

A Substantial Upward Shift of the Alpine Treeline Ecotone
in the Southern Canadian Rocky Mountains.

By

William Morgan Roush
B.A., Middlebury College, 2004

A Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of

MASTER OF SCIENCE

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ABSTRACT

Changes within and beyond the alpine treeline ecotone are hypothesized to respond to climatic changes and to be controlled by site-specific conditions. Repeated photographs show significant changes in the alpine treeline ecotone of Goodsir Pass in Kootenay National Park, B.C. over the past century. Field work revealed increases in tree density within the ecotone, and a 150 vertical metre increase in the elevation of the ecotone, at a rate of 2.2 metres/year. Change within the ecotone of Goodsir Pass is more closely related to temporal climatic variability than to site-specific spatial variability. Repeated photographs from three National Parks in the southern Canadian Rocky Mountains show this change to be a typical but dramatic example. Results at several scales indicate that the occurrence, magnitude and type of change in the alpine treeline ecotone and the drivers of that change are most influenced by the regional ecologic and geo-climatic setting or context.

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In this thesis I seek to understand the changes, or lack thereof, that have occurred in the alpine treeline ecotone (ATE) of the southern Canadian Rocky Mountains over the past two hundred years. The ATE is the zone of transition between continuous subalpine forest and alpine tundra. Encompassing a major boundary between two distinct ecosystems, the ATE is both sensitive to and threatened by climatic changes (Moir et al., 1999; Jobbagy and Jackson 2000; Paulsen et al., 2000; Grace et al., 2002). As the ATE includes the range margins of both tundra and forest species it provides an excellent location to assess the impact of climate change on vegetation (Rocheffort et al., 1994; Cairns, 1999).

Documentation of this change is critical to our understanding of how alpine and subalpine communities respond to climate change and the implications of increased warming for the subalpine and alpine zones (Butler et al., 1994).

In contrast to physical systems (e.g. glaciers, permafrost, snow cover), which often show rapid and tightly-correlated responses to climatic changes (Barry et al., 1995; Rapp, 1996; Haeberli and Beniston, 1998), it is assumed that ecological systems will respond to climatic changes in more complex ways which may include time-lags, ecological inertia, and spatial patterning (Chapin and Starfield, 1997; Körner 1999; Butler et al., 2007). Current research concerning ATE dynamics can be classified into two broad themes: research that shows that recent warming trends cause an upward shift in the elevation of the ATE and research that emphasizes the strong influence that localized geomorphologic and ecologic factors have on the occurrence, magnitude, type and spatial pattern of tree establishment within and beyond the ATE.

In this study I address the need for inquiry that, in the context of an ATE that has undergone significant change in the past one to two centuries, asks whether ATE dynamics are more influenced by coarse-scale climatic events or fine-scaled environmental conditions. Specifically, I will: i) document the type, magnitude, rate, timing, and character of change in

the ATE of Goodsir Pass^{*}; ii) assess the relative impact of drivers of this change; and iii) contextualize the results from Goodsir Pass by examining change in the ATE at a regional scale.

Photographs of the ATE near Goodsir Pass taken in 1906 and 1923, and repeated in 2007 and 2004, serve as a departure point for the research. These images were part of an extensive repeat-photography survey of ATE change in the Canadian Rocky Mountains, the Southern Alps of New Zealand, and the Scands Mountains of Norway, which identified Goodsir Pass as a location where a globally significant increase in the elevation and density of the ATE has occurred (Roush, unpublished photo-pairs). Four photo-pairs of the study site provided substantial information concerning changes that occurred in the ATE in Goodsir Pass over the past century. This initial information constituted several known knowns: tree density has increased; the upper margin of the ecotone has increased in elevation; and the forest structure of the ATE has changed from isolated larger (and presumably older) trees to numerous smaller (and presumably younger) trees. However, large amounts of information are missing from the photo-pairs. These obvious gaps in knowledge informed the three main research questions, what might be termed known unknowns.

- i. What is the magnitude, timing, rate, and type of change that has occurred over the past two centuries in the ATE of Goodsir Pass?
- ii. Are these changes driven primarily by climate shifts that allow change by removing a constraint on the ecotone, or are they primarily controlled by the underlying components - the site-specific environmental variables of the ecotone?
- iii. What changes are occurring in other ATES throughout the southern Canadian Rocky Mountains?

^{*} Goodsir Pass is located in northwestern Kootenay National Park, in the Canadian Rocky Mountains along the eastern edge of British Columbia, Canada. See Figure 3.1 for location and map of the study site.

The study and subsequent analyses also captured a third class of information: unknown unknowns. The inherent complexity of ecological systems makes it unrealistic to presume a foreknowledge of all relevant questions. Consequently, at the outset of this study I was unaware of what conclusions might emerge as important and relevant. Therefore, I collected certain data without a clear indication of what questions they might answer. The importance of these data has only been determined subsequent to analysis, interpretation, and comparison with other results. The most significant interpretations to emerge from this class of information contribute to the field of landscape ecology and indicate that coarse-scale geo-climatic and topographical patterns significantly influence the importance that fine-scale topographical patterns have on the process of tree establishment.

To understand ecological phenomena in general, and ecotones in particular, research must be conducted at multiple scales (Gosz, 1993). Data for this study were gathered at two major scales and employed two distinct methods. First, intensive dendro-ecological field work produced data from Goodsir Pass to determine establishment dates and the geomorphologic and ecologic setting of trees growing in the ATE. As there has been no significant anthropogenic, ecologic or geologic disturbances in Goodsir Pass for over a century the location is well suited to studying long-term landscape change at a sensitive ecological boundary. Second, a series of repeated photographs from Waterton Lakes, Kootenay and Jasper national parks provided data to determine the extent and nature of ATE change across an entire landscape. These coarse-scale image-derived data provide context for the results of the fine-scale data collected in Goodsir Pass. Combining these two methods provides evidence for changes in the ATE from multiple lines of evidence. The information obtained is both qualitative and quantitative, provides a comprehensive spatial view of change in the ATE, and is evocative to broad audiences.

The research undertaken for this thesis is interdisciplinary and contributes to the fields of geography, environmental studies, and landscape ecology. Additionally, the findings from this study contribute to the Mountain Legacy Project, an interdisciplinary research initiative

examining landscape change in the mountains of Western Canada through the use of repeat photography*.

This thesis has seven chapters. Chapter Two is a review of the relevant literature concerning ATE dynamics, first defining the ATE and giving a brief history of ATE research. The bulk of the chapter addresses factors that control the position of the ATE, and causes of change in the ecotone. I then explore the two somewhat conflicting themes concerning change in the ATE: i) ATE change driven by climate at the constraints level; and, ii) ATE change controlled by the site-specific components of the system. Chapter Three contains a description of the study site at Goodsir Pass, how and why it was chosen, and provides background on the geology, climate, ecology and human history of the area. In Chapter Four I describe the collection and analysis of data. Data used in this study fall into three broad categories: field data that were collected in a series of plots laid out near Goodsir Pass, which include trees cores and information concerning vegetative and snow cover, trees, and topography; image data which consist of repeated images both from the study site and from repeat photography surveys in Waterton Lakes, Kootenay and Jasper national parks; and climate records and climate reconstructions. In Chapter Five I present the results of this study, starting with climate data. The majority of the chapter deals with results from analysis of the dendro-ecological field data, and addresses the establishment data, the character, magnitude and rate of change within the ATE, the relationship of tree establishment to climate records, and the relationship of tree establishment to site-specific conditions. I conclude the chapter by presenting results from the repeat photography of both the study site and the broader region. In the latter case, change in the ATE is examined in terms of landscape position and the aspect of the slope on which the change took place.

Chapter Six is a discussion and interpretation of the results. The main conclusions reached from the study are as follows. First, a substantial upward shift (ca. 150 vertical metres) and increase in density of the ATE in Goodsir Pass has occurred in the past one to two centuries. Second, correlations between tree establishment and climate records and the more pronounced temporal, rather than spatial, patterning of tree establishment indicate that

* Repeat photography is the process of locating the exact position from which an existing photograph was taken, occupying that photo-point, and taking a new photograph to create a photo-pair of the same scene.

the change in the ATE of Goodsir Pass is driven primarily by climate. Third, changes are occurring in the ATE throughout the southern Canadian Rocky Mountains; however the environmental context or landscape position strongly influences the type and magnitude of that change. Lastly, coarse scale patterns have a significant effect on the role finer scaled patterns play in the process of tree establishment. In Chapter Seven I conclude the thesis by describing some of the broader implications of this work. In it I suggest that the ecological and geo-climatic (and likely anthropogenic) context of an ATE is the most important factor in determining how and whether change will occur. I also discuss possibilities and needs for future research and the implications of this study for management and conservation of the ATE.

