ON THE SPATIO-TEMPORAL RADIAL GROWTH RESPONSE OF FOUR ALPINE TREELINE SPECIES TO CLIMATE ACROSS CENTRAL LABRADOR, CANADA

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On the spatio-temporal radial growth response of four alpine treeline species to climate across central Labrador, Canada.

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Abstract

This thesis applies standard dendrochronological techniques to contrast and compare between the radial growth responses of alpine treeline species across a climate gradient in central Labrador, Canada. Four species were examined: black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.) and eastern larch (*Larix laricina* (DuRoi) K. Koch). Eighteen tree ring width (TRW) chronologies were constructed at five alpine treeline sites across a 600 km long transect from the Labrador Sea to the Quebec border. The effects of climate and forest disturbance events on radial tree growth were examined at various spatial and temporal scales.

This study is the first to conduct dendrochronological studies on black spruce, fir and larch in Labrador and to use samples from across central Labrador. The chronology statistics are in accordance with regional publications, with the exception of the larch chronologies, which have exceptionally high sensitivity values (MS > 0.3). These results suggest that the radial growth response of each one of the tree species sampled is uniquely adapted to monthly and/or seasonal temperature and precipitation values during the growing season and, in some cases, to winter snowfall amounts. These climate sensitivities are also site-specific and indicative of a strong reliance on the proximity of the Labrador Sea. This study simultaneously compares the radial growth patterns of the four alpine treeline species in a region that, to date, has been largely understudied. As a result, this study has identified possible periods of outbreaks of spruce budworm (*Choristoneura fumiferana* (Clem.)) and larch sawfly (*Pristiphora erichsonii Hartig*), which are synchronous with outbreaks reported from eastern Quebec. The intensity and

frequency of these insect outbreaks is also climate-dependent, and can be so severe as to mask the climate sensitivity in the larch trees. A palaeoclimatic reconstruction (1847-2004) using merged spruce chronologies at one of the sites, the Mealy Mountains, is in accordance with other published records but has weak significance values due to a high degree of variability in climate sensitivity throughout the instrumental record (1942-present). The high degree of variability in the climate sensitivity of spruce trees across central Labrador is partly due to the effect of spruce budworm outbreaks on the radial growth of trees, but other site-specific factors such as moisture effects must also be contributing to the variability. Further studies are needed to determine the cause of this episodic divergence in the relationship between radial tree growth and climate in central Labrador in order to comprehend more fully which environmental factors influence radial tree growth, and how this changes with time.

Key words: Tree ring width, climate, central Labrador, dendroclimatology, disturbance, divergence.

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Chapter One 1. Introduction and Overview

The landscape across central Labrador, Canada, consists of a number of mountain systems whose vegetation cover includes alpine treeline species that are sensitive to climatic fluctuations. This thesis focuses on the radial growth response of four alpine treeline species to local climate in central Labrador, Canada (~53.5°N) (Figure 1.1). Following ice retreat between 10 and 6 ka BP, the regional topography was eventually colonized into various regions of alpine treeline. Currently, these mountain systems are topped by tundra-like vegetation and span a climatic gradient from a marine-like climate along the central Labrador coast to a continental-like climate near the Quebec border (Figure 1.2). At this latitude (~53.3°N), the tundra vegetation exists much further south than its northern counterpart beyond the latitudinal treeline (~57.5°N). With the prospect of a warmer climate in decades to centuries, there is a real possibility that the alpine treeline in central Labrador will eventually migrate upward and encroach on the tundra vegetation. This follows evidence from 4 ka BP, when July temperatures were roughly 1°C higher relative to present conditions due to increased solar insolation, as recorded by local macrofossil and palynological evidence (Engstrom and Hansen 1985; Levac and de Vernal 1997; Kerwin et al. 2004). Evidence also shows that the position of the altitudinal limit of trees in central Labrador was higher during this period and has since receded in tandem with declining July temperatures (1-2°C; Lamb 1985). Knowledge of the specific and current environmental influences on tree growth will provide a better understanding of the forests of northeastern Canada and help manage the potential effects of climate change on them.

Tree ring studies using Labrador trees have shown that measureable relationships exist between tree growth and climate, but these studies have largely been restricted to northern sites (e.g. D'Arrigo et al. 1993; 1996; 2003). However, Labrador's landscape is varied, partly as a result of the proximity of the Labrador Sea, which results in high spatial climate variability (Banfield 1993). As a result, samples are collected from sites across central Labrador, from the coast to the Quebec border, in order to include the various climate regions present. Dendrochronology techniques are applied to four alpine treeline species, three of which have never been sampled in Labrador, and comparative analyses of their radial growth patterns are used to infer site- and species-specific ecological forcings on radial tree growth. Forcings may include ecological factors that impact radial tree growth and that can be identified thought radial growth comparisons, such as insect outbreak events. Dendroclimatological techniques are also applied to investigate how the sensitivity of tree species to climate during the instrumental record may change both spatially and temporally.

1.1.Treelines

The radial growth of trees at alpine treeline is particularly sensitive to changes in climatic trends due to their strong reliance on elements of climate. Globally, studies have shown that the positive relationship between warmer temperatures and the radial growth of trees at the limit of their range is undeniable, but other factors such as moisture and disturbance events can also affect radial growth (Grace et al. 2002). The effects of moisture are not as consistent as those for temperature, but rather are site and season dependent. For example, trees may be sensitive to winter snowfall (Gamache and Payette 2004) and to spring/summer precipitation (D'Arrigo et al. 2003). The latter is due to the fact that during the summer months, trees may suffer from drought stress or moisture saturation, both of which result in narrower tree rings (D'Arrigo et al. 2003).

The radial growth of trees at alpine treeline is also dependent on forest population dynamics and the characteristics and frequency of disturbance events, in particular within the boreal 'forest of disturbance', which maintains its characteristics and diversity through patterns of disturbance (Barbour and Billings 2000). Common disturbances include fire, windthrow, insect outbreaks and predation by animals such as the porcupine (Erethizon dorsatum) (Foster 1985). Fire and windthrow are uncommon across central Labrador; the fire return interval can reach 500 years (Foster 1983) and so does not exert a significant influence on tree radial growth. However, outbreaks of spruce budworm (Choristoneura fumiferana (Clemens) and larch sawfly (Pristiphora erichsonii Hartig) have occurred with regular frequency in the boreal forest of neighbouring Quebec: the return interval is 40 years for the budworm and 25 years (+/- 8.3 years) for the sawfly (Jardon et al. 1994; Boulanger and Arsenault 2004; Simard et al. 2006). These insects are defoliators and can cause widespread tree mortality if their populations reach outbreak proportions and persist for a number of years. Prior to death, however, affected trees allocate resources to needle regeneration at the expense of radial growth, resulting in narrow tree rings. Thus, these outbreaks are easily identifiable through comparative analysis of the radial growth of host and non-host species (e.g. Tardif et al. 2001).

Most studies of the radial growth response of trees focus on a single tree species either due to availability or because only the oldest species is used in order to construct the longest possible record of tree growth. These studies therefore overlook some of the bio-physical complexity and reality of the alpine treeline ecotone. In the present study, all four alpine treeline

species that are common across central Labrador are used. The physiological and ecological characteristics of each study species that may control the status of treeline are outlined below.

1.1.1. Black spruce (Picea mariana (Mill.) B.S.P.)

Black spruce is the most prolific tree species in northeastern Canada, commonly found on northfacing slopes or on sites with relatively small amounts of solar irradiance (Oechel and Lawrence 1985; Payette 1993). This species has a high degree of tolerance for various habitat types and is phenotypically plastic, an adaptation which allows it to survive under harsh conditions, such as those found at the alpine treeline.

Black spruce trees possess semi-serotinous cones, which is an important adaptation to fire (Black and Bliss 1980). Its roots are shallow and wide spreading, making it well-suited for sites that are underlain by bedrock or permafrost, such as Labrador. Unlike white spruce, black spruce is intolerant of coastal environmental conditions in Labrador, which commonly include fog and salt-laden winds. In the spring, the buds of black spruce open one to two weeks after those of white spruce, ensuring that they are less likely to sustain frost damage (Farrar 1995). Black spruce trees are also less likely to sustain damage from spruce budworm compared with either white spruce or balsam fir (Albert and Parisella 1985).

1.1.2. White spruce (Picea glauca (Moench) Voss)

White spruce trees prefer slopes with abundant moisture, good drainage, and high nutrient availability (Engstrom and Hansen 1985). At treeline, it commonly forms isolated tree islands beyond the latitudinal or altitudinal limit of other species, which provide an important seed source for range expansion. In coastal eastern Labrador, it forms treeline in association with black spruce and eastern larch (Payette 1993). Similar to black spruce, white spruce possesses a shallow root system, which makes it well-suited for permafrost terrain (Barbour and Billings 2000). White spruce, like balsam fir, is susceptible to spruce budworm infestation (Albert and Parisella 1985).

1.1.3. Balsam fir (Abies balsamea (L.) Mill.)

Balsam fir is present in central and eastern Canada and increases in density eastward, where the climate is cool and moisture abundant (Ritchie 1987). It prefers mesic soils and acidic loam substrate, a moderate permafrost table and modest nutrient requirements (Barbour and Billings 2000). It is more sensitive to soil conditions than black spruce. Lamb (1985) suggested that fir populations declined and black spruce proliferated as a result of deteriorating soil conditions ~4 ka BP. Balsam fir trees are the preferred host for spruce budworm infestations, which cause defoliation and if persistent, death (Albert and Parisella 1985).

1.1.4. Eastern larch (Larix laricina (DuRoi) K. Koch)

Eastern larch is a shade-intolerant deciduous conifer present throughout the northern portion of the North American boreal forest. It is less common than black or white spruce in Labrador. In subalpine environments, larch occupies upland, moderately drained sites and wetter habitats. The growing season for larch is necessarily shorter than for true evergreens, but it also experiences fast apical growth (Elliot-Fisk 2000). It prefers acidic substrates, a high permafrost table, mesichygric soil moisture, and has low nutrient requirements (Elliot-Fisk 2000). It does not tolerate warm climates or dry substrates. Eastern larch has a shallow and dense root system (Sternberg and Wilson 2004) and like deciduous species, it allocates energy in the spring to the production of fresh needles, which are subsequently lost in the fall.

Eastern larch is susceptible to larch sawfly infestations. Tree ring studies conducted in subarctic Quebec have shown evidence of larch sawfly outbreaks starting as early as 1744 (Jardon et al. 1994). The observed intensification and frequency of larch sawfly activity around 1880 may have been the result of climate change (Jardon et al. 1994).

1.2. Climate

The climate of Labrador is spatially varied as a result of its proximity to Arctic, continental and marine influences. Across central Labrador, the climate is the result of synoptic-scale systems that originate over the North American continent and the Northwest Atlantic. To the west, the prevailing westerlies of the mid latitudes carry relatively warm and dry air over central Labrador during the growing season (Banfield 1993). To the east, the cold Labrador Sea carries cold water southward, resulting in frequent fog and increased atmospheric moisture along coastal regions. This climatic pattern is reflected in the distribution of ecoregions across central Labrador and suggests a close relationship between climate and vegetation in the region (Meades 1989).

Along the coast, winters are relatively mild and summers are cool, whereas inland winters are cold and summers are relatively warm (Figure 1.3). In the spring, the adjacency of colder water coupled with offshore winds result in a higher incidence of fog, with on average 70 less hours of bright sunshine along the coast compared to farther inland (Banfield 1993). In July, the conditions are more uniform: 198 hours of bright sunshine at the coast compared to 197 hours inland across central Labrador (Banfield 1993). The last day of frost is synchronous across

central Labrador, whereas the first day of frost is approximately two weeks earlier inland (Banfield 1993). Annually, values for the total precipitation are uniform across central Labrador, but inland the majority of the precipitation falls as snow: 90 days with snow at the coast compared to 120 days inland (Banfield 1993).

1.3. Labrador Highlands Research

The research carried out in this thesis was conducted as part of the activities of the Labrador Highlands Research Group at Memorial University. Since 2001, this multidisciplinary research group has focused on the past, present and future responses of tundra and taiga ecosystems in Newfoundland and Labrador to climatic changes. Other alpine treeline systems around the world have documented recent shifts in treeline position and it is proposed that the first environmental effects of climate change in Labrador may be detected in these climatically-sensitive systems. Moreover, highland systems such as the ones found in Labrador, are topped by tundra vegetation which is located significantly farther south than its northern counterparts (Figure 1.2). This summit vegetation provides habitat for both plant and animal species, including the endangered woodland Mealy Mountain caribou (*Rangifer tarandus caribou*) and the rock ptarmigan (*Lagopus mutus*). It has also been suggested that a 1°C increase in air temperature in this region may cause treeline to migrate 140 m upslope, effectively eliminating the tundra vegetation (Labrador Highlands Research Group 2007). Should this migration occur, it would also effectively eliminate the habitat for these endangered species.

The Labrador Highlands Research Group has found evidence in the Red Wine Mountains that there were erect trees above the present limit of trees 4 ka BP, a time during which,

according to several independent studies, summer temperatures were warmer than present (Engstrom and Hansen 1985; Levac and de Vernal 1997; Kerwin et al. 2004). These findings suggest that an upslope shift of trees as a response to the observed warming which began in the early 1990s is a strong possibility. Local studies have shown that black spruce, balsam fir and paper birch (*Betula papyrifera*) seeds were able to germinate and overwinter under experimental warming conditions above present treeline (Munier 2006). These studies also indicate that although soil temperatures are cooler (2°C) above the current limit of trees than within the adjacent forest, the soil chemistry is suitable for seedling establishment (Yurich 2006). Studies in the Red Wine Mountains indicate that black spruce saplings are found at the highest elevations above treeline as compared to other species, likely due to their phenotypic plasticity and layering abilities (Bussey 2006).

