, longitude, and elevation inputs. Model outputs include monthly temperature and precipitation variables, as well as annual derived variables such as frost-free period, continentality, growing-degree days, and heat-moisture index. Spittlehouse (2006) discusses ClimateBC model validation and limitations.

Seasonal and annual variables were derived by averaging climate station monthly values (for the regional climate-growth relationships analysis) and ClimateBC monthly values (for the climatic gradient analysis) (Table 2.5). Where monthly values were missing in the climate station record (Table 2.4), the associated derived seasonal variable was computed as a non-number and omitted pair-wise from analysis. Growth was compared to climate variables from the previous year's July to the current year's October because climate in the preceding year affects the current year's growth (Fritts 1976).

Seasonal and annual heat - moisture index variables were calculated from derived seasonal/annual temperature and precipitation data using the following formula (similar to Wang et al. 2006):

1) $HM = (TMX + 10)/(PPT/1000)$

where: HM = seasonal or annual heat-moisture index

TMX = seasonal or annual mean of monthly average maximum temperatures (°C)

PPT = seasonal or annual mean of monthly precipitation totals (mm)

El Niño Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) are two quasi-periodic ocean-atmosphere processes (Allan 2000, Mantua et al. 1997) that influence climate in British Columbia (Shabbar 2006, Shabbar et al. 1997, BC MoE 2007, BC MWLAP 2002) and have been linked to Douglas-fir growth in the Pacific Northwest United States (US) (Case and Peterson 2005). The Pacific-North American index (PNA) is a mid-tropospheric pressure anomaly influenced by ENSO and strongly correlated with North American winter temperature and precipitation (Leathers et al. 1991, Shabbar 2006, Shabbar et al. 1997). Seasonal and annual ENSO, PDO, and PNA indices were derived from monthly indices obtained from the US Department of Commerce's National Oceanic and Atmospheric Administration (http://www.cdc.noaa.gov/ClimateIndices/List/) (Table 2.5).

2.2.3.2.2 Regional climate-growth relationships

Regional climate-growth relationships were quantified by computing Pearson simple correlation coefficients between growth variation (as represented by the regional PCs) and local climate station data (see below for a description of climate data), from 1940 to 2004 (65 years), a time period common to all climate stations. Growth variation was also correlated to ENSO, PDO, and PNA indices over the full available records (see below). The objective of this analysis was to identify important regional climate-growth limitations and to compare these limitations between ecologically similar sites in all three study regions. Bootstrapped bias-corrected accelerated (BCA) 95% confidence intervals were calculated for each correlation coefficient using 1000 iterations (Moore and McCabe 2006, The Mathworks Inc. 2007).

Climate and tree-growth (PC) data were screened for normality using the Lilliefors test (The Mathworks Inc. 2008, Meko 2007, Conover 1980) prior to climate-growth analysis, and natural logarithm transforms were applied to data failing the Lilliefors test at the 95% significance level (The Mathworks Inc. 2007). The Lilliefors test was then repeated to ensure that data transformation was successful (this transformation was successful in all cases).

2.2.3.2.3 Climatic gradient analysis

Variations in population-level Douglas-fir climate-growth relationships were analyzed along a climatic gradient across all sites. This was done in two steps. First, regression and correlation coefficients were calculated between the 33 chronologies and site-specific climate data (e.g. annual precipitation) generated by the ClimateBC model, from 1940 to 2002 (63 years). We chose this time period to match the regional PC climate-growth relationship analysis (historical ClimateBC data extends only to 2002, thus there was a difference of 2 years between the two analyses). In the second step of this analysis, the 33 regression and correlation coefficients calculated for a given variable were regressed against site-specific climate normals (1961-1990 period, Spittlehouse 2006) such as annual heat-moisture index (AHM), MAT, MAP, and others, produced by the ClimateBC model (Table 2.2). In this way, it was possible to determine if a site's climatic conditions could predict growth association (represented by the correlation coefficient) or sensitivity (represented by the regression coefficient) to local climate variability. A similar analysis was completed using population-level responses to PDO and PNA winter indices. Chronology statistic variation along a climatic gradient was also examined using similar methods. An example of how we performed the climatic gradient analysis is presented in Appendix C.

2.3 Results

2.3.1 Chronologies

Final chronologies were built using from 15 to 31 trees, and chronology lengths ranged from 113 to 373 years (Table 2.1). All sites had relatively high average intrasite correlations ranging from 0.352 to 0.695. The expressed population signal for all chronologies exceeded 0.85 (data not shown), indicating a sufficient population signal for climate analysis (Wigley et al. 1984). Mean sensitivity ranged from 0.136 to 0.448 and standard deviation ranged from 0.126 to 0.375.

Chronology mean sensitivity, intrasite correlations, and standard deviation increased linearly with site AHM normals (Figure 2.5). When examined against the individual components of AHM, chronology statistics had no relationship with temperature normals (MAT), and an apparent non-linear relationship with precipitation normals (MAP), however, it should be noted that MAP data were positively skewed. Similar results (data not shown) were found when chronology statistics were regressed against summer heat-moisture index (SHM), and its components (mean warmest month temperature and mean summer precipitation).

2.3.2 Multivariate analysis

2.3.2.1 Northern Interior sites

PCA of Northern Interior chronologies extracted three principal components (PCs) that represented 75.4% of the total chronology variance (Table 2.7). The three retained PCs explained 30.8%, 25.9%, and 18.7% of the variance, respectively.

Visual analysis of chronology-PC relationships revealed that PC1 (hereinafter referred to as 'NIPC1', see Table 2.6) had the strongest correlations with the northernmost (north of ~54°N) and westernmost (west of ~123.5°W) sites in this region (Figure 2.12). This geographic pattern was confirmed by the high loadings of the Fort St. James sites and two sites north of Prince George (Kerry and McLeod) on this PC (Table 2.7, Figure 2.2). When the NIPC1-chronology correlation coefficients were plotted against climate normals, sites with low mean annual temperature (MAT) and mean coldest month temperature (MCMT) had a stronger relationship with this PC (Figure 2.12). NIPC1 also represented sites with lower precipitation and higher heat-moisture indices. Based on these observations, NIPC1 was interpreted to best represent northernmost and westernmost sites with cold and dry conditions; these sites are located near the northern margins of the species' range in the province (Table 2.6).

The second PC (NIPC2) had a stronger correlation with the southernmost sites of the study area (Figure 2.12). This was also confirmed by the high loadings of the Gregg11, Gregg24, and PG1412 sites on this PC (Table 2.7 and Figure 2.2). NICP2 had higher correlations to sites with lower MAP, higher MAT, and lower precipitation as snow (PAS) (Figure 2.12). This PC was interpreted to represent the warmer and drier (southernmost) sites in the Northern Interior study region (Table 2.6).

The third PC (NIPC3) correlated most with the easternmost, high-elevation sites (Figure 2.12) located on the western slopes of the Rocky and Cariboo Mountains east of Prince George (Figure 2.2). This PC was correlated to sites with low MAT and high precipitation/snowfall (Figure 2.12). This was also confirmed by high loadings (Table 2.7) with the three sites located in subalpine (Engelmann Spruce-Subalpine Fir BEC zone, Meidinger and Pojar 1991) forests (Table 2.2). NIPC3 was interpreted to represent radial growth variation for high-elevation sites that are at the wet and snowy extremes for Douglas-fir in this region (Table 2.6).

2.3.2.2 Southern Interior sites

The Southern Interior chronologies had two modes of variability that represented 67.6% of the total variance (Table 2.7). The two retained PCs explained 35.3% and 32.3% of the total variance, respectively.

The first PC (SIPC1, Table 2.6) was best correlated to low-elevation sites in the study area (Figure 2.13). Sites with high average temperatures and low precipitation correlated strongly with SIPC1. This PC had the highest loadings with the hottest and driest sites (Figure 2.13), and therefore was interpreted to represent Douglas-fir growing at its warm and dry margins in the region (Table 2.6).

The second PC (SIPC2) was correlated mostly to high-elevation sites in the study area (Figure 2.13). Radial growth variation represented by this PC best represented sites with lower annual and summer temperatures, and higher precipitation (annual, summer and snow, Figure 2.13). The wettest and snowiest sites in the region (Wap 1 and Wap 2) had the strongest correlation with SIPC2 (Table 2.7). This PC seemed to represent similar ecological conditions as NIPC3 from the Northern Interior study region, and was interpreted to represent Douglas-fir at its upper elevation and precipitation extremes in this region (Table 2.6).

2.3.2.3 Chilcotin Plateau sites

The Chilcotin chronologies had two modes of variability that represented 79.5% of the original chronologies' variance (Table 2.7). The first two principal components explained 43.2% and 36.2% of the variance, respectively.

This first PC (CHPC1, Table 2.6) was best correlated to the easternmost sites in the region (Figures 2.3 and 2.14). The four driest sites of the region (and entire study, Table 2.2) had strong correlations with this PC (Table 2.7 and Figure 2.14). Two of these sites (Hoodoo and Gang) are located along the forest-grassland transition in the Bunchgrass BEC zone (Meidinger and Pojar 1991); growth variation represented by this PC was interpreted to represent Douglas-fir growing at the dry extremes in the region (Table 2.6).

The second PC (CHPC2) best represented the four westernmost sites (Figures 2.3 and 2.14). This PC was strongly correlated to sites with higher mean annual precipitation totals and lower annual heat-moisture index than sites represented by CHPC 1 (Figure 2.14).

2.3.3 Climate-growth relationships

Correlation and regression coefficients were calculated for all annual, seasonal, and monthly variables, however, only annual and seasonal variables are presented because they explained more growth variation than monthly variables (e.g., Littell 2006, Watson and Luckman 2002). Rather than present results for all seasonal and annual variables, we focused our results and discussion on the annual and seasonal variables that appeared important in explaining growth variation.

2.3.3.1 Regional climate-growth relationships

2.3.3.1.1 Northern Interior sites

Douglas-fir growth at cold sites along its northern range margins (as represented by NIPC1) was positively correlated to spring rainfall and annual PNA index, and was positively (negatively) correlated to spring rain (heat-moisture index) (Table 2.8). Warmer and drier sites in the Northern Interior (NIPC2) tended to have high radial growth in years with relatively high annual, prior summer, and spring precipitation and low annual, prior summer, and spring heat-moisture indices. High-elevation sites in the Northern Interior (NIPC3) had a climate-growth relationship distinct from other sites in the region. Radial growth in these sites was positively related to annual and winter temperatures and negatively related to winter snowfall. Winter PNA index was positively correlated to NIPC3 variation.

2.3.3.1.2 Southern Interior sites

Douglas-fir growth at warm and dry sites in the Southern Interior (SIPC1) had a positive relationship to annual and spring precipitation. Maximum temperatures in the previous summer and current spring tended to negatively influence growth on these sites. Heat-moisture index variables for annual, prior summer, and current spring were also negatively correlated to SIPC1 growth.

Radial growth in high-elevation sites in the Southern Interior (SIPC2) tended to be higher during warmer years. The strongest relationships to climate were a negative correlation to winter snowfall and a positive correlation to winter temperatures. Rainfall in the previous summer had a positive relationship to SIPC2 growth. These sites were the only ones of the study with a significant relationship (positive) to annual, winter, and previous summer PDO and ENSO indices. Annual and winter PNA indices were also positively correlated to SIPC2 growth.

2.3.3.1.3 Chilcotin Plateau sites

Both Chilcotin PCs (CHPC1 and CHPC2) had similar relationships to local climate. Growth across the sampling area appeared to be strongly limited by annual precipitation and heat-moisture index. Growth represented by CHPC1 was also correlated to prior summer and spring rain. CHPC2 growth was correlated to annual and prior winter mean temperatures.

2.3.3.2 Climatic gradient analysis

Correlation coefficients computed between each of the 33 ring-width chronologies and site-specific annual precipitation (1940-2002) varied linearly along a climatic gradient defined by site AHM (Figure 2.6) and SHM (Figure 2.7). Linear slopes of natural log-transformed (due to skewness) regression coefficients vs. site AHM and SHM indicated that growth sensitivity (represented by the regression coefficient) increased by approximately 16 and 7% per one-unit increase in AHM and SHM, respectively. Correlation and regression coefficients computed between growth and spring/prior summer precipitation varied similarly but had weaker linear relationships with heat-moisture indices than annual precipitation (data not shown).

When plotted against a precipitation (MAP, MSP, and PAS) gradient, non-linear relationships between the correlation and regression coefficients and site climate were strongly apparent, with a response threshold evident at approximately 700 millimetres per year (Figure 2.8, MSP and PAS not shown). MAP, MSP, and PAS data were positively skewed, and log transformations resulted in significant linear relationships (e.g., Figure 2.9, MSP and PAS not shown). Results using log-transformed MAP indicated that a 1% decrease in MAP would increase a population's correlation coefficient with annual precipitation by approximately 0.0032 units and would also increase the regression coefficient with annual precipitation by approximately 3.3%.

No relationships were found when site-specific temperature normals such as MAT, mean warmest month, mean coldest month, and continentality were used to define the climatic gradient (data not shown). As well, no patterns were found with coefficients computed between the chronologies and derived ClimateBC variables such as frost-free period and growing-degree days. This was also found for coefficients computed between the chronologies and temperature variables.

Correlation and regression coefficients computed between the chronologies and October-March PDO and PNA indices (1901-2005 and 1951-2005, respectively) varied linearly along an AHM gradient (Figures 2.10 and 2.11). Sites with a low AHM (i.e., the coldest and/or wettest sites) had the strongest (positive) relationship to both indices. Only three chronologies were significantly correlated to ENSO, therefore, we did not complete a climatic gradient analysis using ENSO index.

2.4 Discussion

2.4.1 Ecological growth patterns

Visual analysis of PC-chronology relationships indicated that in all three study regions, Douglas-fir growth patterns differentiate primarily along precipitation and temperature gradients, which are somewhat associated with elevation (Case and Peterson 2005, Körner

2007). This supports similar findings for Douglas-fir in coastal environments at smaller spatial scales (Case and Peterson 2005, Zhang and Hebda 2004).

Leading modes of growth variation in each region tend to be dominated by sites located at the climatic extremes, however, these modes also characterize trees growing in moderate climatic conditions. For example, the first PC in the Southern Interior (SIPC1) was most correlated to Douglas-fir growth on a site in the hot and dry Ponderosa Pine xeric-hot BEC zone/subzone (Meidinger and Pojar 1991), but was also significantly correlated to Douglas-fir growth in the Interior Cedar-Hemlock BEC zone (Meidinger and Pojar 1991), a much wetter ecosystem. This pattern was also found in the visual plots of PC-chronology loadings. Therefore, climatic factors that are significantly correlated to this PC (e.g., annual precipitation) are likely most limiting to Douglas-fir growing at the hot and dry climatic extremes, but may also be limiting (although to a lesser degree) in ecosystems with a more moderate climate (Littell 2006).

2.4.2 Climate-growth relationships

2.4.2.1 Low- to mid-elevation dry sites

Principal components explaining the majority of variation in all three regions were generally most correlated to precipitation and integrated precipitation - temperature (heat-moisture index) variables. This suggests that moisture is likely the most limiting environmental factor to Douglas-fir growth across most of its range in the BC Interior, and supports similar findings for this species (e.g., Zhang and Hebda 2004, Case and Peterson 2005, Daniels and Watson 2003, Littell 2006, Adams and Kolb 2005, Watson and Luckman 2002). Growing season water deficits reduce Douglas-fir photosynthesis, gas exchange, and transpiration, resulting in less cambial growth (Lopushinsky and Klock 1974, Lassoie and Salo 1981) (possibly at the expense of root growth; Waring 1991), as this species has relatively poor stomatal control during droughts (Lassoie and Salo 1981) and low sapwood water storage capacity (Lopushinksy 1991). Water stress thresholds (and other climate-growth limitations) may vary with age, microsite conditions, and genetics (Littell 2006).

Annual precipitation amounts generally resulted in higher correlations than seasonal and monthly precipitation amounts, likely reflecting an integration of previous growing season, winter, and spring precipitation influence on growth (Watson and Luckman 2002, Littell 2006, Case and Peterson 2005, Daniels and Watson 2003). Numerous physiological mechanisms may explain this climate-growth relationship. For example, primordial tissues are formed during the end of the growing season, and water availability during the late summer influences carbohydrate allocation to the following year's formative tissues (Fritts 1976, Littell 2006, Kozlowski and Pallardy 1997). Needle drop as a result of late growing-season moisture stress may reduce photosynthetic surface area and result in lower growth the following year (Zhang and Hebda 2004). Trees may allocate more carbohydrates to root systems during the growing season after a dry summer to compensate for drought-reduced root growth, resulting in a smaller annual ring (Lassoie and Salo 1981). Winter snow and spring precipitation can be important because they provide early season soil moisture (Carrer and Urbinati 2006), especially for Douglas-fir, as its needles tend to be fully grown and photosynthesizing relatively early in the year (Watson and Luckman 2002).

The climatic gradient analysis showed that growth responses to annual precipitation, as well as chronology statistics (mean sensitivity, standard deviation, and intrasite correlations), are strongest in Douglas-fir growth in dry areas, and further showed how these responses vary with site local conditions over the entire study domain. Climatic gradient analysis results suggest that Douglas-fir growth will become strongly associated with, and more sensitive to, annual precipitation where local climate becomes warmer and/or drier (i.e. annual heat-moisture index increases). Non-linear increases in growth-precipitation sensitivity along a gradient defined by MAP suggest that if sites receive, on average, less than approximately 700 millimetres of annual precipitation, growth sensitivity to precipitation will increase very rapidly. A decrease in available soil moisture in dry-climate sites could conceivably result in significant productivity declines and potential mortality.

When predicting population growth responses to annual precipitation using a climatic gradient analysis, using the interactions between site temperature and precipitation (i.e., heat-moisture index) to define the site climatic characteristics explained the most variation in climate-growth responses and chronology statistics. Climatic gradients defined by log-transformed precipitation-only variables also significantly explained climate-growth response variation (although less than heat-moisture indices), whereas temperature-only variables did not significantly explain variation. Heat-moisture indices likely reflect the importance of soil moisture to Douglas-fir growth by integrating moisture inputs (precipitation) and evaporation/transpiration forcings (temperatures) (Wang et al. 2006). The integrative effects of temperature-precipitation changes on forest ecosystems must be considered when adapting forest management to climate change, as they may impact forest ecosystem functioning and processes more than either temperature or precipitation dynamics alone (Littell and Peterson 2005).

Only the hottest sites in the study (Southern Interior, SIPC1) had negative growth relationships to temperatures, with the exception of NIPC2 (negatively correlated to spring maximum temperatures). As negative Douglas-fir growth relationships to temperatures have been extensively documented in British Columbia and other regions (Case and Peterson 2005, Zhang and Hebda 2004, Laroque and Smith 2005, Feliksek and Wilczyński 2003, Daniels and Watson 2003, Watson and Luckman 2001), we expected a somewhat broader negative temperature response. Our results indicate that in hot and dry sites in the Southern Interior, summer and spring temperatures may exceed species-specific photosynthesis threshold limits (Brubaker 1980), which can be as low as ~20-25 °C for Douglas-fir (Salo 1974, Doehlert and Walker 1981). As a comparison, Hadley (1969) found that ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) had optimal photosynthesis at temperatures of 25-35 °C. Although these thresholds are specific to their respective study areas, they do suggest that Douglas-fir may have an upper temperature-growth threshold that is low relative to other drought-resistant species (Brubaker 1980). An increase in temperature affects respiration and transpiration processes (Balatinecz and Anderson 1986, Kimmins 1997) and may reduce growth by increasing water loss, reducing nutrient storage, and decreasing foliage efficiency (Laroque and Smith 2005, Kimmins 1997, Balatinecz and Anderson 1986). Projected sustained temperature increases across the province (BC MoE 2007, Christensen et al. 2007) may result in broader negative temperature-growth responses in Douglas-fir.

The climate-growth relationship analysis also revealed relatively uniform climatic limitations to Douglas-fir growth on the Chilcotin Plateau. The eight sites sampled in the Chilcotin Plateau were the driest of the entire study, and all appear to be strongly limited by annual precipitation and heat-moisture index. Although the PCA indicated two significantly different growth patterns in this study region, these growth patterns may simply reflect geographic (longitudinal) differences in temporal precipitation patterns, and not different climate-growth relationships.

2.4.2.2 High-elevation sites

High-elevation Douglas-fir populations have similar growth relationships in the Northern and Southern Interior regions and appear to be unique from the mid- to low-elevation populations in that low annual temperatures and winter snowfall are primary limiting factors. This result is consistent with similar findings in coastal high-elevation Douglas-fir populations in BC (Zhang and Hebda 2004) and the Pacific Northwest US (Case and Peterson 2005). In cold environments with ample moisture supply, low temperatures are often assumed to be primary climatic growth limitations (Littell 2006, Pfeifer et al. 2005), as they reduce glucose utilization, CO_2 uptake, and photosynthesis (Körner 1998, Kimmins 1997, Grace et al. 2002), can cause damage tree tissues (Körner 1998, Chhin et al. 2008), and may be associated with shorter growing seasons (Zhang and Hebda 2004, Littell 2006, Grace et al. 2002). Colder winter temperatures may also be associated with higher snowfall, which was negatively correlated to growth in both the Northern and Southern Interior regions. Negative snow-growth responses have also been found in other high-elevation Douglas-fir populations (Case and Peterson 2005) as well as other tree species in western North America (Ettl and Peterson

1995, Peterson et al. 2002, Laroque and Smith 2005) and Siberia (Vaganov et al. 1999). Higher snowfall and corresponding snowpacks can limit growth by delaying the start of the growing season, as cambial and root growth generally only begin when the upper soil layers have thawed after snowmelt (Vaganov et al. 1999, Emmingham and Waring 1977, Graumlich and Brubaker 1986, Zhang and Hebda 2004). Wind and snow breakage may limit growth in high-elevation environments, however, their effects on growth would be non-linear and therefore likely not reflected in interannual growth patterns (Littell 2006).

Although growth appears to be most limited by temperatures and snowfall in high-elevation environments, growth in both regions was also correlated to prior summer rain, which is consistent with other cold-environment Douglas-fir populations (Case and Peterson 2005, Laroque and Smith 2005, Feliksek and Wilczyński 2003). Trees growing in cold environments may respond to drought events because these stressful periods further reduce an already short growing season (Zhang and Hebda 2004).

Annual and seasonal PDO and ENSO indices were strongly correlated to Douglas-fir growth at high-elevations in the Southern Interior; similar growth relationships have been observed in Douglas-fir in the Pacific Northwest US (Case and Peterson 2005) and in other tree species as well (Holman and Peterson 2006, D'Arrigo et al. 2001, Biondi et al. 1999). PDO and ENSO signals did not appear in high-elevation sites in the Northern Interior, suggesting these climatic processes may be regional in their influence in the British Columbia Interior. High PDO and ENSO index values correlate to warm and dry weather patterns (Hare and Mantua 2001, Shabbar et al. 1997, Shabbar 2006) in British Columbia (BC MoE 2007, BC MWLAP 2002), which may result in longer growing seasons through lower snowpack depths and warmer soils (Case and Peterson 2005). Winter PNA index was correlated to high-elevation growth in both regions. PNA index values are correlated to surface winter and early spring temperature and precipitation variation over much of North America (Leathers et al. 1991), and may provide a good indication of high-elevation Douglas-fir growth over a large spatial range.

The climatic gradient analysis showed that Douglas-fir growing in wet and cold environments (those with a relatively low annual heat-moisture index) have stronger growth relationships with PDO and PNA variation, and that these relationships weaken linearly as sites become warmer and/or drier. Projected temperature increases and snowfall decreases (Christensen et al. 2007, BC MoE 2007, BC MWLAP 2002) may result in an increase in site heat-moisture index and a subsequent future weakening of the influence of PDO and PNA on high-elevation Douglas-fir growth.

2.4.2.3 Sites at the northern geographic limits

The PCA indicated that Douglas-fir populations at the northern geographic margins are unique from other populations in the Northern Interior region, however, these populations have a somewhat similar climate-growth relationship as warmer sites in the North in that growth appears to be most limited by spring precipitation. As low temperatures are assumed to limit Douglas-fir range along its northern margins (Jull 1999, Delong 1999, Vyse et al. 1991), we expected a potentially strong temperature signal in NIPC1, however, the climate influence on growth appears to be relatively low.

There are several possible reasons for relatively weak climate-growth correlations. Douglas-fir along their northern limit may be limited by severe growing season frost events (Jull 1999, Delong 1999, Vyse et al. 1991), which can damage mature needles and reduce radial growth by inhibiting hormonal system functioning (Feliksek and Wilczyński 2003). Growing season frosts and other short-term climatic extremes may affect tree physiology more than average climatic conditions in some environments (Graham et al. 1990, Innes 1994), but would not be reflected in the monthly temperature data used for this study. Climate-growth relationships in this environment may also be non-linear or vary over time.

2.4.3 Conclusions

As forest managers prepare for climate change, a better understanding of forest species vulnerability to climate change (BC MoFR 2006) across large regions and climatic gradients is required (Peterson and Peterson 2001, Case and Peterson 2005). Using high-resolution spatiotemporal climate data from the ClimateBC model (Wang et al. 2006), we were able to sample and develop 33 Douglas-fir growth chronologies covering a wide climatic and geographic range in the interior of British Columbia. Across most of its range in the province's interior, Douglas-fir annual growth appears to be chiefly limited by precipitation totals from the previous July to current June, with the strongest sensitivity in population growth at the dry margins. Even at the northern margins of the species' range near Fort St. James, Douglas-fir growth appears to be mostly limited by precipitation, and we were unable to detect a strong cold-temperature limitation on growth in these presumably cold-margin populations. Future decreases in soil moisture availability as a result of increasing temperatures (Christensen et al. 2007) may result in a widespread increase in precipitation sensitivity and growth declines, with initial and strong changes in drier areas.

At the high-elevation margins of its range, Douglas-fir growth is more limited by annual and winter temperatures and snowfall, and strong associations with PDO, ENSO, and PNA indices may reflect the influence of Pacific Ocean – atmosphere climate systems on winter conditions in mountainous environments. Warmer temperatures and less snowfall may increase Douglas-fir productivity in these environments.

2.5 Literature cited

Aber, J., R.P. Neilson, S. McNulty, J.M. Lenihan, D. Bachelet, and R.J. Drapek. 2001. Forest processes and global environmental change: predicting the effects of individual and multiple stressors. BioScience 51: 735-752.