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2.1 Introduction.

Geographical shifts by both plant and animal species have been widely recorded in response to climatic changes (Walther et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003). These shifts are especially pronounced at the northern and upper margins of species' ranges (Grabherr et al., 1994; Sturm et al., 2001; Chapin et al., 2004; Hickling et al., 2006) supporting the hypothesis that species will move upward or northward as a response to rising temperatures. In mountainous areas, upward shifts are likely to be non-linear. Rather than moving upward in defined bands, shifting plant assemblages are influenced by local topography and soil moisture (Hall and Fagre, 2003). Individual plants, unlike animals, are stationary and are thus able to shift their ranges only between generations rather than within a lifetime. This results in slower rates of change among plant species in response to warming and likely links these rates to species traits (e.g. generation period, lifeform, and geographic distribution pattern) (Parolo and Rossi, 2008). Mountainous plant species, species with shorter life cycles, and grassy (rather than woody) species have been reported to shift upward more rapidly (Lenoir et al., 2008). Thus, the alpine treeline ecotone (ATE) as an assemblage of mountainous species and existing at the upward range of the tree species that compose it, is likely to respond markedly to climate shifts. The easily distinguishable transition between forest and tundra vegetation assemblages allows for these shifts to be measured, and when change is documented these changes suggest research questions into the timing, character, magnitude, and cause of shifts in ATE position.

Past research has shown ATE position to be the result of numerous interrelated factors (Cairns and Malanson, 1998) many of which are ultimately dependent on climatic variables (Hessl and Baker, 1997). While many recent studies have de-emphasized temperature as the primary driver of the location of the ATE (e.g.: Minnich, 1984; Cairns 1999; Holtmeier and Moir et al, 1999; Holtmeier, 2003; Bekker, 2005; Maher and Germino, 2006; Resler, 2006, Butler et al., 2007; Malanson et al., 2009) temperature in particular, and climate in general, remain two of the most frequently-cited controls of current ATE position and possible

future ATE change (e.g.: Stevens and Fox, 1991; Taylor, 1995; Hessler and Baker, 1997; Luckman and Kavanagh, 1998; Alftine et al., 2003; Lloyd et al., 2003; Körner and Paulsen, 2004; Roush et al., 2007; Vittoz et al., 2008).

This chapter begins by offering a definition of the ATE, outlines the history of research trends, describes the most common reasons given for the position of the ATE and ends by describing a framework for viewing recent and pertinent research on changes in the ATE. This framework suggests that change within the ATE can be driven by large-scale climate constraints and variability or by small-scale site-specific components of the ATE. I position much of my research to reflect this dichotomy and will try to answer which set of mechanisms exert greater influence on change within the ATE.

2.2 Defining the Alpine Treeline Ecotone.

The diversity of forms displayed by the ATE has generated an equally varied number of terms to describe it. This diversity often leads to ambiguity and confusion. Two of the more common definitions used in describing the ATE are: “timberline,” defined as “the upper limit of tall, symmetrical, closed canopy forest species” (Walsh and Kelly, 1990:24) or a full forest usually with at least 30% cover (Heikkinen, et al., 2002; Holtmeier, 2003); and “treeline” that occurs at a higher latitude or altitude and has been defined as the “upper limit of all tree species,” (Walsh and Kelly, 1990:24) or the “limit of upright trees” (Lloyd et al., 2003:1). Specific tree heights and densities have been used to demarcate the boundary between the forest and the ATE. Variation among species and site conditions makes this definition of limited use in many circumstances, especially those in which the ATE is controlled by a combination of factors. In contrast, Holtmeier’s (2003:27) definition, of “the transition zone between the closed forest and the upper limit of crippled trees” provides a balance between the need for specificity in research methods and the reality of natural variation.

Biologically, the upper limit of the ATE is hypothesized to exist at an altitude where the annual carbon balance of the trees equals zero (Stevens and Fox, 1991; Hessler and Baker, 1997; Cairns and Malanson, 1998; Cairns 2001). In this thesis I use the phrase “Alpine Treeline Ecotone” (ATE) to describe the functional and physiognomic transition zone

between densely growing tall trees and the alpine tundra. In this transition zone, trees become gradually shorter, grow in less dense stands and usually have slower growth rates. Within the ATE the extreme plasticity of tree physiognomy becomes apparent; trees become krummholz, often appear stunted, and may grow horizontally rather than vertically (Figure 2.1). Within the ATE, regeneration and growth are controlled less by the position and dynamics of other trees (as occurs within the forest) and more by environmental factors (Holtmeier, 2003).

Figure 2.1 Subalpine fir, in the Elk Mountains, Colorado, growing as a krummholz, a common growth form of trees in the ATE. (photograph by W. Roush).



The ATE is not simply a line at which the forest stops and the tundra begins; it is an ecotone where the character of trees changes. Therefore, recognizing and describing change in the altitudinal position of the ATE is not limited to shifts in the altitude of the uppermost tree in the ecotone. Instead a change in the altitudinal position of the ATE includes changes in tree density, tree growth form, tree height, and tree location.

The ATE, in addition to being hard to define as a true line (indeed “swath” might better describe the ecotone), is not only a phenomenon at high altitudes, but also occurs as a result of other physical and biological forces. The various types of treeline ecotones include: upper and lower altitudinal, latitudinal, drought, cold, moisture, salt-caused, orographic (cliffs or

talus), anthropogenic, and edaphic. In this study I focus on upper altitudinal treeline ecotones, though reference will be made to orographic treeline ecotones.

Holtmeier and Broll (2005) identify three types of ATEs that vary in sensitivity to environmental and climatic changes. *Orographic and edaphic treelines* have a constrained response due primarily to the inability of trees to establish in areas where geomorphologic processes are actively occurring or where the soil is too dry. *Anthropogenic treelines* have been significantly affected by past land use (in most cases a depression of the ATE elevation has occurred). A general shift away from logging and grazing in alpine areas (primarily in Europe) means that these ATEs are likely to increase significantly in elevation not as a response to climate but rather as a release from the past control of land use. *Climatic treelines* are not constrained by dramatic orography or anthropogenic influences; they respond to the interaction between climate and local- to landscape-level environmental variables. This response can take three forms: a physiognomic change of already established trees (e.g. krummholz forming upright leaders); a change in tree density within the ATE; and a change in elevation of the extent of the ATE caused either by establishment above the current ATE or by dieback at the upper margin of the ATE.

2.3 History of Alpine Treeline Ecotone Research.

Research concerning the causes of and changes in the ATE is extensive and extends back over 200 years, although it was not until the 1930s that treeline was considered from an ecological point of view (Holtmeier, 2003). Additionally, older studies focused more on the link between thermal conditions and the ATE, rather than taking into consideration the full complexity of variables influencing the ecotone (Holtmeier, 2003). This early research often noted the correlation between treeline position and the ten °C isotherm of the warmest month (e.g. Brink, 1959), which is valuable in predicting potential treeline elevation but does not provide any further insight into the causes of treeline position, or, as is often the case, the actual ATE elevation (Cairns and Malanson, 1997). Studies carried out within the past thirty years have emphasized and examined in greater detail the numerous other environmental factors influencing the ATE. Experimental research into ATE eco-physiology is less common than field observation and highlights the difficulty of generalizing results between or even within mountain regions (Holtmeier, 2003). Recently, particular

attention has been paid to whether a warming climate will cause an upward shift in the elevation of the ATE and how localized factors (including geomorphology, pathogens, animals, snow deposition, and previously existing vegetation) will influence, prevent or accelerate this shift (Butler et al., 2007). ATE research is most abundant from the European Alps, Scandinavia, and North America, while research concerning tropical and southern hemispheric ATEs is less extensive (Holtmeier, 2003).