This thesis will focus on the radial growth of mature trees within the highlands of Labrador and their response to climate. This information can subsequently be used to assess the vulnerability of alpine treeline species to future climate scenarios.

1.4. Dendrochronology

Dendrochronology, the study of tree rings, has provided significant knowledge of the controlling factors affecting tree growth. A tree's annual growth commences in the spring using energy stored during the previous year's growth. Cells formed in the spring have thin walls and are called earlywood cells, whereas cells formed at the end of the growing season have thicker walls and are called latewood cells. The latter cells have a darker appearance when compared to the earlywood and it is this sharp transition between dark latewood and the next year's earlywood

which results in a visible annual ring. Both tree ring width and wood density measurements have been shown to capture a slightly different climate signal. In a study encompassing the entire extra-tropical northern hemisphere, Briffa et al. (2002) showed that tree ring density series are sensitive to air temperatures from April to September whereas tree ring width series are more sensitive to June to August temperatures (Briffa et al. 2002). Tree ring research in Labrador has primarily focused on the relationship between tree ring density and climate (density only: D'Arrigo et al. 1996; D'Arrigo and Jacoby 1999, ring width and density: D'Arrigo et al. 1993; 2003).

Annually-resolved tree ring records can be accurately dated using crossdating techniques. This process is based on the fact that all trees, in particular those of the same species, growing in the same regional setting, must experience the same environmental conditions and so have similar radial growth patterns. Crossdating is a process whereby the tree ring pattern between samples is matched in order to assess the data quality and to anchor the tree ring pattern in time. The resulting dated tree ring chronology is called the master chronology. The crossdating process can also be used to extend the length of the tree ring chronology by matching the ring width pattern of an undated sample to the master chronology. This process can be repeated indefinitely and has resulted in millennia-long chronologies (Fritts 1976; Luckman and Wilson 2005).

Once a tree ring chronology is accurately crossdated, it is standardized to produce a unitless index of radial growth. This process is necessary because there are a variety of factors – biological, ecological and climatic – which together produce an annual ring. The standardization process removes unwanted (commonly age-related) trends in radial growth by fitting a theoretical curve to a time series and subtracting or dividing it by the idealized curve. For

example, the most common standardization method is a negative exponential which removes the age-related radial growth of a tree; younger trees produce wider rings due to their smaller circumference and so their radial growth pattern is mimics a negative exponential trend. This so-called rigid detrending only removes low-frequency patterns, such as age, from the data. There are several detrending options, however, which remove various amounts of high and low frequency data, depending on the focus of the research (Helama et al. 2004).

1.5. Dendroclimatology

Dendroclimatology relates the radial growth trends of trees to climate. This application is based on the fact that the radial growth of trees living at the edge of their range are limited by a single climatic factor; a slight change in this factor produces a measurable change in the ring characteristics for that year. Using the relationship between the tree's radial growth and instrumental climate, we can reconstruct annually-resolved climate for several centuries using dendroclimatology. Dendroclimatic reconstructions are an important tool in determining past climatic variability at local, regional and hemispheric scales. In Labrador, these reconstructions have captured well-known circumpolar climatic events such as the Little Ice Age, which ended ca. 1850, and cool periods associated with volcanic eruptions (D'Arrigo and Jacoby 1999).

1.5.1. Divergence

The relationship between tree rings and climate can be used to reconstruct palaeoclimate as long as it is static in time. There is, however, increased awareness that the sensitivity of tree rings to climate may have changed in recent decades; where there was once a strong relationship between tree rings and climate, it is now statistically insignificant (D'Arrigo et al. 2008). The overall

consequence of this phenomenon is that palaeoclimatic reconstructions may need to be reconsidered. A recent review paper on this 'Divergence Problem' has shown that this loss in sensitivity is circumpolar in the northern latitudes, and may be due to a number of biological and ecological factors and/or methodological issues (D'Arrigo et al. 2008). Further, the loss of sensitivity is not limited to temperature, but also precipitation. To date, the divergence problem has been observed in western Canadian tree rings but no attempt has been made to determine its occurrence in alpine tree of eastern North America. From a dendroclimatic perspective, it is imperative that the stability of the relationship between radial tree growth and climate be assessed.

1.6. Thesis focus

This thesis focuses on the direct relationship between tree radial growth and climate in order to determine which environmental conditions exert influence on the radial tree growth of alpine treeline species across central Labrador. Dendroclimatological techniques will be applied to the four species that make up the alpine treeline in order to identify which climate variables are most limiting to radial growth. These relationships, should they be strong enough, will be used to reconstruct past climate over the last several centuries. A palaeoclimatic reconstruction can eventually provide a context for current and future climatic conditions in Labrador. The influence of forest disturbance events, such as insect outbreaks, will also be assessed through the comparative analysis of the radial growth patterns and confirmed through verification with data from neighbouring Quebec. Last, this thesis will analyse the temporal stability of alpine tree sensitivity to climate in order to test for the presence of the 'divergence problem' in Labrador.

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Table 1.1: Physiological characteristics of four alpine treeline species.Source: Elliott-Fisk in Barbour and Billings in all cases except those marked by a *.* Source: Jim Cornish, NL. http://www.cdli.ca/CITE/artsmarts/boreal_factsheets.PDF (accessed January 2009)

	Black spruce	White spruce	Balsam fir	Eastern larch
	Yukon to	Yukon to	Prairies to	Yukon to
Canadian range	Labrador*	Labrador*	Labrador*	Labrador*
Maximum age	350	600	200	350
Maximum height (m)	20*	40*	15-30*	15-25*
Evergreen	yes	yes	yes	no
Growth rate	moderate	moderate	moderate	rapid
Frost free period (days)	60	60	80	75
Site requirements:				
Substrate preference	acidic	basic loam	acidic loam	acidic
Permafrost table	high	low	moderate	high
Soil moisture	xeric-hygric	xeric-mesic	mesic	mesic-hygric
Nutrient requirements	low	moderate	moderate	low



Figure 1.1: Map of Labrador showing study area in relation to the Atlantic Ocean and continental Canada. Inset shows position of Labrador within North America. The study area for this thesis is in the vicinity of the 54°N line, with key locations (from east to west): Cartwright, Mealy Mountains, Red Wine Mountains, Churchill Falls and Labrador City.







Figure 1.3: Picture of alpine treeline taken in the Red Wine Mountains. The photographer is standing atop a mountain, overlooking a sharp transition from forest to tundra vegetation, located in background of photo. The alpine treeline composition includes black spruce, white spruce, balsam fir and eastern larch and is located at approximately 610 m asl. Copyright T. Bell (2004).

Co-authorship Statement

The design and development of the research proposal were completed by me, with input from Trevor Bell, Colin Laroque, John Jacobs and Luise Hermanutz;

The practical aspects of the research were completed by me, with logistical support by Trevor Bell, Colin Laroque, John Jacobs and Luise Hermanutz;

All data analysis was completed by myself;

All manuscript preparation was completed by me with comments and editorial suggestions from Trevor Bell, Colin Laroque, John Jacobs and Luise Hermanutz.

Chapter 3, "On the divergence problem in eastern Canada: changing climatic sensitivities of two spruce species across a moisture gradient has been submitted for publication to Dendrochronologia, October 2008.

Chapter Two

2. Dendroclimatic response of alpine treeline species in Central Labrador: a multi-species perspective

2.1. Introduction

This chapter describes the radial growth patterns of four alpine treeline species in central Labrador, Canada, and investigates the climate mechanisms that control their radial growth. To date in Labrador only 12 dendroclimatic studies from seven sites have investigated the statistical relationships between radial tree growth and regional climate variables. Radial tree growth has been significantly correlated to the North Atlantic Oscillation (NAO) and the Arctic Oscillation, both of which are based on atmospheric pressure differences and climatic series, including Arctic temperatures (D'Arrigo et al. 2003a; 2003b). In addition, the positive sea ice anomalies in the Labrador Sea during the 1960s-70s and 1990-1991 have been linked to narrow tree rings in coastal northern Labrador (D'Arrigo et al. 1992; 1996). Moisture also influences radial tree growth in Labrador as identified by D'Arrigo et al. (2003a) through drought-related stress effects in spring growth. Together these studies have established that there is a measurable relationship between radial tree growth and climate in Labrador.

Previous studies of tree ring growth in Labrador relied exclusively on white spruce tree ring chronologies and in many cases local data were merged with other circumpolar sites to establish hemispheric climate signals (Schweingruber et al. 1993; D'Arrigo et al. 1993; 2003b; Briffa et al. 1994). In other cases, single-site chronologies focused on coastal trees and indicated that radial growth responses to recent warming were opposite to inland trees, largely due to

mechanical damage resulting from wind exposure (Payette 2007). For those studies that investigated the radial growth response of trees at non-coastal sites, most used tree ring density measurements, which capture a different climate signal than tree ring widths (D'Arrigo et al. 1992; 1996; Schweingruber et al. 1993). This study analyzes tree ring width chronologies from four different species at a single site in central Labrador and investigates their radial growth response to primarily terrestrial climate.

Tree species commonly found at higher elevations in Labrador include: black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glau*ca (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.) and eastern larch (*Larix laricina* (DuRoi) K. Koch). This multispecies perspective has the potential to identify species-specific climatic drivers and disturbance events such as insect outbreaks, which may have a significant impact on the radial growth of its host (Tardif et al. 2001). The study also isolates the strong climate signal inherent in trees growing at their biological limit, but in contrast to most other studies the focus is on altitudinal treeline at latitudes farther south in Labrador.

This study is part of a multidisciplinary research initiative of the Labrador Highlands Research Group of Memorial University of Newfoundland, which aims to study the potential impacts of climate change on highland ecosystems in Labrador. Thermally-limited "edge" ecosystems are particularly sensitive to climatic fluctuations and therefore are ideal locations to study climate effects on tree species (Fritts 1976). To date, studies of seedling germination and establishment indicate that the growth of tree species within the forest-tundra of central Labrador is limited by temperature (Munier 2006). Should this temperature sensitivity also apply to mature

trees, then their tree ring record should preserve an enhanced climate signal at alpine sites (Fritts 1976).

2.2. Methods

2.2.1. Study Area

The study area is located within the Mealy Mountains (53.61°N, 58.84°W), the main field site for the Labrador Highlands Research Group in central Labrador. The site is located approximately 115 km from the Labrador Sea and 20 km south of Lake Melville (Figure 1.1). The mountain tops within the study area reach 1092 m above sea level (a.s.l.) and consist of exposed bedrock, whereas the valleys are predominantly covered by coniferous forest composed of mixed stands of the four tree species employed in this study.

Forest density decreases from the limit of tree growth (approximately 600 m a.s.l.) into a deciduous shrub and a forest-tundra subzone, culminating in tundra-like vegetation on land summits. A climate station located at the upper limit of the open canopy forest at 570 m a.s.l. has recorded hourly temperature observations since 2001 (Labrador Highlands Research Group 2007).

2.2.2. Climate

The study site experiences long cold winters and short cool summers. Labrador is within the path of the prevailing westerlies that dominate the northern mid-latitudes and so continental air masses carry relatively cool and dry air into the region in the winter, and warmer, moist air in the summer. Mean monthly temperatures are above 0°C between May and September. To the east of
the study site, the cold Labrador Current carries Arctic-origin waters southward along the Labrador coast, thereby moderating terrestrial temperatures (Banfield and Jacobs 1998).

Since the end of the Little Ice Age (LIA, ca. 1850), the climate of eastern Canada has experienced an overall increase in both temperature and precipitation (Lamb 1985). However, over the last 30 years, climate trends indicate cooler and drier winters in the region (Labrador Highlands Research Group 2007). In contrast, regional observations show that growing season (June-September) temperatures have been warmer than the average recorded by the instrumental record (1942-2005, 12.75°C) every year since 1998 (Environment Canada 2007).

2.2.3. Sampling

Master tree ring width chronologies for each species were developed based on 60 tree cores collected at breast height (~1.3 m), using a 5.1 mm increment borer. Two cores were collected at right angles to each other from each tree. Cores were mounted onto boards for processing following standard dendrochronological techniques (Stokes and Smiley 1968). Tree cross-sections were also collected at breast height from coarse woody debris (CWD) in order to allow for the possibility of extending the chronology using crossdating techniques. Crossdating is a process where the tree-ring width pattern of an undated sample is matched to that of a master (i.e. a dated chronology). All samples were sanded to expose the tree rings and measured using WinDENDRO software (version 2005a), a semi-automated imaging software which measures tree ring widths with 0.001 mm precision (Guay et al. 1992). Two radii were measured for each CWD disk. CWD samples were identified to the species-level based on cellular characteristics, using the presence (spruce) or absence (fir) of resin ducts (Robichaud et al. 2007). Larch species were visually distinguished based on distinct earlywood/latewood transitions.

2.2.4. Chronology development

The accuracy of tree ring chronology measurements for each of the four species was first assessed visually and then through the application of COFECHA software (Holmes 1983). COFECHA creates a master tree ring chronology by averaging all the tree ring width measurements. The measurements from each core (now called a series) were sequentially assessed against the master chronology using a correlation analysis. CWD was crossdated into the master chronologies using similar correlation analyses. It was not possible to distinguish between the two spruce species using visual analysis alone. Consequently, the unidentified CWD disks were fit into both master white and black spruce chronologies and only kept in that master spruce chronology where they correlated most strongly to the master. This method seemed to easily distinguish between the two species.

The statistical rigor of the chronologies was also assessed using the descriptive statistics provided by COFECHA. The commonality of the signal within each chronology was assessed using the mean interseries correlation value, which is an average of the correlation coefficients between each core and the master chronology created from all the other measurements. The standard deviation about the mean determines the spread of that signal and the autocorrelation was used as a measure of the influence of the radial growth of one year on the next year's growth. Mean sensitivity is a measure of how sensitive the rings are from one year to the next, irrespective of the previous year's growth. The expressed population signal (EPS) was also used as a measure of the predictive ability of the chronology, using the equation:

Equation 1

$$EPS = \frac{nr}{nr + (1 - r)}$$

where: $n = \text{sample size and } \overline{r} = \text{mean interseries correlation value. A value above 0.85 is}$ generally deemed statistically acceptable for climatic reconstruction (Wigley et al. 1984; Briffa and Jones 1990).