Adams, H.D. and T.E. Kolb. 2005. Tree growth response to drought and temperature in a mountain landscape in northern Arizona, USA. Journal of Biogeography 32: 1629-1640.

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

Allan, R.J. 2000. ENSO and climatic variability in the past 150 years, p. 3-56. *In* El Nino and the Southern Oscillation: multiscale variability and global and regional impacts. Diaz, H. F. and Markgraf, V. (eds). Cambridge University Press, New York.

Arno, S.F. 1991. Ecological relationships of interior Douglas-fir, p. 47-51. *In* Interior Douglas-fir: The species and its management symposium proceedings. Baumgartner, D. M. (ed). Department of Natural Resource Sciences, Washington State University, Pullman, Washington.

Balatinecz, J.J. and H.W. Anderson. 1986. Effects of climatic factors on the formation of wood and its quality, p. 195-200. *In* Climate Applications in Forest Renewal and Forest Production, Proceedings of Forest Climate 1986. MacIver, D. C., Street, R. B., and Auclair, A. N. (eds). Canadian Forestry Service, Ottawa, Ontario.

Barber, V., G. Juday, and B. Finney. 2000. Reduced growth of Alaska white spruce in the twentieth century from temperature-induced drought stress. Nature 405: 668-672.

BC MoE. 2007. Environmental Trends in British Columbia: 2007. State of Environment Reporting. BC Ministry of Environment, Victoria, B.C.

BC MoFR. 2006. Preparing for climate change: Adapting to impacts on British Columbia's forest and range resources. BC Ministry of Forests and Range, Victoria, BC.

BC MWLAP. 2002. Indicators of climate change for British Columbia, 2002. Indicators of climate change for British Columbia, 2002. BC Ministry of Water, Land and Air Protection, Victoria, B.C.

Biondi, F., D.R. Cayan, and W.H. Berger.1999. Decadal-scale changes in southern California tree-ring records, p. pp. 303-306. *In* Proceedings of the 10th Symposium on Global Change Studies. Karl, T. R. (eds). American Meteorological Society, Boston, MA.

Biondi, F. and Swetnam, T.W. 1987. Box-Jenkins Models of forest interior tree-ring chronologies. Tree-Ring Bulletin 47: 71-96.

Biondi, F. and K. Waikul. 2004. Dendroclim2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. Computers & Geosciences 30: 303-311.

Brubaker, L.B. 1980. Spatial patterns of tree growth anomalies in the Pacific Northwest. Ecology 6: 798-807.

Carrer, M. and C. Urbinati. 2006. Long-term change in the sensitivity of tree-ring growth to climate forcing in *Larix decidua*. New Phytologist 170: 861-872.

Case, M.J. and D.L. Peterson. 2005. Fine-scale variability in growth-climate relationships of Douglas-fir, North Cascade Range, Washington. Canadian Journal of Forest Research 35: 2743-2755.

Cayan, D.R., M.D. Dettinger, H.F. Diaz, and N.E. Graham. 1998. Decadal variation of precipitation over Western Northern America. Journal of Climate 11: 3148-3166.

Chhin, S., E.H. Hogg, V.J. Lieffers, and S. Huang. 2008. Influences of climate on the radial growth of lodgepole pine in Alberta. Botany 86: 167-178.

Christensen, J.H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R.K. Kolli, W.-T. Kwon, R. Laprise, V. Magaña Rueda, L. Mearns, C.G. Menéndez, J. Räisänen, A. Rinke, A. Sarr, and P. Whetton. 2007. Regional Climate Projections, p. 848-940. *In* Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Solomon, S. D., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. M. (eds). Cambridge University Press, New York.

Conover, W. 1980. Practical Nonparametric Statistics. John Wiley and Sons, New York.

Cook, E. 1985. A time series analsysis approach to tree-ring standardization. PhD Dissertation. University of Arizona. Tucson, Arizona.

Cook, E. and L. Kairiukstis. 1990. Methods of dendrochronology: Applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, Netherlands.

Cook, E.R. and P. Krusic. 2005. Users Manual for Program ARSTAN. Tree-Ring Lab, Lamont-Doherty Earth Observatory, Columbia University, New York. http://www.ldeo.columbia.edu/res/fac/trl/public/publicSoftware.html.

D'Arrigo, R., R. Villalba, and G. Wiles. 2001. Tree-ring estimates of Pacific decadal climate variability. Climate Dynamics 18: 219-224.

D'Arrigo, R., R. Wilson, B. Liepert, and P. Cherubini. 2007. On the 'Divergence Problem' in Northern Forests: A review of the tree-ring evidence and possible causes. Global and Planetary Change 289-305.

Dai, A., K.E. Trenberth, and T.R. Karl. 1999. Effects of clouds, soil moisture, precipitation, and water vapor on diurnal temperature range. Journal of Climate 12: 2451-2473.

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

Daniels, L.D. and E. Watson. 2003. Climate-fire-vegetation interactions in the Cariboo forests: a dendrochronological analysis. Report to Forest Innovation and Investment. Forest Innovation and Investment Research Program, Vancouver, BC.

Davis, M.B. and Shaw. R.G. 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292: 673-679.

Delong, S.C. 1999. Ecology of Douglas-fir at its northern limits, p. 27-28. *In* Ecology and management of interior Douglas-fir (*Pseudotsuga menziesii* var *glauca*) at the northern extreme of its range. Proceedings of a workshop held 7-9 October 1996 in Fort St. James, British Columbia. Lousier, J. D. and Kessler, W. B. (eds). University of Northern British Columbia, Prince George, BC.

Doehlert, D.C. and R.B. Walker. 1981. Photosynthesis and photorespiration in Douglas-fir as influenced by irradiance, CO_2 concentration, and temperature. Forest Science 27: 641-650.

Douglas, M.E. 1993. Analysis of sexual dimorphism in an endangered Cyprinid fish (*Gila cypha* Miller) using video image technology. Copeia 1993: 334-343.

Easterling, D.R., G.A. Meehl, C. Parmesan, S.A. Changnon, T.R. Karl, and L.O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. Science 289: 2068-2074.

Emmingham, W.H. and R.H. Waring. 1977. An index of photosynthesis for comparing forest sites in western Washington. Forest Science 7: 165-174.

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

Feliksek, E. and S. Wilczyński. 2003. Dendroecological characterization of Douglas-fir (*Pseudotsuga menziesii* Franco) in the Wielkopolska region. Electronic Journal of Polish Agricultural Universities 6: Series: Forestry.

Fritts, H.C. 1976. Tree rings and climate. The Blackburn Press, New Jersey.

Gates, D.M. 1990. Climate change and forests. Tree Physiology 7: 1-5.

Grace, J., F. Berninger, and N. Laszlo. 2002. Impacts of climate change on the tree line. Annals of Botany 90: 537-544.

Graham, R.L., M.G. Turner, and V.H. Dale. 1990. How increasing CO_2 and climate change affect forests. Bioscience 40: 575-587.

Graumlich, L.J. 1991. Subalpine tree growth, climate, and increasing CO_2: An assessment of recent growth trends. Ecology 72: 1-11.

Graumlich, L.J. and L.B. Brubaker. 1986. Reconstruction of annual temperature (1590-1979) for Longmire, WA, derived from tree rings. Quaternary Research 25: 223-234.

Hadley, E.B. 1969. Physiological ecology of *Pinus ponderosa* in southwestern North Dakota. American Midland Naturalist 81: 289-314.

Hamann, A. and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87: 2773-2786.

Hansen, A.J., R.P. Neilson, Dale. V.H., C.H. Flather, L.R. Iverson, D.J. Currie, S. Shafer, R. Cook, and P.J. Bartlein. 2001. Global change in forests: responses of species, communities, and biomes. BioScience 51: 765-779.

Hanson, P.J. and J.F. Weltzin. 2000. Drought disturbance from climate change: response of United States forests. The Science of the Total Environment 262: 205-220.

Hare, S.R. and N.J. Mantua. 2001. An historical narrative on the Pacific Decadal Oscillation, interdecadal climate variability and ecosystem impacts. Report of a talk presented at the 20th NE Pacific Pink and Chum workshop, Seattle, WA, 22 March 2001. http://www.iphc.washington.edu/Staff/hare/html/papers/pcworkshop/pcworkshop.pdf.

Hermann, R.K. and D.P. Lavender.1990. Douglas-fir. *In* Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. Burns, R. M. and Honkala, B. H. (eds). U.S. Department of Agriculture, Washington, DC. http://www.na.fs.fed.us/spfo/pubs/silvics_manual/Volume_1/pseudotsuga/menziesii.htm.

Holman, M.L. and D.L. Peterson. 2006. Spatial and temporal variability in forest growth in the Olympic Mountains, Washington: sensitivity to climatic variability. Canadian Journal of Forest Research 36: 92-104.

Holmes, R. 1983. Computer-assisted quality control in tree-ring dating and measuring. Tree-Ring Bulletin 43: 69-78.

Innes, J.L. 1994. Climatic sensitivity of temperate forests. Environmental Pollution 83: 237-243.

Josza, L. 1988. Increment core sampling techniques for high quality cores. Special Publication SP-30. Forintek Canada Corp., Vancouver, BC.

Jull, M.J. 1999. Douglas-fir silviculture "on the edge": silvicultural systems at the northern range of the species, p. 34-44. *In* Ecology and management of interior Douglas-fir (*Pseudotsuga menziesii* var *glauca*) at the northern extreme of its range. Proceedings of a workshop held 7-9 October 1996 in Fort St. James, British Columbia. Lousier, J. D. and Kessler, W. B. (eds). University of Northern British Columbia, Prince George, BC.

Karl. T.R., Jones. P.D., R.W. Knight, G. Kukla, N. Plummer, V. Razuvayev, K.P. Gallo, J. Lindsaey, R.J. Charlson, and T.C. Peterson. 1993. A new perspective on recent global warming: asymmetric trends of daily maximum and minimum temperature. Bulletin of the American Meteorological Society 74: 1007-1023.

Kimmins, J. P. 1997. Forest Ecology. Prentice-Hall Inc., New Jersey.

Knowles, N., M.D. Dettinger, and D.R. Cayan. 2006. Trends in snowfall versus rainfall in the Western United States. Journal of Climate 19: 4545-4559.

Kozlowski, T. T. and Pallardy, S. G. 1997. Growth control in woody plants. Academic Press, San Diego.

Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. Oecologia 155: 445-459.

Körner, C. 2007. The use of 'altitude' in ecological research. TRENDS in Ecology and Evolution 22: 569-574.

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

Lassoie, J.P. and D.J. Salo. 1981. Physiological response of large Douglas-fir to natural and induced soil water deficits. Plant physiology and biochemistry 11: 139-144.

Leathers, D.J., B. Yarnal, and M.A. Palecki . 1991. The Pacific/North American Teleconnection Pattern and United State Climate. Part I: Regional Temperature and Precipitation Associations. Journal of Climate 4: 517-528.

Leung, L.R., Y. Qian, X. Bian, W.M. Washington, J. Han, and J.O. Roads . 2004. Mid-century ensemble regional climate change scenarios for the western United States. Climatic Change 62: 75-113.

Littell, J. S. 2006. Climate impacts to forest ecosystem processes: Douglas-fir growth in north-western U.S. mountain landscapes and area burned by wildfire in western U.S. eco-provinces. PhD Dissertation. University of Washington. Seattle, WA.

Littell, J.S. and D.L. Peterson. 2005. A method for estimating vulnerability of Douglas-fir growth to climate change in the northwestern U.S. The Forestry Chronicle 81: 369-374.

Lloyd, A.H. 2005. Ecological histories from Alaskan tree lines provide insight into future change. Ecology 86: 1687-1695.

Lloyd, A.H. and C.L. Fastie. 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. Climatic Change 52: 481-509.

Loehle, C. 2000. Forest ecotone response to climate change: sensitivity to temperature response functional forms. Canadian Journal of Forest Research 30: 1632-1645.

Lopushinksy, W. 1991. Water relations of interior Douglas-fir, p. 35-46. *In* Interior Douglas-fir: The species and its management symposium proceedings. Baumgartner, D. M. (ed). Department of Natural Resource Sciences, Washington State University, Pullman, Washington.

Lopushinksy, W. and G.O. Klock. 1974. Transpiration of conifer seedlings in relation to soil water potential. Forest Science 20: 181-186.

Mantua, N.J. and S.R. Hare. 2002. The Pacific Decadal Oscillation. Journal of Oceanography 58: 35-44.

Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace, and R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78: 1069-1079.

Meehl, G.A., W.M. Washington, W.D. Collins, J.M. Arblaster, A. Hu, L.E. Buja, W.G. Strand, and H. Teng. 2005. How much more global warming and sea level rise? Science 307: 1769-1772.

Meidinger, D. and J. Pojar. 1991. Ecosystems of British Columbia. BC Ministry of Forests, Victoria, B.C.

Mekis, É. and W.D. Hogg . 1999. Rehabilitation and analysis of Canadian daily precipitation time series. Atmosphere-Ocean 37: 53-85.

Meko, D. M. 2007. GEOS 585A: Applied Time Series Analysis. Page accessed: 2007. URL: http://www.ltrr.arizona.edu/~dmeko/geos585a.html

Mitchell, T.D. and P.D. Jones. 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. International Journal of Climatology 25: 693-712.

Moore, D. S. and McCabe, G. P. 2006. Introduction to the Practice of Statistics. W.H. Freeman and Co., New York, N.Y.

Neilson, R.P. 1993. Transient ecotone response to climatic change: some conceptual and modelling approaches. Ecological Applications 3: 385-395.

Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37-42.

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

Peterson, D.W., D.L. Peterson, and G.J. Ettl. 2002. Growth responses of subalpine fir to climatic variability in the Pacific Northwest. Canadian Journal of Forest Research 32: 1503-1517.

Pfeifer, K., W. Kofler, and W. Oberhuber. 2005. Climate related causes of distinct radial growth reductions in *Pinus cembra* during the last 200 yr. Vegetation History and Archaeobotany 14: 211-220.

Regent Instruments Inc. 2005. WinDENDRO™. An image analysis system for tree-rings analysis. Regent Instruments Inc. Quebec

Rising, J.D. and K.M. Somers. 1989. The measurement of overall body size in birds. The Auk 106: 666-674.

Salo, D. J. 1974. Factors affecting photosynthesis in Douglas-fir. PhD Dissertation. University of Washington. Seattle, WA.

Shabbar, A. 2006. The impact of El Niño-Southern Oscillation on the Canadian climate. Advances in Geosciences 6: 149-153.

Shabbar, A., B. Bonsal, and M. Khandekar. 1997. Canadian Precipitation Patterns Associated with the Southern Oscillation. Journal of Climate 10: 3016-3027.

Spittlehouse, D. 2006. ClimateBC: Your access to interpolated climate data for BC. Streamline Watershed Management Bulletin 9: 16-21.

Spittlehouse, D.L. and R.B. Stewart. 2003. Adaptation to climate change in forest management. BC Journal of Ecosystem Management 4: 1-11.

Spittlehouse, D. 2003. Water availability, climate change and growth of Douglas-fir in the Georgia Basin. Canadian Water Resources Journal 28: 673-688.

Stephenson, N.L. and P.J. van Mantgem. 2005. Forest turnover rates follow global and regional patterns of productivity. Ecology Letters 8: 524-531.

Tabachnick, B. G. and Fidell, L. S. 1989. Using Multivariate Statistics. Harper Collins Publishers, Inc., New York.

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

Trenberth, K.E. 1990. Recent observed interdecadal climate changes in the Northern Hemisphere. Bulletin of the American Meteorological Society 71: 988-993.

Vaganov, E.A., M.K. Hughes, A.V. Kirdyanov, F.H. Schweingruber, and P.P. Silkin. 1999. Influence of snowfall and melt timing on tree growth in subarctic Eurasia. Nature 400: 149-151.

Vincent, L.A. and D.W. Gullett . 1999. Canadian historical and homogenous temperature datasets for climate change analyses. International Journal of Climatology 19: 1375-1388.

Vincent, L.A., X. Zhang, B.R. Bonsal, and W.D. Hogg . 2002. Homogenization of daily temperatures over Canada. Journal of Climate 15: 1322-1334.

Vyse, A., R.A. Smith, and B.G. Bondar. 1991. Management of interior Douglas-fir stands in British Columbia: past, present, and future, p. 177-185. *In* Interior Douglas-fir: The species and its management symposium proceedings.Department of Natural Resource Sciences, Washington State University, Pullman, Washington.

Walther, G.-R. 2003. Plants in a warmer world. Perspectives in Plant Ecology, Evolution, and Systematics 6: 169-185.

Walther, G.-R., E. Post, P. Convey, A. Menzei, C. Parmesan, T.J.C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416: 389-395.

Wang, T., A. Hamann, D.L. Spittlehouse, and S.N. Aitken. 2006. Development of scale-free climate data for western Canada for use in resource management. International Journal of Climatology 26: 383-397.

Waring, R.H. 1991. Responses of evergreen trees to multiple stresses, p. 371-390. *In* Response of plants to multiple stresses. Mooney, H. A., Winner, W. E., and Pell, E. J. (eds). Academic Press, San Diego.

Watson, E. and B.H. Luckman. 2002. The dendroclimatic signal in Douglas-fir and ponderosa pine tree-ring chronologies from the southern Canadian Cordillera. Canadian Journal of Forest Research 32: 1858-1874.

Wigley, T.M.L., P.D. Jones, and K.R. Briffa. 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. Journal of Climate and Applied Meteorology 23: 201-213.

Zhang, Q.-B. and R.J. Hebda. 2004. Variation in radial growth patterns of *Pseudotsuga menziesii* on the central coast of British Columbia, Canada. Canadian Journal of Forest Research 34: 1946-1954.

Zhang, X., F.W. Zwiers, G.C. Hegerl, F.H. Lambert, N.P. Gillett, S. Solomon, P.A. Stott, and T. Nozawa. 2007. Detection of human influence on twentieth-century precipitation trends. Nature 448: 461-465.

Table 2.1. Site descriptions and chronology statistics.

Site	Region	Lat. (°N)	Long. (°W)	Elev. (m)	Trees (n)	Chronology (years)	Mean sensitivity	Rbar	St.Dev.
Alexis	CH	52.12	123.57	1020	24	2006-1750 (257)	0.283	0.616	0.360
Gang	CH	51.73	122.42	680	21	2006-1768 (239)	0.375	0.602	0.341
Hoodoo	CH	51.82	122.56	700	15	2006-1829 (178)	0.448	0.641	0.375
Martin	CH	51.92	124.65	1040	21	2006-1794 (213)	0.244	0.546	0.206
Martin2	CH	51.96	124.71	1240	20	2006-1824 (183)	0.281	0.644	0.236
Newton	CH	52.03	123.56	1050	24	2006-1678 (329)	0.341	0.695	0.311
Tat	CH	51.62	124.38	920	22	2006-1832 (175)	0.231	0.503	0.211
Tat2	CH	51.64	124.39	860	23	2006-1762 (245)	0.289	0.617	0.244
Arch	NI	54.73	124.30	860	27	2006-1880 (127)	0.174	0.461	0.153
Battleship	NI	54.56	124.40	860	21	2006-1887 (120)	0.156	0.474	0.137
Bison	NI	54.72	124.35	840	23	2006-1844 (163)	0.198	0.473	0.176
Bowron	NI	53.94	122.10	780	25	2005-1818 (188)	0.175	0.406	0.147
Dolphin	NI	54.80	124.43	940	21	2006-1799 (208)	0.184	0.415	0.185
Ferndale	NI	53.95	122.46	780	21	2005-1833 (173)	0.203	0.493	0.171
Gregg11	NI	53.67	123.21	815	18	2005-1860 (146)	0.220	0.496	0.184
Gregg24	NI	53.68	123.24	840	23	2005-1868 (138)	0.222	0.592	0.180
Hedrick	NI	54.01	120.97	1250	23	2005-1754 (252)	0.148	0.414	0.135
Ispah	NI	53.68	122.19	840	25	2005-1861 (145)	0.157	0.460	0.138
Kerry	NI	54.70	122.82	800	23	2005-1837 (169)	0.171	0.436	0.139
Mcleod	NI	54.91	122.98	740	26	2005-1884 (122)	0.150	0.433	0.130
Narrow	NI	53.57	121.92	1300	22	2005-1853 (153)	0.157	0.376	0.134
Parsnip	NI	54.57	121.99	1200	20	2005-1633 (373)	0.155	0.381	0.139
PG1412	NI	53.50	123.10	740	31	2005-1865 (141)	0.199	0.458	0.168
Pinchi	NI	54.65	124.42	880	26	2006-1880 (127)	0.156	0.450	0.135
LaCasa	SI	50.10	119.51	425	27	2005-1863 (143)	0.268	0.445	0.236
Queest	SI	50.94	118.82	520	24	2005-1883 (123)	0.181	0.435	0.157
Shorts	SI	50.17	119.58	1340	26	2005-1739 (267)	0.211	0.440	0.199
Sicamous	SI	50.85	119.00	370	25	2005-1889 (117)	0.203	0.376	0.168
Star	SI	50.35	119.11	1540	25	2005-1893 (113)	0.153	0.428	0.129
Wap1	SI	50.86	118.36	1320	20	2005-1880 (126)	0.138	0.352	0.126
Wap2	SI	50.86	118.38	1340	19	2005-1869 (137)	0.136	0.367	0.137
Wap3	SI	50.89	118.45	920	24	2005-1855 (151)	0.187	0.447	0.157
Whiteman	SI	50.21	119.55	700	25	2005-1840 (166)	0.210	0.493	0.182

Lat. = latitude. Long. = longitude. Elev. = elevation. Rbar = average series correlation with master chronology. St. Dev. = standard deviation.

Table 2.2. Sample site climate normals.

Site	BEC	MAT	MWMT	MCMT	TD	MAP	MSP	AHM	SHM	PAS
Alexis	IDF dk4	2.3	13.7	-9.9	23.6	335	201	36.8	68.2	106
Arch	SBS dw3	1.8	13.7	-11.2	24.9	604	255	19.6	53.6	266
Battleship	SBS dw3	2.1	13.9	-11.2	25.1	512	229	23.7	60.6	213
Bison	SBS dw3	1.9	13.7	-11.1	24.8	603	255	19.7	53.7	264
Bowron	ICH wk4	3.1	14.6	-9.9	24.5	804	346	16.2	42.1	304
Dolphin	SBS mk1	1.5	13.3	-11.3	24.6	663	270	17.3	49.2	307
Ferndale	SBS wk1	3.5	14.8	-8.9	23.7	861	389	15.7	38.1	298
Gang	BG xw2	4.7	16.4	-8.7	25.1	372	211	39.5	77.9	105
Gregg11	SBS dw3	3	14.6	-10.1	24.7	582	255	22.4	57.3	226
Gregg24	SBS dw3	2.8	14.3	-10.1	24.4	593	260	21.6	55	235
Hedrick	ESSF wk2	1.7	12.7	-9.8	22.6	1386	525	8.4	24.3	637
Hoodoo	BG xw2	4.2	15.9	-8.9	24.7	341	202	41.8	78.4	94
Ispah	SBS wk1	2.9	14.1	-9.5	23.6	733	332	17.6	42.3	273
Kerry	SBS wk1	2.2	14	-11.2	25.3	755	279	16.1	50.3	339
LaCasa	PP xh1	7.3	18.7	-4.5	23.2	394	173	43.9	108.3	92
Martin	SBPS xc	2	12.9	-10	23	421	178	28.6	72.6	185
Martin2	SBPS xc	1.5	12.3	-10.3	22.7	493	202	23.4	61	226
Mcleod	SBS mk1	2.1	14.3	-12	26.3	713	252	17	56.8	331
Narrow	ESSF wk1	1.9	12.6	-9.6	22.2	992	443	12	28.4	400
Newton	IDF dk4	2.4	13.7	-9.7	23.4	338	192	36.8	71.3	113
Parsnip	ESSF wk2	1.8	13.5	-10.4	23.9	1064	386	11.1	35	477
PG1412	SBS dw3	3.5	14.6	-9.1	23.7	680	309	19.8	47.2	242
Pinchi	SBS dw3	2	13.7	-11.2	24.9	549	240	21.8	57.2	235
Queest	ICH mw3	5.6	17	-6.6	23.6	917	368	17	46.2	273
Shorts	ICH mk1	3.8	14.8	-7.3	22.1	615	255	22.4	58	236
Sicamous	ICH mw2	7.4	18.9	-5	24	848	379	20.5	50	169
Star	ICH mk1	2.4	13.5	-8.5	22	867	325	14.3	41.5	410
Tat	IDF dw	2.8	12.4	-8	20.4	461	183	27.6	68	185
Tat2	IDF dw	3	12.9	-7.8	20.7	452	174	28.9	74.2	179
Wap1	ICH vk1	2.5	13.9	-9.4	23.3	2077	676	6	20.5	983
Wap2	ICH vk1	2.7	14.1	-9.3	23.4	2062	680	6.1	20.7	952
Wap3	ICH wk1	3.6	15	-8.3	23.3	1255	483	10.8	30.9	488
Whiteman	IDF mw3	5.8	17	-5.9	22.9	499	217	31.6	78.4	145

Note: Abiotic ecological descriptors are for climate normal period of 1961-1990 (Wang et al. 2006). BEC=biogeoclimatic zone/subzone/variant (Meidinger and Pojar 1991). MAT=mean annual temperature (°C). MWMT=mean warmest month temperature (°C). MCMT=mean coldest month temperature (°C). TD=continentality (°C). MAP=mean annual precipitation (mm). MSP=mean summer precipitation (mm). AHM=annual heat-moisture index. SHM=summer heat-moisture index. PAS=precipitation as snow (cm).

Table 2.3. Summary of meteorological records used in Chapter 2.

Station name	Latitude (°N)	Longitude (°W)	Elevation (m)	Station ID	Data length (years)
Northern Interior					
Fort St. James	54.45	124.25	686	1092970	110 (1895-2004)
Prince George	53.89	122.68	691	1096450	94 (1913-2006)
Southern Interior					
Vernon Coldstream Ranch	50.22	119.2	482	1128580	98 (1900-1997)
Vernon Bella Vista*	50.26	119.31	427	1128553	21 (1985-2005)
Chilcotin					
Williams Lake**	52.18	122.05	940	1098940	69 (1939-2007)
Tatlayoko	51.67	124.41	870	1088010	76 (1930-2005)

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

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

Table 2.4. Missing precipitation data in meteorological records (between 1940 and 2004).