2.4 Factors Controlling the Position of the Alpine Treeline Ecotone.

Numerous causes for the position of the ATE have been posited and the topic remains central to the study of treeline dynamics. While most studies concede that a suite of factors affect the position of the ATE and the potential for movement, many disagree about which factors are primary in their effect on ATE location and character. Most studies find climate or other factors ultimately influenced by climate to exert the strongest control on ATE position. In the most general sense, the upper margin of the ATE is caused by heat deficiency. Thus, the ATE decreases in elevation as the latitude increases and as the climate becomes more maritime (Holtmeier, 2003). Other factors mentioned as significant causes include microtopography -including tree islands themselves- (Holtmeier and Broll, 1992; Bekker, 2004), soil composition (Cairns, 1999), fire (Rocheport et al., 1994), winter injury (Cairns and Malanson, 1998), and aspects of tree reproduction including seed bank location and abundance (Cairns and Malanson, 1997). Additionally, the traits of individual tree species may result in a depressed upper limit of the ATE as is the case in New Zealand where exotic northern hemisphere species grow up to three hundred m above the native *Nothofagus* species (Wardle, 1983). While the growth and reproductive traits of trees growing in the ATE are significantly influenced by the current climate (Lloyd et al., 2005; Danby and Hik, 2007a) the position of the ATE is commonly a function of past climatic conditions (Payette et al., 2001; Holtmeier and Broll, 2005). Five of the factors most directly involved in determining the position of the ATE (carbon balance, tree form, climate, geomorphology, and human influences) are discussed below.

2.4.1 Carbon Balance.

Broadly speaking, the ATE will occur where the annual carbon balance of trees equals zero. This occurs when carbon sequestration equals carbon lost to respiration or outright loss of

tissue (Cairns, 2001). Trees have an annual carbon budget in which summertime accumulation makes up for wintertime loss (Holtmeier, 2003). In the ATE, these winter losses are often severe and include desiccation and winter injury. While many factors can influence the carbon balance of a tree, climate is the primary determinant of whether a tree has an annual net gain or loss of carbon (Hessl and Baker, 1997). Of the variety of climatic conditions influencing the carbon balance of a tree, temperature likely plays the major role as it directly influences the photosynthetic capabilities of the tree (Grace et al., 2002). A 0.5 °C decrease in daily temperatures is equivalent to a 46% reduction in insolation or a 50% increase in snow amount (Cairns and Malanson, 1998). Increased temperatures, especially in the late spring and summer, benefit krummholz both by providing increased water through snowmelt and by determining the inception date for photosynthesis (Cairns and Malanson, 1998). Other factors influencing the carbon balance of a tree include: (ranked in order of decreasing importance) winter injury, leaf area index, soil depth, rainfall, insolation and snowfall (Cairns and Malanson, 1998).

Not all research points to carbon balance as the primary factor that determines treeline elevation. In fact, it may be the ability of a tree to use available carbon - carbon allocation rather than carbon balance – which is most important to tree growth and survival within the ATE (Holtmeier, 2003). Tree growth is not limited by carbon supply (Körner, 2003); rather, it is a tree's effective use of carbon to produce growth rather than the initial ability to gain carbon that deteriorates with decreasing temperature. Cairns and Malanson (1997) found that while climatic conditions and the carbon balance of ATE trees are closely linked, the elevation of the ATE in Glacier National Park, Montana, was largely decoupled from the carbon balance of individual trees. From this, they conclude that tree carbon balance is useful in predicting the potential ATE elevation but not the present one.

2.4.2 Tree Form.

Stevens and Fox (1991) propose several reasons for the position of the ATE largely based on the phenotypic characteristics of trees. These characteristics place them at a disadvantage relative to herbaceous tundra vegetation in their ability to colonize the nutrient poor and high-stress environment of the tundra. Specifically, the high stature of trees relative to all other tundra vegetation causes them experience colder temperatures and more extreme

microclimate conditions than both trees growing within the forest canopy and tundra vegetation (Grace et al., 2002; Körner and Paulsen, 2004).

2.4.3 Climate Components.

As mentioned, climate (namely temperature and precipitation) exerts a primary influence on the position of the ATE, and can be divided into specific variables. These include length of the growing season, summer temperatures, winter temperatures and conditions (including winter injury and desiccation), snowpack depth and persistence, rainfall, frost-free days, evapotranspiration, precipitation during or outside of growing season, amount of light, relative humidity, and effective temperature sum (Heikkinen et al., 2002). Many studies have examined the importance of these variables, either singly or in combination, to determine their relative effect on the position of the ATE.

2.4.3.1 Length of the Growing Season.

Walsh and Kelly (1990:24) consider the length of the growing season to be “the most important factor influencing the location and quality of the treeline zone” and postulate that at least a two-month growing season is necessary for seeding establishment and sufficient growth to withstand winter. This hypothesis is also held by Wardle (1993) who argues that this constraint is the central factor in limiting trees’ ability to grow at higher altitudes.

Körner and Paulsen (2004) accept that this may be the case regionally, but that on a global scale the growing season varies greatly, from three months to a full year, and so is likely not the dominant factor in determining the position of the ATE.

2.4.3.2 Isotherms.

Various isotherms have been suggested as determining the elevation of the ATE, but regional variability, due to non-thermal conditions, in the correspondence between ATE elevations and isotherm elevations suggests that the ATE position cannot be predicted by an isotherm alone. While not explanatory on a global scale, a mean growing season isotherm of five to seven °C usually shares the same altitudinal limit as the ATE (Körner, 1998). On the North-American continent a mean isotherm of ten °C in the warmest month provides a rough indicator of the elevation of the ATE (Holtmeier, 2003).

Use of mean air temperature isotherms as predictors of the ATE elevation is complicated by the frequent use of low elevation climate stations as a method to calculate isotherms near the ATE using the adiabatic lapse rate. Körner and Paulsen (2004) found substantial evidence for the importance of ground temperature isotherms in determining ATE elevation on a global scale. While isotherm temperatures varied slightly by taxon and continent, ground thermal conditions were found to serve as a predictive tool for determining ATE elevation. Lastly, mean temperatures should only serve as proxies or indicators. Mean temperature is not a real ecological phenomenon and thus cannot be considered a direct casual factor in determining ATE position.

2.4.3.3 Temperature.

Temperature has long been thought to be the main factor controlling the position of the ATE, though recent research suggests its impacts are more diffuse and malleable. Taylor (1995:207) found “climate, especially temperature exerts a strong control on tree growth and tree population dynamics” and Hessel and Baker (1997) conclude that temperature is generally considered to be the primary factor controlling treeline. Rather than an isolated factor affecting ATE position through influence on individual trees, temperature is a meta-variable that is heterogeneous in space and time and exerts the greatest influence on ATE position by affecting factors specific and proximate to individual trees.

Temperature influences the position of the ATE most directly by imposing limitations on tree growth. Rates of photosynthesis and other biosynthetic processes are decreased at lower temperatures; which limits radial and apical growth (Grace et al., 2002). At a certain elevation low temperatures limit tree growth so severely that tree seedlings cannot survive. While the relative importance of temperature in determining ATE position shows a high degree of variability, several studies have conclusively shown the positive effect of warming on the growth of already established trees in the ATE both experimentally (Weih and Karlsson, 2001; Danby and Hik, 2007b) and by comparing growth and climate records (Gindl et al., 2000; Paulsen and Körner, 2000; Solberg et al., 2002; Frank and Esper, 2005).

Temperature at a given location is influenced most directly by slope aspect and elevation. Of these two variables, Cairns and Malanson (1998) showed that aspect has a greater effect

on temperature than most medium-scale (hundreds of m) elevation changes. This effect is dramatically evident in a rising ATE in the southwest Yukon where Danby and Hik (2007a) document a sixty-five m asl to eighty-five m asl increase in ATE elevation on southern slopes but no advance on northern slopes.

2.4.3.4 Precipitation.

While the absolute amount of precipitation certainly influences ATE dynamics by providing moisture to trees and ensuring that the roots of seedlings do not dry out, the timing of precipitation (either rainfall or release of snowpack melt water) may play a greater role in determining the position and character of the ATE (Cairns and Malanson, 1998).

Kusnierczyk and Ettl (2002) found that short-term tree growth had no correlation with temperature but was most influenced by non-growing-season precipitation, indicating the importance of moisture stored in snow. Other studies have shown establishment at the ATE to be positively correlated with normal or above normal precipitation (Taylor, 1995). The effect of precipitation on the ATE is likely influenced by local environmental factors and depends on the autecology of trees as much as the absolute amount of precipitation. In the Olympic Mountains, Washington increased tree establishment of mountain hemlock (*Tsuga mertensiana* [Bong.] Carr.) occurred in wet sites during periods of below-average precipitation, while increased tree establishment of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) occurred in dry sites during periods of above-average precipitation (Woodward et al., 1995).