Standardization, a statistical procedure that removes non-climatic (i.e. biological and ecological) growth-effects from tree ring chronologies, was accomplished using ARSTAN software (Cook 1985). The program fits a theoretical growth curve to each series and divides the actual measurement by this idealized curve, thereby producing an index of tree radial growth. The 'fit' of this theoretical curve determines the characteristics of the data in the resulting chronology. A curve with a rigid fit will remove very little environmental information from the tree rings, whereas a more flexible curve will conserve mostly interannual high-frequency variability. In this study, a relatively-conservative single-detrending negative exponential or linear regression was applied. This method retains a large amount of the low and high frequency variability present in the tree ring chronologies, thereby exposing long-term patterns that are appropriate for an exploratory-type study (Helama et al. 2004).

2.2.5. Climate data

Air temperature

In order to assess the relationship between radial tree growth and local air temperature, the record from the 'local' climate station (600 m asl) was extended using a linear regression. This local station is located within the sampling area. Nearby Environment Canada climate stations include Goose Bay (1942-present, Station ID 8501900) (~80 km) and Cartwright (1938-present, Station ID 8501100) (~100 km). Growing season temperature and precipitation values are comparable between the three climate stations (Table 2.1). For each month, multiple regression equations of mean daily air temperature were established among the three stations for the period of overlap (2001-2006). For example, a multiple regression was calculated for all of the "January" days from 2001 to 2006 using Goose Bay, Cartwright and Mealy Mountains records. The equations were then applied to the instrumental records on a monthly basis, thereby reconstructing daily data for the study site from 1942 to present. The data were then averaged to produce monthly air temperature values ($r^2=0.985$, p<0.000, n=1826), producing a new local "Mealy Mountains" temperature record.

Precipitation

The Goose Bay and Cartwright precipitation data were used because bulk local precipitation measurements from the Mealy Mountains were not reliable and so it was impossible to conduct a similar scaling analysis as was done for temperature. Average annual precipitation (530.5 mm in Cartwright and 557.3 mm in Goose Bay) and snowfall amounts (474.7 cm in Cartwright and 463.8 cm in Goose Bay) are comparable for both stations. In order to assess the sensitivity of each tree species to precipitation and since there is no prior knowledge on the sensitivity of tree species to precipitation in the Mealy Mountains, total monthly precipitation values from each station were used.

Species response to climate

The program DENDROCLIM was used to assess the relationship between monthly local air temperature, precipitation and radial tree growth (Biondi and Waikul 2004). This program computes bootstrapped (1000 simulations) confidence intervals to calculate Pearson correlation coefficients between climate variables and radial growth with a 95% confidence interval. Bootstrapping involves removing a random sample of the data set and repeating the correlation analysis with this random sample. This process is repeated 1000 times in DENDROCLIM in order to reduce the possibility of erroneously producing statistically significant results (Biondi and Waikul 2004).

Climate reconstruction

Climate reconstruction was accomplished using linear regression, and standard calibration/verification methods (Fritts 1976). For the calibration step, only the tree ring data from 1971 to 2005 (or one half of the instrumental record period) was regressed against the climate data. This regression was then applied to the remaining time period (1942-1970) in order to test the statistical rigor of this model. If the regression is statistically significant (r<0.05) for both time periods, then the model is deemed acceptable. The statistical rigor of the entire reconstruction (1942-2005) was assessed using the Reduction of Error (RE) statistic, which is a measure of the fit between the estimated and instrumental data sets (Cook and Kairiukstis 1990).

Any value above zero in this statistical analysis indicates that the reconstruction has predictive ability.

2.3. Results

2.3.1. Chronology statistics

The four tree ring chronologies span a maximum of 201 years (1805 to 2006, Table 2.2). The interseries correlation value is highest for the white spruce (r=0.581) chronology and lowest for larch (r=0.470). Values for the descriptive statistics are comparable between all species with the exception of larch, which has exceptionally high mean sensitivity values (Table 2.2).

Correlation analysis illustrates that the two spruce chronologies are significantly similar (r=0.668, p<0.000, n=157) and, to a lesser extent, so are the white spruce and balsam fir chronologies (r=0.285, p<0.05, n=92; Table 2.3). The radial growth patterns for larch and fir are significantly dissimilar (r=-0.308, p<0.05, n=92).

2.3.2. Tree ring indices

The four tree ring time series are illustrated in Figure 2.1. The two spruce chronologies share very similar growth patterns from the mid-1800s to the present, including decade-long periods of below-average growth in the 1850s, 1910s, 1960s and 1970s. During the period 1920-1950, a marked difference in the two spruce chronologies occurs; black spruce rings widen and white spruce narrow. Further, during this same period the radial patterns in the white spruce chronology are more similar to fir than black spruce. The larch chronology is characterized by high interannual variability and periods of growth suppression which occur every 20 to 30 years and last between 5 and 20 years. All species experience narrow radial growth during the 1960s

and 1980s. Since the 1990s, all species except larch have experienced reduced variability in ring width.

2.3.3. Species response to climate

Temperature

In order to evaluate the sensitivity of the tree ring width chronologies to climate, each series was correlated to the Mealy Mountains record of monthly mean air temperature for a period of 19 months, including the growing season prior to ring formation (

Figure 2.2). All species are positively correlated to temperature. Correlations using DENDROCLIM software indicate that black and white spruce trees are sensitive to summer temperature during the year of ring formation. Fir is positively and significantly correlated with fall temperatures in the year prior to ring formation and larch is positively associated with fall temperatures in the year of ring formation, indicating that this species' radial growth continues to be dependent on temperature into the fall months.

Precipitation

All species demonstrated stronger correlations to precipitation at Goose Bay than Cartwright (Figure 2.3). Balsam fir trees are the least sensitive to precipitation when compared to the other three species. The radial growth of all tree species in the Mealy Mountains is negatively impacted by total precipitation values during the growing season of the year of ring formation and in the case of black spruce and larch the previous growing season too. White spruce radial growth benefits from high amounts of precipitation in the winter months prior to ring formation (Figure 2.3). Statistically significant correlations between radial tree growth and precipitation are

more frequent during the early and late portions of the growing season, in particular for white spruce and larch trees.

2.3.4. Climate reconstruction

Growing season (June-September) temperature was reconstructed using the black and white spruce chronologies (1847-2004). This merging of the two chronologies was done because the addition of a predictor variable, in the form of another chronology, greatly improved the predictive ability of the regression model. Calibration (1971-2004) and verification (1942-1970) estimates are low but significant (Table 2.4, Figure 2.4), which may be due to the fact that from the late 1990s to 2001 the tree ring indices diverge from the temperature record. The calibration/verification periods each explain 12.4% (adjusted for degrees of freedom) of the variance in the temperature data. This new temperature record portrays cool periods in the Mealy Mountains in the 1850s, 1910s, 1960s, 1970s and the 2000s. Higher temperatures were associated with the 1860s, 1900s and 1950s. The proxy record also illustrates that temperatures over the last two decades of the record are close to average values.

2.4. Discussion

Interseries correlations and mean sensitivity values suggest that all four species are appropriate for dendrochronological analysis. The white spruce chronology has the highest interseries correlation value, indicating that this species is responding to a common signal. Species-specific comparisons with other dendrochronological studies are hindered by the lack of nearby chronologies, with the exception of white spruce. Black spruce, white spruce and balsam fir statistics are comparable to Tardif et al. (2001) in western Quebec (black spruce, r = 0.310, white spruce, r = 0.310, balsam fir, r = 0.340), whereas white spruce statistics are slightly weaker than other Labrador tree ring width chronologies (r = 0.659, r = 0.704) (D'Arrigo et al. 2003a). The high standard deviation and mean sensitivity values for the larch chronology indicate that the radial growth of this species has a tendency to fluctuate on an inter- and intra-annual basis, yet a consistent pattern can be found within the master chronology on the mean interseries correlations for the species (Table 2.2).

2.4.1. Tree ring indices

The lack of synchronicity of the four chronologies indicates that there is no single climatic forcing mechanism influencing the radial growth of all treeline species in the Mealy Mountains. As suggested by the high inter-chronology correlation values, the two spruce species have very similar radial growth patterns and climate sensitivities (Table 2.3). The divergence in the radial growth pattern of the spruce trees from 1920 to 1950 may be related to a species-specific event. White spruce is a secondary host for spruce budworm whereas black spruce is less susceptible due to the timing of bud burst in the growth year (Ascoli and Albert 1985). However, the lack of a concurrent growth suppression of balsam fir trees (the primary host species for budworm) during this time period suggests that a spruce budworm infestation did not occur in the Mealy Mountains at this time. It is concluded therefore that the reduction in spruce radial growth during this decade is climatic in nature. Similarly, the highly-fluctuating radial growth pattern in the larch chronology may be indicative of a species-specific disturbance. Jardon et al. (1994) reported that growth suppression episodes from larch sawfly infestations in Quebec persist on average 9.7 years and the mean period between infestations was 25 years (+/- 8.3 years), a temporal pattern that resembles the one reconstructed here (Figure 2.1). Larch radial growth is

exceptionally narrow during the years: 1794, 1843, 1857, 1874, 1896, 1943, 1951, 1961 and 1979, yielding an average return interval of 23 years.

The program OUTBREAK compares the radial growth patterns of host and non-host species and identifies episodes of insect outbreaks when the radial growth of those host species falls below a threshold value. This identification of periods of insect outbreaks is therefore primarily based on all species having similar radial growth patterns overall except when a hostspecific insect outbreak occurs. In the present case, however, there is poor synchronicity in the radial growth patterns of all species and so it is difficult to identify periods when a host species decouples from a non-host. In particular, larch is the only species that serves as a non-host for spruce budworm infestations in the Mealy Mountains, but this species has exceptionally high MS values, indicating that is it responding to a unique set of variables, and so is not appropriate to be used under the OUTBREAK application. It is concluded then that the program cannot be used to identify episodes of spruce budworm or larch sawfly outbreaks in the present study.

2.4.2. Species response to climate

The sensitivity of four treeline species to local and regional climate variables was assessed using correlation analysis. Bootstrapped correlations illustrated that the two spruce species are positively sensitive to temperature during the growing season, whereas all species for the most part are negatively sensitive to Goose Bay precipitation.

Previous studies in Labrador have shown that northern white spruce trees experience drought-related stress in the spring as evidenced by negative correlations between tree rings and spring air temperature (D'Arrigo et al. 2003a). Similar results, or significant positive correlations to spring precipitation, were not observed in the Mealy Mountains data, likely because the

underlying bedrock inhibits drainage in the thin soils of the region, thereby maintaining adequate soil moisture.

Balsam fir trees are the least sensitive to temperature and precipitation in the Mealy Mountains, being hindered by high levels of precipitation in the late summer months during ring formation. The radial growth of fir trees is aided by warm temperatures during the late summer the year prior to ring formation. These conditions allow trees to build up carbohydrate reserves which can be used during growth initiation the next spring.

White spruce trees benefit from high levels of precipitation in the winter. This is likely an indication of the severe winter winds in the Mealy Mountains (e.g. Hadley and Smith 1983). Icy winds damage needles and other tissues on exposed trees, necessitating that they allocate resources to healing in the spring. These results are similar to those reported by Payette (2007) using white spruce in northern Labrador, where exposed white spruce trees suffered from defoliation due to mechanical damage incurred by wind. Although snow persistence into the growing season was not sufficient to protect trees in the Mealy Mountains, it is likely that the snow pack protects white spruce against wind stress during the winter months. The depth of the snow line is variable but readily evident throughout the study area through the occurrence of damaged leaders, especially on white spruce trees, which occupy the most exposed sites.

All species have negative sensitivity to summer precipitation in the Mealy Mountains. These results may be related to solar radiance effects, through the incidence of cloud cover. The proximity of the Labrador Sea can contribute significant amounts of moisture to the Mealy Mountains in the form of fog. Such conditions are detrimental to radial tree growth not only because of the amounts of moisture added to the region, but also the decrease in solar radiation

receipt at the surface. Studies in Greenland have also reported that the high incidence of coastal fog is detrimental to tree radial growth (Bocher 1977).

2.4.3. Climate reconstruction

The combined spruce tree ring width series was the most effective at reconstructing past summer (June-September) air temperature in the Mealy Mountains (1847-2005). This is similar to other published results from Labrador which indicated that spruce trees are appropriate for dendroclimatic reconstruction of growing season conditions (D'Arrigo et al. 1993). The reduction of error (RE, measures the common variance between the observed and reconstructed temperature records) statistic indicates that the reconstruction has predictive ability (Table 2.4).

The newly reconstructed temperature record illustrates a cool period in the 1910s that is of note because it has been interpreted differently by various studies (Figure 2.5). Blais (1981) used white and black spruce tree species to investigate the occurrence of spruce budworm outbreaks in eastern Quebec, and inferred an infestation during this decade, as did dendroentomological studies throughout Quebec (Boulanger and Arsenault 2004). However, there is no reduction in the radial growth of balsam fir trees (the primary host species) during this time period in the Mealy Mountains, and it is concluded that this decade was cool in the Mealy Mountains, which agrees with other dendrochronological studies (Grand Banks SSTs, D'Arrigo et al. 1996; Northern hemisphere temperatures, Jacoby et al. 1989). During the 1960s, trees-rings in all species narrow, possibly as a response to cool and dry conditions due to positive sea ice anomalies related to a positive NAO index (e.g. Brazdil 1988). This cool event was also recorded in white spruce trees in Newfoundland and Labrador, white pine (*Pinus strobus*) trees in Newfoundland and birch (*Betula pubescens*) in Greenland (D'Arrigo et al. 1992).