Station name	year	month	Variable(s)
Vernon Coldstream Ranch	1963	August	Rain, snow, PPT
Williams Lake A	1947	September	Rain, snow, PPT
		October	Rain, snow, PPT
	1960	June	Rain, snow, PPT
	1979	October	Rain, snow, PPT
		November	Rain, snow, PPT
Tatlayoko Lake	1977	April	Rain, snow, PPT
		May	Rain, snow, PPT
	1985	June	Rain, PPT
	1998	May	Rain, snow, PPT
		October	Rain, snow, PPT
		November	Rain, snow, PPT
		December	Rain, snow, PPT
	1999	January	Rain, snow, PPT
		February	Rain, snow, PPT
		March	Rain, snow, PPT
		April	Rain, snow, PPT
		May	Rain, snow, PPT
		June	Rain, snow, PPT
		July	Rain, snow, PPT
		August	Rain, snow, PPT

Table 2.5. Monthly climate values used to derive annual and seasonal variables used for correlation analysis.

Variable	Monthly inputs
Annual	Prior July to current June
Prior summer	Prior July to prior September
Winter	Prior October to current March
Spring	April to June
Summer	July to September

Table 2.6. Principal components used for climate-growth analysis.

Region	PC Number	Identifier	Ecological conditions	Corresponding climate station
Northern Interior	1	NIPC1	Northernmost sites in the province; characterized by low MAT and relatively low MAP. These are among the coldest sites of the study.	Fort St. James
	2	NIPC2	Low-elevation sites near Prince George; characterized by relatively warm and dry conditions.	Prince George
	3	NIPC3	High-elevation sites near Prince George on the western slopes of the Rocky and Cariboo Mountains; characterized by cold temperatures and high precipitation/snowfall.	Prince George
Southern Interior	1	SIPC1	Low-elevation sites near Vernon; characterized by hot and dry conditions. These are the hottest sites of the entire study.	Vernon
	2	SIPC2	High-elevation sites near Vernon and Revelstoke; characterized by cold temperatures and high precipitation/snowfall. These are the snowiest sites of the entire study.	Vernon
Chilcotin	1	CHPC1	Eastern sites on the Chilcotin Plateau near Williams Lake; characterized by very low precipitation. These are the driest sites of the entire study.	Williams Lake
	2	CHPC2	Western sites on the Chilcotin Plateau near Tatlayoko Lake; characterized by cold temperatures and slightly higher precipitation than CHPC1. These are among the coldest sites of the entire study.	Tatlayoko Lake

Note: Ecological conditions associated with each PC are based on visual interpretation of chronology-PC loadings.

Table 2.7. Principal components analysis summary.

	Northern Interior			Southern Interior			Chilcotin Plateau		
Component	1	2	3		1	2		1	2
Eigenvalues	9.21	1.56	1.29		3.98	2.11		4.92	1.44
Variance (%)	57.6	9.7	8.1		44.2	23.4		61.5	17.9
Cumulative variance(%)	57.6	67.3	75.4		44.2	67.6		61.5	79.5
Rotation sums of squared loadings									
Eigenvalues	4.93	4.14	2.99		3.18	2.91		3.46	2.9
Variance (%)	30.8	25.9	18.7		35.3	32.3		43.2	36.3
Cumulative variance (%)	30.8	56.7	75.4		35.3	67.6		43.2	79.5
Loadings									
Arch	**0.868**	0.272	0.199	Lacasa	**0.773**	-0.188	Alexis	**0.846**	0.309
Battle	**0.797**	0.302	0.213	Queest	**0.661**	0.379	Gang	**0.858**	0.16
Bison	**0.899**	0.254	0.149	Shorts	**0.676**	0.562	Hoodoo	**0.874**	0.15
Bowron	0.261	**0.645**	0.484	Sicamous	**0.813**	0.063	Martin	0.482	**0.687**
Dolphin	**0.747**	0.285	0.239	Star	0.059	**0.743**	Martin2	0.468	**0.717**
Ferndale	0.327	**0.763**	0.216	Wap1	-0.002	**0.889**	Newton	**0.867**	0.325
Gregg11	0.47	**0.78**	0.129	Wap2	0.036	**0.876**	Tat	0.095	**0.919**
Gregg24	0.391	**0.806**	0.036	Wap3	**0.588**	0.543	Tat2	0.172	**0.906**
Hedrick	0.186	-0.03	**0.823**	Whiteman	**0.823**	-0.002			
Ispah	0.126	0.517	**0.673**						
Kerry	**0.551**	0.306	0.503						
Mcleod	**0.597**	0.227	0.423						
Narrow	0.109	0.548	**0.691**						
Parsnip	0.487	0.19	**0.636**						
PG1412	0.299	**0.802**	0.273						
Pinchi	**0.758**	0.421	0.100						

Loading (correlation coefficient) significance levels: 0.191 (95%), 0.249 (99%), and 0.315 (99.9%), based on N=106.

Bolded values refer to highest loadings.

Table 2.8. Correlation coefficients between Douglas-fir growth variation and annual/seasonal climatic variables.

	Northern Interior			Southern Interior		Chilcotin	
	NIPC 1	NIPC 2	NIPC 3	SIPC 1	SIPC 2	CHPC 1	CHPC 2
Annual							
Precipitation		0.557**		0.387*		0.534**	0.589**
Mean temperature			0.352*		0.429**		0.261
HM		-0.498**		-0.387*		-0.467**	-0.585**
PDO					0.456**		
ENSO					0.349**		
PNA	0.274				0.466**		
Prior winter							
Snow			-0.432**		-0.523**		
Mean temperature			0.397*		0.530**		0.283
PDO					0.476**		
ENSO					0.342**		
PNA			0.400**		0.593**		
Prior summer							
Rain		0.324*			0.272	0.324	
HM		-0.271		-0.251			
Max. temperature				-0.403**	-0.257		
PDO					0.324**		
ENSO					0.390**		
PNA							
Spring							
Rain	0.365*	0.437**		0.327*		0.328*	
HM	-0.406*	-0.463**		-0.317*			
Max. temperature		-0.304		-0.317			
PDO					0.337**		
ENSO							
PNA							
Summer							
Rain							
Heat-moisture index							
Max temp.							

All relationships are significant at $p<0.05$ (bootstrapped confidence intervals). * = $p<0.01$ **=$p<0.001$
All relationships calculated from 1940 to 2004 (n=65), except PDO (1901-2005, n=105), ENSO (1900-2003, n=104), and PNA (1951-2005, n=55).
HM=heat-moisture index.

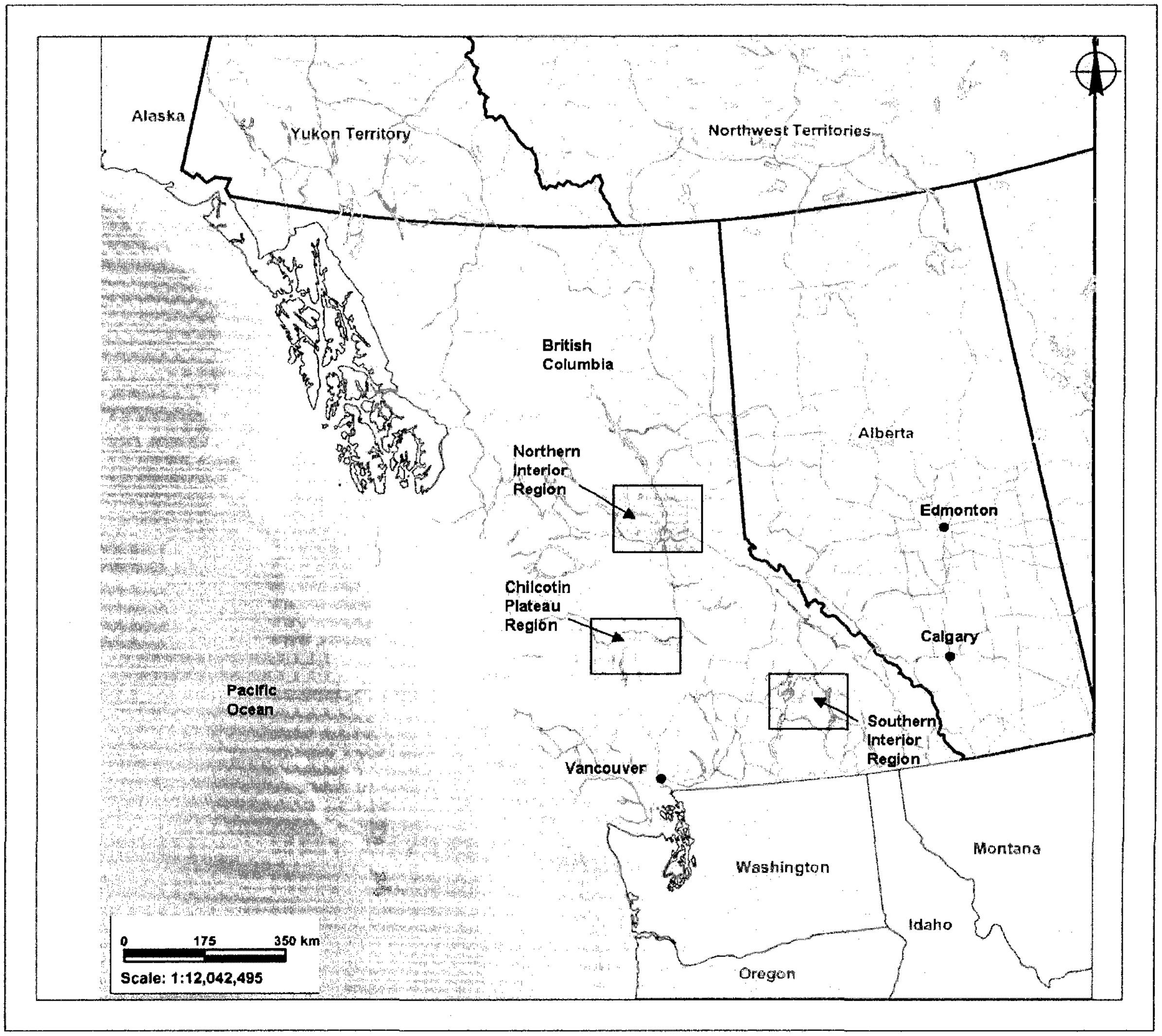


Figure 2.1. Sampling region overview map.

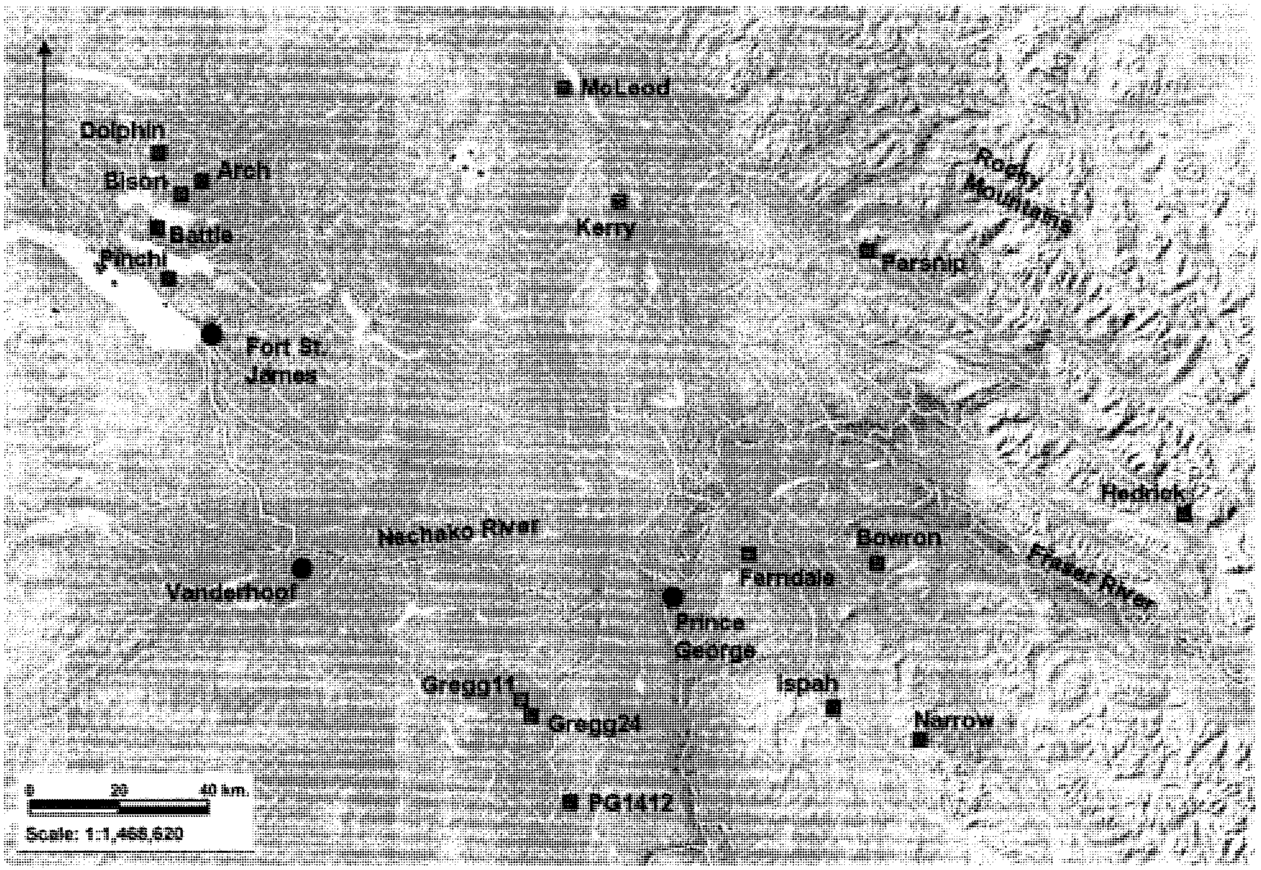


Figure 2.2. Sampling site locations in Northern Interior study region. Red squares are sampling sites, black dots are settlements.

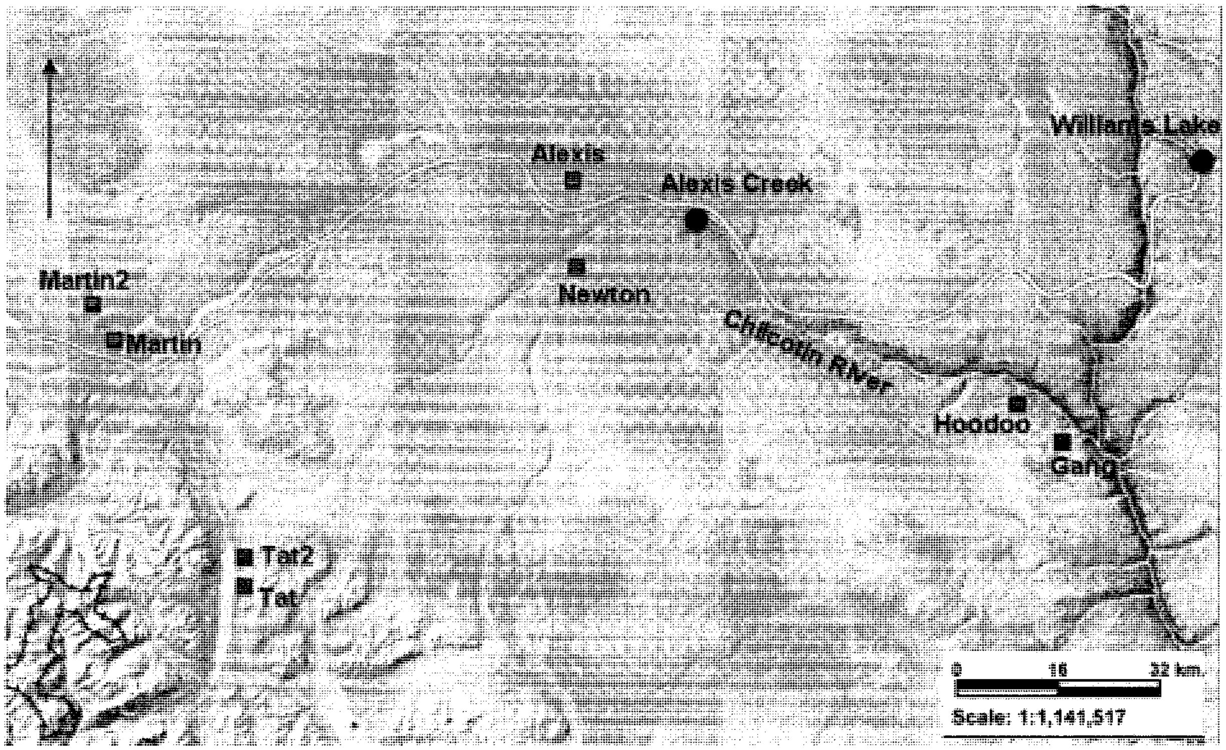


Figure 2.3. Sampling site locations in Chilcotin Plateau study region. Red squares are sampling sites, black dots are settlements.

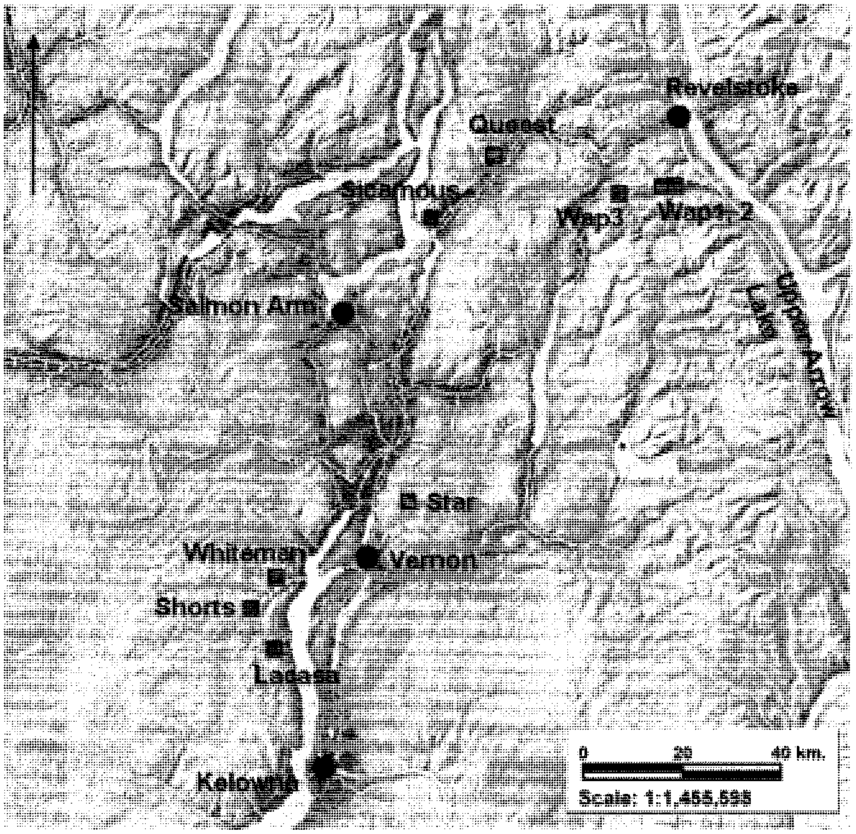


Figure 2.4. Sampling site locations in Southern Interior study region. Red squares are sampling sites, black dots are settlements.

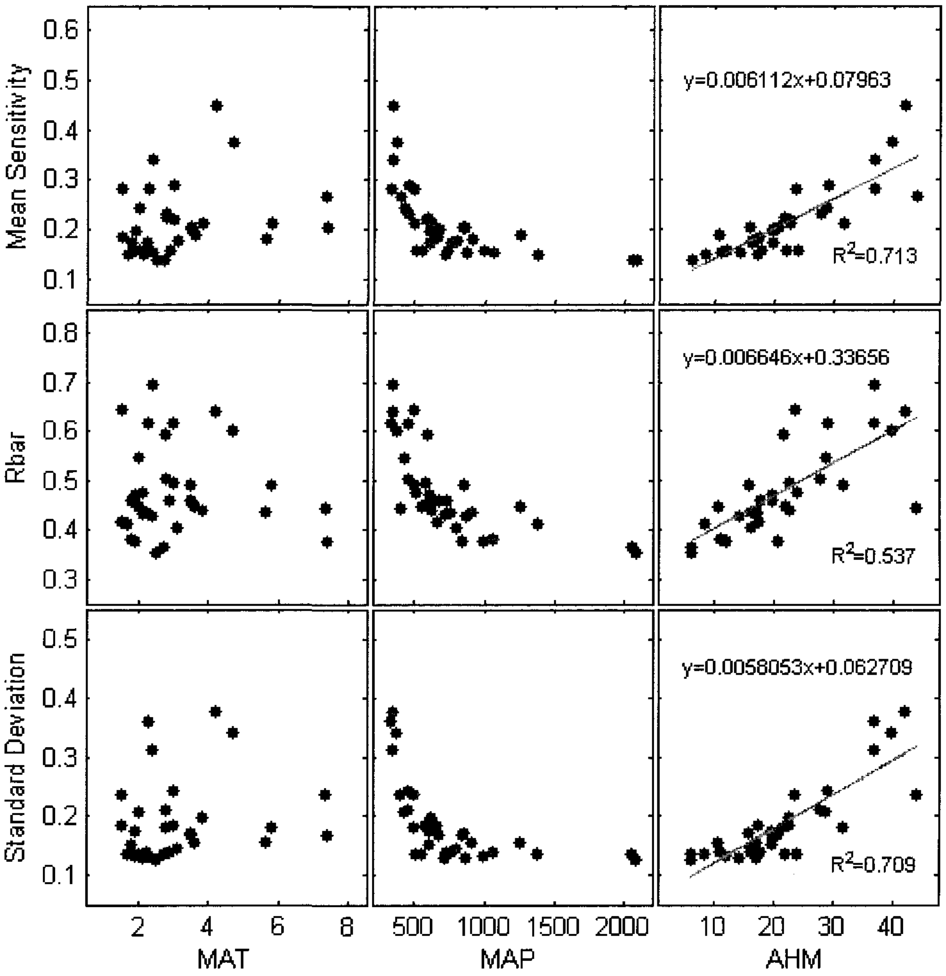


Figure 2.5. Chronology statistics against sample site mean annual climate normals. Rbar=average intrasite series correlation with chronology. MAT=mean annual temperature (°C), MAP=mean annual precipitation (mm). AHM=annual heat-moisture index. Relationships between chronology statistics and AHM are all significant at $p<0.0001$.

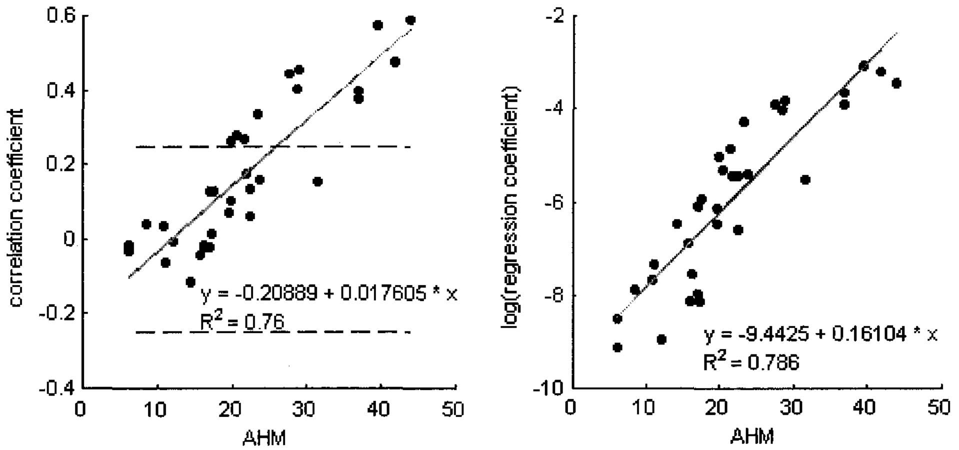


Figure 2.6. Variation in annual precipitation-growth correlation and regression coefficients over annual heat-moisture index normals. AHM=annual heat-moisture index. Regression coefficients were log transformed prior to analysis. Relationships are significant at $p<0.0001$. Black dashed lines represent 95% significance levels for correlation coefficients.

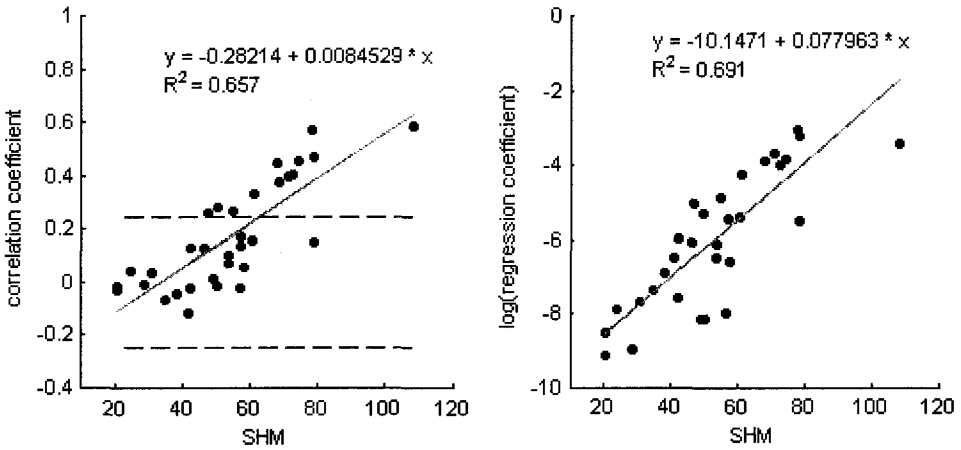


Figure 2.7. Variation in annual precipitation-growth correlation and regression coefficients over summer heat-moisture index normals. SHM=summer heat-moisture index. Regression coefficients were log transformed prior to analysis. Relationships are significant at $p<0.0001$. Black dashed lines represent 95% significance levels for correlation coefficients.