2.4.3.5 Snow.

Snow has a variety of effects on the ATE position by influencing tree health and growth and seedling establishment in the ATE. Often the effects are so dramatic that snow depth and wind velocity can be deduced by examining the height, severity, and direction of damage to trees within the ATE (Wooldridge et al., 1996). With the exception of blown snow causing abrasion of plant tissue (Cairns, 2001), and avalanching (Walsh et al., 1994), these damaging effects of snow are a function of snow depth, snow water equivalent (SWE) and late spring/early summer snow-covered area. As a global predictor of the position of the ATE, snowpack is likely unreliable because tropical treelines exist in areas that receive no snow

(Körner and Paulsen, 2004). However, in the temperate and arctic zones, snowpack plays a significant role in ATE position.

Snowpack depth and duration has been both positively and negatively correlated with establishment, growth and continued survival of both seedlings and mature trees (Rocheftort et al., 1994). Negative impacts include: i) trunk and branch damage due to snow weight, slumping and avalanching (Walsh and Kelly, 1990); ii) shortening of the growing season due to persistence of spring snow (Franklin et al., 1971; Taylor, 1995); iii) growth of snow fungi (Rocheftort et al., 1994); and iv) shading of lower branches due to deep snow accumulated around the base of the tree (Cairns, 2001).

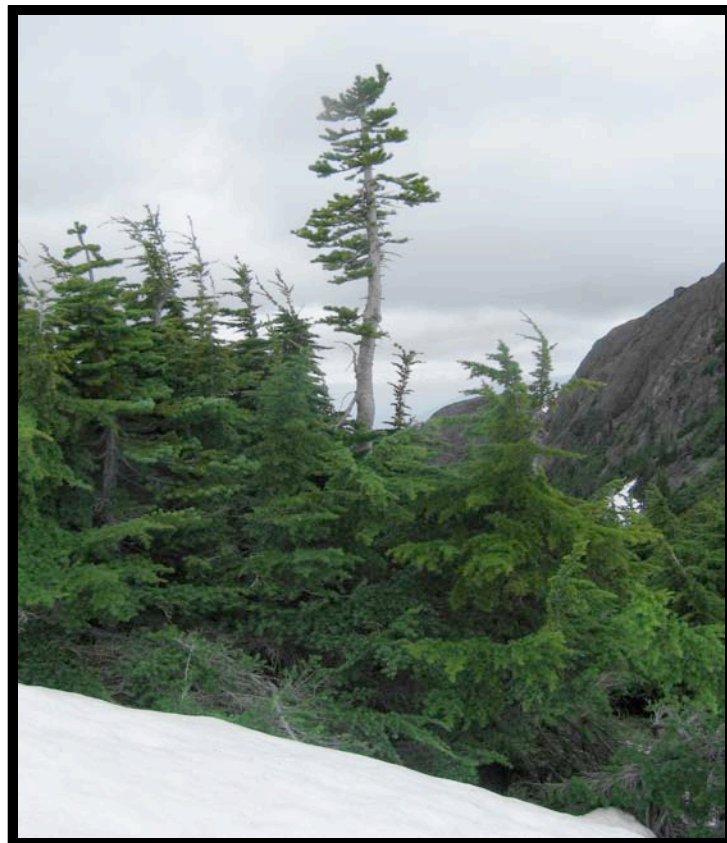
Positive impacts of a deeper snowpack include: i) insulation of seedlings (Cairns and Malanson, 1997); ii) protection from winter winds and drying (Walsh and Kelly, 1990); iii) prevention of summer drought due to increased soil moisture (Rocheftort et al., 1994; Walsh et al., 1994); iv) collection and deposition of nitrogen from the atmosphere (Cairns, 1999); and v) reduction of herbaceous vegetation (Magee, 1992).

Once established, tree survival, health and physiognomy are influenced by a variety of snow-related processes. Blown snow and ice crystals cause abrasion of bark and needles and can reduce a tree's carbon balance, especially for trees growing above the winter snowpack (Cairns, 2001). This is often displayed as flagging in which branches along the stem are stripped in the zone where saltation and blowing are most intense (Figure 2.2). Snow cover is also important for tree survival as it reduces winter water stress and prevents desiccation. In a planted tree experiment in the subalpine zone near Davos, Switzerland, Frey (1983) found that seedling mortality of Norway Spruce and European Larch was 20% and 40% higher respectively for seedlings that were kept snow-free during the winter. While avalanches do not affect trees across the entire ATE they do so dramatically in specific locations. Recurring avalanches on yearly or decadal scales creates a disturbance regime that affects the spatial extent and character of the ATE (Butler and Malanson, 1990). The main impacts of avalanches include localized depressions of the ATE due to slide paths, damage to trees above the snowpack and suppression of establishment and growth in runout zones where patches of late-lying snow are created (Malanson and Butler, 1986; Walsh et al., 1994).

2.4.4 Geomorphology and Topography.

The importance of site history and the local ecological and geological conditions in determining the position and character of the ATE has become an increasingly common topic of study (e.g. Brown, 1994; Butler and Walsh, 1994; Cairns, 1994; Malanson and Butler, 1994). Research has highlighted the role of geomorphology in determining ATE position (Malanson and Butler, 2007) and the role that micro-site shelters (in the form of soil risers, boulders and previously established trees) play in establishment patterns (Resler et al., 2005; Resler, 2006).

Figure 2.2 Blowing snow and ice crystals cause abrasion of bark surfaces and needles and a reduction in branch density within the zone of blowing snow, resulting in ‘flagging’ of this subalpine fir in the ATE on Mt. Arrowsmith, Vancouver Island, B.C. (photograph by W. Roush).



Geomorphology affects ATE position at all spatial scales. This is most obvious at larger scales (e.g. mountain ranges create the elevational gradient over which the ATE position varies). However, Butler et al. (2007) suggest that even at fine scales (a mountain slope or

ridge) where climate would be expected to be the primary factor in determining ATE position, microsites and shelters have a profound influence on whether and where tree establishment occurs. Specifically, Resler et al. (2005) identify the role that terrace risers and boulders play, first in creating sites suitable for trees to establish within the ATE, and then in creating micro-shelters conducive to growth and survival of young trees. Of 211 surveyed trees at three locations in the eastern portion of Glacier National Park, Montana, 206 established in sheltered sites, primarily on terrace risers. The authors attribute the positive impact of small-scale topography on seedling establishment and survival to nurse effects; the shelters moderate local temperatures, reduce wind speed, create seed traps, limit competition and increase soil moisture.

Topography also influences the location of trees within the ATE through complex interactions with multiple environmental variables. The interactions of wind, topography and snow produce similar annual spatial patterns of snow deposition, scouring, drifting, and meltout (Leydecker et al., 2001; Hiemstra et al., 2006). Topographically-controlled wind flows redistribute snow within the ATE, and the subsequent pattern of snow depth and timing of melt-out influence tree survival and establishment (Minnich, 1984; Moir et al., 1999). Specifically, upwind topography and the overall exposure for a given point play a significant role in determining snow depth and density (Winstral and Marks, 2002; Erickson et al., 2005). Anderton et al. (2004) examined the importance of upwind topography at various distances relative to the overall exposure of a given point and found that while upwind topography roughly thirty m distant from a site exerted more influence than closer or further terrain, it is overall exposure that exerts the most control on deposition of wind-transported snow for any given location. This observation points to the role of sheltered sites in trapping snow (Erickson et al., 2005) and likely explains the importance of boulders and terrace risers for tree establishment documented by Resler et al. (2006) in dry environments (where snow buries and protect seedlings and provides additional early summer moisture) such as eastern Glacier National Park, Montana.