The radial growth pattern of the spruce and fir trees is stable over the last two decades of the record despite an observed increase in instrumental temperatures (1-2°C) since 1998. This pattern is also seen in other northern studies and may be due to a change in the radial growth response to temperature (i.e. Briffa et al. 1998). Briffa et al. (1996) first reported on the incidence of reduced sensitivity of tree rings to temperature throughout the Northern Hemisphere and D'Arrigo et al. (2008) recently published a comprehensive review of studies reporting similar effects, terming it the "divergence effect". Although there is a clear indication that the spruce trees in the Mealy Mountains are experiencing some kind of divergence effect, a more indepth study is needed to highlight the specific causes of this effect given the important implications for dendroclimatic reconstructions in Labrador.

2.5. Conclusion

This paper has presented the first dendroclimatic assessment of black spruce, balsam fir and eastern larch in Labrador. It is also the first to explore the radial growth response of four treeline species simultaneously at a single site to local climate in Labrador, and to include the effects of moisture on these treeline species in eastern Canada.

The simultaneous use of multiple treeline species at a single site has highlighted that their radial growth pattern is the result of a response to a unique set of climatic and/or ecological variables for each species. Although black and white spruce have very similar growth patterns and responses to climate, species-specific sensitivities to disturbance events help maintain a constant diversity in growth patterns between all species. Further investigations are needed to confirm the occurrence of species-specific ecological disturbance, such as insect infestations, to

trees in the Mealy Mountains, but inferences have been made based on infestations that have occurred in eastern Quebec, insect migration rates and visual analysis of radial growth patterns.

Precipitation and growing season length are significant contributors to the radial growth of trees in the Mealy Mountains. While precipitation totals are ample for radial tree growth and summer temperature sensitivities are generally weak, all species are at times sensitive to temperature during the spring and fall seasons. It is concluded that in the Mealy Mountains the length of time available to grow new tissue is more important than ambient air temperature.

The newly reconstructed climate record for the Mealy Mountains is in accordance with regional published results, but the predictive ability of this new record is weak. The reconstruction underestimates extremes in temperature, as illustrated in the verification period (1942-1970) and so is not reliable. The temperature reconstruction has also highlighted the occurrence of the divergence effect in Labrador.

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2.7. Tables

Table 2.1: Comparison of mean growing season (June-September) climate values at three stations in central Labrador for the period of common overlap (2001-2005). Temperature (°C) values for Mealy Mountains and two adjacent climate stations are shown (Environment Canada 2007). Total precipitation (mm) values are available from Environment Canada sites only.

	Temperature (°C)	Precipitation (mm)
Cartwright	10.48	88.92
Mealy Mountains	10.60	n/a
Goose Bay	12.75	94.88

Table 2.2: Statisti	cal characteristics	s of tree ring	, width	chronologies	generated	by the comp	outer
		program C	OFECI	HA.			

Species	# series*	Period	r †	SD‡	ACf§	MS	¶ EPS >0.85
Black spruce	32	1825-2003	0.509	0.335	-0.035	0.267	1847
White spruce	45	1758-2004	0.581	0.376	-0.025	0.252	1805
Balsam fir	23	1826-2004	0.509	0.348	-0.001	0.275	1913
Eastern larch	52	1717-2004	0.470	0.379	-0.028	0.345	1829

* Number of measured segments (series) in the final chronology.

† Mean Interseries correlation values (using 50-year segments) averaged over the chronology.

‡ Standard deviation of the mean tree ring measurements

§ Filtered autocorrelation value.

Mean sensitivity value.

¶ The year when the EPS >0.85.

		White spruce	Balsam fir	Eastern larch
Black spruce	r	0.668	0.173	0.082
	Sig	0.000	0.102	0.309
	N	157	91	157
White spruce	r		0.285	-0.027
	Sig		0.006	0.718
	N		92	176
Balsam fir	r			-0.308
	Sig			0.003
	Ň			92

Table 2.3: Matrix of two-tailed Pearson correlation coefficient values (r) and their statistical significance (Sig) values between tree ring chronologies. Sample size (N) used in each calculation is shown.

Table 2.4: Statistical characteristics of calibration (1971-2005) and verification (1942-1970)
periods for climate reconstruction, using the merged black-white spruce chronology. Percent
variance explained by the model and significance value (p) are also given.

Calibration years	Verification years	Adjusted r ²	p-value	RE*
1971-2005		0.124	0.029	0.994
	1942-1970	0.124	0.030	0.994

* Reduction of error statistic measures the common variance between the observed and reconstructed temperatures. A positive value of RE indicates an acceptable predictive ability.



Figure 2.1: Time series of the four tree ring width (TRW) chronologies. Thick black line represents the TRW record where the EPS value > 0.85, whereas the thick gray line represents the time period when the EPS value < 0.85 (left axis). Total sample depth (right axis) is shown by a thin gray line, CWD sample depth is shown by light dashed line, and live core sample depth is shown by a black dashed line.



Figure 2.2: Pearson correlation coefficient (r) values between tree ring widths and monthly Mealy Mountains temperature values. The histograms show the r-values between tree ring chronologies and estimated mean monthly temperature for the 17 month period. Significant correlations (p<0.05) are shaded.



Figure 2.3: Pearson correlation coefficient (r) values between tree ring widths and monthly Goose Bay precipitation. **The histograms** show the r-values between tree ring chronologies and total monthly precipitation for 17 month period. Significant correlations (p<0.05) are shaded. Precipitation data from Environment Canada (2007).



Figure 2.4: Time series plot of growing season (June-September) temperature (1942-2006) in the Mealy Mountains. Calibration and verification curves are shown. Error bars represent 95% confidence intervals.



Figure 2.5: Reconstruction of mean June-September temperature for the Mealy Mountains (1847-2004). The five-year running mean is shown as bolded line and the 95% error bars in grey.

Chapter Three

3. Dendroecology of alpine treeline across southcentral Labrador

3.1. Introduction

The thermal control of tree growth at alpine treelines around the world is broadly accepted (Körner and Paulsen 2004). In central Labrador, Canada, this relationship has been demonstrated for seedling germination and establishment (Munier 2006), whereas other factors, such as moisture and forest disturbance events, also likely exert influence on tree growth. For example, moisture can be limiting to tree growth when the ground temperature is below zero and the air temperature is warm enough to initiate photosynthesis. This causes drought stress because trees cannot take in water from the frozen ground (Cairns and Malanson 1998; D'Arrigo et al. 2003). Forest disturbance events such as insect infestations can also influence tree radial growth through tissue damage, causing the tree to shift resources towards tissue repair and decreasing the amount allocated to growth (Körner and Paulsen 2004). In neighbouring Quebec, dendrochronological and macrofossil evidence has shown that insect outbreaks have had a mean recurrence interval of 40 years over the last 450 years (Boulanger and Arsenault 2004; Simard et al. 2006). Further, Jardon (2001) reported an increase in the frequency of spruce budworm (*Choristoneura fumiferana* (Clem.)) infestations during the latter half of the 20th century.

The climate of central Labrador is spatially and temporally varied as a result of the interaction of meso- and synoptic-scale systems from both continental and oceanic sources. The region lies in the path of the prevalent westerlies that characterise the northern hemisphere mid-

latitudes. Cold Labrador Sea waters also influence temperature and moisture characteristics on land (Banfield 1993). The ocean effects are most obvious during the late-winter, spring and fall seasons. From February to June, a coastal climate station (Cartwright) consistently received less hours of bright sunshine compared to an inland station (Wabush Lake A; Banfield 1993). In July, the conditions are more uniform: 198 hours at the coast compared to 197 hours inland across central Labrador. The last day of frost is synchronous across central Labrador, whereas the first day of frost is approximately two weeks earlier inland (Banfield 1993). Total annual precipitation is similar across central Labrador, but inland most of the precipitation falls as snow. For instance, precipitation falls as snow at Cartwright approximately 90 days of the year as compared to 120 days at Wabush Lake A (Banfield 1993).

Previous dendrochronological studies in Labrador have shown that the location of trees relative to the coast influences their relationship to climate. In northern regions, white spruce (*Picea glauca* (Moench) Voss) trees are sensitive to both temperature and moisture effects (D'Arrigo et al. 1996. D'Arrigo et al. 2003). Coastal white spruce populations exhibit different growth dynamics and climatic responses compared to their inland counterparts at similar latitudes (Payette 2007). In central Labrador at an inland alpine treeline site situated ca. 115 km from the outer coast and probably affected by both marine and continental influences, black spruce (*Picea mariana* (Mill.) B.S.P.) and white spruce tree species appear to be most sensitive to summer temperature whereas balsam fir (*Abies balsamea* (L.) Mill.) and eastern larch (*Larix laricina* (DuRoi) K. Koch) trees are more sensitive to fall temperature. At the same site, white spruce was found to be sensitive to winter precipitation, while the other tree species were more closely correlated to summer precipitation.

Forest disturbance events associated with periods of insect outbreaks also influence tree radial growth. Spruce budworm and larch sawfly (*Pristiphora erichsonii Hartig*) are both endemic defoliators in this region. Both insects cause tree defoliation which reduces tree vigour and growth, including radial growth, and can lead to death in the case of sustained infestations. One dendrochronological study in central Labrador showed that for some infestations, the effects of insect defoliation are more significant to radial tree growth than climate (Trindade et al. 2008). Williams and Liebhold (2000) found that there exists spatial synchrony between insect populations up to 2000 km from the initial outbreak, indicating that Quebec outbreaks may occur simultaneously in Labrador.

Since the majority of previous dendrochronological studies in Labrador are located in coastal regions, previous tree ring studies focus on white spruce trees exclusively. However, alpine treeline ecotones across central Labrador are composed of four tree species: black and white spruce, balsam fir and eastern larch. Each of these species has evolved unique physiological characteristics and ecological tolerances to environmental conditions (Payette 1993). Black spruce has a high degree of phenotypic plasticity and a high tolerance for different moisture gradients and habitat-types (Payette 1993). As such, it is one of the most common species of the northeastern boreal forest. In contrast to white spruce, black spruce is intolerant of coastal fog and salt-laden coastal winds (Payette and Gagnon 1979). In Labrador, white spruce trees are most common along the coast and they prefer abundant moisture, good drainage, and high nutrient availability (Engstrom and Hansen 1985). Balsam fir is more tolerant of poor organic sites than white spruce, and can survive in a variety of cool, somewhat moist soils (Engstrom and Hansen 1985). Balsam fir is the primary host for spruce budworm infestations in

eastern Canada, but white and black spruce trees are also susceptible (Blais 1981). Larch is a deciduous species and so its growing season is necessarily shorter than for true evergreens because it must allocate energy to the production of fresh needles in the spring which are subsequently lost in the fall. It does not tolerate warmer climates or dry substrates (Elliott-Fisk 2000). Eastern larch is the only species in Labrador that is susceptible to larch sawfly infestations.

This study investigates the radial growth of four alpine treeline species across central Labrador. Comparative analysis of the radial growth time series is used to compare and contrast the patterns of each species across a moisture gradient, from coastal locations inland. The spatial patterns in climate-growth relationships for each species are investigated using local and regional temperature and precipitation records.

3.2. Methods

3.2.1. Study sites

The research described in this paper was derived from tree ring samples collected at five sites located roughly along 53°N latitude. The sites span 660 km of longitude from coastal Labrador at 57°W inland to 66°W (Figure 3.1; Table 3.1). From east to west the sites include: a coastal site at Cartwright (Site 1), a site in the Mealy Mountains (Site 2), a site in the Red Wine Mountains (Site 3), a site at Churchill Falls (Site 4) and a site in Labrador City (Site 5). Species composition was sufficiently diverse throughout the study area to sample four species at most sites (Table 3.1). Sampling focused on high-elevation regions in order to enhance the climate signal within each tree species (Fritts 1976).

Sites 2 and 3 are isolated mountain Sites located more than 20 km from any community. By contrast, Site 1 is less than 10 km away from the coastal community of Cartwright and Sites 4 and 5 are within 5 km and 1 km from Churchill Falls and Labrador City/Wabush, respectively. Sampling time was limited at Site 1 and so all tree samples were collected from a single southeast-facing slope. At all other sites, an effort was made to sample at various micro sites.

3.2.2. Sampling

Thirty trees of each species found at the study sites were cored at breast height (~1.3 m), with a 5.1 mm increment borer. Two cores (at 90° angles) were sampled per tree for a total of 60 core samples per chronology. The cores were glued onto slotted mounting boards for processing following standard dendrochronological techniques (Stokes and Smiley 1968). Tree cross-sections were collected from dead standing snags with minimal rot in an attempt to extend the length of each chronology.

3.2.3. Chronology development

All samples were mounted on slotted boards and sanded to expose the annual ring pattern. Ring widths were measured to the nearest 0.001 mm using the WinDENDRO program (version 2005a; Guay et al. 1992). For each undated snag sample, two radii were measured along the longest possible paths. Snag samples were identified to the species-level using visual properties of the wood cells following methods outlined in Robichaud et al. (2007). Ring patterns from each chronology were first visually crossdated to confirm that similar patterns existed in the wood of each set of samples. COFECHA software was then used to statistically verify the pattern within the master tree ring chronologies, and to assess the quality of the data (Holmes 1983).

COFECHA does this by first averaging all the raw tree ring width measurements and then comparing the fit of each individual series to the average using a Pearson's correlation analysis of overlapping 50-year segments. Standing snags were crossdated into each master chronology using the same method. Where the two spruce species were difficult to distinguish in snags using wood cell analyses, the disks were pattern matched against the black and white spruce master chronologies at the site to establish a potential species match.