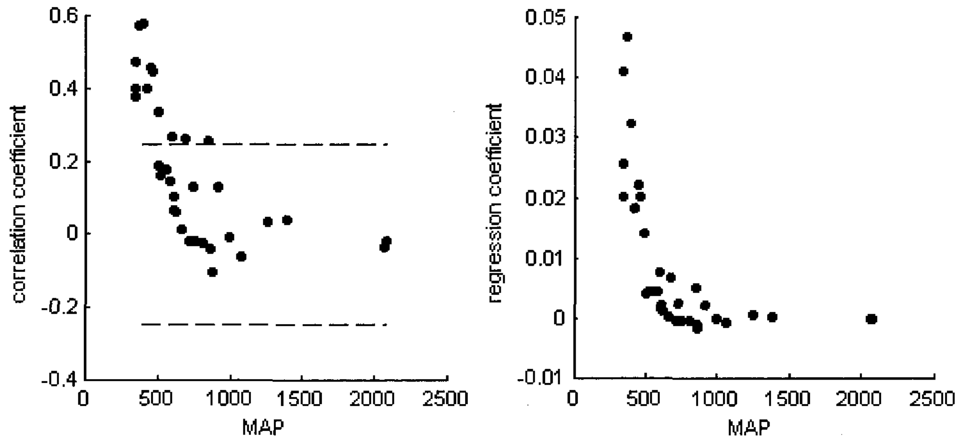


Figure 2.8. Variation in annual precipitation-growth correlation and regression coefficients over mean annual precipitation normals. MAP=mean annual precipitation (mm). Black dashed lines represent 95% significance levels for correlation coefficients. MAP data is positively skewed. Relationships were not tested for significance (see Figure 2.9), and are only presented to demonstrate non-linear relationships.

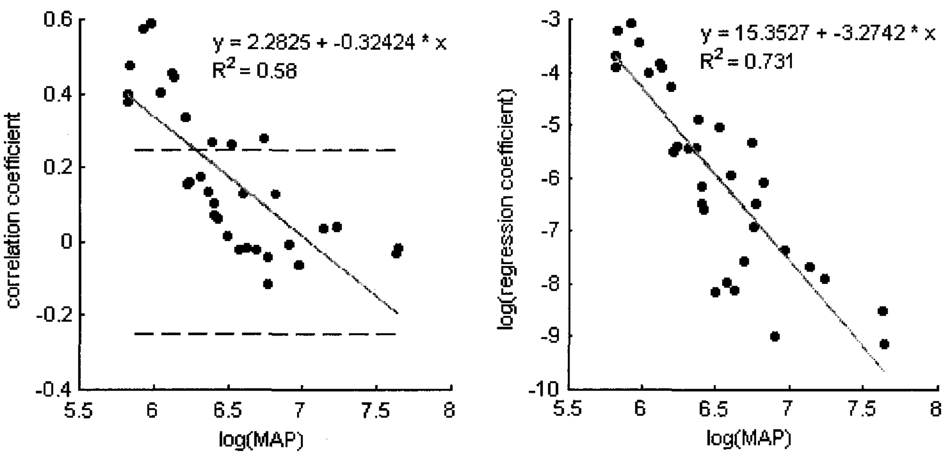


Figure 2.9. Variation in annual precipitation-growth correlation and regression coefficients over (log-transformed) mean annual precipitation normals. MAP=mean annual precipitation (mm). Regression coefficients and MAP data were log transformed prior to analysis. Relationships are significant at $p<0.001$. Black dashed lines represent 95% significance levels for correlation coefficients.

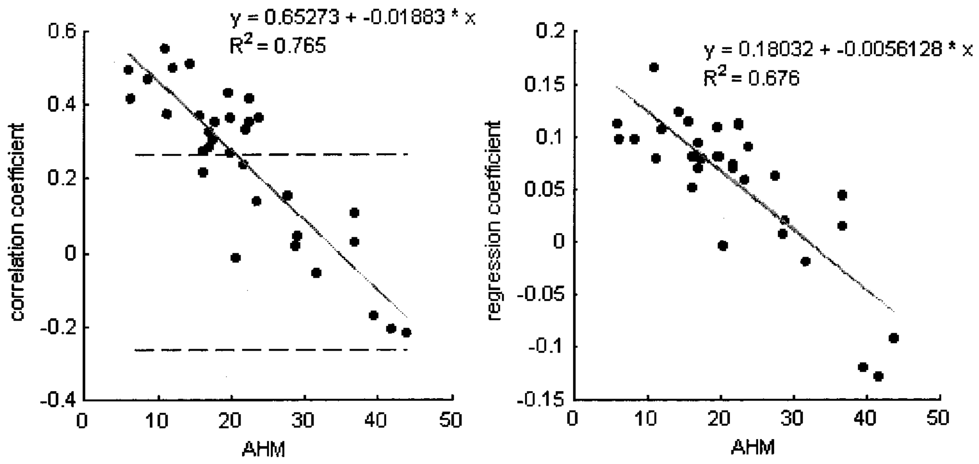


Figure 2.10. Variation in winter PNA index-growth correlation and regression coefficients over annual heat-moisture index. AHM=annual heat-moisture index. Relationships are significant at $p<0.001$. Black dashed lines represent 95% significance levels for correlation coefficients.

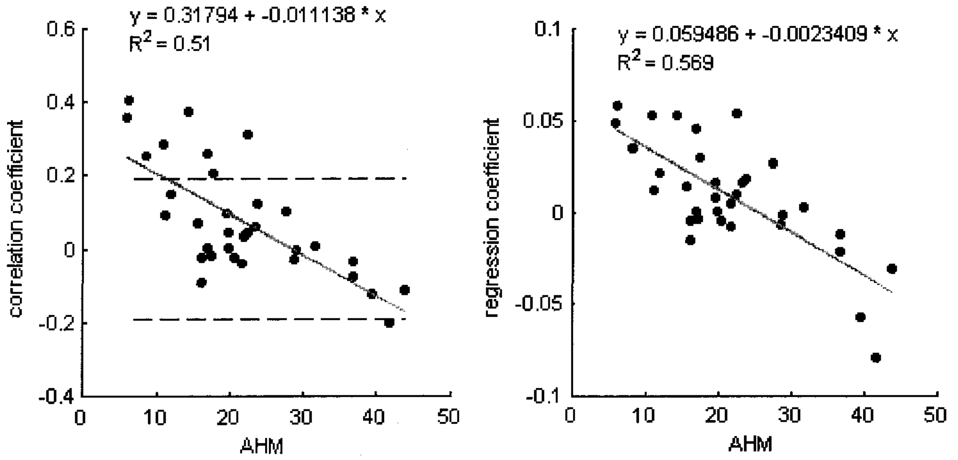


Figure 2.11. Variation in winter PDO index-growth correlation and regression coefficients over annual heat-moisture index. AHM=annual heat-moisture index. Relationships are significant at $p<0.001$. Black dashed lines represent 95% significance levels for correlation coefficients.

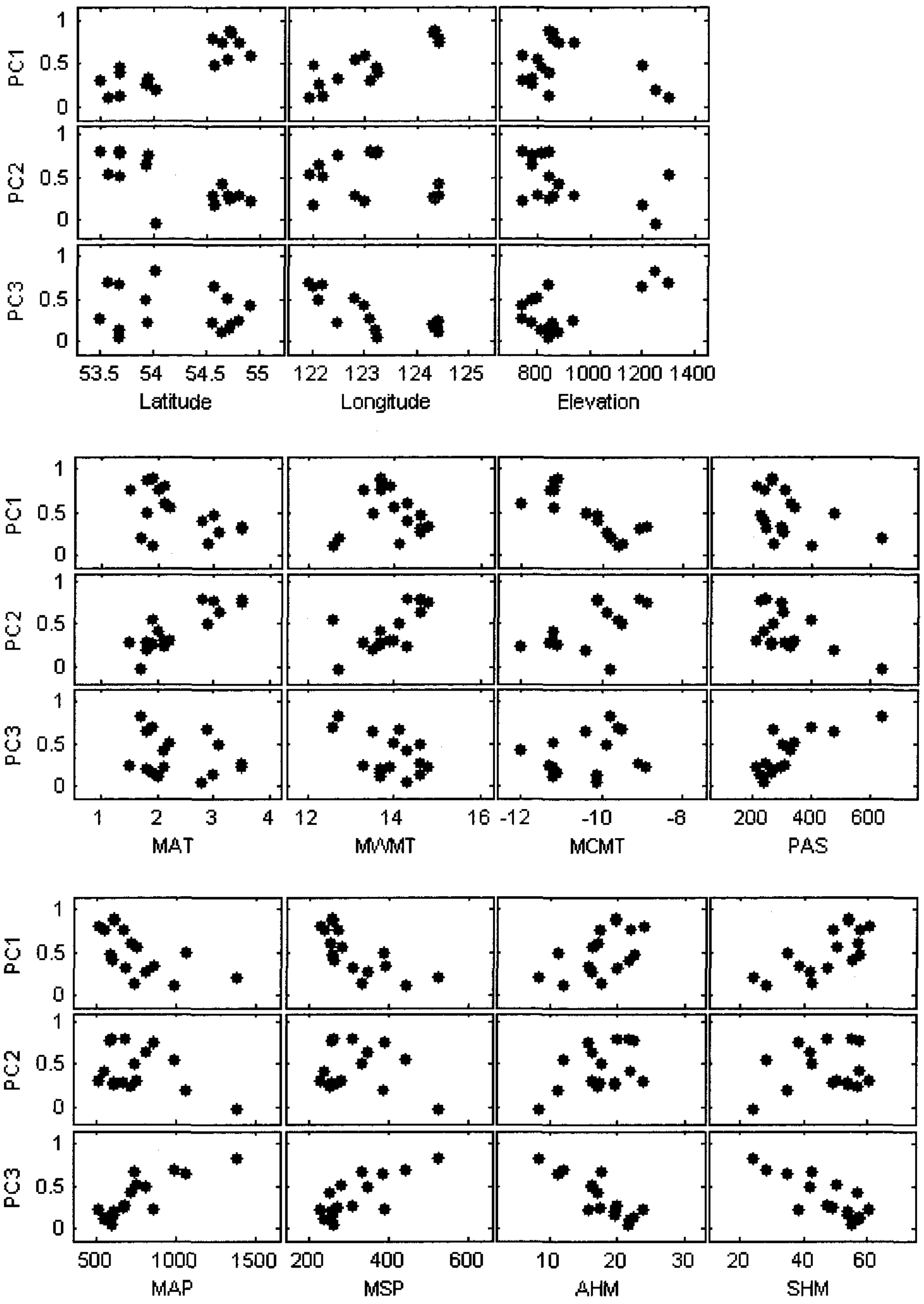


Figure 2.12. Northern Interior PC loads against geographic variables and climatic normals. Latitude units=°N. Longitude units=°W. Elevation units=metres. MAT=mean annual temperature (°C). MWMT=mean warmest month temperature (°C). MCMT=mean coldest month temperature (°C). TD=continentality (°C). MAP=mean annual precipitation (mm). MSP=mean summer precipitation (mm). AHM=annual heat-moisture index. SHM=summer heat-moisture index. PAS=precipitation as snow (cm).

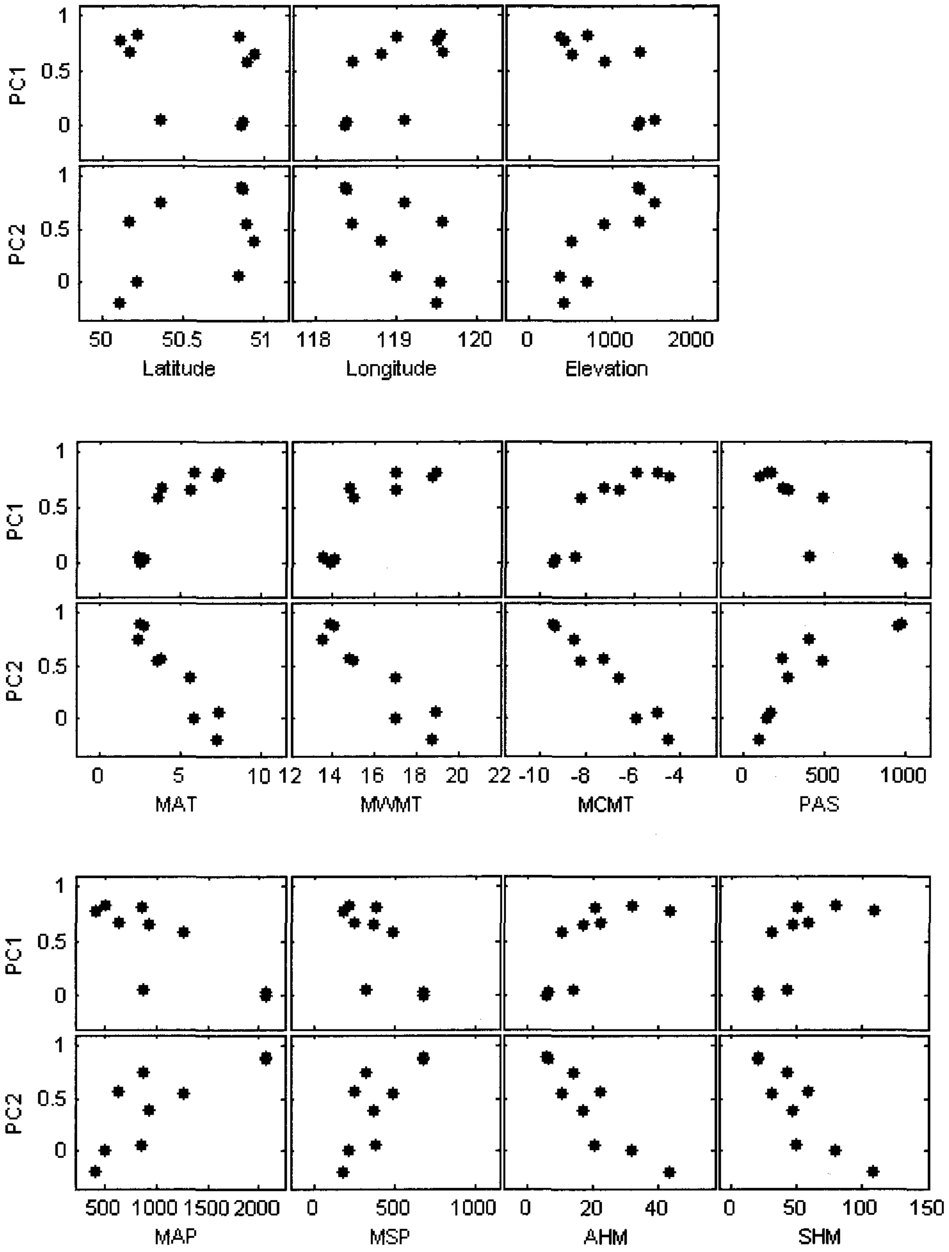


Figure 2.13. Southern Interior PC loads against geographic variables and climate normals. Latitude units=°N. Longitude units=°W. Elevation units=metres. MAT=mean annual temperature (°C). MWMT=mean warmest month temperature (°C). MCMT=mean coldest month temperature (°C). TD=continentality (°C). MAP=mean annual precipitation (mm). MSP=mean summer precipitation (mm). AHM=annual heat-moisture index. SHM=summer heat-moisture index. PAS=precipitation as snow (cm).

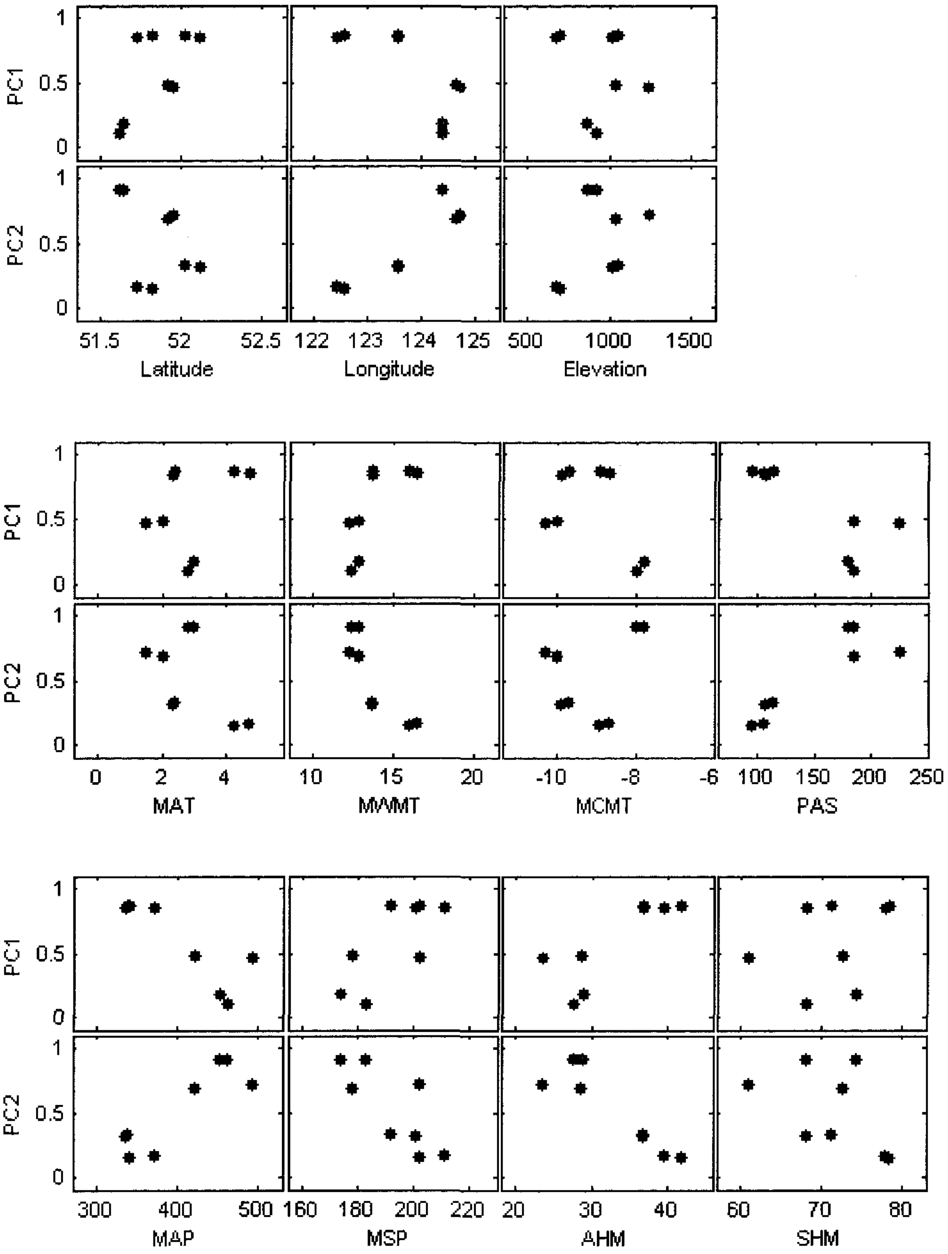
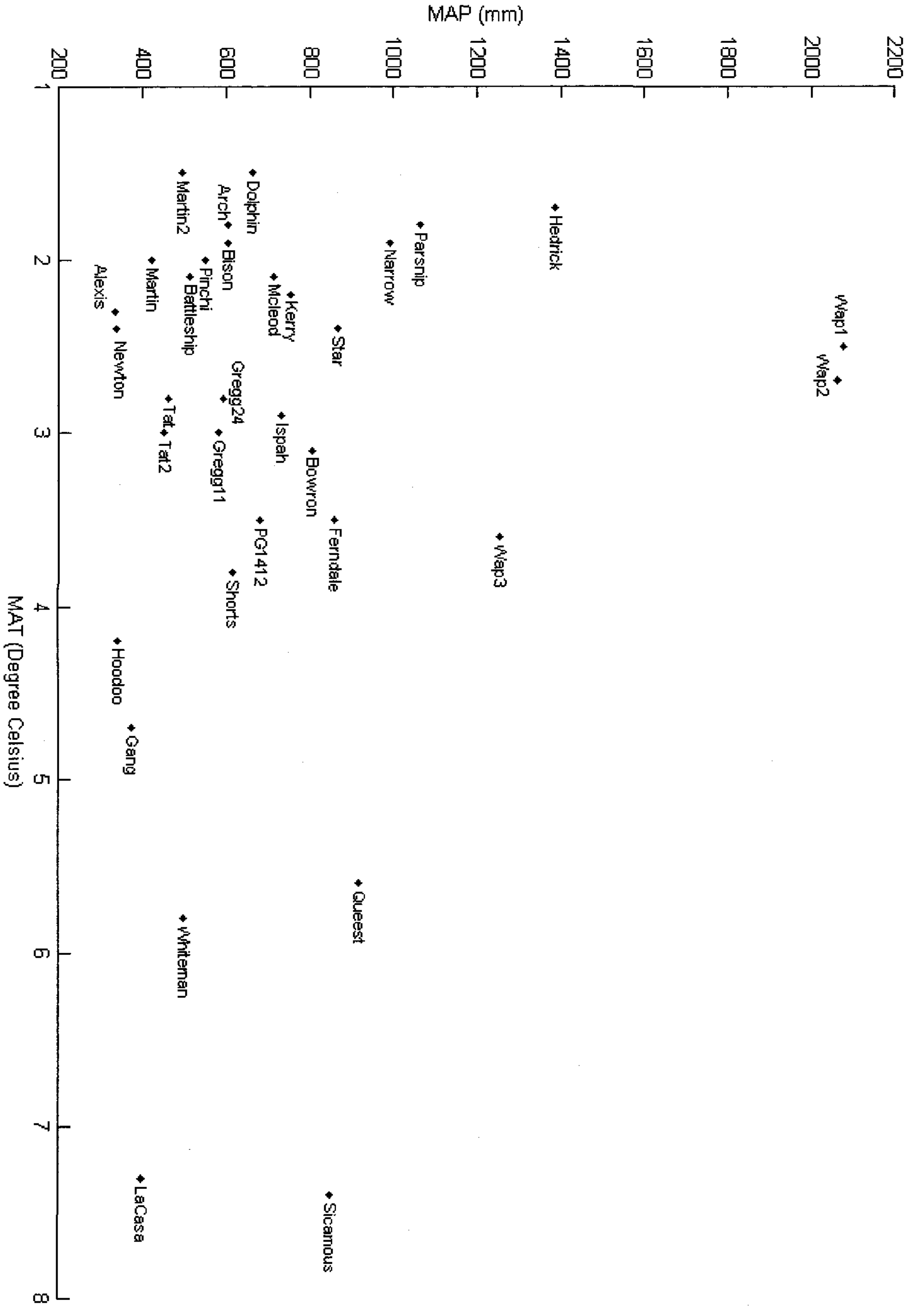


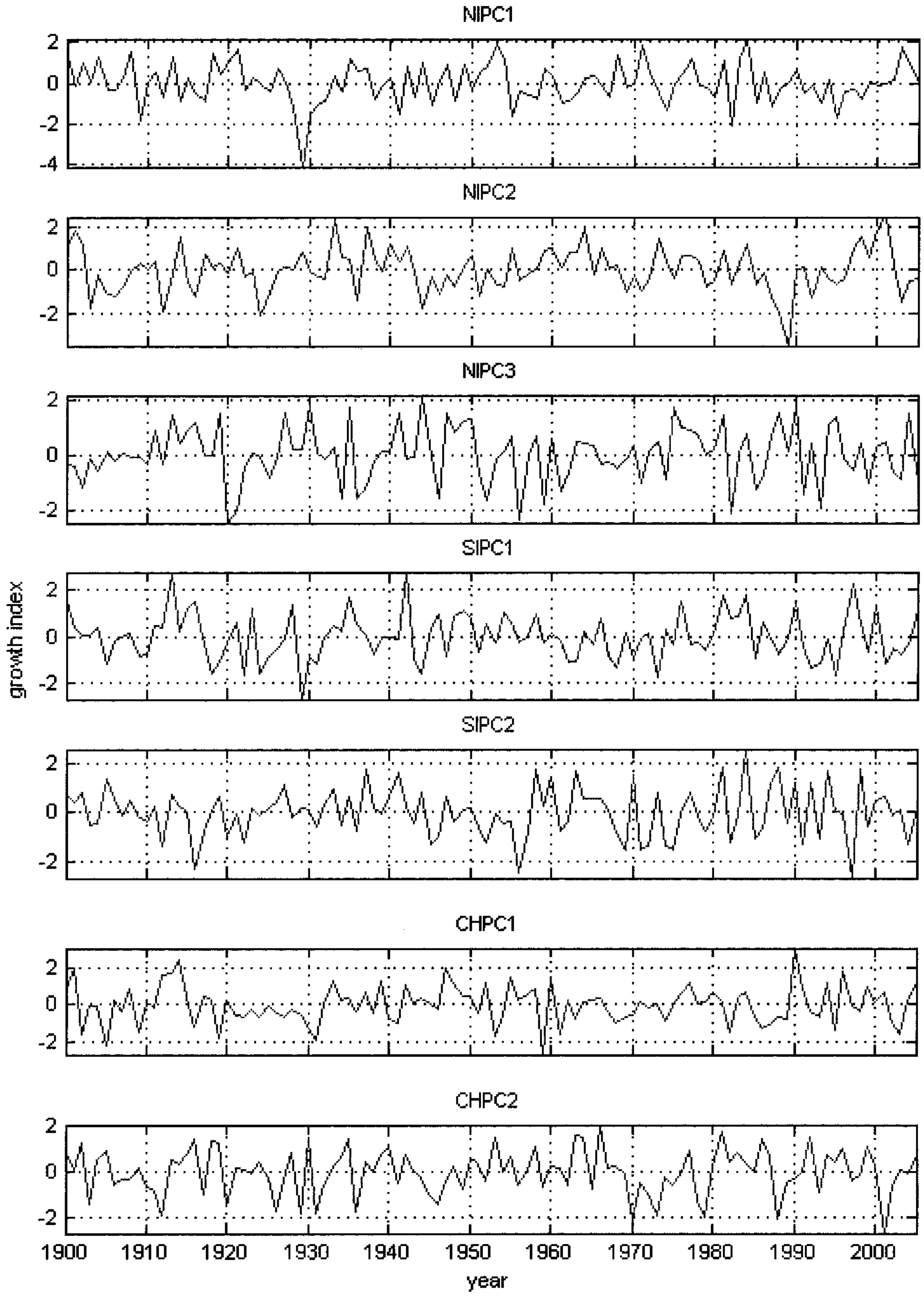
Figure 2.14. Chilcotin Plateau PC loads against geographic variables and climate normals. Latitude units=°N. Longitude units=°W. Elevation units=metres. MAT=mean annual temperature (°C). MWMT=mean warmest month temperature (°C). MCMT=mean coldest month temperature (°C). TD=continentality (°C). MAP=mean annual precipitation (mm). MSP=mean summer precipitation (mm). AHM=annual heat-moisture index. SHM=summer heat-moisture index. PAS=precipitation as snow (cm).