There is a limit to the extent to which topography can affect snow redistribution. The effect of certain topographic features often depends on the relationship between their size and the amount and type of snow received over the course of a winter (Erickson et al., 2005). This

relationship is due both to the importance of snow-surface conditions in dictating how much snow will be redistributed due to wind and to a topographical smoothing effect that often occurs with increased snow depth. Deep snowpacks can lead to more homogeneous snow distribution as the snow itself creates a less abrupt topography, and relative differences in depth are masked by larger absolute values of snow depth (Berg, 1986). Erickson et al. (2005) suggest that while topography strongly controls the snow depth in low precipitation winters, during high precipitation winters it has a smaller effect because the snow creates new topography with reduced spatial relief. Quantifying the effect of topography on establishment patterns within the ATE becomes an especially important consideration if data are collected only over the course of a single season. Similarly, Anderton et al. (2004) point out that within-snow processes such as settling, sloughing, metamorphism and melt may diminish the beneficial effects of wind sheltering or exposure reduction over time. The benefits to trees of increased snow depths caused by wind sheltering is likely greater in continental climates where snow is light and in alpine areas where wind steering by rugged topography is more pronounced (Erickson et al., 2005).

2.4.5 Anthropogenic Influences on Alpine Treeline Ecotones.

While the impact of geomorphology on ATE position has been emphasized in North-America, research efforts in the more heavily human-impacted alpine environments of Europe has focused on the role of past land use in shaping the ATE. Maintenance of alpine pastures, grazing, and forestry within the ATE have combined to reduce the ATE elevation throughout the European Alps (Dirnböck et al., 2003; Holtmeier, 2003). In the Swiss Alps, Gehrig-Fasel et al. (2007) found changes in land use (specifically cessation of grazing) to be responsible for 96% of upward shifts in the ATE. Similarly, the position and character of the ATE in northern Norway has been attributed to grazing patterns over the past century (Dalen and Hofgaard, 2005). Areas used by reindeer for summer grazing are likely to have a depressed and sparse ATE due to increased grazing and trampling (Evans, 1996). However, winter forage for reindeer consists primarily of lichens that serve as a barrier to establishment of mountain birch (*Betula pubescens ssp. czerepanovii*) (Sveinbjörnsson et al., 2002). Thus, not only the presence or absence but also the timing of grazing influences ATE position (Tømmervik et al., 2004). The interactions of specific land-use histories and regional climate regimes combine to produce the structure and position of the ATE

throughout Europe at present. As land use of alpine areas diminishes and shifts to warmer climates become more dramatic, the ATE is likely to increase in density and elevation (Theurillat and Guisan, 2001; Vittoz et al., 2008).

In the southern hemisphere, ATE position has been strongly affected by grazing (Morales et al., 2005) and is frequently abrupt and relatively static reflecting the regeneration traits of the dominate treeline genus' (*Betula*) inability to establish beyond the forest limit and the presence of a subalpine vegetation belt which creates a hostile environment to tree seedlings (Wardle, 2008). Site-specific variables affecting the character of tropical ATEs include the amount of shading from other trees, the prevalence of fire, and photoinhibition (Bader et al., 2008).

2.4.6 Summary of Factors that Affect the Position of the Alpine Treeline Ecotone.

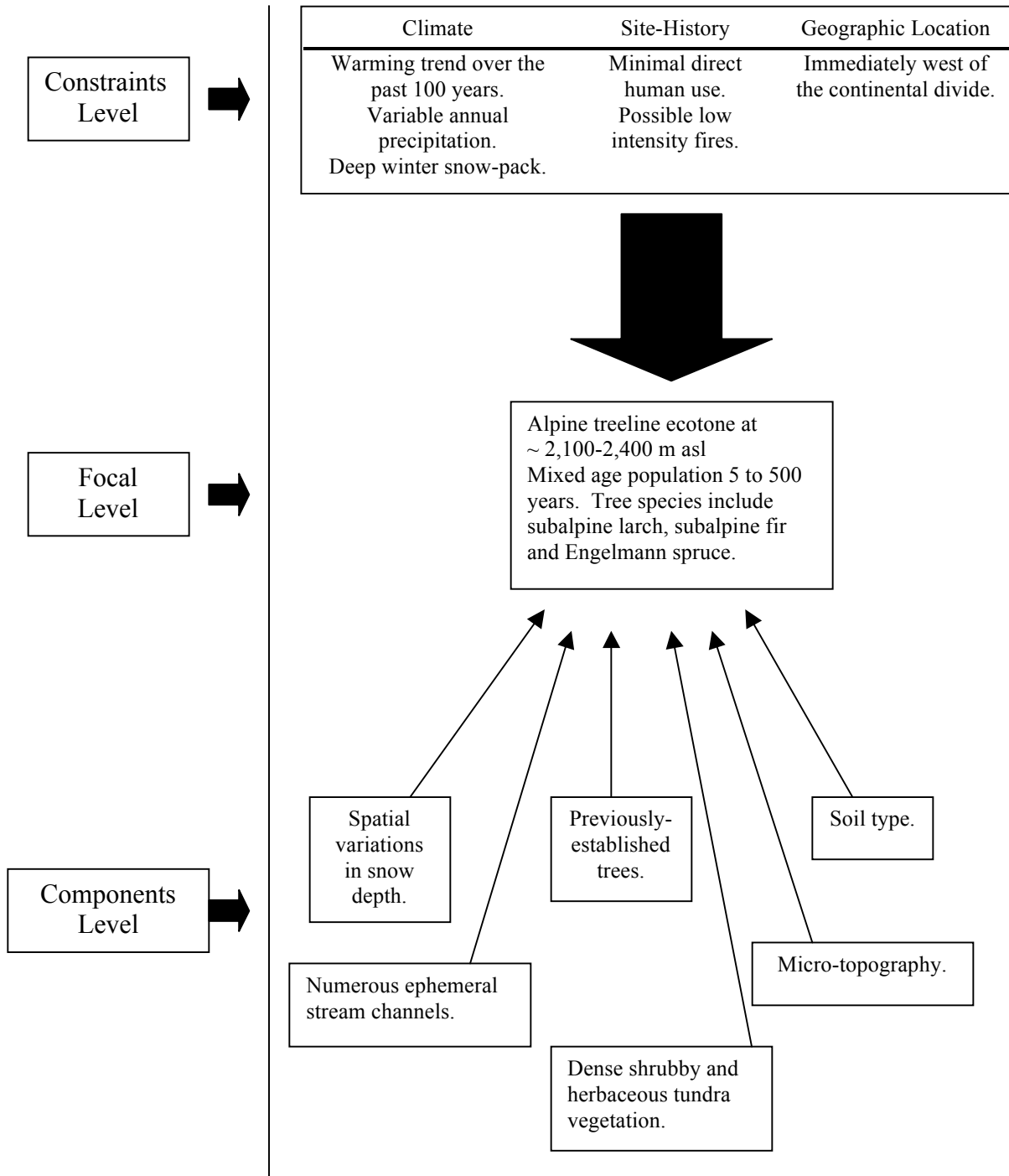
The proximate causes for ATE position are numerous and include carbon balance, tree form, climate, geomorphology, other trees, and humans. Many studies of ATE dynamics examine just one or two variables, and as a result miss a larger more complex picture. Three main conclusions can be drawn from an examination of the literature. First, no single variable is likely to be responsible for the ATE position. As environmental conditions in the ATE change through time the relative importance of certain factors is affected; one variable is not likely to be continuously dominant. Second, the present character and position of the ATE is often a function of past environmental conditions (Szeicz and MacDonald, 1995; Paulsen et al., 2000). Ecological inertia complicates research inquiry as those past conditions cannot be measured or observed directly in the landscape. Finally, it is useful to view the factors influencing the position of the ATE as underlain by basic climatic drivers, the influence of which is seen most commonly at large scales, but often determined most actively by small-scale, localized, and proximate factors. These localized factors (e.g. microtopography, tree island feedback, soils, aspect, and snow depth) exert more control on ATE position depending on: i) the degree to which the local position of the ATE is coupled to climate (e.g. is the ATE a relic - out of phase with current climate conditions) and ii) the intensity, geography, and interactions of the localized site-specific conditions (e.g. the influence of topography and wind on snow distribution within the ATE; or the size and activity of a scree slope).