The statistical rigor of the chronologies was assessed from the descriptive COFECHA outputs. The commonality of the segments within each chronology was assessed using the interseries correlation descriptor 'r'. The standard deviation (SD) about the mean determines the spread of that signal about the mean r-value. Autocorrelation (AC) is a measure of the influence of the radial growth of one year on the next year's growth, and is often used in conjunction with mean sensitivity (MS), a measure of how sensitive rings are in year-to-year variation, irrespective of the previous-year's growth, to help understand the possible ecological effects of one year's growth on the next. The expressed population signal (EPS) was also calculated for each chronology. This statistic is a measure of the signal strength of a chronology based on the sample size and the r-value for the chronology. Values above 0.85 are deemed to be statistically robust (Wigley et al. 1984; Briffa and Jones 1990).

To standardize the tree ring records, a theoretical growth curve was fit to each series and divided by the actual ring measurements. The product was an index of tree radial growth, in which the 'fit' of this theoretical curve determined the characteristics of the data in the resulting chronology. In this study, standardization was accomplished using the computer program ARSTAN (Cook 1985). A double detrending method was used; first, a conservative negative

exponential function was applied to remove the biological growth trend, followed by a relatively flexible cubic spline (32-year window, 50% frequency cut off). The application of this approach was selected to preserve the interannual climatic variability signal in the radial growth of the tree (Helama et al. 2004). ARSTAN's second function combines the standardized rings of all trees into a single master chronology (Cook 1985).

3.2.4. Climate data

As with most northern locations, the instrumental climate record across central Labrador is limited. Environment Canada climate stations exist near Site 1 (Cartwright 1938-present, Station ID 8501100), between Sites 2 and 3 (Goose Bay Station, 1942-present, Station ID 8501900), Site 4 (Churchill Falls Station, 1969-present, Station ID 8501130) and Site 5 (Wabush Lake A, 1961present, Station ID 8504175) (Figure 3.2). Further, instrumental climate stations were established at Site 2 (2001-present) and Site 3 (2004-present) by the Labrador Highlands Research Group of Memorial University.

The length of the instrumental climate record at the Mealy Mountains and Red Wine Mountains sites was extended by establishing linear regression relationships between the local air temperature data and the closest long-term instrumental records available. In the case of the Mealy Mountains site, climate records from Cartwright and Goose Bay were used, whereas for the Red Wine Mountains, records from Goose Bay and Churchill Falls were used. Equations were calculated for each month to account for fluctuations in the climate influence at the site. Daily data were used to compute each regression equation in order to increase sample size. For example, a multiple regression equation was established using all of the "January" days from 2001 to 2006 using Goose Bay, Cartwright and Mealy Mountains records. Each multiple regression equation was then applied to the length of the Environment Canada record and used to estimate the mean air temperature for January in the Mealy Mountains between 1942 and present and for the Red Wine Mountains between 1969 and present (Table 3.1). Precipitation data were obtained directly from the nearest Environment Canada climate station as only bulk measurements were available for Sites 2 and 3. Seasonal values for temperature and precipitation are shown in Figure 3.2.

3.2.5. Response Functions

The climatic response of each tree ring chronology to climate was assessed using the program DENDROCLIM (Biondi and Waikul 2004), a statistical package which estimates confidence intervals using bootstrap methods (1000 iterations). These intervals were then used to estimate the significance of Pearson correlation coefficients between climate and radial growth at the 95% confidence interval.

3.3. Results

3.3.1. Chronology statistics

A total of 18 tree ring chronologies were constructed from the five sites located across central Labrador (Figure 3.3). All four species were sampled at Sites 1, 2 and 3, but white spruce was not located at Site 4 and eastern larch could not be found at Site 5 (Table 3.1). Descriptive statistics of all the chronologies are presented in Table 3.2. R-values values range between 0.402 and 0.622, with the lowest combined r-values at Site 1 (Black spruce: 0.435, white spruce: 0.478, balsam fir: 0.402 and eastern larch: 0.461). SD values are highest at the inland site for all species except black spruce, which has its highest variability at Site 1. There is a consistent decrease in
MS values inland from the coast, indicating a high degree of interannual variability away from the coast. In addition, larch trees have exceptionally high MS indicating that the radial growth of this species has high interannual variability.

A correlation matrix of tree ring chronologies is displayed in Table 3.3. At Site 1, there are significant (p<0.01) negative correlation values between time series for black and white spruce (r=-0.22) and balsam fir and larch (r=-0.24). At all other sites most of the significant (p<0.01) correlation values are positive. Overall, the radial growth pattern of black spruce trees across Labrador is similar to that of white spruce trees and to a lesser extent, balsam fir. In particular, the radial growth patterns of the black and white spruce chronologies at Sites 2 and 3 are very similar (Table 3.3). The tree ring chronologies from Site 4 are not significantly correlated to any of the chronologies at Sites 2, 3 or 5 (Table 3.3). The intra-series correlation values also indicate that the larch chronologies in Labrador are only weakly correlated to other chronologies across central Labrador and that three of the four statistically significant (p<0.01) negative correlations within the matrix involve larch chronologies (Table 3.3).

3.3.2. Climate-growth relationships

Tree ring widths were correlated against seasonal temperature and precipitation values from proximal climate stations using DENDROCLIM software. Using this method, it was determined that the sensitivity of trees at Sites 2 and 3 was consistently stronger when using precipitation from Goose Bay rather than Cartwright, with the exception of balsam fir and larch at Site 3, which correlated to Churchill Falls precipitation only (Figure 3.4).

On the whole, the climate-growth relationships illustrated in Figure 3.4 suggest that the radial growth of trees in Labrador is affected by temperature and precipitation parameters. The

two spruce species are more sensitive to temperature overall than the other two species presented here (Figure 3.4). Fir is sensitive to temperature at Site 1, whereas the larch chronologies do not have any temperature sensitivity across central Labrador. With the exception of black spruce, all species are more sensitive to seasonal precipitation values than temperature. Black and white spruce and balsam fir tree ring chronologies show periods of synchronous decreased radial growth (Figure 3.3). The following reports on species-specific results.

Black spruce

Black spruce tree rings display higher mean sensitivity values along the coast (Table 3.2; Figure 3.3). Two periods of noticeably lower than normal growth in spruce occurred in the 20th century. From 1910 to 1930, black spruce tree rings across Labrador narrow at all sites beginning at slightly different times. For instance, at Site 1, this narrowing begins around 1905 while at Site 5 it begins in the 1920s. In addition, the radial growth of black spruce chronologies narrows at Sites 2-5 during the 1980s, followed by a period (between 3-10 years) of wider than average rings. This period of reduced radial growth lasts several decades at Site 5 (Figure 3.3).

The relationships between the black spruce chronologies and seasonal temperature and precipitation values are strong throughout the growing season and across the study area (Figure 3.4). At all sites except for Site 3, black spruce radial growth is sensitive to both seasonal temperature and precipitation. At Site 3, black spruce growth is only sensitive (negative) to fall precipitation.

White spruce

White spruce trees at Sites 1 and 2 have comparable growth trends until the early 1900s, at which time they decouple slightly (Figure 3.3). Periods of simultaneously narrowing of tree rings occur in the 1910s (Sites 2 and 3 and, to a lesser extent 5), 1930s (Sites 1, 3 and 5), 1960s, 1980s and late 1990s (all sites). All of these episodes are followed by periods (2-10 years) when some of the largest ring sizes are observed in the time series. Further, the periods of narrowing tree rings are not synchronous across the transect, but rather are offset by a number of years. For example, the period of reduced growth in the 1980s appears to have occurred earlier along the coast and later inland.

The relationship between white spruce trees and seasonal climate is weak to non-existent at Sites 1 and 2 (Figure 3.4). At Sites 3 and 5 white spruce tree rings narrow when there are high levels of precipitation during all seasons, and widen when there are warm summer and fall temperatures (Figure 3.4).

Balsam fir

The balsam fir time series display lower interannual variability and mean sensitivity values than the other study species (Table 3.2; Figure 3.3). Intra-series correlation values are significant between fir and all other species across the transect, in particular when compared to the spruce chronologies (Table 3.3). All of the fir time series display long periods of smaller-than-average rings during the 1940s and 1980s. This interval is longer and more severe at Site 5.

Balsam fir tree rings are almost exclusively sensitive to spring and summer precipitation (Figure 3.4). Sensitivity to spring precipitation values alternates between positive (Sites 2 and 4)

and negative (Sites 3 and 5) across central Labrador. At Site 1, balsam fir trees also benefit from warm summer conditions (Figure 3.4).

Eastern larch

The larch chronologies are characterized by highly variable radial growth and exceptionally high MS values which, along with r-values, increase with distance inland (Table 3). Most of the variability in the larch time series stems from consecutive periods of rapid reduction in radial growth followed by a gradual increase in ring width from 1860 to present (Figure 3.3). Some of these episodes occur simultaneously at multiple sites, in other cases they are offset by several years.

The radial growth of larch trees is only climatically sensitive to spring precipitation at Site 2 and summer precipitation at Site 3 (Figure 3.4). Larch radial growth does not appear to be sensitive to temperature in central Labrador.

In summary, these observations show that species are more climatically-sensitive at inland sites than at the coastal site. In particular, the spruce trees are climatically-sensitive to both temperature and precipitation during all three seasons studied here. Fir and larch trees are almost exclusively sensitive to precipitation during spring and summer seasons.

3.4. Discussion

This chapter addresses the climatic sensitivity of 18 tree ring width chronologies from across central Labrador from coastal regions to inland locations. The statistics for the Labrador chronologies are comparable to others reported from Quebec (black spruce, r = 0.310, white spruce, r = 0.310, balsam fir, r = 0.340; Tardif et al. 2001) and Labrador (white spruce, r = 0.659,

0.704; D'Arrigo et al. 2003). The chronology r-values are lowest for all species at coastal Site 1, indicating that the fit between the tree ring width measurements is weakest at this site (Table 3.2). This may be the result of the compound climate factors affecting the coast; in a less complex climatic environment, where a single climate forcing predominates, trees respond uniformly to a distinct variable, resulting in higher r-values. Under the present conditions, trees located at different micro sites along the coast experience a slightly different environment, thereby producing lower overall r-values.

The chronology SD values observed across central Labrador are slightly higher that those from Tardif et al. (2001) from western Quebec, indicating a wider range in ring width values in Labrador than Quebec. The exceptionally high MS values in the larch chronologies are likely a result of a species-specific disturbance, which causes the radial growth to fluctuate widely. Larch radial growth is controlled in part by the larch sawfly, which has been shown to reach outbreak proportions regularly in Quebec (e.g. Jardon et al. 1994).

The spatial pattern in the climatic sensitivities of black and white spruce tree ring chronologies suggests that there is a shift in terrestrial climate around Site 3, located approximately 280 km from the coast (Table 3.1). For black spruce, this is evident in the opposing climate sensitivity results between Sites 2 and 4; at Site 2, black spruce trees rings widen as a result of cool spring, hot and dry summer and dry fall conditions. On the other hand, at Site 4 black spruce tree rings widen as a result of warm and wet spring conditions, cool and wet summers and wet fall conditions. The added moisture on the coastal side is therefore abundant and not limiting to growth at Site 2. There is also a shift in the climate sensitivity of

white spruce trees around Site 3. White spruce trees are not sensitive to any of the climate variables studied at Sites 1 and 2, but are sensitive to moisture and temperature at inland sites.

Black spruce

The radial growth for black spruce trees across Labrador is climatically-limited. Results at Site 4 are similar to those reported by Tardif et al. (2001) from western Quebec, where early-season temperatures were important for the radial growth of all conifers (black spruce, white spruce and balsam fir). Similarly, Hofgaard et al. (1999) found that black spruce trees are most sensitive to spring temperature in northern sites in western Quebec (~ 50°N), and also have a tendency for negative associations with summer temperatures, perhaps indicating moisture stress.

The adjacency of the Labrador Sea to Site 1 results in a higher incidence of cloud cover and fog at this location, which is dissipated by higher temperatures (Banfield 1993). The positive relationship between black spruce and balsam fir and summer and fall temperature may actually be linked to clear days, rather than thermal values. This may also explain the absence of a strong relationship between coastal white spruce and temperature at this site: since white spruce trees are adapted to coastal conditions and therefore not limited by them, it is not expected that they will produce a measurable climate signal.

White spruce

White spruce is climatically-limited only at inland sites. At Site 2, white spruce trees may experience drought stress in the spring, as evidenced by a negative correlation to temperature at that time. This finding is similar to the results reported for white spruce trees in coastal northern sites in Labrador (D'Arrigo et al. 2003) and conifer species in western Quebec (Tardif et al.

2001). However, drought stress evidence is usually accompanied by positive associations with precipitation values, since during a 'drought' episode trees should become sensitive to precipitation, a trend that is not observed in white spruce trees at Site 2. During the spring months (March-May) in Labrador, mean air temperatures are negative (Figure 3.2), and precipitation can be expected to be in the form of snow. Further, ground temperatures are still below freezing at this time and so the lack of associations between white spruce and precipitation at this time is not surprising.

White spruce trees at Site 1 are complacent and have little climatic sensitivity. These results suggest that there is an alternate controlling factor, other than seasonal temperature, moisture or insect infestation, on the radial growth of white spruce along the Labrador coast. Payette (2007) found that exposed white spruce trees at a northern Labrador site failed to respond to monthly temperature and precipitation values due to the mechanical defoliation by wind. Harsh coastal winds cause needle damage, in particular ice-laden winds in the winter months. As a result, during the growing season, white spruce trees allocate resources to needle production rather than producing new xylem cells for radial growth. This effectively eliminates a measurable statistical relationship between growing season climate and tree ring widths. Although this was not observed at the single location sampled for Site 1, which was within the forest-tundra region, it was observed at the most exposed locations at Site 2.