Appendix A. Sample site mean annual temperature and precipitation normals.



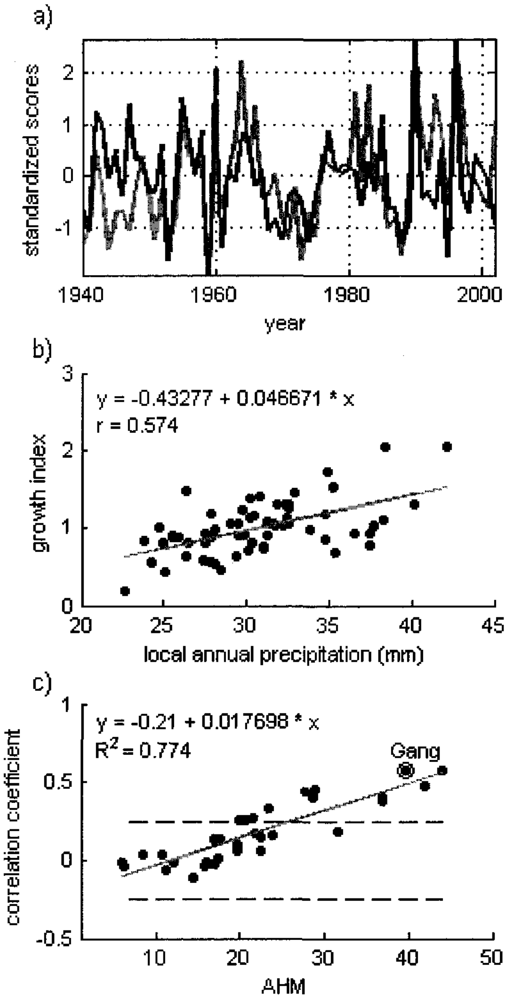
MAT=mean annual temperature (1961-1990). MAP=mean annual precipitation (1961-1990).

Appendix B. Regional growth chronology time series derived from residual growth chronologies.



Appendix C. Example of climate gradient analysis.

	Mean site climate	Growth response to local annual precipitation (1940-2002)	
	AHM	r	β
Alexis	36.8	0.379	0.0203
Arch	19.6	0.064	0.0015
Battle	23.7	0.161	0.0045
Bison	19.7	0.101	0.0021
Bowron	16.2	-0.024	-0.0005
Dolphin	17.3	0.012	0.0003
Ferndale	15.7	-0.043	-0.001
Gang	**39.5**	**0.574**	**0.0467**
Gregg11	22.4	0.144	0.0044
Gregg24	21.6	0.269	0.0077
Hedrick	8.4	0.040	0.0004
Hoodoo	41.8	0.474	0.0411
Ispah	17.6	0.131	0.0026
Kerry	16.1	-0.018	-0.0003
Lacasa	43.9	0.582	0.0323
Martin	28.6	0.402	0.0182
Martin2	23.4	0.336	0.0141
Mcleod	17.0	-0.022	-0.0003
Narrow	12.0	-0.009	-0.0001
Newton	36.8	0.402	0.0256
Parsnip	11.1	-0.065	-0.0006
Pg1412	19.8	0.261	0.0067
Pinchi	21.8	0.176	0.0044
Queest	17.0	0.131	0.0023
Shorts	22.4	0.059	0.0014
Sicamous	20.5	0.259	0.0049
Star	14.3	-0.107	-0.0015
Tat	27.6	0.446	0.0201
Tat2	28.9	0.457	0.0221
Wap1	6.0	-0.018	-0.0001
Wap2	6.1	-0.033	-0.0002
Wap3	10.8	0.035	0.0005
Whiteman	31.6	0.188	0.0041



The climatic gradient analysis was completed in two steps. First, correlation and regression coefficients were computed between each chronology and local annual precipitation from 1940 to 2002. As an example, part a) of this figure shows a time series of Gang site tree growth (blue) and local annual precipitation (red) from 1940 to 2002. Part b) of this figure shows a regression of Gang site tree growth on local annual precipitation from 1940 to 2002 (β=0.0467 and r=0.574). This was performed for all 33 chronologies (see table). In the second step of the climatic gradient analysis, the 33 correlation and regression coefficients (see table) were regressed against site-specific climatic normals such as mean annual heat-moisture index (AHM, see table) to determine if coefficients varied with site climate. Part c) of the figure shows the climatic gradient analysis, with the 33 correlation coefficients plotted against mean site AHM. Note that the data point corresponding to the Gang site is highlighted.

Chapter 3. Temporal variability in climate-growth relationships at the climatic margins of Douglas-fir in British Columbia

Abstract

A growing body of evidence is challenging assumptions around the temporal stability of historical climate-tree growth relationships. This study examined the temporal stability of correlations between regional Douglas-fir growth patterns and climate in three study regions in British Columbia. Growth patterns describing high-elevation Douglas-fir populations have become more correlated with annual temperatures and snowfall over the 20th century, possibly reflecting changing conditions in these environments associated with anthropogenic climate change. Growth patterns describing dry climate Douglas-fir populations show variability in the Southern Interior, possibly associated with PDO phases, an extensive drought in the early 1900s, and the recent development of temperature-growth sensitivity. Ecologically similar sites in the Chilcotin Plateau show more stability in climate-growth relationships, possibly reflecting the dominant drought influence in forest-grassland ecotonal populations. This study adds to the recent studies highlighting historically variable climate-growth relationships and suggests that in BC, Douglas-fir growth responses to climate change will vary over time.

3.1 Introduction

Climate change models project that by 2100, mean annual temperatures in western North America could be two to seven °C above the mean for the previous 1000 years, with the greatest increases occurring during the winter months and at higher latitudes and continental areas (Christensen et al. 2007, BC MoE 2007). Annual (summer) precipitation is also expected to increase (decrease), although there may be a high degree of spatial variability associated with topography, continentality, and other factors (Christensen et al. 2007, BC MoE 2007). The frequency of droughts, severe storms, and other extreme climatic events may also increase in association with climate change (Easterling et al. 2000).

As climate is a key factor influencing tree growth (Fritts 1976, Kimmins 1997), climate change is expected to have a profound impact on future forest productivity and will subsequently challenge many aspects of forest management (Nigh et al. 2004, Littell 2006, D'Arrigo et al. 2007, Spittlehouse 2005). Tree radial growth can indicate species health, productivity, and resilience, therefore, identifying links between specific climate parameters and growth rates can provide information regarding future species viability and resource sustainability (Littell and Peterson 2005, Littell 2006, Nigh et al. 2004). Many studies have shown that species-specific radial growth (productivity) responses to climate may vary by local abiotic conditions (e.g., climate, elevation) (e.g. Littell 2006, Littell and Peterson 2005, Case and Peterson 2005, Zhang and Hebda 2004, Laroque and Smith 2005), with potentially strong and unique responses in populations growing near climatically-controlled range margins (e.g., Barber et al. 2000, Case and Peterson 2005, Zhang and Hebda 2004). Further, recent studies have shown that critical climatic growth limitations in a given environment can vary over time, possibly as a result of changing local conditions associated with long-term climate change and/or anthropogenic non-climatic factors such as pollution and increased atmospheric carbon dioxide concentrations (Biondi 2000, Barber et al. 2000, Lloyd and Fastie 2002, Carrer and Urbinati 2006, Pfeifer et al. 2005, D'Arrigo et al. 2007). In order to more fully understand and predict forest ecosystem responses to climate change, ecological and temporal complexities underlying population-specific climate-growth relationships must be considered in research strategies and can be elucidated by sampling across a species' biophysical range (including its extremes) (Littell 2006, Littell and Peterson 2005, Peterson and Peterson 2001) and examining relationships at different temporal scales (Biondi 2000, Biondi and Waikul 2004, D'Arrigo et al. 2007, Lloyd and Fastie 2002, Carrer and Urbinati 2006, Pfeifer et al. 2005).

Our study incorporated this concept with dendroecological methods (Fritts 1976) to identify and describe temporal variations in Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco) climate-growth relationships in the British Columbia Interior. Interior Douglas-fir is a commercially important conifer with a wide ecological amplitude in BC (Meidinger and Pojar 1991), ranging from dry semi-arid forests in the lee of the Coast Mountains to low- to high-elevation wetbelt forests on the western slopes of the Rocky Mountains (Arno 1991), to cold interior forests near Fort St. James (Jull 1999). Many studies have shown that Douglas-fir radial growth is sensitive to climate, and that its climate-growth relationships change with local ecological conditions (e.g., Daniels and Watson 2003, Case and Peterson 2005, Zhang and Hebda 2004, Littell 2006, Watson and Luckman 2002), however, to our knowledge, there have been no studies in BC (and only one in the US; Biondi 2000) examining temporal variation in Douglas-fir climate-growth responses.

This study addressed this knowledge gap by examining four regional growth chronologies generated from a principal components analysis (PCA, The Mathworks Inc. 2007) of 33 population ring-width chronologies collected over a wide geographic and climatic range in three study regions in the province. Analysis of PCA results (presented in Chapter 2) indicated that regional growth chronologies significantly described growth patterns across each region, but best described populations growing at the climatic margins. Thus, this study assessed temporal stability in regional-scale climate-growth relationships with a focus on stands growing at the climatic margins. The specific study objectives were to:

1) identify and describe temporal variations in important climate-growth relationships in Douglas-fir at the cold and wet (associated with high-elevation environments, hereafter, high-environment) and dry (hereafter, dry site) climatic extremes of its range in BC, and
2) suggest possible causal mechanisms for these temporal variations.

3.2 Materials and methods

3.2.1 Field sampling

We sampled 33 mature stands of Douglas-fir in three geographic regions (Figure 2.1) in the British Columbia Interior: 1) Northern Interior (Figure 2.2), 2) Chilcotin Plateau (Figure 2.3), and 3) Southern Interior (Figure 2.4). The 33 sample stands (sites) were strategically chosen to encompass a wide range of climatic regimes, including stands located at the extremes in each region. Potential sampling sites were identified by overlaying spatial mean annual temperature (MAT) and precipitation (MAP) data (1961-1990 climate normal period, Spittlehouse 2006) obtained from ClimateBC (v3.1, Wang et al. 2006) onto mature Douglas-fir coverage obtained from the BC Ministry of Forest and Range's Vegetation Resource Inventory. Sample site MAT ranged from 1.5 to 7.4 °C, and MAP ranged from 335 to 2077 mm (Table 2.2). The elevation range was 370 to 1540 m (Table 2.1). The sampled sites encompassed seven biogeoclimatic (BEC) zones (Meidinger and Pojar 1991), representing a wide diversity of ecosystems (Table 2.2).

Sample sites and trees were chosen to maximize the climate signal in growth variation. Sites without evidence of edaphic limiting factors (e.g., shallow rocky soils, cold air ponding, steep northerly aspects) or recent abiotic or biotic disturbance were selected in order to minimize the growth impacts of non-climatic factors. The influence of inter-tree competition was minimized by sampling trees with a dominant canopy position. We avoided sampling trees with obvious growth defects or evidence of disease, fire scarring, or insect attacks as much as possible. At each site, between 18 and 40 mature trees greater than 100 years old were sampled to build a robust population sample. A single increment core was taken from each sample tree at approximately breast height (1.3m, Josza 1988). Where sampling occurred on slopes, increment cores were taken perpendicular to the slope direction to avoid compression and tension wood (Josza 1988).

3.2.2 Processing and chronology development

Increment cores were mounted and sanded to enhance the contrast of tree ring boundaries. Cores were then visually crossdated to assign calendar years to annual growth rings (Cook and Kairiukstis 1990). Ring widths were measured using WinDendro™ image analysis software (Regent Instruments Inc. 2005) to the nearest 0.01mm. Crossdating was verified using COFECHA software (Holmes 1983). After checking for measurement errors, cores that did not crossdate with the master chronology were excluded from the final chronology (Daniels and Watson 2003).

The ARSTAN software (Cook and Krusic 2005) was used to remove the age-related growth trend from each series, as this trend usually dominates the variance and masks the climate signal (Fritts 1976, Cook and Kairiukstis 1990, Cook 1985). A cubic smoothing spline with a 50% frequency response cutoff of 60 years was used to remove very low-frequency (i.e., age-related trend) variation (Cook 1985, Cook and Kairiukstis 1990). Cubic smoothing splines remove unwanted variation by filtering data in the frequency domain; the spline used in this study removed 50% of the signal amplitude at a frequency of 1 cycle/60 years, and an increasing (decreasing) percentage of the signal amplitude at frequencies lower (higher) than 60 years (Cook 1985, Cook and Kairiukstis. 1990).

After detrending, ARSTAN was used to analyze autocorrelation and apply a common autoregressive model to each series for a given site (Cook and Krusic 2005, Cook 1985). Residuals from autoregressive modeling were then averaged together using robust mean calculation to produce a residual growth chronology that represented stand growth variation with autocorrelation removed (Cook and Krusic 2005). Removing autocorrelation from growth chronologies is a common procedure in dendroecological studies (e.g., Chhin et al. 2008, Case and Peterson 2005, Littell 2006, Pfeifer et al. 2005) because autocorrelation has statistical implications (Pfeifer et al. 2005, Littell 2006, Meko 2007) and may be a function of non-climatic processes such as stand-level disturbances and morphological influences on growth (Littell 2006, Cook 1985, Fritts 1976). A preliminary analysis of this dataset revealed that autocorrelation confounded climate-growth relationships (i.e. autocorrelation may have resulted from non-climatic sources, Chhin et al. 2008, Biondi and Swetnam 1987). Robust mean calculation is more resistant to outliers, which may serve to reduce noise from tree-level growth disturbances (Cook 1985, Cook and Kairiukstis 1990).

3.2.3 Principal components analysis

For each of the 3 regions, PCA was used to consolidate the variation in annual radial growth expressed in the chronologies of each region. Leading principal components (PC) represented regional growth patterns and were retained as composite chronologies to be used in determining climate-growth relationships. In order to determine what climatic and geographic attributes were represented by each regional PC, we calculated correlation coefficients (also referred to as 'loadings') between the original chronologies and the PCs in each region, and then visually examined these against corresponding climatic normals (Table 2.2) and geographic variables (Table 2.1) for each chronology (Case and Peterson 2005, Zhang and Hebda 2004). This visual analysis revealed that sites at climatic extremes were best represented (had the highest correlations) to regional PCs, however, sites growing in more moderate conditions also had significant (albeit lower) correlations with each PC. Thus, we interpreted each PC to represent populations growing at the climatic margins of the species' range in each region, but also representing populations growing under more moderate conditions. PCA results, analysis, and discussion are presented in Chapter 2.

For this study, we used four of the regional composite chronologies: 2 chronologies representing high-elevation interannual growth variation from 1900 to 2005 in the Southern and Northern Interior study regions, and 2 chronologies representing interannual dry site growth variation from 1900 to 2005 in the Chilcotin Plateau and Southern Interior study regions. The 1900 to 2005 period was chosen to allow for analysis with complete climate records where possible (see below).

3.2.4 Climate data

Environment Canada climate station temperature and precipitation data were used as predictor variables to determine climate-growth relationships with the regional PCs (see below for details on this analysis). Climate stations corresponding to regional PCs were chosen based on spatial and ecological interpretations of the PCA results, proximity to sample sites, and sufficient time series length. Adjusted monthly precipitation records (Mekis and Hogg 1999) and homogenized monthly temperature records (Vincent and Gullett 1999, Vincent et al. 2002) provided by the Climate Research Division of the Meteorological Service of Canada (http://www.cccma.bc.ec.gc.ca/hccd/) for the chosen climate stations were used to account for non-climatic variation in the instrumental records caused by changes in station location, measurement procedures, instrument changes, and other factors (Mekis and Hogg 1999, Vincent and Gullett 1999, Vincent et al. 2002).

We made further adjustments to two data records. The Williams Lake temperature record was not homogenized at the time of this study (Vincent, pers. comm.), therefore we used the observed data. However, the station moved location (and over 300m up in elevation) in 1961, which likely introduced inhomogeneities in the climate record. We accounted for this by using ClimateBC elevation-adjusted and interpolated homogenized historical temperature data (Wang et al. 2006, Mitchell and Jones 2005) from 1939-1960 (see below for a description of the ClimateBC model). A visual comparison of Williams Lake observed temperature data and ClimateBC temperature data from 1939 to 2002 (data not shown) indicated a possible step change in recorded temperatures around 1960, which presumably could be associated with the change in station location and elevation.

At the time of this study, adjusted precipitation, rain, and snow data for the Vernon Coldstream Ranch were only available up to April 1997. To create a time series that matched the other records used in the analysis, we used observed precipitation, rain, and snow data from a nearby station (Vernon Bella Vista) to extend the record to 2005.

Climate station data are summarized in Table 3.1. All climate stations had some missing precipitation, rain, and snow data, which are summarized in Table 3.2. We did not replace missing precipitation data due to a high potential for errors in estimating precipitation (Mekis and Hogg 1999).

Seasonal and annual variables were derived by averaging monthly values (Table 3.3). Where monthly values were missing in the climate station record (Table 3.2), the associated derived seasonal variable was computed as a non-number and omitted pair-wise from analysis. Growth was compared to climate variables from the previous year's July to the current year's October because climate in the preceding year affects the current year's growth (Fritts 1976).

Seasonal and annual heat - moisture index variables were derived from monthly temperature and precipitation data using the following formula (similar to Wang et al. 2006):

1) $HM = (TMX + 10)/(PPT/1000)$

where: HM = seasonal or annual heat-moisture index

TMX = seasonal or annual mean of monthly average maximum temperatures (°C)

PPT = seasonal or annual mean of monthly precipitation totals (mm)

El Niño Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) are two quasi-periodic ocean-atmosphere processes (Allan 2000, Mantua et al. 1997) that influence climate in British Columbia (Shabbar 2006, Shabbar et al. 1997, BC MoE 2007, BC MWLAP 2002) and have been linked to Douglas-fir growth in the Pacific Northwest United States (US) (Case and Peterson 2005). The Pacific-North American index (PNA) is a mid-tropospheric pressure anomaly influenced by ENSO and strongly correlated with North American winter temperature and precipitation (Leathers et al. 1991, Shabbar 2006, Shabbar et al. 1997). Index values used for this study were derived by averaging October to March monthly index values obtained from the US Department of Commerce's National Oceanic and Atmospheric Administration (http://www.cdc.noaa.gov/ClimateIndices/List/).

3.2.5 Analysis of climate-growth relationships and inter-regional growth patterns

Climate-growth relationships were assessed by 1) examining climate-growth relationships within the Northern and Southern Interior study regions, and 2) comparing temporal growth patterns between ecologically similar stands in disparate regions (e.g., comparing high-elevation annual growth rates between the Northern and Southern Interior) (hereafter, inter-regional growth patterns).

Analyses were performed using annual, seasonal, and monthly variables, however, results involving only annual and seasonal variables are presented because they explained more growth variation than monthly variables (e.g., Littell 2006, Watson and Luckman 2002).

Two approaches were used to examine temporal variation in climate-growth relationships and inter-regional growth patterns:

1) Sub-period correlation analysis was used to detect changes in climate-growth relationships and inter-regional growth patterns between the first and second half of the 20th century. Climate and tree growth records were split into two sub-periods using 1950 as a breakpoint (Lloyd and Fastie 2002, Wilmking et al. 2004). Regional climate records vary in length, therefore, the sample size for the pre-1950 climate-growth analysis differed for each region. The Williams Lake climate record does not contain pre-1939 data, therefore, no sub-period analysis was computed for the Chilcotin Plateau region. The post-1950 analysis was computed over the 1951-2005 period.

2) Finer-scale changes in temporal variation were examined using moving correlation functions (D'Arrigo et al. 2007, Wilson and Elling 2004, Carrer and Urbinati 2006, Biondi 2000, Biondi and Waikul 2004). A moving correlation function (MCF) calculates correlation coefficients between two time series using a fixed-length time window that is incrementally moved over the full series; time-dependent variation in the coefficients provides a measure of temporal stability in the linear relationship (Biondi and Waikul 2004, Biondi 2000). MCFs were computed using a 31-year window offset in one-year increments (D'Arrigo et al. 2007), over the full available climate record in each region.

Values presented for a given year refer to the 31-year period ending at that year. Missing data in the climate records was omitted pair-wise from analysis, therefore, the sample size was less than 31 over some periods. Bootstrap bias-corrected accelerated 95% confidence intervals were calculated for each correlation coefficient using 1000 iterations (Moore and McCabe 2006, The Mathworks Inc. 2007).

MCFs using all climatic variables would have produced too many results for reasonable interpretation and discussion, therefore, we focused the MCF analysis on a subset of climatic variables that explained a relatively high proportion of growth variation. Interpretation of MCF results focused on identifying changes in correlation coefficients over time and consistent periods of significant climate-growth relationships (i.e., multiple consecutive 31-year windows with significant correlations). Significant correlation coefficients over only a few consecutive time windows were treated as potentially spurious, and moving scatterplots (data not shown) were examined to assess the influence of potential outliers. Because the MCF analysis focused on identifying periods of significant correlations, confidence limit adjustments such as Bonferonni (Meko 2007, Biondi et al. 1997*)* or False Discovery Rate (Benjamini and Hochberg 1995) techniques were not employed (Meko 2007).

Moving regression functions were also calculated in a similar fashion as MCFs to detect changes in the regression slopes. The output from both analyses was virtually identical (slopes increased with correlation), therefore, only MCF results are presented and discussed.

3.3 Results

3.3.1 Temporal variation in high-elevation growth and climate-growth relationships

3.3.1.1 Inter-regional growth patterns

Annual radial increment patterns in high-elevation populations of Douglas-fir were similar for the Northern and Southern Interior study regions over the 1900 - 2005 period ($r = 0.457$, $p<0.001$), with a stronger correlation for the 1951 - 2005 period ($r=0.564$, $p<0.0001$) than the 1900 - 1950 period ($r=0.304$, $p<0.05$) (data not shown). The MCF confirmed an increasing common growth signal over time (Figure 3.2a). Since ca. 1940, growth patterns converged and have remained significantly correlated over subsequent 31-year periods.

3.3.1.2 Temperature-growth relationships

Prior to ca. 1950, growth in the Northern Interior study region was not correlated to any seasonal or annual climatic variables, and growth in the Southern Interior was correlated to winter and annual temperatures (Figure 3.1). Since ca. 1950, growth in both regions was positively correlated to fall, winter, and annual temperatures and heat-moisture index (growth tended to be higher during warmer and drier years). Annual minimum temperatures generally had stronger correlations with growth than maximum temperatures.

MCF using annual average temperatures confirmed an increasing association with growth since ca. 1950 and revealed a similar pattern in temporal coefficient variation between both regions (Figure 3.2b). Growth became increasingly associated with temperatures after the 1920-1950 period ($r \sim 0$), developing the strongest association over the ca. 1968-1998 period (r > 0.4) in both regions. MCFs using average maximum and minimum temperatures as well as winter season temperatures produced similar results (data not shown).

3.3.1.3 Snowfall-growth relationships

Prior to 1950, growth at high-elevation sites in both regions was not correlated with annual or winter snowfall (Figure 3.1), although Southern Interior populations had a positive growth correlation with spring snowfall. After ca. 1950, growth in both regions became negatively correlated with snowfall and positively correlated with winter heat-moisture index (radial growth tended to be higher after warmer and drier winters). Post-1950 growth had stronger correlations with annual vs. winter snowfall in both regions. MCF using annual snowfall indicated that temporal variations in correlation functions differed between the regions (Figure 3.2c). Douglas-fir in the Northern Interior maintained a relatively stable negative growth relationship to snowfall after ca. 1950, whereas in the Southern Interior, growth correlations to annual snowfall were more dynamic. After the 1926-1956 period (r ~ 0), snowfall became increasingly associated (negative) with growth. The 31-year period with the strongest association was 1968 to 1998; annual snowfall explained approximately 50% of growth variation during this period.

3.3.1.4 Ocean-atmosphere climate indices-growth relationships

At high elevation, Southern Interior growth was significantly correlated to ENSO, PDO, and PNA indices over the full available record (Table 3.3), while Northern Interior growth was correlated with PNA and PDO. MCFs indicated that growth at high-elevation sites in the Southern Interior was consistently correlated to ENSO and PDO over most 31-year windows in the latter half of the 20th century, while in the Northern Interior, growth correlations with ENSO and PDO were insignificant over most time windows (Figures 3.2d and 3.2e). Growth in both regions was significantly correlated to PNA over most 31-year periods (Figure 3.2f).

3.3.2 Temporal variation in dry-site inter-regional growth patterns and climate-growth relationships

3.3.2.1 Inter-regional growth patterns

Dry sites in the Southern Interior and Chilcotin Plateau had correlated growth patterns from 1900 to 2005 ($r = 0.359$, $p<0.001$, not shown). Growth patterns were significantly correlated over both sub-periods, with a slightly weaker correlation for the 1951 - 2005 period ($r=0.327$, $p<0.05$, not shown) than the 1900 - 1950 period ($r=0.390$, $p<0.01$, not shown). However, MCF results revealed this relationship was dynamic, particularly in the latter half of the century (Figure 3.4a). Correlations decreased after the 1913-1943 period and growth patterns are insignificant for many 31-year periods in the latter portion of the 20th century.

3.3.2.2 Temperature-growth relationships

In the Southern Interior, correlation analysis using the two sub-periods indicated that prior summer, spring, and annual temperature became negatively associated with growth over the last half of the century, whereas prior to ca. 1950, only prior summer average maximum temperatures were negatively correlated with growth (Figure 3.3). MCFs revealed that prior summer maximum and average temperatures and spring maximum temperatures became negatively correlated to growth in recent decades, although prior summer temperatures were more strongly correlated to growth for a period around the middle of the 20th century (Figures 3.5a to 3.5c).

Chilcotin Plateau Douglas-fir growth from 1951 - 2005 was not correlated to any temperature variables (Figure 3.3), although MCFs revealed that growth and spring maximum temperatures became significantly negatively correlated in recent decades (Figure 3.5c).

3.3.2.3 Precipitation-growth relationships

Southern Interior growth relationships to annual and spring precipitation variables remained significant (positive) over the two sub-periods, with generally higher correlations over the 1900-1951 period (Figure 3.3). MCFs revealed a dynamic signal strength with annual, spring, and prior summer precipitation variables over the past century (Figures 3.4b to 3.4f). After ca. 1950, significant growth responses to annual precipitation, rain, and heat-moisture index and spring/prior summer precipitation gradually began to weaken; associations were insignificant over the ca. 1950 - 1980 period. After this period, correlations between growth and annual, spring, and prior summer precipitation rapidly increased and became significant again. A moving scatterplot analysis confirmed that this rapid correlation increase was due to post-1980 values (data not shown).