2.5 Alpine Treeline Ecotone Change: Influences at the Constraint and Component Levels.

Initial descriptions of hierarchy theory suggest that landscape patterns can be explained by processes operating at lower level scales (Allen and Starr, 1982); for example, the pattern of vegetation across a landscape may be explained by examining soil moisture levels and the ability of individual plant species to survive in varying moisture regimes. Turner et al. (2001) offer a more comprehensive model. Building on Koestler's (1967) concept of a *holon* - "entities that were at the same time composed of parts, yet were also a whole that fits within its environment" (Turner et al., 2001: 34), the authors argue that three levels of scale must be considered in any study. The first is the *focal* level; the level at which the research question is being asked (the ATE in this study). The level above the focal level consists of *constraints* that control lower levels and provides a context for the phenomena observed at the focal level. The level below the focal level consists of *components*, the details of which explain the behavior of the focal level. This model creates a framework into which past ATE research can be examined and more focused future research strategies developed. Figure 2.3 applies the model of hierarchy theory as described by Turner et al. (2001) to the ATE in Goodsir Pass. In this study I use the concept of the *constraint* level to discuss large-scale drivers of ATE change, such as climate variability, and the concept of the *component* level to discuss site-specific conditions such as local geomorphology. Both tree populations and individual trees constitute the *focal* level.

Most investigations of changes in the ATE do not explicitly recognize hierarchy theory as a context for their research (exceptions include Resler et al., 2005; Resler, 2006). However, the theory provides a useful means of comparing results, conclusions and theories. Research that identifies climate as a significant driver of changes in the ATE position emphasizes the importance of the *constraint* level in driving ecotone dynamics. Here climatic changes have the potential to shift the position of the ATE by altering a limiting factor on tree establishment. Consistent change in ATE position and character, with variation in response

Figure 2.3. The model of Hierarchy Theory applied to the ATE in Goodsir Pass. Variables at both the constraint and component levels influence the character of change at the focal level, the ATE in this study. One of the research goals of this thesis is to ask whether the observed changes in the ATE are influenced more strongly by variables acting at the constraints level or variables acting at the components level.



occurring at the meso- to macro-scale*, is expected. Research that explains the position and character of the ATE as a function of geomorphology, vegetation and other site-specific variables emphasizes the *component* level as a driver of treeline dynamics. Here the assumption is that fine-scaled processes control the pattern of tree establishment. This type of research expects to find response of the ATE to climate change to be highly variable in space.

These two lines of thinking are not entirely mutually exclusive. The first (emphasizing the constraints level) assumes climate will exert a powerful enough control on the ATE to cause spatially-ubiquitous tree establishment regardless of variability in the landscape, with observable episodic pulses of establishment and mortality that coincide with a regional climate signal. The second approach (emphasizing the components level) positions climate as subservient to local conditions, and expects the response of the ATE to be highly spatially variable but generally consistent through time.

2.5.1 Climatically Controlled Change: Temporally Variable - Spatially Consistent.

Climate change is expected to force a change in the altitudinal range-margin of plant species (Grace, 1997). Recent studies have documented a contemporary increase in a variety of mountain species (Lenoir et al., 2008) including trees (Kullman, 2008). Tree establishment in the ATE has responded to both short- and long-term climate patterns at a variety of scales (Franklin et al., 1971; Woodward et al., 1995; Rochefort and Peterson, 1996; Kullman, 2000 and 2002). The most dramatic establishment has occurred in sharp pulses in which entire meadow systems were taken over by seedlings (Kearney, 1982; Taylor, 1995; Rochefort and Peterson, 1996). Many of these establishment pulses occurred despite considerable variation in site moisture and environment (Magee and Antos, 1992; Jakubos and Romme, 1993); however, the strength and type of the climate signal in temporal patterns of tree establishment shows substantial variation, which has led to skepticism as to whether it can be accurately identified as a causal factor (Holtmeier, 2003).

*In this study I use the terms micro, meso, and macro to describe the spatial extent of many patterns and processes. “Micro” refers to a scale of approximately one cm. to five m. “Meso” refers to a scale of approximately five m to five km. “Macro” refers to a scale of greater than five km.

2.5.1.1 The Response of Alpine Treeline Ecotones to Short-Term Climate Shifts.

Abundant research (Franklin et al., 1971; Kullman, 1991; Taylor, 1995; Suarez et al., 1999; Lloyd et al., 2003) shows that short-term (decadal or yearly rather than century-long) shifts in ATE position are possible and that such shifts may be episodic in nature (Hessl and Baker, 1997; Cullen et al., 2001). On the Seward Peninsula, Alaska, Lloyd et al. (2003) document spruce expansion coincident with the end of the Little Ice Age, and take this as evidence against a hypothesis of long lags in tree response to climate change. Similarly, Franklin et al.'s (1971) study in the northern Cascade Mountains of Washington State showed that the bulk of tree establishment into subalpine meadows occurred during a narrow temporal window (1928–1937) when the mass budget of the nearby Nisqually Glacier was negative; this relationship suggests a closely-linked system in which ecological response does not lag climate shifts. Expansion of mountain hemlock in the dry ATE of Lassen Volcanic National Park, California, showed a strong establishment pulse from the mid 1880s through 1915 that corresponds with an interval of mesic conditions (Taylor, 1995).

Kullman (1991:36) showed a close association between increases in tree growth and summer temperature rise, and concluded that the ATE responds to climate changes (both positively and negatively) in “dynamic equilibrium.” More detailed documentation from a twenty-five year ATE monitoring study by Kullman (2000) in the Swedish Scandes records an upward shift in the tree-limit of 100 to 130 m between ca. 1915 and 2000. This shift is likely related to a 0.7 °C increase in summer temperatures over the same period. The link between temperature and ATE rise is supported by similar episodic patterns in both chronologies. The greatest period of ATE upslope migration occurred between 1920 and 1950, which was also the period of greatest temperature increase (0.9 °C). When both summer and winter temperatures cooled between 1951 and 1987, establishment stopped.

Several dramatic short-term changes in the ATE have been documented below the upper limit of trees (e.g. Jakubos and Romme, 1993; Klasner and Fagre, 2002; Roush et al., 2007). These changes cause an infilling of the existing ecotone and are often characterized as subalpine meadow invasions rather than establishment beyond the current ATE. Both Jakubos and Romme (1993) and Roush et al. (2007) identified climate as a significant driver of this change due to ubiquitous change over an area in which site conditions varied.

2.5.1.2 The Response Alpine Treeline Ecotones to Long Term Climate Shifts.

Several factors make accurate documentation of the impact of long-term climate trends on the position and character of the ATE challenging. Documenting the response of the ATE to longer-term climate trends is difficult due to a lack of instrumental records prior to 1900. Unfortunately, limiting examination of change in the ATE to the twentieth century can result in erroneous conclusions both because of the brevity of the climate record and because climate for the past three centuries has been altered by human activity. Further confounding the issue is the differential response of trees in the ATE to positive and negative climatic shifts. Climatic shifts that encourage or increase tree establishment are likely to be recorded in the historical record as immediate establishment, which will increase the elevation and density of the ATE. However, during a period of unfavorable climate, when seed-based establishment stops, the ATE will remain at the same elevation as existing trees age and create a relict ATE out of context with the existing climate (Holtmeier, 2003). Only extremely poor climate conditions will cause a decrease in ATE elevation. Thus, long-term negative impacts of climate on the position of the ATE are more difficult to observe than are long-term positive impacts. Holtmeier (2003) makes the additional point that ATE and temperature fluctuations are not likely to be synchronous as a result of the strong influence of factors such as competition, precipitation, and seed production on establishment processes. If trees are limited by several factors, they are unlikely to respond rapidly to climate amelioration, especially in the short-term. Heikkinen et al. (2002) proposed that ATE shifts to higher latitudes and altitudes occur over long time scales. They note that the ATE is most likely to advance as a result of climate amelioration lasting several decades or centuries. They also note that unfavorable climates may not cause retreat, except over the very long term, but can prevent further seedling establishment.

This strong directional nature of change in the tundra-forest boundary (with tundra advancing more slowly into the taiga than taiga does into the tundra) is also noted by Holtmeier (2003), who attributes the time lag in retreating timberline to the shade intolerance of most tundra species. The morphological plasticity of trees in the ATE also biases the direction of change in favor of forest vegetation. For example, established *krummholz* respond quickly to favorable conditions by growing upright leaders. While, branch dieback may occur during unfavorable conditions, individual trees are likely to persist

over long time scales (Holtmeier and Broll, 2005) (Figure 2.4). In an extreme case, an individual Norway Spruce (*Picea abies*) tree has been shown to have lived and occupied the same site for 9,550 years in northern Sweden (Umea University, 2008).