Balsam fir

Balsam fir trees are sensitive to spring and summer precipitation across central Labrador. Their positive relationship to temperature observed at Site 1 may be linked to the prevalence of fog and solar radiation intensity in a manner similar to black spruce. In addition, balsam fir's sensitivity

to precipitation is probably linked to both local climate factors and the severity of spruce budworm outbreaks. High amounts of precipitation during the spring prevent spruce budworm larvae from reaching epidemic proportions (Simard and Payette 2001; Gray 2008).

Episodes of budworm outbreaks reported in western Quebec are illustrated by black arrows in the balsam fir time series in Figure 3.3. Given that the study area lies in the path of the dominant westerlies of the mid-latitudes, it is expected that outbreaks progress from west to east; outbreaks occurring in Quebec could eventually 'migrate' several years later into Labrador. Spruce budworm insects can migrate at a rate of 50-100 km per year (Greenbank et al. 1980) and there exists spatial synchronicity in insect outbreaks up to 2000 km as evidenced through the cross correlations of defoliation in eastern Canada (Williams and Liebhold 2000). The distance between the eastern Quebec outbreaks and those in Labrador City is only 500 km, indicating a possibility that the Quebec outbreak migrated into Labrador within a period of several years. In the proposed 1910s outbreak, periods of narrowing rings occurred in fir and spruce trees at inland Sites several years prior to the eastern Sites, suggesting that a possible budworm outbreak migrated eastward.

Trindade et al. (2008) concluded that the 1910s outbreak reported from Quebec did not occur at Site 2, based on the fact that the radial growth of spruce, not balsam fir, was suppressed. It was concluded therefore that the cause of the narrow spruce rings was climatic in nature, rather than pathogenic. With the larger area used in the present study, it is possible to infer a spatiotemporal pattern in growth suppression, from west to east. As such, the 1910s outbreak from Quebec likely passed through Labrador beginning in the late 1910s at Site 5 and only experienced epidemic proportions at Site 2 in the 1930s. This illustrates the advantage of using a

large area to infer the occurrence of insect outbreaks using dendrochronological techniques alone.

During the 1940s, a westward-moving budworm outbreak is evident in the fir and white spruce time series (not in black spruce) across central Labrador, as evidenced by periods of narrow rings commencing earlier along the coast (Figure 3.3). These results suggest that local climate factors may be sufficient to promote the initiation of an outbreak and that large-scale climate may play a role in budworm migration, but may not be exclusive in determining outbreak movement. This is supported by evidence presented by Gray (2008), who describes the theory of 'climatic release', which states that spruce budworm populations are more likely to reach epidemic proportions under warm and dry spring conditions. This also explains the small number of outbreaks observed along the Labrador coast, which experiences cool and wet spring conditions.

Eastern larch

The climatic sensitivity of eastern larch trees across central Labrador is low to negligible. Rather, the larch chronologies are characterized by high interannual variability and periods of significant growth suppression that occur every 20-30 years and last between 5 and 20 years (Figure 3.3). Jardon et al. (1994) have reported that growth suppression episodes from larch sawfly infestations in Quebec lasted on average 9.7 years and the mean time between infestations was 25 years (+/- 8.3 years), a pattern that is observed in this study. Further, the trends seen here are synchronous with periods of known sawfly outbreaks in Quebec (Figure 3.3) and strongly suggest that the larch sawfly exerts a significant control over the radial growth of larch trees in Labrador. This effect was also seen in western Quebec, where larch sawfly disturbance, along

with spring and fall moisture effects, were concluded to be the principal controlling factors for the radial growth of larch trees (Girardin et al. 2001).

3.5. Conclusion

This study has shown that the radial growth of trees across central Labrador is influenced by location, species and forest disturbance events. At the coast site, climate sensitivity is weak for all species except white spruce. This is likely due to white spruce's adaption to the environmental conditions at coastal site: higher incidence of fog and stronger winds. There also appears to be a shift in climate sensitivity, in most cases, in the vicinity of the Red Wine Mountains. This may be the result of the influence of the Labrador Sea. Prior to this study, the geographical extent on which the Labrador Sea influenced tree radial growth, was unknown. Based on the climate sensitivity results shown here, it appears that there is a shift from maritime-like to continental-like climate 300 km inland.

Both spruce species have similar climate sensitivities across the transect. This is also reflected in their radial growth patterns at each site, and in their apparent susceptibility to insect (spruce budworm) outbreaks. On the other hand, balsam fir and larch trees have relatively unique radial growth patterns, not similar to any other species. These results highlight that each species has different adaptations to environmental conditions and also that fir and larch are the primary hosts for local insects, spruce budworm and larch sawfly.

All species are vulnerable to large-scale insect infestations, which are in tandem with outbreaks in Quebec, suggesting rapid, large scale movement of insects across Quebec-Labrador. Although for most species the episodic occurrence of insect outbreaks does not 'mask' climate

sensitivity, for larch, insect predation is most significant as a forcing mechanism on tree radial growth in Labrador. This study has also highlighted an advantage of using a large region to study the occurrence of insect outbreaks. When using comparative analysis of radial growth patterns at a single site, it is more difficult to differentiate between climatic and pathogenic origins for a reduction in radial growth, whereas results are clearer using a broader spatial scale.

3.6 References

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3.6. Tables

Table 3.1: Geographical	description of sites san	mpled. Sites are order	ed from coast (top) i	nland
(bottom). Species	used to build tree ring	width chronologies at	each site are listed.	

Site	Site name	Latitude (N)	Longitude (W)	Elevation (meters above sea level)	Approximate Distance from Labrador Sea (km)	Chronologies created
1	Cartwright	53° 43.0'	57° 25.0'	550	40	Black sp. White sp. Balsam fir Eastern larch
2	Mealy Mountains	53° 36.5'	59° 48.5'	570	140	Black sp. White sp. Balsam fir Eastern larch
3	Red Wine Mountains	53° 47.5'	62° 5.0'	574	280	Black sp. White sp. Balsam fir Eastern larch
4	Churchill Falls	53° 33.6'	64° 5.4'	550	450	Black sp. Balsam fir Eastern larch
5	Labrador City	52° 55.8'	66° 52.4'	730	660	Black sp. White sp. Balsam fir

Table 3.2: Statistical characteristics of 18 tree ring chronologies created across Labrador. Sites are organized from the coast (top) inland (bottom). Bs = black spruce, Ws = white spruce, Bf = balsam fir and El = eastern larch.

Site	Site name	Species	#series*	Period	r [†]	SD [‡]	AC_{f}^{\S}	MS [∥]	EPS¶	
	Charlin II.	Bs	27	1851-2006	0.435	0.390	-0.035	0.292	1881	
		Ws	23	1823-2004	0.478	0.388	-0.032	0.251	1855	
1	Cartwright	Bf	26	1891-2006	0.402	0.426	-0.003	0.239	1913	
		EI	21	1871-2005	0.461	0.418	0.000	0.415	1950	
		Bs	32	1824-2005	0.509	0.335	-0.035	0.267	1847	
2	Mash Mauntaina	Ws	45	1758-2006	0.581	0.376	-0.025	0.251	1805	
L	Meary Mountains	Bf	23	1826-2005	0.509	0.348	-0.001	0.275	1914	
		El	52	1794-2002	0.470	0.379	-0.028	0.345	1829	
		Bs	22	2 1813-2006 0.	0.456	0.272	-0.023	0.218	1866	
2	Red Wine	Ws	23	1840-2006	0.520	0.311	-0.011	0.232	1907	
2	Mountains	Bf	20	1886-2005	0.460	0.308	-0.024	0.210	1942	
		EI	38	1681-2006	0.600	0.376	-0.015	0.311	1764	
	Churchill Falls	Bs	21	1771-2005	0.471	0.260	-0.025	0.200	1872	
4		Bf	21	1926-2006	0.495	0.370	-0.031	0.196	1945	
		El	31	1900-2006	0.622	0.511	0.006	0.267	1951	
		Bs	24	1755-2006	0.486	0.289	-0.028	0.184	1785	
5	Labrador City/Wabush	Ws	24	1868-2006	0.509	0.452	-0.020	0.202	1881	
	<i>2-0,</i>	Bf	27	1887-2006	0.562	0.499	-0.016	0.199) 1911	

* Number of radii sampled to produce final chronology (2 per tree).

† Interseries correlation value averaged over the entire chronology.

‡ Standard deviation about the mean.

§ Filtered autocorrelation value as per COFECHA.

|| Mean sensitivity value averaged over the entire chronology.

¶ The year when the EPS value becomes statistically reliable

			1				2				3				4			5	
		Bs	Ws	Bf	El	Bs	Ws	Bf	El	Bs	Ws	Bf	El	Bs	BF	EL	BS	WS	
	Ws	22*																	
1	Bf	.27	06																
	El	.00	05	24*															
	Bs	.05	.01	.31*	02														
2	Ws	04	.11	.01	.05	.43*													
2	Bf	.02	.02	03	.04	15	.01												
	El	.12	17	.23	.13	.21*	03	05											
	Bs	18	.13	.09	08	.32*	.41*	16	02										
2	Ws	.01	.12	.25*	12	.49*	.38*	10	.18	.70*									
	Bf	23	04	.07	.15	02	09	05	.11	.15	10								
	El	.12	28*	.08	07	01	06	01	.00	17	12	27*							
	Bs	05	02	.09	01	01	04	.06	13	08	12	.02	.04						
4	Bf	.05	.39*	.08	09	.15	03	.09	22	.23	.28	03	01	.22					
	El	.12	.16	11	.11	.02	09	.09	01	06	.06	10	02	15	.40*				
	Bs	.06	19	09	.26	.01	.13	.00	.14	.02	.10	.25*	.01	08	19	.17			
5	Ws	.06	13	.20	.04	.27	.09	16	.08	.20	.44*	.03	.08	04	.23	.23	.20		
	Bf	.12	12	13	.01	15	.21	.05	18	05	.07	12	.10	11	13	.14	.45*	.26*	

Table 3.3: Correlation matrix of all the chronologies in this study. Sites are organized from coast (top-left) inland (right and bottom). Significant correlations at the 99% level are bolded and illustrated by a *. Bs = black spruce, Ws = white spruce, Bf = balsam fir and El = eastern larch.

3.7. Figures



Figure 3.1: Map of Labrador showing study area. Black circles show the location of the five study sites.



Figure 3.2: Seasonal temperature and precipitation patterns across the study transect. Sites are organized from the coast (left) inland (right). A) Average seasonal temperature values for the Mealy Mountains and Red Wine Mountains are derived from Cartwright, and Goose Bay, and Churchill Falls sites, respectively. B) Total seasonal precipitation values from Environment Canada climate stations.

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1580 1700 1720 1740 1750 1780 1800 1820 1840 1860 1880 1900 1920 1940 1960 1980 2000

Figure 3.3: Time series of the radial growth for all tree ring chronologies, per species. Sites are ordered from coast (top) inland (bottom). Times series show periods when EPS values are below (grey) and above (black) 0.85. Triangles on fir and larch graphs depict decades when spruce budworm (Boulanger and Arsenault 2004) and larch sawfly (Jardon et al. 1994) insect infestations were reported for Quebec.



Figure 3.4: Significant (95%) bootstrapped correlation (r) values between black spruce chronologies and seasonal climate variables. Y-axis represents the r-value, and x-axis represents the study sites, ordered from the coast (left) inland (right). Filled figures represent temperature, open figures precipitation. Squares, triangles and circles represent spring, summer and fall conditions, respectively. At Site 3, balsam fir and eastern larch are correlated against Churchill Falls precipitation. All other cases are correlated to Goose Bay data.

Chapter Four

4. On the divergence problem in eastern Canada: changing climatic sensitivities of two spruce species across a moisture gradient

4.1.Introduction

Climate reconstructions from tree rings are a significant source of long-term, highresolution data on past climate variability and can incorporate various spatial scales (i.e., hemispheric, Haugen 1967; regional, Schweingruber et al. 1993). A key component of the dendroclimatological approach is the assumption that the relationship between tree rings and climate is stable over time, as dictated by the *uniformitarian principle*. The application of this principle requires that present-day limitations on tree ring variability must have remained unchanged in the past in order for palaeoclimatic reconstructions to be reliable (Fritts 1976). Increasingly, studies are showing that the sensitivity of tree growth to climate may not be stable (Jacoby and D'Arrigo 1995; Briffa et al. 1998; D'Arrigo et al. 2008). These findings raise concerns about the accuracy of dendroclimatic reconstructions; if present environmental controls on tree growth are unstable then the reconstruction of past climate and the prediction of growth under future climate scenarios may be unreliable. This occurrence has been termed the "divergence problem" (D'Arrigo et al. 2008).

The divergence problem is defined as a recent weakening in the relationship between tree rings and temperature or a change between these previously-determined

synchronous trends (D'Arrigo et al. 2008). Briffa et al. (1998) first reported on the reduced sensitivity of trees to temperature during the second half of the 20th century throughout the northern hemisphere. Recently, other researchers identified a similar phenomenon in Alaska (Jacoby and D'Arrigo 1995; Wilmking and Myers-Smith 2008) and the Italian Alps (Carrer and Urbinati 2006; Oberhuber et al. 2008). There has been no consensus on the cause of divergence, although some results suggest that moisture effects may be playing a role. In particular, Wilmking and Myers-Smith (2008) found that microtopography, through peatland versus drier open canopy sites, affects climate sensitivity, where the drier sites are more time-stable. This chapter documents the occurrence of divergence in recently acquired radial growth records in spruce trees from central Labrador, northeastern North America, and investigates its spatial and temporal patterns.

Central Labrador (Latitude ~53°N) is on the eastern extent of the North American boreal forest and its climate is affected by both continental and marine influences. The proximity of the Labrador Sea shapes the climate of Labrador and in turn, these climatic patterns shape the current tree distribution (Meades 1989). Inland, a more continental-like climate dominates throughout the year, whereas further to the east the proximity of the Labrador Sea commonly ensures a late spring and cool summers. The occurrence of highlands across central Labrador with a well-defined forest-tundra ecotone, permits sampling near treeline where the climate signal in tree rings should be amplified (Fritts 1976).