A sub-period analysis was not computed for the Chilcotin Plateau region, as the Williams Lake climate record does not contain pre-1939 data. MCFs calculated for Chilcotin Plateau growth and annual precipitation, rain, and heat-moisture index from 1940 to 2005 revealed a relatively stable response (Figures 3.4b to 3.4d). Correlation strengths varied somewhat over time, with the strongest relationship occurring over the ca. 1950-1980 period. Relationships with prior summer and spring precipitation weakened and became insignificant in recent decades (Figures 3.4e and 3.4f).

3.4 Discussion

This study detected temporally variable climate-growth relationships in Douglas-fir populations in the British Columbia Interior, thus broadening the spatial, species, and ecological extent of this recently described phenomenon (e.g., D'Arrigo et al. 2007, Wilmking and Myers-Smith 2008, Carrer and Urbinati 2006, Pfeifer et al. 2005). Temporally variable climate-growth relationships will impact various management areas that rely on ecological process data such as carbon cycle modeling, growth and yield, the management of climatically sensitive populations, species distribution models, and the use of tree-rings as historical climate proxies because they challenge current paradigms based on assumptions of "stable" ecosystem responses (D'Arrigo et al. 2007, Carrer and Urbinati 2006, Barber et al. 2000, Millar et al. 2006). The adaptation of forest management to climate change will require a greater understanding of the temporal and ecological complexities of species-specific climate-growth relationships that may result in unexpected responses and conditions (D'Arrigo et al. 2007, Carrer and Urbinati 2006, Wilmking et al. 2004, Pfeifer et al. 2005, Zhang and Hebda 2004, Littell and Peterson 2005, Peterson and Peterson 2001).

Isolated mechanisms behind unstable climate-growth relationships are difficult to identify as many climatic and non-climatic (e.g., increased CO_2, global dimming, pollution, and nitrogen deposition) factors potentially responsible for this phenomenon covary (D'Arrigo et al. 2007, Carrer and Urbinati 2006). If non-climatic factors were primary contributors to the instability in the climate-growth relationships studied here, it would be reasonable to expect an overall loss of sensitivity to climate variables over time (Lloyd and Fastie 2002), however, this was not the case. The Douglas-fir populations examined in this study developed new climatic sensitivities over the last half of the 20th century, implying that the underlying mechanism is at least partially climatic in nature (Lloyd and Fastie 2002, D'Ariggo et al 2007, Carrer and Urbinati 2006). Multi-decadal climatic variation as a result of 20th century linear temperature/precipitation trends and/or quasi-periodic ocean-atmosphere climate systems such as PDO has been suggested as a causal factor in other studies (e.g., Fagre et al. 2003, Daniels and Veblen 2004, Barber et al. 2000, Lloyd and Fastie 2002) and is discussed below as a potential primary contributor to the unstable climate-growth relationships observed in this study.

3.4.1 High-elevation sites

Our results indicate that high-elevation Douglas-fir growth patterns and climate-growth relationships in both the Northern and Southern Interior study regions have become more synchronized over the 20th century, possibly reflecting an increasing macro-regional influence of linear temperature/precipitation increases. We expected that positive temperature-growth correlations in high-elevation populations would decrease over the 20th century as temperatures rose and became less limiting in these cold environments (Körner 1998, 2003, Kimmins 1997, Littell 2006), however, growth in both regions actually became more responsive to annual, prior fall, and winter temperatures after ca. 1950. This unexpected result may be related to a co-occurring increase in annual/summer precipitation

(BC MWLAP 2002, BC MoE 2007, Cayan et al. 1998, Zhang et al. 2007) and cloudiness (Dai et al. 1999, Henderson-Sellers 1992) in both regions that may have introduced new environmental conditions such as excessive soil moisture, lower daytime maximum temperatures and/or reduced direct sunlight. In high-elevation environments, these integrated factors can negatively influence photosynthesis and growth (Helms 1965, Peterson and Peterson 2001, DeLucia and Smith 1987) or at least shift critical growth limitations from soil moisture to thermal energy (Littell 2006) and correlated factors such as sunlight, possibly explaining the strengthening growth-temperatures correlations.

We note that annual and winter temperatures are highly correlated (e.g., $r > 0.9$, $p<0.00001$ for 1900-2005 Southern Interior and 1912-2005 Northern Interior annual and winter average temperatures), therefore, it is difficult to identify the important variable (annual vs. winter) that may be influencing growth. Warmer annual temperatures may simply reflect more days with optimum temperatures for photosynthesis (Helms 1965, Doehlert and Walker 1981), whereas warmer winter temperatures may reflect an earlier snowmelt date and a correspondingly longer growing season (Vaganov et al. 1999).

Although snowfall can be a critical forest growth limitation in high-elevation environments (Case and Peterson 2005, Peterson et al. 2002, Laroque and Smith 2005), our results indicate that snow-growth responses in high-elevation Douglas-fir populations can vary over time and by region. In both regions, growth did not become correlated to snowfall until the latter half of the 20th century, and MCFs highlighted regional differences in snow-growth responses that may reflect unique climatic limitations in each region. For example, the high-elevation populations in the Southern Interior had the highest snowfall normals of the entire study

(Table 2.2), and may be particularly sensitive to snowfall increases. Growth in these populations has become increasingly negatively associated with annual snowfall since ca. 1950, and the period of strongest correlations (ca. 1968 to 1998) corresponds with a period of anomalously high October to March precipitation recorded at Vernon climate stations (ca.1970 to 2000, Appendix A). Much of this winter precipitation would likely have been snowfall at higher elevations, therefore, snowpacks during this period may have been anomalously high. The period of high precipitation ended ca. 2000 and MCF results indicate that growth correlations with snowfall began to weaken around this time.

While high-elevation Douglas-fir populations in the Northern Interior also developed a negative growth response to snowfall after ca. 1950, MCF results indicate a relatively stable response to this variable over the latter half of the 20th century. An analysis of Prince George climate did not reveal any strong possible climatic mechanisms. Projected significant decreases in winter snowfall and corresponding snowpacks over much of the province (BC MoE 2007, BC MWLAP 2002, Christensen et al. 2007) may result in a decrease in snow-growth responses in both regions as this climatic limitation becomes alleviated.

After ca. 1950, Southern Interior high-elevation growth developed a positive (negative) response to prior summer rain (temperatures). With a potentially shorter growing season as a result of deep snowpacks over the ca. 1970 to 2000 period, tree growth may have become increasingly sensitive to growing season drought events (Zhang and Hebda 2004). High-elevation sites are usually assumed to have ample moisture, however, high summer temperatures in these environments can cause drought-like soil conditions (Anfodillo et al. 1998) and shorten the growing season (Zhang and Hebda 2004), negatively affecting growth.

We note that higher snowpacks in the Southern Interior may have also resulted in greater soil moisture availability during the subsequent growing season, although this would presumably result in a reduced growth response to prior growing season variables, which was not observed.

ENSO and PDO indices strongly influenced Southern Interior high-elevation growth (particularly over the latter half of the 20th century), but were generally not reflected in northern high-elevation tree growth. Other studies have shown these indices influence the growth of Douglas-fir (Case and Peterson 2005) and other tree species (Holman and Peterson 2006, D'Arrigo et al. 2001, Biondi et al. 1999) in other (mostly high-elevation coastal) regions of North America. High index values are correlated with warm and dry weather patterns (Mantua et al. 1997, Hare and Mantua 2001) in British Columbia (BC MWLAP 2002), which may result in longer growing seasons through lower snowpack depths (Case and Peterson 2005). While PDO and ENSO indices were regional in their influence on high-elevation Douglas-fir growth, the PNA index appears to have a broad growth influence, as it was correlated to growth in both regions. PNA may represent a different mode of variability in surface temperatures and precipitation than PDO and ENSO; research into differences between these climate systems and their possible effects on forest growth may provide useful information about future productivity (Case and Peterson 2005, Fagre et al. 2003, Daniels and Veblen 2004).

Climate-growth relationships may have recently changed in both regions, as MCFs indicated that common growth patterns and growth responses to annual temperatures, snowfall, and PNA weakened after ca. 1998. As well, Southern Interior growth responses to PDO and

ENSO have weakened somewhat since ca. 1998. Moving scatter plots (data not shown) showed that the gradual weakening in correlation values after 1998 were a result of post-1998 values. Although preliminary, these changes may signal a weakening macroregional climate influence or changing climatic growth limitations in high-elevation environments. Over time, growth may become more limited by local climate processes and/or different climate variables than those identified in this study, resulting in a greater divergence in growth patterns and climate-growth relationships between northern and southern populations.

3.4.2 Dry sites

Synchronized growth patterns in the first half of the 20th century in Southern Interior and Chilcotin Plateau dry sites suggest a similar large-scale climatic process influenced growth in both regions during this period (Zhang and Hebda 2004, Carrer and Urbinati 2006). Tree-ring precipitation reconstructions for many areas in western North America, including Williams Lake, indicate that a drought covered a large area of western North America from the early 1900s until the mid-1940s (Watson and Luckman 2004, Daniels and Watson 2003). This drought may have been the longest and most extensive in the past three centuries in western North America (Watson and Luckman 2004). Annual precipitation recorded in Vernon also indicates a prolonged period of below-average precipitation in the first half of the 20th century, particularly before 1940 (Appendix B). As climatic events such as droughts may cause widespread and synchronized climatic sensitivities (and possible mortality) in forests (van Mantgem and Stephenson 2007, Breshears et al. 2005), a prolonged macroregional drought may be a primary causal factor behind the correlated inter-regional growth patterns observed in dry sites in both regions.

A divergence between the regional growth patterns after ca. 1943 may be related to the end of the large-scale drought as well as a ca. post-1950 negative temperature-growth response that developed in the Southern Interior but not the Chilcotin Plateau. Warmer spring and summer temperatures in the Southern Interior may now exceed a species- and region-specific optimal photosynthesis limit (which can be as low as 20-25 °C for Douglas-fir; Salo 1974, Doehlert and Walker 1981) and/or causing physiological stress (Kimmins 1997, Balatinecz and Anderson 1986, Kozlowski and Pallardy 2002). A general lack of temperature response in Chilcotin Plateau populations may reflect cooler temperatures and/or the dominant growth influence of drought in this region, however, growth in recent decades has developed a negative growth correlation with spring maximum temperatures. This may indicate that temperatures are beginning to exceed tolerances in the Chilcotin Plateau region; projected future temperature increases (BC MoE 2007, BC MWLAP 2002) could result in more negative temperature-growth responses developing, as well as a possible convergence in growth patterns with dry sites in other regions.

Chilcotin Plateau population growth responses to annual precipitation variables were relatively strong and stable over time, possibly reflecting persistent local drought conditions associated with forests located at the forest-grassland ecotonal boundary (these sites were the driest of the entire study). We note that correlations were somewhat stronger over a period of anomalously dry conditions in the Williams Lake climate record (ca. 1940 to 1975, Appendix C); in these types of ecotonal populations, a higher drought frequency associated with climate change (Easterling et al. 2000) may increase growth sensitivity to precipitation, and eventually cause pronounced and widespread forest growth declines and possible mortality (van Mantgem and Stephenson 2007, Breshears et al. 2005).

Unlike the Chilcotin Plateau populations, Southern Interior growth responses to annual and seasonal precipitation variables fluctuated substantially over the 20th century. The period of strong correlations during the early portion of the century concurs with the prolonged period of low precipitation discussed above (Appendix B), whereas the strengthening of correlations between growth and precipitation in recent decades may reflect a temperature-induced drought signal as a result of warming temperatures (Wilmking et al 2004, Littell 2006, Oberhuber et al. 2007). Shifts in Southern Interior population precipitation-growth responses may also be related to PDO phases. The two periods of high correlation with annual precipitation concur approximately with positive (warm/dry) PDO phases (ca. 1925 to 1945, and ca. 1977 to present day; Mantua et al. 1997, D'Arrigo et al. 2001, Mantua and Hare 2002, Gedalov and Mantua 2002), and the period of low growth response to this variable occurs during a negative (cool/wet) PDO phase (ca. 1946 to 1976; Mantua et al. 1997, D'Arrigo et al. 2001, Mantua and Hare 2002, Gedalov and Mantua 2002). This relationship was also observed in drought-sensitive ponderosa pine in the Pacific Northwest US (Fagre et al. 2003) and may reflect PDO influence on factors related to tree growth such as precipitation, temperatures, growing season length, and snowfall. PDO-related climate-growth relationship shifts were not observed in the Chilcotin Plateau populations, possibly indicating the limited spatial extent of PDO influence on local climate and/or the persistent drought influence in the Chilcotin Plateau.

3.4.3 Conclusions

Future broad-scale forest productivity shifts will have significant ecological and socioeconomic impacts and will create a challenge for forest managers (Millar et al. 2007). Long-term shifts in local climate regimes will result in altered temperature-precipitation interactions and subsequently, new climatic growth limitations may develop. By examining climate-growth relationships over different temporal scales, it is possible to analyze how climate-growth relationships have historically changed as well as detect potential recent changes related to climate change. These changes can provide important information regarding future responses.

In the British Columbia Interior, Douglas-fir growth in high-elevation and dry environments appears to be changing, possibly in response to climate change, and these climatically sensitive populations may serve as indicators of broader future responses. High-elevation populations are becoming more sensitive to annual temperatures and snowfall, possibly reflecting limitations associated with co-occurring increases in precipitation and cloudiness. The influence of PDO and ENSO has become stronger in Southern Interior high-elevation populations over the 20th century, whereas PNA influence on growth in both regions has been relatively stable since 1950.

Dry site populations of Douglas-fir in the Southern Interior and the Chilcotin Plateau may have been similarly affected by an extensive drought in the early portion of the 1900s. Over the 20th century, Southern Interior populations have had a variable relationship with precipitation and temperatures, whereas Chilcotin Plateau populations have generally been consistently limited by the very low annual precipitation in that region. These differences may reflect unique local site limitations.

Although the use of these temporal variations in climate-growth relationships may be limited in terms of predictive abilities, the variations themselves highlight the dynamic nature of climate-growth relationships in Douglas-fir forests and must be considered when adapting future forest management to climate change. These and other findings challenge assumptions of stable ecosystem processes and highlight the considerable uncertainty facing forest managers regarding future forest responses to current rapid environmental changes (Millar et al. 2007, Spittlehouse and Stewart 2003, Spittlehouse 2005).

3.5 Literature cited

Allan, R.J. 2000. ENSO and climatic variability in the past 150 years, p. 3-56. In El Nino and the Southern Oscillation: multiscale variability and global and regional impacts. Diaz, H. F. and Markgraf, V. (eds). Cambridge University Press, New York.

Anfodillo, T., S. Rento, V. Carraro, L. Furlanetto, C. Urbinati, and M. Carrer. 1998. Tree water relations and climatic variations at the alpine timberline: seasonal changes of sap flux and xylem water potential in Larix decidua Miller, Picea abies (L.) Karst. and Pinus cembra L. Annales des Sciences Forestieres 55: 159-172.

Arno, S.F. 1991. Ecological relationships of interior Douglas-fir, p. 47-51. In Interior Douglas-fir: The species and its management symposium proceedings. Baumgartner, D. M. (eds). Department of Natural Resource Sciences, Washington State University, Pullman, Washington.

Balatinecz, J.J. and H.W. Anderson. 1986. Effects of climatic factors on the formation of wood and its quality, p. 195-200. In Climate Applications in Forest Renewal and Forest Production, Proceedings of Forest Climate 1986. MacIver, D. C., Street, R. B., and Auclair, A. N. (eds). Canadian Forestry Service, Ottawa, Ontario.

Barber, V., G. Juday, and B. Finney. 2000. Reduced growth of Alaska white spruce in the twentieth century from temperature-induced drought stress. Nature 405: 668-672.

BC MoE. 2007. Environmental Trends in British Columbia: 2007. State of Environment Reporting. BC Ministry of Environment, Victoria, B.C.

BC MoFR. 2006. Preparing for climate change: Adapting to impacts on British Columbia's forest and range resources. BC Ministry of Forests and Range, Victoria, BC.

BC MWLAP. 2002. Indicators of climate change for British Columbia, 2002. Indicators of climate change for British Columbia, 2002. BC Ministry of Water, Land and Air Protection, Victoria, B.C.

Benjamini, Y. and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society. Series B 57: 289-300.

Biondi, F. 2000. Are climate-tree growth relationships changing in north-central Idaho, U.S.A.? Arctic, Antarctic, and Alpine Research 32: 111-116.

Biondi, F. 1997. Evolutionary and moving response functions in dendroclimatology. Dendrochronologia 15: 139-150.

Biondi, F., D.R. Cayan, and W.H. Berger.1999. Decadal-scale changes in southern California tree-ring records, p. pp. 303-306. In Proceedings of the 10th Symposium on Global Change Studies. Karl, T. R. (eds). American Meteorological Society, Boston, MA.

Biondi, F. and Swetnam, T.W. 1987. Box-Jenkins Models of forest interior tree-ring chronologies. Tree-Ring Bulletin 47: 71-96.

Biondi, F. and K. Waikul. 2004. Dendroclim2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. Computers & Geosciences 30: 303-311.

Breshears, D.D., N.S. Cobb, P.M. Rich, K.P. Price, C.D. Allen, R.G. Balice, W.H. Romme, J.H. Kastens, M.L. Floyd, J. Belnap, J.J. Anderson, O.B. Myers, and C.W. Meyer. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences 102: 15144-15148.

Carrer, M. and C. Urbinati. 2006. Long-term change in the sensitivity of tree-ring growth to climate forcing in Larix decidua. New Phytologist 170: 861-872.

Case, M.J. and D.L. Peterson. 2005. Fine-scale variability in growth-climate relationships of Douglas-fir, North Cascade Range, Washington. Canadian Journal of Forest Research 35: 2743-2755.

Cayan, D.R., M.D. Dettinger, H.F. Diaz, and N.E. Graham. 1998. Decadal variation of precipitation over Western Northern America. Journal of Climate 11: 3148-3166.

Chhin, S., E.H. Hogg, V.J. Lieffers, and S. Huang. 2008. Influences of climate on the radial growth of lodgepole pine in Alberta. Botany 86: 167-178.

Christensen, J.H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R.K. Kolli, W.-T. Kwon, R. Laprise, V. Magaña Rueda, L. Mearns, C.G. Menéndez, J. Räisänen, A. Rinke, A. Sarr, and P. Whetton. 2007. Regional Climate Projections, p. 848-940. In Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Solomon, S. D., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. M. (eds). Cambridge University Press, New York.

Cook, E. 1985. A time series analsysis approach to tree-ring standardization. PhD Dissertation. University of Arizona. Tucson, Arizona.

Cook, E. and L. Kairiukstis. 1990. Methods of dendrochronology: Applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, Netherlands.

Cook, E.R. and P. Krusic. 2005. Users Manual for Program ARSTAN. Tree-Ring Lab, Lamont-Doherty Earth Observatory, Columbia University, New York. http://www.ldeo.columbia.edu/res/fac/trl/public/publicSoftware.html.

D'Arrigo, R., R. Villalba, and G. Wiles. 2001. Tree-ring estimates of Pacific decadal climate variability. Climate Dynamics 18: 219-224.

D'Arrigo, R., R. Wilson, B. Liepert, and P. Cherubini. 2007. On the 'Divergence Problem' in Northern Forests: A review of the tree-ring evidence and possible causes. Global and Planetary Change 289-305.

Dai, A., K.E. Trenberth, and T.R. Karl. 1999. Effects of clouds, soil moisture, precipitation, and water vapor on diurnal temperature range. Journal of Climate 12: 2451-2473.

Daniels, L.D. and T.T. Veblen. 2004. Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. Ecology 85: 1284-1296.

Daniels, L.D. and E. Watson. 2003. Climate-fire-vegetation interactions in the Cariboo forests: a dendrochronological analysis. Report to Forest Innovation and Investment. Forest Innovation and Investment Research Program, Vancouver, BC.

DeLucia, E.H. and W.K. Smith. 1987. Air and soil temperature limitations on photosynthesis in Engelmann spruce during summer. Canadian Journal of Forest Research 17: 527-533.

Doehlert, D.C. and R.B. Walker. 1981. Photosynthesis and photorespiration in Douglas-fir as influenced by irradiance, CO2 concentration, and temperature. Forest Science 27: 641-650.

Easterling, D.R., G.A. Meehl, C. Parmesan, S.A. Changnon, T.R. Karl, and L.O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. Science 289: 2068-2074.

Fagre, D.B., D.L. Peterson, and A.E. Hessl. 2003. Taking the pulse of mountains: Ecosystem responses to climatic variability. Climatic Change 59: 263-282.

Fritts, H.C. 1976. Tree rings and climate. The Blackburn Press, New Jersey.

Gedalov, Z. and N.J. Mantua. 2002. A multi-century perspective of variability in the Pacific Decadal Oscillation: new insights from tree rings and coral. Geophysical Research Letters 29: 1-4.

Hare, S.R. and N.J. Mantua. 2001. An historical narrative on the Pacific Decadal Oscillation, interdecadal climate variability and ecosystem impacts. Report of a talk presented at the 20th NE Pacific Pink and Chum workshop, Seattle, WA, 22 March 2001. http://www.iphc.washington.edu/Staff/hare/html/papers/pcworkshop/pcworkshop.pdf.

Helms, J.A. 1965. Diurnal and seasonal patterns of net assimilation in Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, as influenced by environment. Ecology 46: 698-708.

Henderson-Sellers, A. 1992. Continental cloudiness changes this century. GeoJournal 27: 255-262.

Holman, M.L. and D.L. Peterson. 2006. Spatial and temporal variability in forest growth in the Olympic Mountains, Washington: sensitivity to climatic variability. Canadian Journal of Forest Research 36: 92-104.

Holmes, R. 1983. Computer-assisted quality control in tree-ring dating and measuring. Tree-Ring Bulletin 43: 69-78.

Josza, L. 1988. Increment core sampling techniques for high quality cores. Special Publication SP-30. Forintek Canada Corp., Vancouver, BC.

Jull, M.J. 1999. Douglas-fir silviculture "on the edge": silvicultural systems at the northern range of the species, p. 34-44. In Ecology and management of interior Douglas-fir (Pseudotsuga menziesii var glauca) at the northern extreme of its range. Proceedings of a workshop held 7-9 October 1996 in Fort St. James, British Columbia. Lousier, J. D. and Kessler, W. B. (eds). University of Northern British Columbia, Prince George, BC.

Kimmins, J. P. 1997. Forest Ecology. Prentice-Hall Inc., New Jersey.

Kozlowski, T.T. and S.G. Pallardy. 2002. Acclimation and adapative responses of woody plants to environmental stresses. The Botanical Review 68: 270-334.

Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. Oecologia 155: 445-459.

Laroque, C.P. and D.J. Smith. 2005. Predicted short-term radial-growth changes of trees based on past climate on Vancouver Island, British Columbia. Dendrochronologia 22: 163-168.

Leathers, D.J., B. Yarnal, and M.A. Palecki . 1991. The Pacific/North American Teleconnection Pattern and United State Climate. Part I: Regional Temperature and Precipitation Associations. Journal of Climate 4: 517-528.

Littell, J. S. 2006. Climate impacts to forest ecosystem processes: Douglas-fir growth in north-western U.S. mountain landscapes and area burned by wildfire in western U.S. eco-provinces. PhD Dissertation. University of Washington. Seattle, WA.

Littell, J.S. and D.L. Peterson. 2005. A method for estimating vulnerability of Douglas-fir growth to climate change in the northwestern U.S. The Forestry Chronicle 81: 369-374.

Lloyd, A.H. and C.L. Fastie. 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. Climatic Change 52: 481-509.

Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace, and R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78: 1069-1079.

Meidinger, D. and J. Pojar. 1991. Ecosystems of British Columbia. BC Ministry of Forests, Victoria, B.C.

Mekis, É. and W.D. Hogg . 1999. Rehabilitation and analysis of Canadian daily precipitation time series. Atmosphere-Ocean 37: 53-85.

Meko, D. M. 2007. GEOS 585A: Applied Time Series Analysis. Page accessed: 2007. URL: http://www.ltrr.arizona.edu/~dmeko/geos585a.html

Millar, C., R. Neilson, D. Bachelet, R. Drapek, and J. Lenihan. 2006. Climate change at multiple scales, p. 30-60. In Forests, carbon and climate change: a synthesis of science findings.Oregon Forest Resources Institute, Portland, Oregon.

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

Mitchell, T.D. and P.D. Jones. 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. International Journal of Climatology 25: 693-712.

Moore, D. S. and McCabe, G. P. 2006. Introduction to the Practice of Statistics. W.H. Freeman and Co., New York, N.Y.

Nigh, G.D., C.C. Ying, and H. Qian. 2004. Climate and productivity of major conifer species in the interior of British Columbia, Canada. Forest Science 50: 659-671.

Oberhuber, W., W. Kofler, K. Pfiefer, A. Seeber, A. Gruber, and G. Wieser. 2007. Long-term changes in tree-ring-climate relationships at Mt. Patscherkofel (Tyrol, Austria) since the mid-1980s. Trees.

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

Pfeifer, K., W. Kofler, and W. Oberhuber. 2005. Climate related causes of distinct radial growth reductions in Pinus cembra during the last 200 yr. Vegetation History and Archaeobotany 14: 211-220.

Regent Instruments Inc. 2005. WinDENDRO™. An image analysis system for tree-rings analysis. Regent Instruments Inc. Quebec

Salo, D. J. 1974. Factors affecting photosynthesis in Douglas-fir. PhD Dissertation. University of Washington. Seattle, WA.

Shabbar, A. 2006. The impact of El Nińo-Southern Oscillation on the Canadian climate. Advances in Geosciences 6: 149-153.

Shabbar, A., B. Bonsal, and M. Khandekar. 1997. Canadian Precipitation Patterns Associated with the Southern Oscillation. Journal of Climate 10: 3016-3027.

Spittlehouse, D. 2006. ClimateBC: Your access to interpolated climate data for BC. Streamline Watershed Management Bulletin 9: 16-21.

Spittlehouse, D.L. 2005. Integrating climate change adaptation into forest management. Forestry Chronicle 81: 691-695.