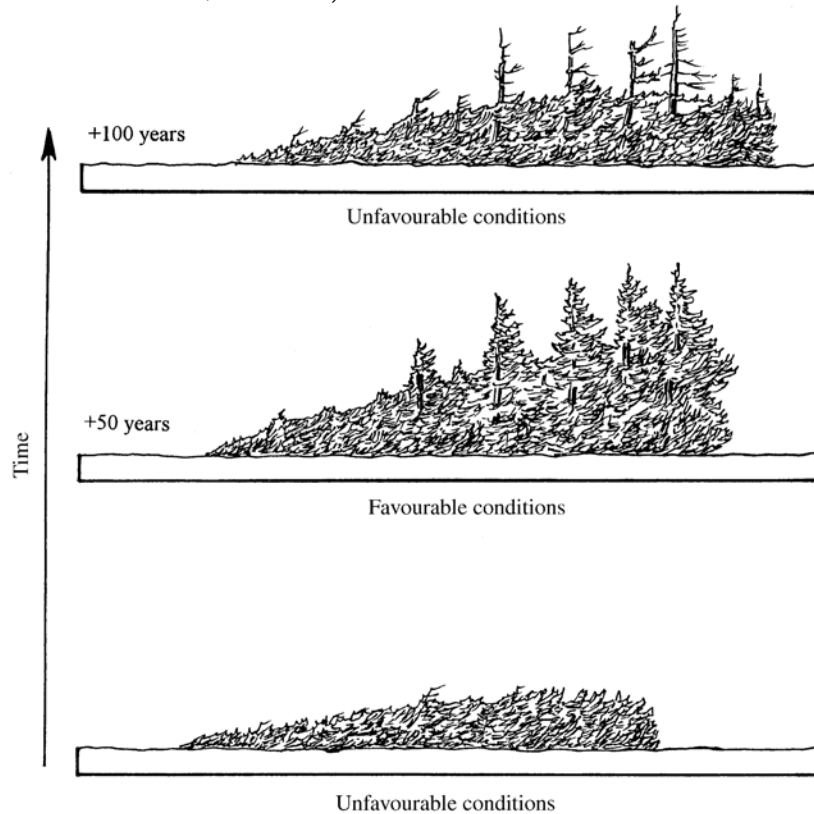
Areas with highly variable interannual temperatures may be less likely to experience a climatically-driven response as seed production, establishment and seedling growth all require favorable conditions for several contiguous years (Camarero and Gutiérrez, 2004). The impact of one or two years of severe conditions in a generally ameliorating climate may be enough to reduce or prevent tree recruitment due to the greater vulnerability of tree seedlings to climate extremes (Tranquillini, 1979).

2.5.1.3 Snow and the Interactions of Climate Variables in Time and Space.

While the majority of research linking climate change to ATE dynamics has focused on temperature there is growing recognition that snow plays a significant role as well. Brink (1959) first recognized its importance, and concluded that increased establishment in the ATE within Garibaldi Provincial Park, British Columbia, was likely caused by a decreasing snowpack.

Snowpack is unlikely to be the sole driver of change in the ATE and several studies have concluded that interactions between snow and temperature produce variations in the temporal patterns of tree establishment in the ATE. Both Rochefort and Peterson (1996) and Franklin et al. (1971) demonstrate the importance of these interactions, stemming from research on Mt. Rainer, Washington. Their research found that regional patterns of snow depth interact with annual temperature variability to play a significant role in the timing of subalpine fir establishment. Warm dry summers facilitated establishment on the snowier west side of Mt. Rainer, while cool wet summers had the same effect on the east side of Mt. Rainer, which has a thinner snowpack. They identified the importance for tree establishment of warm spring temperatures in areas with high snowfall that create rain on snow events, and thus lengthen the growing season.

Figure 2.4 Morphological plasticity of Krummholz through time. The figure shows how, despite unfavorable conditions within the ATE, trees are likely to persist over long periods of time. (Holtmeier and Broll, 2005:209).



In the northern California Cascades, Taylor (1995) found that mountain hemlock establishment was negatively correlated with April snowpack depth. Establishment was greatest during two periods of historically warmer temperatures and low April snowpack, which led to a longer snow-free growing season. In Rocky Mountain National Park, Colorado, however, Hessler and Baker (1997) found that both high temperatures and deep snow depths must occur simultaneously for several years if tree establishment is to occur.

The discrepancy between these two studies can be understood by considering their locations. Rochefort et al. (1994) point out that in continental climates cold soils and high winds are the largest limiting factor to tree establishment, whereas in maritime climates moderate moisture is ideal for tree establishment. Thus, a deep snowpack year in the continental environment of Rocky Mountain National Park reduces the negative effects of cold soils and high winds by insulating seedlings and providing spring moisture, while a thinner snowpack

in the wet maritime Cascade climate allows for a longer growing season with year round precipitation supplying the required moisture. Woodward et al. (1995) working in the Olympic Mountains of Washington state examined establishment patterns along a strong precipitation gradient. Establishment was greatest in areas with a deep winter snowpack during periods with warm dry summers. In contrast, in areas where there was only a shallow winter snowpack, establishment occurred only when wetter conditions prevailed. These observations suggest that tree establishment occurs most commonly when precipitation and temperature combine to produce mesic conditions.

On smaller spatial scales the persistence of drifted snow correlates not only with establishment patterns, but also with stand canopy damage and tree physiognomy. On Mt. San Geronio, California, Minnich (1984) observed stable populations of lodgepole pines (*Pinus contorta* [Dougl.] ex. Loud.) on exposed windward slopes. In contrast, burial by periodic late spring snow events on lee slopes resulted in variable establishment events and sporadic mortality

In general, sheltered areas along the periphery of snow patches create the best establishment zones as they provide suitable moisture, do not shorten the growing season, and provide adequate snow cover during the winter to protect against desiccation and ice damage (Hattenschwiler and Smith, 1999). Similar to open alpine environments, the spatial pattern of snow within the ATE shows little interannual variability (Hiemstra et al., 2002). Snow distribution is largely controlled by interactions between wind and ground surface features such as boulders, topography and vegetation (Elder et al., 1991; Bloschl and Kirnbauer, 1992; Luce et al., 1998; Prasad et al., 2001; Winstral et al., 2002). These features are largely immobile, which results in low interannual variability in snow cover.

In a few situations researchers have noted circumstances where individual trees have successfully established at higher elevations and extended the boundaries of the ATE (Rocheftort et al., 1994). When this occurs, the spatial pattern of snow within the ATE will change. As trees establish they cause the peripheral environment, conducive to tree establishment, to expand and a positive feedback loop results in which trees become an autogenic control on their environment (Geddes et al., 2005) (Figure 2.5).

Figure 2.5. Patterns of snow deposition as a result of dense clumps of subalpine fir in the ATE of Mt. Arrowsmith, British Columbia. Prevailing wind is upslope from the left side of the picture. Note the exposed ground on the windward side of the trees and the increased deposition of snow in the lee of the trees. This interaction between existing vegetation and snow distribution affects future establishment patterns by providing sheltered locations with increased moisture that are more suitable to establishment (photograph by W. Roush).



2.5.2 Environmentally Controlled Change: Spatially Variable – Temporally Consistent.

A relatively uniform increase in the elevation of the ATE as a response to a warming climate has been commonly hypothesized. This hypothesis assumes that the ATE corresponds to an isotherm or other thermal regime (Jobbagy and Jackson, 2000) and, if temperatures increase, the isotherm will move up in elevation and the ATE will follow (Holtmeier, 2003); however, as noted previously, isotherms do not reliably predict the position of the ATE (Körner and Paulsen, 2004). Thus, many investigators have examined additional factors that may cause variability in the uniform elevation rise predicted under the isotherm-related hypothesis. These parameters include feedback responses between vegetation and topography (Bekker, 2005), vegetation and snow (Geddes et al., 2005), vegetation and wind (Alftine and Malanson, 2004), vegetation and fire (Bader et al., 2008), seasonal and regional climate and browsing patterns (Dalen and Hofgaard, 2005), land use (Morales et al., 2005; Gehrig-Fasel et al., 2007; Vittoz et al., 2008), invasive pathogens (Tomback and Resler, 2007; Resler and Tomback, 2008), animal activity (Cairns et al., 2007), invasibility of the alpine

tundra vegetation (Magee and Antos, 1992; Rochefort and Peterson, 1996; Moir et al., 1999; Maher and Germino, 2006; Malanson et al., 2009), disturbance (Cullen et al, 2001); dispersal traits of tree species (Dullinger et al., 2004), large-scale geologic and geomorphic features (Butler et al., 2007), meso- or slope-scale landscape differences (e.g. aspect or slope steepness) (Danby and Hik, 2007a), micro-scale geomorphic sheltering features (Resler et al., 2005; Resler, 2006), and human-created hiking trails (Klasner and Fagre, 2002).