Four species are found at alpine treeline in Labrador: black spruce, white spruce, balsam fir (*Abies balsamea* (L.) Mill.) and eastern larch (*Larix laricina* (DuRoi) K.

Koch). Dendroclimatic studies from central Labrador have shown that, of the aforementioned species, the radial growth of spruce trees is particularly dependent on both temperature and precipitation (Schweingruber et al. 1993; Trindade et al. 2007; Trindade et al. 2008). Furthermore, the characteristics of the radial growth /climate relationship in northern Labrador are heavily reliant on proximity of the ocean – in this case the Labrador Sea (Payette 2007). In northern Labrador, the relationship between spruce radial tree growth and temperature is reversed between coastal sites and those further inland; along the coast, white spruce trees are growing in tandem with global climate trends whereas those trees located further inland are retreating, possibly as a result of exposure, as they are located on upper sites.

Currently, knowledge on the temporal pattern and of the relationship between tree rings and climate is largely unknown, as are the causes for these patterns. This chapter uses the two most climatically-sensitive species –black and white spruce – available in central Labrador to assess whether their climate sensitivity is stable and whether this sensitivity is related to proximity of the Labrador Sea. It describes the spatial and temporal patterns of their sensitivity to climate with reference to temperature and precipitation. In order to do so, spruce trees were sampled at alpine treeline sites across central Labrador, at varying distances from the Labrador Sea.

4.2. Methods

Samples were collected along the same lines of latitude (~53-55°N) and at varying distance from the Labrador Sea (Figure 4.1; Table 4.1). At all sites an effort was made to sample trees near their limit of growth.

Eight tree ring width chronologies were constructed from four sites across central Labrador from black and white spruce trees (Figure 4.1; Table 4.1). Each chronology was constructed based on 60 cores sampled at breast height from 30 trees using a 5.1 mm increment borer. Two cores were taken per tree at right angles to each other. Samples were processed using standard mounting and sanding procedures in order to expose the tree rings (Stokes and Smiley 1968). Ring widths were measured to 0.001 mm accuracy using WinDENDRO software (version 2005a) (Guay et al. 1992).

Following preliminary visual analysis where damaged cores were removed from the analysis, crossdating of the measured radii was accomplished using COFECHA software (Holmes 1983). Sample cores that did not crossdate into the master chronology were removed. Master chronologies were standardized in ARSTAN using a double detrending method to retain as much high-frequency data as possible while removing long term trends (Cook 1985). The method used was first to employ a negative exponential curve followed by a 32-year-cubic spline with 50% cut off. This procedure resulted in a unitless index of radial tree growth for each species at each site.

Climate data

Climate data were obtained from local Environmental Canada stations (Figure 4.1; Table 4.1). Growing season temperature and precipitation are comparable across the transect: June-September average precipitation ranges from 88 to 98 mm and air temperature from 10.4 to 12.8°C (Environment Canada 2008). The maritime influence on terrestrial climate, however, is most obvious during the spring and fall; the coast experiences on average 70 hours less bright sunshine in the spring due to the higher incidence of fog

along the coast. The first frost occurs approximately two weeks earlier at inland sites (Banfield and Jacobs 1998).

Running correlations were used to track the relationship between radial growth and each climate variable over the time span of the eight master chronologies. To do this, a correlation was established between the first 11 years of the climate record and the corresponding years for the tree ring record. The resulting correlation value was positioned in the middle of section. That is, if a running correlation was run for the years 1950-1960, the corresponding correlation value was plotted in 1955. The same process was repeated, with a 1-year lag, to the end of the climate record.

The use of shorter-term running correlations was necessary given the shorter length of the instrumental climate records in Labrador (Table 4.1). Although it would be possible to apply longer running correlations at Sites 1 and 2, it was necessary to preserve the same methods across the transect, and so adjustments were made to accommodate the shorter climate records at Sites 3 and 4. Longer running correlation lengths enhance longer term shifts and smooth out short-term aberrations (Jacoby and D'Arrigo 1995; Carrer and Urbinati 2006; Wilmking and Myers-Smith 2008), whereas shorter correlation lengths highlight fluctuations in sensitivity thus amplifying results in the immediate past. Given the lack of knowledge on the issue of divergence, it is argued that the use of short running correlations is appropriate here, especially given the limited instrumental data set.

4.3. Results

At Sites 1 and 2, the climate data used were from the Cartwright station (Figure 4.1; Table 4.1). At this climate station, records show that June-September precipitation values

have increased from an average value of 82 mm from 1938 to 1974 to an average value of 97.6 mm from 1975 to 2004, a trend that is apparent in Figure 4.2 (Sites 1D and 2D). June-September temperatures have also risen, from a low value of 9.4°C in 1985 to 11.5°C in 2004 (Figure 4.2). At Site 3, tree ring width data were correlated against climate data from the Goose Bay station (Figure 4.1; Table 4.1). Similar to Cartwright, the Goose Bay data show that precipitation totals have increased from 82 mm (average from 1943 to 1974) to 96.3 mm (1975-2004) and temperature has risen from a low value of 12.7°C in 1985 to 13.4°C in 2004 (Figure 4.2). The climate data at Site 4 is from the Wabush climate station (Figure 4.1; Table 4.1). There is no discernable pattern in the precipitation data in this short climate record, but there has been an overall rise in June-September temperature at this site since the early 1990s (Figure 4.2).

Site 1- Cartwright

The radial growth patterns for the two spruce species at Site 1 are similar over the instrumental period, but they do at times deviate significantly. In particular, the tree ring index values for the two species differed in the 1950s, around 1970, and during the 1980s and 1990s (Figure 4.2). Figure 4.2 shows that sensitivity to temperature reverses at several points in the record. Temperature sensitivities are generally positive for black spruce and negative for white spruce. There is a notable reversal from these trends in the 1950s and 1980s for both species (Figure 4.2). The two species also deviate from their respective sensitivities to precipitation (negative for black spruce and positive for white spruce) during the 1960s and 1980s (Figure 4.2). Both species' relationship to precipitation has had a positive trend since the 1980s, which is synchronous with rising temperatures and precipitation values (Figure 4.2).

Site 2 - Mealy Mountains

The radial growth patterns for black and white spruce at Site 2 are similar through the instrumental climate record (Figure 4.2), as do their sensitivities to temperature and precipitation (Figure 4.2). Both species are positively correlated to temperature, but black spruces' thermal sensitivity is weak during the early 1950s, and both species experience weak thermal sensitivity during the late 1960s. Further, there is a trend towards lower thermal sensitivities for both species during the late 1990s (Figure 4.2). The running correlation values for precipitation are negative overall for both species, although the values deviate from this trend in the late 1940s/early 1950s, late 1960s and the entire 1980s decade (Figure 4.2).

Site 3 – Red Wine Mountains

The radial growth trends for black and white spruce trees at Site 3 are similar, although the patterns deviate slightly during the late 1960s and early 2000s (Figure 4.2). Similarly, the running correlation values between spruce radial growth and temperature at Site 3 are similar to the values from Site 2 (Figure 4.2). At both sites, species experience a loss in thermal sensitivity during the late 1960s/early 1970s and during the 1990s. At Site 3, however, black spruce sensitivity reverses during this latter decade, and becomes negative (Figure 4.2). The sensitivity of spruce trees to growing season precipitation values is more variable than that for temperature (Figure 4.2). In particular, there are reversals in the running correlation values for precipitation during the late 1960s and 1980s (Figure 4.2).

Site 4 – Labrador City/Wabush

The radial growth patterns of the two species at Site 4 are similar from the early 1980s to the present, but prior to this, the patterns are divergent, notably during the early 1940s, mid to late 1950s, early to mid 1960s and mid to late 1970s (Figure 4.2). The running correlation values in Figure 4.2 reverse and change frequently during this short instrumental record. The running correlation values for precipitation are less variable, as they only reverse in sign once and shift towards 'zero' during the 1970s, 1980s and 1990s (Figure 4.2).

4.4. Discussion

Figure 4.4 summarizes the trends in running correlation values. The nature of the correlations was arbitrarily classified based on a running r-value of 0.1: a running correlation value above 0.1 was classified as positive, below -0.1 as negative and between 0.1 and -0.1 as neutral. This method was used to differentiate between reversals in climate sensitivities vs. shifts towards weaker or non-sensitivity. The total number of reversals in black spruce, when all running correlation values at all sites were taken into account is 25, compared with 22 for white spruce and the total number of shifts was 15 for black spruce compared with 18 for white spruce, thereby weakening the possibility that there was a species-specific origin for the divergence problem in Labrador when using spruce trees.

The use of 11-year running correlation rather than 31-year correlations was necessary in order to accommodate for the length of the instrumental climate stations, in particular those at Sites 4 and 5 (Figure 4.2). Shorter running correlations affect the interpretation of the results because they highlight more details in the tree's climate sensitivity. A comparison of the results using 11-year (Figure 4.2) and 31-year (Figure

4.3) correlations illustrates this. The running correlation lines in Figure 4.3 are more stable and cross over the zero line with less frequency. However, the overall trends between the graphs using the 11-year and 31-year correlations are similar. For example, at Sites 1 and 2 and, to a lesser extent Site 3, the running correlation values in all graphs shift towards neutral sensitivity in the late 1960s-early 1970s. However, at Site 3, this shift is only observed in the 31-year running correlations to precipitation whereas it is seen in the running correlations to temperature and precipitation when using the 11-year correlations.

The interpretation of the data assessed from using a 11-year or 31-year running correlations can yield different conclusions. In particular, the use of 31-year running correlations smoothes out the variability in the sensitivity of trees to climate. A comparison between the results from 11-year correlations (Figure 4.2) and from 31-year correlations (Figure 4.3) shows that some of the most distinct patterns, such as the loss in climate sensitivity at most Sites in the late 1960s-early 1970s, are still present, and so the differences between the two methods may not always be pronounced. Given the lack of knowledge on the characteristics and causes of the stability of the relationship between tree rings and climate, I argue that those results with the higher variability, using 11-year running correlation, are desirable. Should divergence be caused by a high-variability issue, it will only be visible when using the 11-year data.

Forest disturbance events

Forest disturbance events such as insect outbreaks may also play a role in the occurrence of shifts in climate sensitivity. Figure 4.4 shows that all sites experience shifts in sensitivity to temperature and precipitation during the early 1950s, late-1960s and early

1970s, and from the 1980s to present. Disturbance events such as insect outbreaks cause narrow tree rings and can induce a loss in climatic sensitivity (Boulanger and Arsenault 2004). This occurs because insects defoliate trees, which causes the tree to allocate a portion of its resources to needle regeneration rather than radial growth, thereby causing a loss in climate sensitivity (Kulman 1971). Both black and white spruce are susceptible to spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks and outbreak events have been documented in eastern Quebec and, synchronously, across central Labrador in the 1950s, 1970s and 1980s (Boulanger and Arsenault 2004).

The spruce budworm can migrate at a rate of 50-100 km per year (Greenbank et al. 1980) and the distance between sites sampled in eastern Quebec and western Labrador is approximately 500 km. These outbreaks have also been shown to last between 1-25 years (Williams and Leopold 2000; Boulanger and Arsenault 2004; Gray 2008) and so it is likely that a period of budworm outbreak in eastern Quebec overlaps temporally with one in Labrador. Given the length of period of neutral sensitivity to temperature at Sites 2 and 3 in the early 1970s (between 5-10 years, without taking into account that the data are transformed through the application of an 11-year running mean), it is possible that a period of spruce budworm outbreak in Labrador caused the spruce trees to loose their sensitivity to climate during this time period.

Although it is difficult to assess with absolute certainty whether these episodes of reduced climate sensitivity are solely the result of insect outbreaks, there is marked synchronicity between the Quebec insect infestation history and the variability in radial growth/climate relationships shown here. Based on these results, it appears that episodes of insect outbreaks are coincident with shifts in climate sensitivity rather than reversals,

which must be caused by another factor. These factors include, but are not limited to, those that are anthropogenic in origin, methodological, biological, or climatic (D'Arrigo et al. 2008).

Temperature

There is a noticeable difference in the number of temperature-related (17) and precipitation-related (30) reversals over the entire study area. Summer temperatures in Labrador have been rising since the early-1990s, following global trends. This is evident in Figure 4.2. At all four Sites, the sensitivity of spruce trees to temperature either tends towards neutral or is neutral during the later portions of the temperature running correlations graphs (Figure 4.2). This pattern may support the hypothesis for the anthropogenic origin for the divergence problem, proposed by Briffa et al. (1998) and D'Arrigo et al. (2008)

Moisture

Although Wilmking and Myers-Smith (2008) noticed these differences with respect to soil moisture whereas in the present case it is with respect to precipitation levels, it appears that in Labrador, like in Alaska, moisture availability plays a role in tree sensitivity to climate. In Alaska, trees growing on sites with abundant soil moisture were less climatically-sensitive than those growing under drier conditions (Wilmking and Myers-Smith 2008). In Labrador, a similar pattern is detected at several Sites using precipitation values only. For example, at Site 1 (Figure 4.2), the two spruce species' sensitivity to precipitation tends towards zero during the period of peak rainfall (~1990). Post-1980 at Site 2 (Figure 4.2) spruce trees experience a loss in sensitivity to precipitation simultaneously with an increase in precipitation in the instrumental record

(Figure 4.2). At Site 3 the running correlation values to precipitation fluctuate from negative to neutral at the same time as the precipitation values increase, from the beginning of the record to peak precipitation values in the late 1960s. This association continues from 1980 to present, when precipitation values decrease, and the running correlation values fluctuate from neutral to negative. At Site 4, running correlation values are neutral or near-neutral for most of this short record and, at this site, the seasonal precipitation values never fall below 90 mm, as they do at times at the other sites.