Spittlehouse, D.L. and R.B. Stewart. 2003. Adaptation to climate change in forest management. BC Journal of Ecosystem Management 4: 1-11.

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

Vaganov, E.A., M.K. Hughes, A.V. Kirdyanov, F.H. Schweingruber, and P.P. Silkin. 1999. Influence of snowfall and melt timing on tree growth in subarctic Eurasia. Nature 400: 149-151.

van Mantgem, P.J. and N.L. Stephenson. 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. Ecology Letters 10: 909-916.

Vincent, L.A. and D.W. Gullett . 1999. Canadian historical and homogenous temperature datasets for climate change analyses. International Journal of Climatology 19: 1375-1388.

Vincent, L.A., X. Zhang, B.R. Bonsal, and W.D. Hogg . 2002. Homogenization of daily temperatures over Canada. Journal of Climate 15: 1322-1334.

Wang, T., A. Hamann, D.L. Spittlehouse, and S.N. Aitken. 2006. Development of scale-free climate data for western Canada for use in resource management. International Journal of Climatology 26: 383-397.

Watson, E. and B. Luckman. 2004. Tree-ring based reconstructions of precipitation for the Southern Canadian Cordillera. Climatic Change 65: 209-241.

Watson, E. and B.H. Luckman. 2002. The dendroclimatic signal in Douglas-fir and ponderosa pine tree-ring chronologies from the southern Canadian Cordillera. Canadian Journal of Forest Research 32: 1858-1874.

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

Wilmking M. and I. Myers-Smith. 2008. Changing climate sensitivity of black spruce (Picea mariana Mill.) in a peatland-forest landscape in Interior Alaska. Dendrochronologia 25: 167-175.

Wilson, R. and W. Elling. 2004. Temporal instability in tree growth/climate response in the Lower Bavarian Forest region: implications for dendroclimatic reconstruction. Trees 18: 19-28.

Zhang, Q.-B. and R.J. Hebda. 2004. Variation in radial growth patterns of Pseudotsuga menziesii on the central coast of British Columbia, Canada. Canadian Journal of Forest Research 34: 1946-1954.

Zhang, X., F.W. Zwiers, G.C. Hegerl, F.H. Lambert, N.P. Gillett, S. Solomon, P.A. Stott, and T. Nozawa. 2007. Detection of human influence on twentieth-century precipitation trends. Nature 448: 461-465.

Table 3.1. Meteorological records used in Chapter 3.

Station name	Latitude (°N)	Longitude (°W)	Elevation (m)	Station ID	Data length (years)
Northern Interior					
Prince George	53.89	122.68	691	1096450	95 (1912-2006)
Southern Interior					
Vernon Coldstream Ranch	50.22	119.2	482	1128580	98 (1900-1997)
Vernon Bella Vista*	50.26	119.31	427	1128553	21 (1985-2005)
Chilcotin					
Williams Lake**	52.18	122.05	940	1098940	69 (1939-2007)

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

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

Table 3.2. Missing rain, snow, and precipitation data in meteorological records.

Station name	Year	Month(s)
Vernon Coldstream Ranch	1900	January to April
		October
	1901	February
		March
		November
	1902	February to May
		October
	1903	February
		December
	1905	January
	1912	March
	1924	January
	1963	August
Williams Lake A	1947	September
		October
	1960	June
	1979	October
		November
Prince George	1912	January to December
	1913	December
	1914	January
		February
	1915	January
		February
		October to December
	1916	January
	1917	June

Table 3.3. Monthly variables used to create seasonal variables for climate-growth analyses.

Season	Monthly variables
Prior summer	Prior July to September
Winter	October to March
Spring	April to June
Summer	July to September
Annual	Prior July to June

Table 3.4. Correlation coefficients between high-elevation Douglas-fir growth and ocean-atmosphere climate system indices.

	PDO (1900 - 2005)	ENSO (1900 - 2003)	PNA (1951 - 2005)
Northern Interior	0.198, $p<0.05$	-	0.400, $p<0.01$
Southern Interior	0.476, $p<0.0001$	0.342, $p<0.001$	0.593, $p<0.0001$

PDO = Pacific Decadal Oscillation; ENSO = El Niño Southern Oscillation; PNA = Pacific/North American teleconnection index

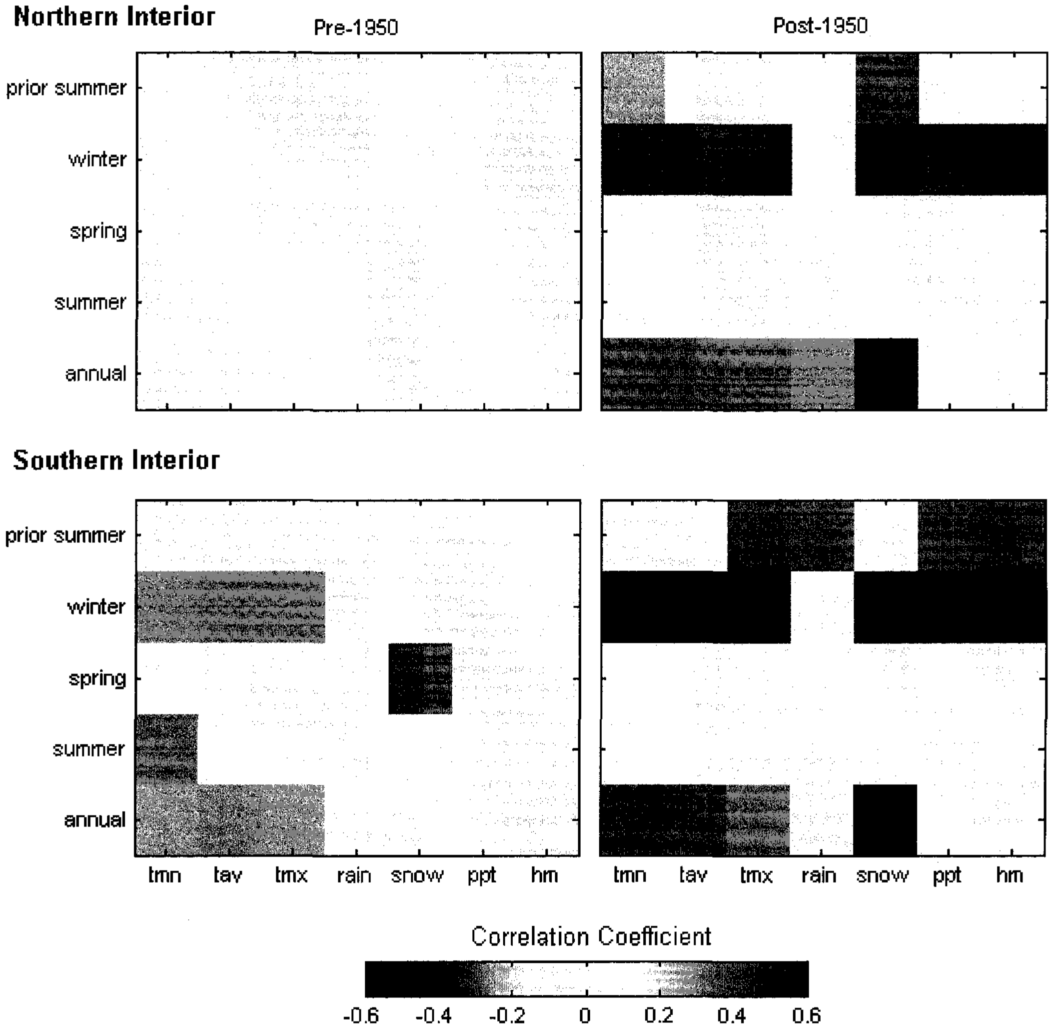


Figure 3.1. Correlations between climate and growth for high-elevation Douglas-fir populations in two regions of British Columbia over two sub-periods. Due to different climate station record lengths, pre-1950 climate-growth relationships were calculated over different time periods (Northern Interior: 1912 to 1950, Southern Interior: 1900-1950). Post-1950 climate-growth relationships were calculated from 1951 to 2005. Climate variables are seasonal averages of monthly values. tmn=monthly mean minimum temperature, tav=monthly mean temperature, tmx=monthly mean maximum temperature, ppt=precipitation, hm=heat-moisture index. Correlations shown are significant ($p<0.05$).

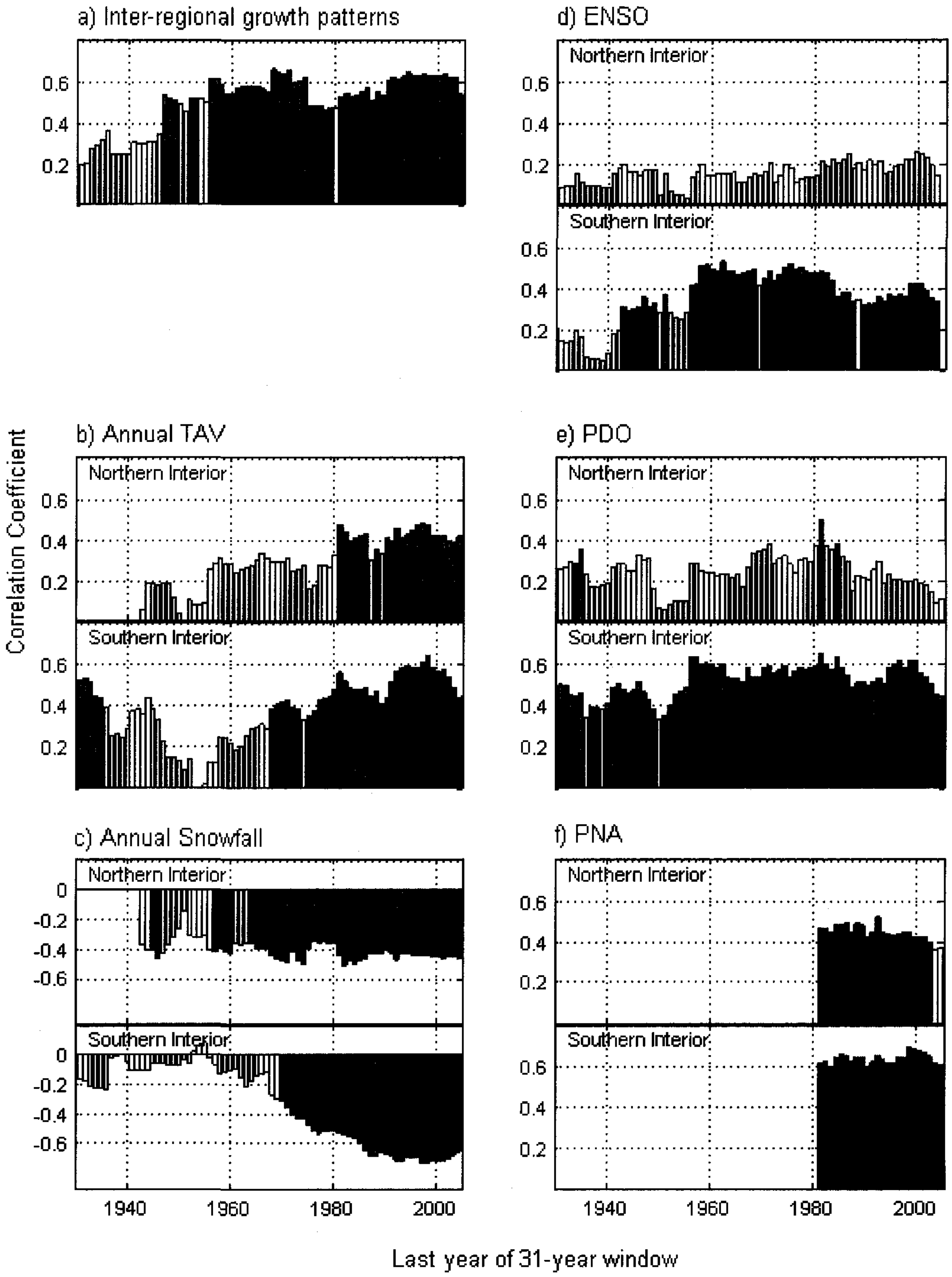


Figure 3.2. Moving correlation functions between climate and growth for high-elevation Douglas-fir populations in two regions of British Columbia. TAV=monthly mean temperatures, ENSO=El Niño Southern Oscillation index, PDO=Pacific Decadal Oscillation index, PNA=Pacific/North American teleconnection index. Significant correlation coefficients ($p<0.05$) are shaded.

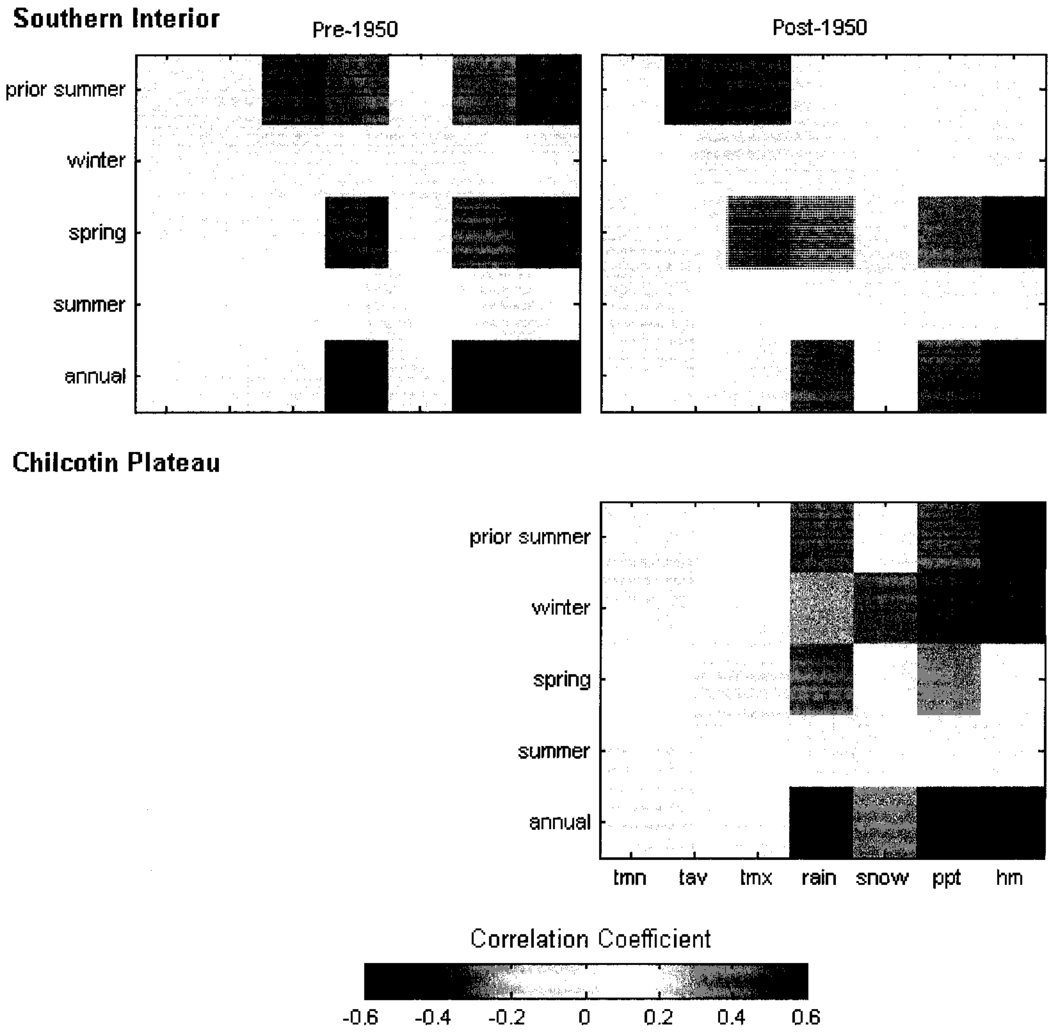


Figure 3.3. Correlations between climate and growth for Douglas-fir populations growing in dry climates in two regions of British Columbia over two sub-periods. No pre-1950 climate-growth relationships were calculated for Chilcotin Plateau growth because the Williams Lake climate station record length is too short. Post-1950 climate-growth relationships calculated from 1951 to 2005. Climate variables are seasonal averages of monthly values. tmn=monthly mean minimum temperature, tav=monthly mean temperature, tmx=monthly mean maximum temperature, ppt=precipitation, hm=heat-moisture index. Correlations shown are significant ($p<0.05$).

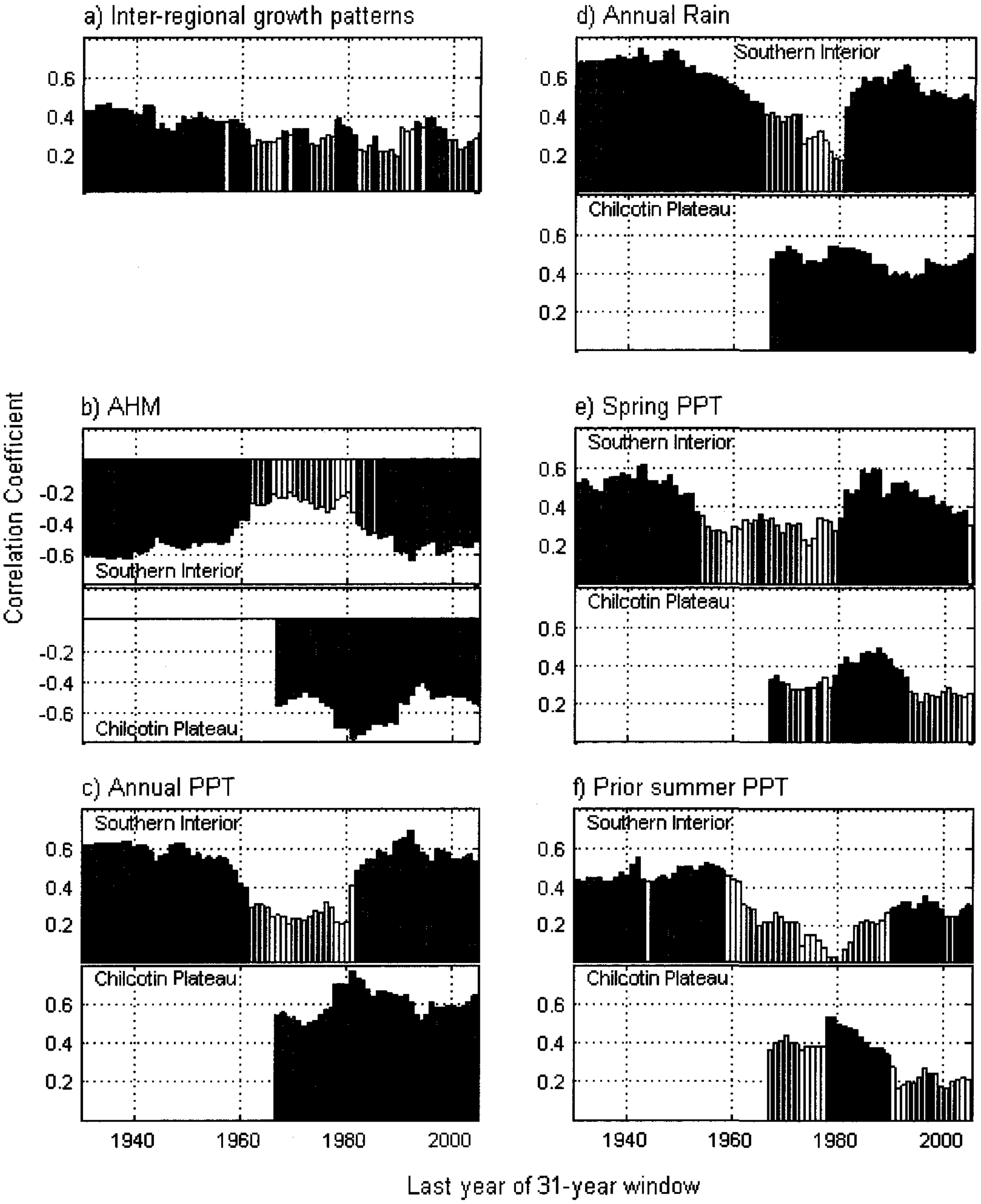


Figure 3.4. Moving correlation functions between climate and growth for Douglas-fir populations growing in dry climates in two regions of British Columbia. AHM=annual heat-moisture index, PPT=precipitation. Shaded values represent significant ($p<0.05$) correlation coefficients.

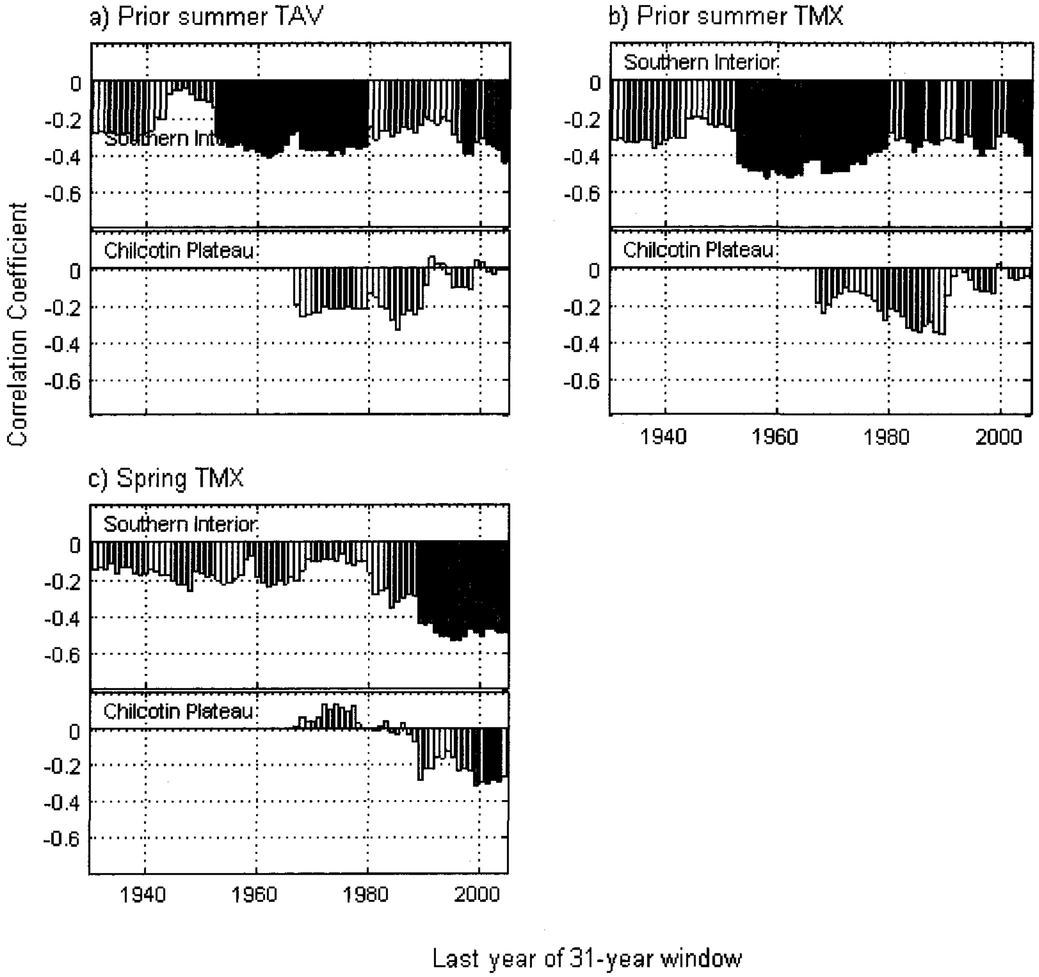
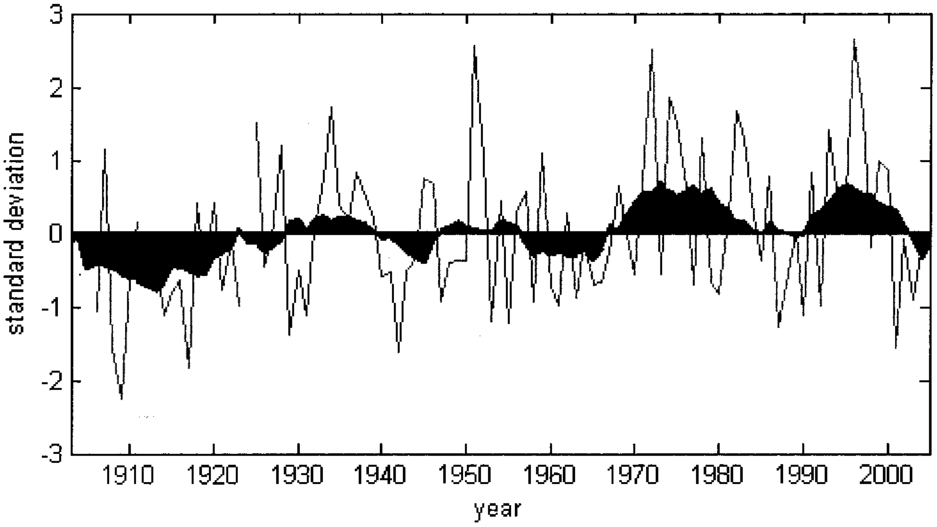


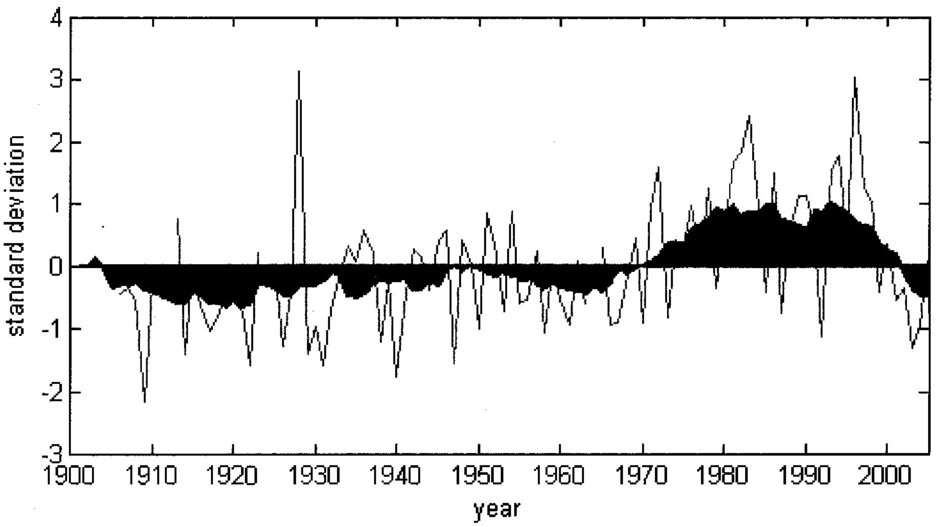
Figure 3.5. Moving correlation functions between temperatures and growth for Douglas-fir populations growing in dry climates in two regions of British Columbia. TAV=mean monthly temperatures, TMX= mean monthly maximum temperatures. Significant correlation coefficients ($p<0.05$) are shaded.