Ecologically, negative sensitivity to precipitation implies that trees benefit from less precipitation; this may be due to trees experiencing water saturation as a result of increased precipitation, in particular when periods of high precipitation occur in tandem with cooler periods. In these cases, trees can suffocate, as poor soil drainage decreases the efficiency of nutrient uptake by roots and low temperatures decrease evapotranspiration, resulting in narrow annual radial growth. Across central Labrador, these periods of peak rainfall are sometimes coincident with narrow radial tree rings, in particular at Sites 1, 2 and 3. Although it is not possible to conclude that rainfall amount is directly responsible for changes in the sensitivity of trees to precipitation, it appears that high levels of moisture in this already wet environment affects the stability of the relationship of tree radial growth to precipitation across central Labrador.

Proximity of the Labrador Sea

There is no noticeable difference in the frequency or timing of reversals between the four sites in the Labrador transect. At the coastal site, for instance, the climate is strongly influenced by the proximity of the Labrador Sea and, it was expected that this would yield site-specific patterns in climate sensitivity (Banfield and Jacobs, 1998). However, a

major climatic difference between the coastal site and inland Labrador is in amount of solar radiance in the spring and/or the timing of the first frost in the fall (Banfield and Jacobs 1998). Since the climate data in the present study encompasses June-September values of temperature and precipitation only, this difference between the coastal and inland sites may have been overlooked. A future study focusing on monthly climatic values, may therefore verify if the influence of the proximity of the Labrador Sea affect species' climatic sensitivity differently throughout the year.

The trends in the running correlation values at Sites 2 and 3 are very similar. In particular, the climate sensitivities to temperature are more stable at these two sites than the coastal or inland sites. Both Sites 2 and 3 only have three shifts in their sensitivity to temperature and, at Site 2 there are no reversals in temperature sensitivities and only two reversals at Site 3. The climate data used at Sites 2 and 3 are from two different stations and the tree ring width chronologies constructed at these sites have the highest interseries correlation values, suggesting that there is commonality between them (Tables 4.1 and 4.2). Sites 2 and 3 are topped by large areas of tundra-like vegetation, whereas at the other two sites, the tundra zone is much smaller. As such, trees at Sites 2 and 3 may be closer to their limit of growth, and therefore have a more stable and cohesive climate signal (Fritts 1976). On the other hand, the trees at Sites 1 and 4 may be responding to a more compound climate, since they are not as close to the edge of their range and therefore display additional variability in their sensitivity to climate.

4.5. Conclusion

Until recently, it was generally assumed that the correlation value between a tree ring index for a climatically sensitive species and the climate variable in question was
constant over the instrumental period. Thus, depending on the strength of the correlation any reconstruction of past climate made on the basis of the statistical relationship would generate a reliable palaeoclimate record. More recently, the recognition of the divergence problem illuminated the issue of variable correlation over time and, as the name suggests, an increasingly weaker correlation between radial tree growth and climate.

To date, the divergence problem has been largely defined as a recent effect, with implications that its causes are at least in part, anthropogenic in origin. However, this study and others (Wilmking and Myers-Smith 2008) have shown that the relationship between tree radial growth and climate is not always temporally stable over time periods that are not limited to the recent past. As such, these latter studies imply that climate instability is a natural phenomenon that is misunderstood. Climate instability appears to be linked to local environmental factors such as insect infestations and moisture amounts, but the exact nature of that relationship remains to be confirmed.

The results presented here suggest that there needs to be increased vigilance on future dendroclimatic reconstructions. The presentation of a running correlation graph of climate sensitivity, along with the standard calibration/verification graph would demonstrate the data quality on palaeoclimatic reconstructions. This chapter has also shown that some sites are not suitable for dendroclimatic reconstructions, even if they appear to be so *a priori*. For instance, an alpine treeline may be climatically limited, and as such deemed appropriate for a climatic reconstruction, but deeper analysis may reveal periods of insect outbreaks, which effectively eliminate the relationship between radial tree growth and climate and weaken the dendroclimatic reconstruction.

4.6. References

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4.7. Tables

Table 4.1: Site characteristics for locations from where tree ring chronologies wereconstructed. The names of the climate stations used for each site are shown, along with
the length of the instrumental record at each station.

Site	Site name	Latitude (N)	Longitude (W)	Elevation (m asl)	Approximate Distance from Sea (km)	Climate data
1	Cartwright	53° 43.0'	57° 25.0'	550	40	Cartwright (1938-present)
2	Mealy Mountains	53° 36.5'	59° 48.5'	570	140	Cartwright (1938-present)
3	Red Wine Mountains	53° 47.5'	62° 5.0'	574	280	Goose Bay (1942-present)
5	Labrador City	52° 55.8'	66° 52.4'	730	660	Labrador City (1961-present)

Table 4.2: Characteristics of tree ring width chronologies. Segments are the number of cores taken to build each chronology. The r-value is a measure of the overall fit between the segments used to build the chronology. The SD determines the spread of that fit and the AC_f is a measure of the influence of the radial growth of one year on the next year's growth. The MS measures how much ring widths change from one year to the next, irrespective of the previous-year's growth.

Site	Species	segments	Period	Mean tree age (range)	Interseries correlation (r)	Standard deviation (SD)	Filtered Autocorrelation (AC _f)	Mean Sensitivity (MS)
1	Black Spruce	27	1851-2006	58 (22-111)	0.435	0.390	-0.035	0.292
	White spruce	23	1823-2004	96 (54-152)	0.478	0.388	-0.032	0.251
2	Black Spruce	32	1824-2005	88 (25-172)	0.509	0.335	-0.035	0.267
	White spruce	45	1758-2006	97 (33-205)	0.581	0.376	-0.025	0.251
3	Black Spruce	22	1813-2006	94 (43-160)	0.456	0.272	-0.023	0.218
	White spruce	23	1840-2006	78 (41-160)	0.520	0.311	-0.011	0.232
4	Black Spruce	24	1755-2006	105 (58-154)	0.486	0.289	-0.028	0.184
	White spruce	24	1868-2006	88 (25-139)	0.509	0.452	-0.020	0.202

4.8. Figures



Figure 4.1: Map of Labrador, showing location within North America and location of four sites sampled. Site 1 = Cartwright, Site 2 = Mealy Mountains, Site 3 = Red Wine Mountains, Site 4 = Labrador City/Wabush. Black triangles depict the location of the three Environment Canada climate stations used in this study.



Figure 4.2: Time series, correlation and climate results for black spruce and white spruce for four sites across central Labrador. In all cases, the black line represents black spruce and grey line is white spruce tree ring width indices. The radial growth time series are shown in (A). The 11-year running correlation values for tree ring index and (B) temperature and (C) precipitation. Dashed lines about the zero line in (B) and (C) represent the cut-off value of 0.1, identifying periods of positive, negative and neutral associations to climate. D) Illustrates averaged June-September climate data with 11-year running mean applied. Line is temperature, bars is precipitation data.



Figure 4.3: Correlation results using 31- year running means. Solid lines represent correlations to temperature (black for black spruce and grey for white spruce), dashed lines represent correlations to precipitation.



Figure 4.4: Summary graph of all correlation values presented. White bars represent a positive correlation, black bars negative correlation and grey bars no correlation.

Chapter Five 5. Conclusion

This thesis was the first to simultaneously apply dendrochronological techniques to multiple alpine treeline species across central Labrador. It has presented annuallyresolved tree ring evidence on three new species and contributed to the knowledge on the radial growth response of four alpine treeline species to climate. This work has also answered several spatio-temporal questions concerning the changing climatic sensitivity of alpine treeline species across a moisture gradient in Labrador and therefore has filled a large spatial gap in northeastern Canada.

The effects of the proximity of the Labrador Sea on climate are evident in the distribution of ecoregions, as suggested by Meades (1989). The results presented in this thesis suggest that trees experience ample moisture up to ~300 km from the coast, as observed through a shift in spruce tree's climatic sensitivity in the vicinity of the Red Wine Mountains. This is due to systems originating in the North Atlantic loosing moisture as they move inland. Consequently, east of the Red Wine Mountains, there is abundant moisture which originates from the Labrador Sea in addition to continental moisture carried by the predominant westerlies of the northern latitudes, whereas inland Labrador receives moisture from the latter only.

The palaeoclimatic reconstruction in the Mealy Mountains necessitated the merging of two tree ring chronologies in order to be statistically significant and highlighted the first instance of the divergence problem in northeastern Canada which weakens dendroclimatic reconstructions from the area. The comparative analysis of

several treeline species has also detected multiple periods of insect infestations which are temporally synchronous and characteristically similar to data from neighbouring Quebec. *Radial growth comparisons*

This thesis applied comparative analysis of the radial growth patterns of host and nonhost species in conjunction with reports of insect outbreaks events from eastern Quebec to infer the occurrence of insect infestation events across Labrador. This tentative conclusion would be reinforced by using specialized statistical software such as the dendroentomological program OUTBREAK, which flags an outbreak event when the radial growth of the host falls below a threshold value, when compared to that of a nonhost. All four species used in this study are sometimes-hosts for insects; black spruce, white spruce and balsam fir are hosts for spruce budworm and eastern larch is a host for the larch sawfly. As a result, the *a priori* assumption that all tree species follow an overall similar radial growth pattern except during periods of insect outbreaks is not valid. As a result, the use of the program OUTBREAK was not appropriate for this study, as it requires that one species not be susceptible to insect outbreaks, a condition that is not met here.

The radial growth comparison of four alpine treeline species was indispensable to this thesis. Most importantly, comparisons of the radial growth patterns of host and nonhost species has highlighted periods of reduced radial growth for local species which overlaps periods of known insect outbreaks from eastern Quebec, for a time period spanning the last two centuries. These periods of reduced growth are inferred to be the result of insect infestations. Further, the description of the frequency and characteristics of these proposed sawfly outbreaks in Labrador helped to explain the lack of climate

sensitivity observed in larch trees in Labrador. The concurrent comparison of all tree species has also confirmed that a period of radial growth reduction seen in the spruce trees in the Mealy Mountains in the early 20th century is more likely climatic in nature at this site, rather than insect-related, as it is in some parts of Quebec (i.e. insect outbreaks reported in: Blais 1961; 1965; 1981; Boulanger and Arsenault 2004, but not in: Krause 1997; Morin et al. 1993).

The abundant atmospheric moisture in coastal regions diminishes the frequency and severity of insect outbreaks along the coast. This is in accordance with Peltonen et al. (2002), who found that regional weather patterns determine spatial synchrony in insect populations. Wet spring conditions are more common along the coast and probably prevent spruce budworm larvae to progress into epidemic proportions (Simard and Payette 2001; Gray 2008). This also follows the theory of 'climate release' which states that insect populations may reach outbreaks levels due to local climate variability, such as consecutive dry summers and/or warm and dry spring conditions (Gray 2008). Both budworm and sawfly outbreaks are more common inland Labrador.

Temperature reconstruction

The temperature reconstruction in the Mealy Mountains is in accordance with other palaeotemperature records from Labrador (D'Arrigo and Jacoby 1993; D'Arrigo et al. 1996; 2003). The calibration and verification statistics of the reconstruction are significant, but very weak. This is in part due to the presence of the divergence problem in Labrador which reduces the reliability of the results. In this case, the divergence problem is defined as reversals and/or shifts in climate sensitivity which occur throughout the instrumental record period, rather than being limited to the recent past, as suggested

by D'Arrigo et al. (2008). Although shifts in climate sensitivity are synchronous with period of insect outbreaks, further studies are needed to confirm the cause of reversals. Moisture effects appear to play a stronger role that temperature effects on the climate sensitivity of tree species across central Labrador, but the specific cause of the shifts and reversals in climate sensitivity are unknown. The results presented here, along with those presented in studies in western North America, are suggestive of site-specific reasons (Wilmking and Myers-Smith 2008).

This thesis has emphasized the potential for the application of dendrochronological and dendroclimatological analysis in Labrador. Dendrochronology provides local-, regional- and hemispheric-scale annually-resolved information on the relationship between tree growth and climate. Prior to this work, tree ring analysis in Labrador was limited to white spruce at (predominantly) northern sites. These studies focused on merging tree rings chronologies from Labrador to others from Quebec, yielding large-scale inferences on the relationship between tree rings and climate, or on local and northern site-specific tree ring chronologies. This thesis complemented this by focusing on both local and Labrador-wide sites, across a moisture gradient, to study the relationship between tree rings and climate. Further, the simultaneous application of dendrochronological techniques to multiple species has highlighted some of the complexity of the forest characteristics in Labrador, such as the prevalence of insect infestations across central Labrador.

The results presented in this thesis provide insight on the potential response of forests across central Labrador to future environmental changes. Knowledge of the potential response of alpine treeline species in central Labrador to climate change is

significant due to the presence of the tundra vegetation located above the treeline, rendering it vulnerable to treeline migration. The most climatically-sensitive species, black and white spruce, will likely experience changes in radial growth variability that is directly related to local changes in temperature and precipitation. On the other hand, the radial growth of balsam fir and eastern larch trees is indirectly related to climate through the reliance of insect populations on climate. These insights can provide local stakeholders with site-specific information on the potential changes to the forests of central Labrador, with respect to climate.

This thesis has also highlighted areas where additional research on the relationship between tree growth and climate is necessary. In particular, the root cause of the instability of the relationship between tree rings and climate is still unknown. The strength of the relationship between tree radial growth and climate is site-specific and closely related to disturbance events and moisture levels in Labrador, but the exact nature of this relationship still needs to be discovered. Future studies should also focus on reinforcing the occurrence of insect infestations in Labrador, as these exert a significant influence on the radial growth of most alpine treeline species in Labrador.

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