Appendix A. Time series of October-March precipitation anomalies for Vernon, British Columbia, from 1904 to 2004.



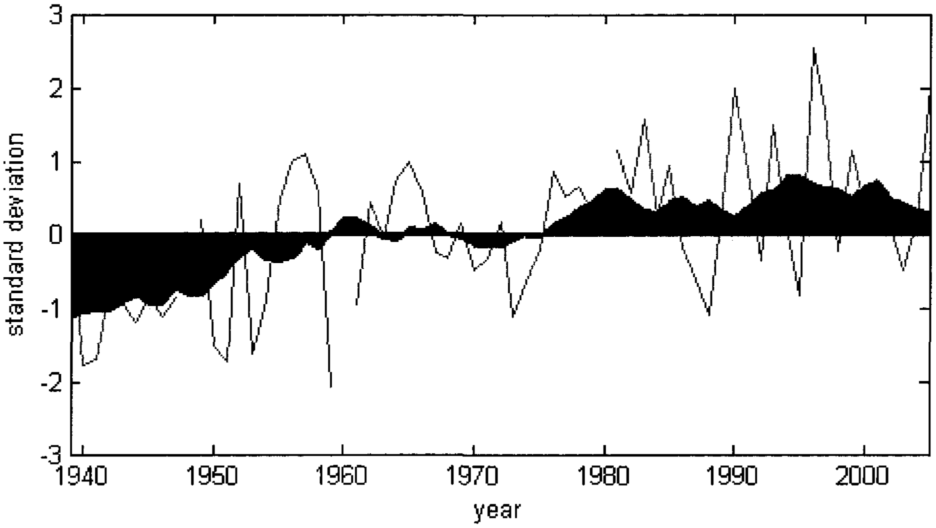
Decadal variation highlighted with moving 11-year average filter.

Appendix B. Time series of annual (prior July to current June) precipitation anomalies for Vernon, British Columbia, from 1904 to 2004.



Decadal variation highlighted with moving 11-year average filter.

Appendix C. Time series of annual (prior July to current June) precipitation anomalies for Williams Lake, BC, from 1940 to 2005.



Decadal variation highlighted with moving 11-year average filter.

Chapter 4. Summary and management implications

4.1 Introduction

This research project addressed a knowledge gap regarding Douglas-fir radial growth responses to climatic variability across its climatic and geographic range in the interior of British Columbia (BC). We sampled 33 chronologies in three large study regions spanning a wide range of climatic conditions, including stands located at the ecological and geographic margins of the species' range in the province, in order to 1) identify key historical climatic sensitivities, 2) link these sensitivities to local climate regimes, and 3) examine how sensitivities change over a climatic gradient. As well, we examined some climate-growth relationships at different temporal scales in order to assess their temporal stability. Below, we briefly summarize the key findings of this study and discuss potential management implications.

4.2 Key study results and management implications

In all three study regions, Douglas-fir growth patterns tended to be highly correlated between sites and are differentiated mainly by site climate conditions. For example, mid- to low-elevation dry sites in a given region tended to have correlated growth patterns whereas high-elevation wetter sites tended to be more correlated. Highly correlated growth patterns between ecologically similar stands separated by considerable distances (400+ km) suggest that across the species' range in BC, Douglas-fir growth is regulated mostly by regional-scale precipitation and temperature patterns and corresponding responses to changes in these climate patterns will be widespread.

4.2.1 Mid- to low-elevation dry-site Douglas-fir populations

Regional growth patterns describing Douglas-fir growth in relatively dry and/or warm environments at mid- to low-elevations in all study regions were strongly correlated to annual (prior July to current June) precipitation, which likely represents the dominant influence of soil moisture availability across most of the species' range. When examined at a smaller (population-level) scale, the strength of this response appeared to be largely a function of local site climate conditions, especially precipitation. When a site's annual precipitation regime was considered, we found that Douglas-fir became exponentially more sensitive to annual precipitation with dryness. Temperature (and variables derived solely from temperature such as frost-free period and degree-days) did not explain any variation in population precipitation-growth relationships, however, integrating temperature and precipitation together into a heat-moisture index explained the most variation and may be the most accurate way to describe a site's local climate conditions (and corresponding growth sensitivity to annual precipitation). By reflecting both precipitation inputs as well as evaporation/transpiration forcings (Wang et al. 2006), heat-moisture indices may provide a good indication of available soil moisture.

Predictive models are integral to forest management in BC (BC MoFR 2006) and the incorporation of climate variables and related biological responses into growth and yield, carbon cycle, and species distribution models has been recommended as an important step in improving future management decisions (Spittlehouse 2005, Ogden and Innes 2007, Aitken et al. 2008, O'Neill et al. 2008). For example, species distribution models that predict changes in the fundamental and realized niche of a species based on the concept of a bioclimate envelope (Pearson and Dawson 2003, Hamann and Wang 2006) may be improved if the climatic envelope used is biologically relevant (e.g., with respect to this study, if annual heat-moisture index is used instead of more typical variables such as mean annual temperatures) to the species in question and the model considers specific biological responses (e.g., growth responses to annual precipitation) (Aitken et al. 2008). Further, these types of models may improve their predictive ability if they consider response variation among populations (e.g., with respect to this study, increasing sensitivity to annual precipitation with site heat-moisture index) across the species' climatic envelope instead of assuming a more uniform species response (O'Neill et al. 2008).

We can examine our results against future projections of annual heat-moisture index (AHM) and annual precipitation in BC to suggest possible outcomes in terms of Douglas-fir productivity. In all three study regions, temperatures are projected to increase at a faster rate than precipitation, resulting in increased AHM (Figure 4.1). Based on these projections, our results suggest that growth in all populations will become 1) more variable (as measured by mean sensitivity), 2) more correlated among individuals within the same population (as measured by rbar, thus reflecting a stronger climate signal), 3) more correlated with annual precipitation, and 4) sharply more sensitive (as measured by regression slope) to annual precipitation where local AHM increases above approximately 20 (Figure 4.2) or where local MAP decreases below approximately 700mm per year (Figure 4.3). Although annual precipitation is expected to modestly increase over most of BC (BC MoE 2007), including the three study regions (Figure 4.1), accelerating temperature increases may result in net drying (Christensen et al. 2007) and create temperature-induced drought conditions (Barber et al. 2000). Projected declines in winter snowfall and summer precipitation in some areas (Figure 4.1) could further reduce the availability of soil moisture during the growing season.

Under this scenario, long-term Douglas-fir growth rates could be negatively affected across the species' range, with pronounced and initial responses likely in populations growing near the warm and/or dry climatic margins. Projected AHM increases are highest for the Chilcotin Plateau region (Figure 4.1), where some of the most sensitive populations already exist; continued exponential increases in growth sensitivity in these populations could conceivably result in eventual mortality. Douglas-fir stands near the dry and/or warm margins of the species' range in the province (e.g., relatively high AHM), especially those at the forest-grassland transition (e.g. in the Chilcotin Plateau and elsewhere in the province in the Bunchgrass BEC Zone, Meidinger and Pojar 1991), should be highlighted as especially vulnerable to climate change and future drought events.

Declining Douglas-fir stands can be targeted for harvesting to allow for conversion to more suitable genotypes or species (such as lodgepole pine, *Pinus contorta* Douglas ex Louden, Case and Peterson 2005), or can be thinned to increase resource availability for remaining trees (Ogden and Innes 2007), however, dry margin sites tend to have limited productivity due to the severe environmental conditions and may therefore not be economically suitable for intensive management. At the very least, these populations should be carefully monitored as early indicators of potential forest dieback stemming from climate change.

Historical data are often used to form baselines that are incorporated into models and decision-making frameworks (Millar et al. 2007), however, the temporal variations in climate-growth relationships found in this study support similar findings elsewhere (e.g., Lloyd and Fastie 2002, Carrer and Urbinati 2006, D'Arrigo et al. 2007) that highlight the potential limitations of extrapolations from historical relationships. Our results suggest that in certain environments, Douglas-fir climate-growth relationships have varied in the past (possibly associated with drought events and/or Pacific Decadal Oscillation phases) and may also be changing now as a result of anthropogenic climate change. In other environments, such as dry sites in the Chilcotin Plateau, climate-growth relationships appear to be more stable over time, perhaps reflecting the chronic strong drought limitations in forest-grassland ecotonal populations. The use of moving correlation functions and other techniques designed to detect temporal variation in climate-growth relationships should be incorporated into future research to improve assessments of ecosystem responses and to detect possible early responses as a result of climate change. Although temporal variability in climate-growth relationships will be difficult to incorporate into models or decision-making frameworks, it must be considered when making future management decisions based on historical ecological relationships.

Our study did not explicitly consider the influence of within-species genetic diversity in climate-growth relationships. Douglas-fir growth-related traits have been shown to vary steeply along environmental clines, and this variation has been attributed to a relatively high species genetic diversity that allows populations to adapt to a broad spectrum of environmental conditions across the species' geographic range (St. Clair et al. 2005, Arno 1991, Rehfeldt 1991). Populations that are closely adapted to local conditions may have narrow climatic tolerances and could become maladapted if local climate regimes move outside of those tolerances; therefore, from a species perspective, maladaptation could be expressed across a wide geographic range (Aitken et al. 2008, O'Neill et al. 2008). Results from our regional climate-growth analysis support this suggestion, as they showed that leading growth patterns in all three regions were sensitive to annual precipitation anomalies.

However, our results from the population climate-growth analyses also suggest that across the species' range in BC, populations vary in their adaptation to local climate (assuming that growth sensitivity can be used as one measure of local adaptation) along a precipitation and heat-moisture gradient. Thus, sensitivity to annual precipitation may be a species-wide genetic trait that is expressed more strongly as a site becomes warmer and/or drier.

4.2.2 High-elevation Douglas-fir populations

High-elevation Douglas-fir populations appear to be unique from others in this study in that cold winter/annual temperatures and snowfall tend to limit growth more than annual precipitation, especially over the latter half of the past century. The increase in growth sensitivity to temperatures over that time was somewhat unexpected, as we hypothesized this signal would weaken in the growth records as temperatures increased and became less limiting in these cold environments. This type of unexpected growth response may represent the difficulty of predicting ecosystem responses to changes in a single variable (e.g., temperature), as growth may be controlled more by the integrated influence of temperature and precipitation changes rather than temperature alone (Littell and Peterson 2005). For example, in high-elevation environments, growth benefits from warmer temperatures over the past 50 years may have been buffered by limitations imposed by higher precipitation and cloudiness (BC MoE 2007, Henderson-Sellers 1992, Dai et al. 1999, Cayan et al. 1998, Zhang et al. 2007) over the same period, resulting in new (and unexpected) growth sensitivities. When assessing species vulnerability in complex habitats such as high-elevation environments where multiple climatic variables are shown to limit growth, the integrative effect of temperature and precipitation changes on growth should be considered as much as possible.

Forest management must also consider the growth influence of climate processes at various spatial scales (Littell and Peterson 2005, Tessier, 1989). The strong synchronization between high-elevation growth patterns and climate-growth relationships in the Northern and Southern Interior (400+km apart) over the 20th century likely reflects strengthening macroregional climatic processes (e.g., anthropogenic temperature/precipitation trends, ocean-atmosphere climate systems) that can override the influence of local factors such as topography, soils, and aspect on growth (Littell and Peterson 2005, Tessier 1989). When large-scale climatic processes weaken, growth patterns across large areas will diverge and instead reflect local climate conditions (Littell and Peterson 2005, Tessier 1989). Shifts between macroregional and local climatic influences are important drivers of forest productivity and should be examined further.

The influence of quasi-periodic ocean-atmosphere climate systems on BC local winter conditions appears to be strongly reflected in high-elevation Douglas-fir growth. The Pacific/North American teleconnection index (PNA) was reflected similarly in both regions, whereas the Pacific Decadal Oscillation (PDO) and El Niño/Southern Oscillation (ENSO) indices had strong influences on southern populations but not northern. These indices may be useful in predicting high-elevation growth rates and climate-growth relationships as well as increasing our understanding of low-frequency large-scale climatic influences on ecosystem processes. A better understanding of how PNA differs from PDO and ENSO in its influence on local conditions may help elucidate specific climatic parameters that limit growth in both regions.

High-elevation Douglas-fir productivity may benefit from warmer temperatures, less snowfall, and longer growing seasons, and populations from other locations may provide seed source for new forests that are suited to future conditions in these environments. More research would be required, however, before this species is artificially regenerated extensively in such areas. Douglas-fir is especially vulnerable to harsh conditions such as snow press and frost events during early developmental stages (Jull 1999), and unique silviculture strategies may be required if it is to regenerate successfully and form an important timber species at high-elevations.

4.3 Research limitations and future directions

The recent development of high-resolution spatiotemporal climate normals and historical data models such as ClimateBC is an important step in assessing species vulnerability to climate change (BC MoFR 2006) across wide biophysical ranges (Littell 2006, Peterson and Peterson 2001). To our knowledge, this is the first study of tree radial growth responses along such a broad climatic gradient in British Columbia, and we recommend this approach be applied to other tree species in the province. Species such as western red cedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and larches (*Larix* spp.), whose range (and possible climatic) limits are found in the province of BC, as well as other species identified as particularly vulnerable to climate change (Hamann and

Wang 2006) could be targeted to provide additional information regarding responses to climate change both in marginal populations and across climatic gradients.

One of the limitations of the standard dendroecological approaches used in this study is that only relative growth rates are analyzed and compared between sites (i.e., measurements are converted into a unitless index to form the growth chronology). Estimates of productivity impacts from climate change would be potentially improved by using absolute growth rates (e.g., millimetres per year) and converting them to a productivity measure common to forest management, such as basal area increment or volume, which could be then used as part of a plot-based sampling strategy to determine annual productivity increment per unit area (e.g., hectare). This approach would also allow for stand-level biological factors such as species, age, crown-class and abiotic factors such as soil moisture/nutrient regime to be considered when assessing climate-growth relationships, thus providing information at a finer scale (both spatial and biological) that could complement data from larger scale studies such as this one. The main drawback to this approach would be the increased time and resources required for data collection, which may make this approach more feasible for local stand-level assessments of productivity impacts from climate variability.

4.4 Conclusions

This study revealed important Douglas-fir climate-growth relationships across the species' range in the British Columbia Interior, complementing other studies examining similar questions in different regions and at different spatial scales (e.g., Littell and Peterson 2005, Case and Peterson 2005, Zhang and Hebda 2004). Although this study provides deterministic information that may guide forest management, it is important to acknowledge the high uncertainty regarding forest responses to climate change. Environmental changes without historical precedent are expected to occur resulting in complex and unpredictable ecosystem responses (Millar et al. 2007, Spittlehouse 2005). Forest managers will need a wide range of tools to accommodate these changes (Millar et al. 2007, Spittlehouse and Stewart 2003, Littell and Peterson 2005); flexible and adaptive strategies with careful monitoring will be required to deal with complex and unpredictable future challenges.

4.5 Literature Cited

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

Arno, S.F. 1991. Ecological relationships of interior Douglas-fir, p. 47-51. *In* Interior Douglas-fir: The species and its management symposium proceedings. Baumgartner, D. M. (eds). Department of Natural Resource Sciences, Washington State University, Pullman, Washington.

Barber, V., G. Juday, and B. Finney. 2000. Reduced growth of Alaska white spruce in the twentieth century from temperature-induced drought stress. Nature 405: 668-672.

BC MoE. 2007. Environmental Trends in British Columbia: 2007. State of Environment Reporting. BC Ministry of Environment, Victoria, B.C.

BC MoFR. 2006. Preparing for climate change: Adapting to impacts on British Columbia's forest and range resources. BC Ministry of Forests and Range, Victoria, BC.

Carrer, M. and C. Urbinati. 2006. Long-term change in the sensitivity of tree-ring growth to climate forcing in *Larix decidua.* New Phytologist 170: 861-872.

Case, M.J. and D.L. Peterson. 2005. Fine-scale variability in growth-climate relationships of Douglas-fir, North Cascade Range, Washington. Canadian Journal of Forest Research 35: 2743-2755.

Cayan, D.R., M.D. Dettinger, H.F. Diaz, and N.E. Graham. 1998. Decadal variation of precipitation over Western Northern America. Journal of Climate 11: 3148-3166.

Christensen, J.H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R.K. Kolli, W.-T. Kwon, R. Laprise, V. Magaña Rueda, L. Mearns, C.G. Menéndez, J. Räisänen, A. Rinke, A. Sarr, and P. Whetton. 2007. Regional Climate Projections, p. 848-940. *In* Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Solomon, S. D., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. M. (eds). Cambridge University Press, New York.

D'Arrigo, R., R. Wilson, B. Liepert, and P. Cherubini. 2007. On the 'Divergence Problem' in Northern Forests: A review of the tree-ring evidence and possible causes. Global and Planetary Change 289-305.

Dai, A., K.E. Trenberth, and T.R. Karl. 1999. Effects of clouds, soil moisture, precipitation, and water vapor on diurnal temperature range. Journal of Climate 12: 2451-2473.

Flato, G.M., G.J. Boer, W.G. Lee, N.A. McFarlane, D. Ramsden, M.C. Reader, and A.J. Weaver. 2000. The Canadian centre for climate modelling and analysis global coupled model and its climate. Climate Dynamics 16: 451-467.

Hamann, A. and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87: 2773-2786.

Henderson-Sellers, A. 1992. Continental cloudiness changes this century. GeoJournal 27: 255-262.

Jull, M.J. 1999. Douglas-fir silviculture "on the edge": silvicultural systems at the northern range of the species, p. 34-44. *In* Ecology and management of interior Douglas-fir (*Pseudotsuga menziesii* var *glauca*) at the northern extreme of its range. Proceedings of a workshop held 7-9 October 1996 in Fort St. James, British Columbia. Lousier, J. D. and Kessler, W. B. (eds). University of Northern British Columbia, Prince George, BC.

Littell, J.S. and D.L. Peterson. 2005. A method for estimating vulnerability of Douglas-fir growth to climate change in the northwestern U.S. The Forestry Chronicle 81: 369-374.

Lloyd, A.H. and C.L. Fastie. 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. Climatic Change 52: 481-509.

Meidinger, D. and J. Pojar. 1991. Ecosystems of British Columbia. BC Ministry of Forests, Victoria, B.C.

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

O'Neill, G.A., A. Hamann, and T. Wang. 2008. Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. Journal of Applied Ecology 45: 1040-1049.

Ogden, A.E. and J. Innes. 2007. Incorporating climate change adaptation considerations into forest management planning in the boreal forest. International Forestry Review 9: 713-733.

Pearson, R.G. and T.P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate models useful? Global Ecology and Biogeography 12: 361-371.

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

Rehfeldt, J. 1991. The genetic resource of Douglas-fir in the interior northwest, p. 53-62. *In* Interior Douglas-fir: The species and its management symposium proceedings. Baumgartner, D. M. (ed). Department of Natural Resource Sciences, Washington State University, Pullman, Washington.

Spittlehouse, D.L. 2005. Integrating climate change adaptation into forest management. Forestry Chronicle 81: 691-695.

Spittlehouse, D.L. and R.B. Stewart. 2003. Adaptation to climate change in forest management. BC Journal of Ecosystem Management 4: 1-11.

St. Clair, J.B., N.L. Mandel, and K.W. Vance-Borland. 2005. Genecology of Douglas Fir in Western Oregon and Washington. Annals of Botany 96: 1199-1214.

Tessier, L. 1989. Spatio-temporal analysis of cliamte-tree ring relationships. New Phytologist 517-529.

Wang, T., A. Hamann, D.L. Spittlehouse, and S.N. Aitken. 2006. Development of scale-free climate data for western Canada for use in resource management. International Journal of Climatology 26: 383-397.

Zhang, Q.-B. and R.J. Hebda. 2004. Variation in radial growth patterns of *Pseudotsuga menziesii* on the central coast of British Columbia, Canada. Canadian Journal of Forest Research 34: 1946-1954.

Zhang, X., F.W. Zwiers, G.C. Hegerl, F.H. Lambert, N.P. Gillett, S. Solomon, P.A. Stott, and T. Nozawa. 2007. Detection of human influence on twentieth-century precipitation trends. Nature 448: 461-465.

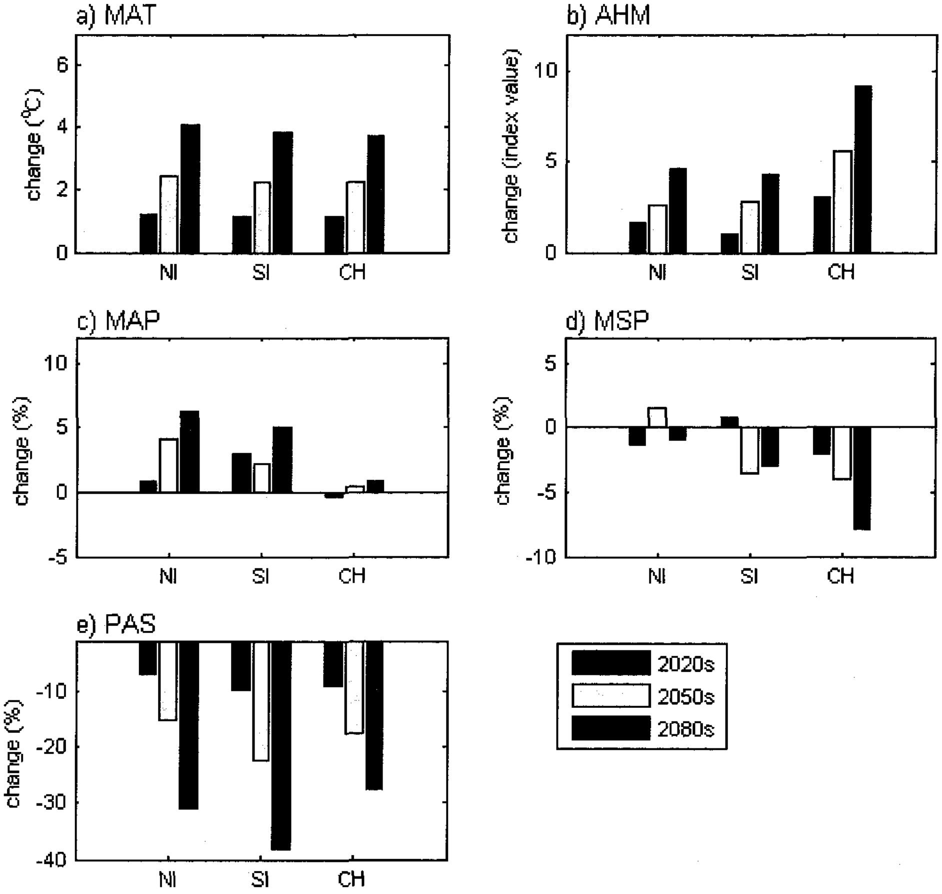


Figure 4.1. Projected future climate for Douglas-fir sample sites in the three study regions.Changes are an average of all sample sites in each study region, and represent the difference between the 1961-1990 reference period and the 2020s, 2050s, and 2080s. The ClimateBC model was used to generate future climate conditions, based on the CGCM2-A2x scenario of the Canadian Centre for Climate Modeling and Analysis (Wang et al. 2006, Flato et al. 2000). NI=Northern Interior, SI=Southern Interior, CH=Chilcotin Plateau, MAT=mean annual temperature, AHM=annual heat-moisture index, MAP=mean annual precipitation, MSP=mean summer precipitation, PAS=precipitation as snow.

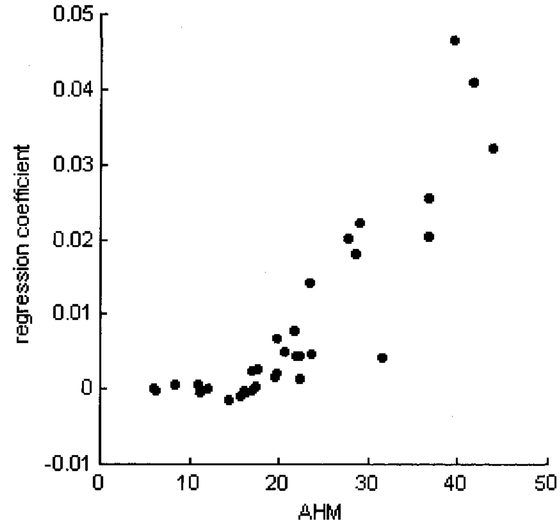


Figure 4.2. Growth-annual precipitation regression coefficients against site annual heat-moisture index. Note: this relationship was quantified using log-transformed regression coefficients (due to skewness) in Chapter 2 (Figure 2.6). Figure is presented to demonstrate non-linear relationship and possible response threshold at AHM = ~20.

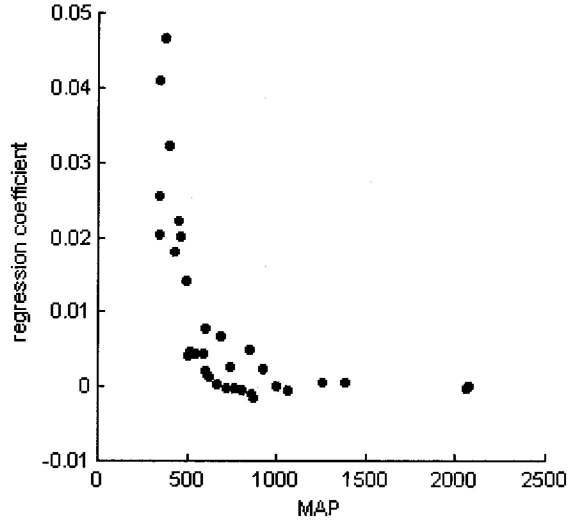


Figure 4.3. Growth-annual precipitation regression coefficients against site mean annual precipitation. MAP=mean annual precipitation (mm). Note: this relationship was quantified using log-transformed regression coefficients and MAP data (due to skewness) in Chapter 2 (Figure 2.9). Figure is presented to demonstrate non-linear relationship and possible response threshold at MAP = ~700mm.