2.5.2.1 Regeneration.

An increase in the elevation of the ATE or in the density of trees within the ATE can occur either through vegetative- or seed-based regeneration. Vegetative regeneration is largely decoupled from the conditions driving seed-based regeneration. During harsh conditions when seed-based reproduction occurs at very low rates, mature trees create a favorable microclimate - protecting clones from wind and blowing snow and providing nutrients and moisture (Holtmeir, 2003). Expansion of the ecotone however, is spatially limited as it can only occur within a small radius of existing trees. In contrast, seed-produced regeneration results in dramatic advance of the ATE beyond its present limits (Cooper, 1986; Kullman, 2002 and 2004).

2.5.2.2 Microtopography.

Much of the argument for the importance of site-specific environmental variables stems from the theory that seed-based regeneration is highly dependent on safe sites or shelter in which seeds are more likely to germinate and seedlings have a better chance of survival (Butler et al., 2004; Resler et al., 2005; Maher and Germino, 2006; Malanson et al., 2009). Specifically, microtopographical features have been shown to influence the occurrence and spatial pattern of seedling establishment. Following her study of the effect of terrace risers and boulders on tree establishment in the ATE of Glacier National Park, Montana, Resler (2006) concluded that the direction and character of ATE advance will vary spatially depending on interactions between micro- and macro-topography, and that initial patterns of establishment are controlled by shelter availability. Butler et al. (2004) identified a close spatial association between conifer seedlings and turf exfoliation sites in the same location.

2.5.2.3 Tundra Vegetation.

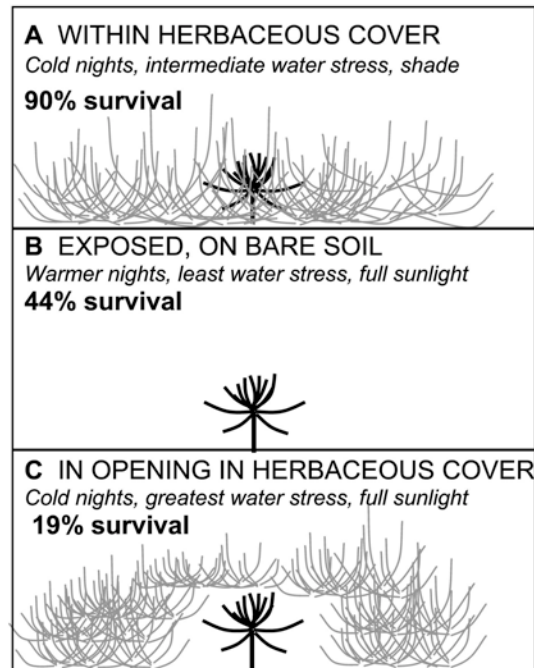
Maher and Germino (2006) found cover provided by surrounding herbaceous vegetation to increase survivorship of both subalpine fir and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) seedlings. The positive effect of tundra vegetation was less relevant for seedlings establishing under trees and for older seedlings, an indication of the importance of tundra plants for initial establishment but not for continued survival.

In an experimental study conducted in an ATE in southeastern Wyoming, Germino et al. (2002) examined the relative effects of facilitation vs. competition on survival of Engelmann spruce seedlings. Seedlings found growing within herbaceous cover had a 90% survival rate compared to seedlings found growing on exposed soil (44% survival) or in an opening surrounded by herbaceous cover (19% survival) (Figure 2.6). They attribute the high survival rate to the protection herbaceous vegetation provides from the increased night-time cooling as a result of sky exposure as well as insulation from cold air drainage. Lower survival rates for seedlings separated from herbaceous cover indicate that the positive effects of facilitation outweigh the negative effects of competition (Smith et al., 2003).

2.5.2.4 Animal Activity.

Animal activity can influence the patterning of trees within the ATE through direct action, such as occurs following the caching of seeds by birds (Tomback, 2001). However, this activity is often limited to a single species as is the case with the caching of Whitebark pine (*Pinus albicaulis* Engelm.) seeds by Clark's nutcrackers (*Nucifraga columbiana*). More generally, browsing and trampling of newly-established seedlings will prevent expansion of the ATE, while browsing and trampling of non-tree species can reduce competition with tundra plants and create favorable regeneration sites by exposing mineral soil (Cairns et al., 2007). In extreme cases insect outbreaks can decimate entire treeline forests and result in a depressed ATE. This has been most thoroughly documented in Scandinavia where autumnal moth (*Epirrita autumnata*) outbreaks in 1954-1955 caused massive defoliation of the mountain birch (*Betula pubescens* ssp. *czerepanovii*) forests resulting in decreased radial growth and tree mortality (Hoogesteger and Karlsson, 1992).

Figure 2.6 Effect of herbaceous plants on tree seedling survival in the alpine (Germino et al., 2002: 162).



2.5.2.5 Feedback Mechanisms.

Feedback mechanisms between established trees and site-specific environmental conditions influence the spatial patterning of subsequent tree establishment within the ATE. Initial investigations focused on the effects of tree islands and krummholz patches on soil formation (Holtmeier and Broll, 1992) and snow redistribution (Minnich, 1984; Hiemstra et al., 2002; Geddes, 2005) and then recognized the connection to subsequent patterns of tree establishment (Bekker, 2005; Resler, 2006; Resler and Tomback, 2008). I begin this section by describing the impact of trees on the ATE environment and then show how this affects tree establishment within the ecotone.

Influence of Trees on the Alpine Treeline Ecotone Environment.

By influencing wind velocity, trees exert considerable control over pedoecological conditions in the ATE. Holtmeier and Broll (1992) found that tree islands on Niwot Ridge, Colorado, increased the deposition of alpine loes in the lee of the island, and that ratios of organic matter and nutrients in the soil depended upon the location relative to tree islands. This sorting caused differential formation of inceptisol varieties and influenced the distribution of

non-matrix material. Cobbles and gravel were found in higher percentages in soils on the windward side of the tree island because the wind stripped the finer particles away. Thus, windward soils have a greater percentage of coarse materials than leeward soils or soils interior to the tree islands.

In Glacier National Park, Montana, Geddes et al. (2005) mapped vegetation in relation to snow depth and found it to be the most important variable in predicting May SWE regardless of topography. Their findings were similar to those reported by Anderton et al. (2002) who noted that trees function in a manner that is similar to topography in redistributing snow, but may do so in a more pronounced manner due to the abruptness of their physical structure and the effective slowing of wind through dense conifer branches. Hiemstra et al. (2006) showed that ribbon forests (continuous lines of trees usually found on long topographic highs) within the ATE serve as highly efficient snow fences that created drifts from three to seven m deep in the Medicine Bow Mountains, Wyoming.

Completing the Loop: Feedback within the Alpine Treeline Ecotone.

Building upon findings that show trees as significant modifiers of the ATE, a body of research has documented the subsequent feedback mechanisms that influence further establishment in the ATE. Resler (2006: 131) succinctly summarized this process as, “improved site conditions as a result of these sheltering effects initiate[s] positive feedbacks. As trees become established, their presence modifies the local environment and makes local conditions more favorable for additional seedlings to grow.” An absence of feedback mechanisms may even be the cause of the static nature of ATEs in the tropics where shade-dependent species are unable to invade the tundra zone without the presence of previously established trees (Bader et al., 2008). This is likely part of the reason for the similarly static state of the *Nothofagus* sp. ATE in New Zealand where recruitment within the ATE is limited to disturbed areas that occur infrequently and only within but not beyond the forest limit (Cullen et al., 2001).

Positive feedback leading to increased tree establishment in the ATE has been extensively documented in the Rocky Mountains of North America. Much of this research documents the effect trees have on snow redistribution and the subsequent consequences for further

tree establishment. Initial tree establishment increases snow deposition immediately around trees (Hiemstra, 2006), which provides increased protection during the winter and greater soil moisture during the spring; both processes encourage increased establishment (Geddes et al., 2005).

Feedback mechanisms may also be linked to larger climatic patterns. In Glacier National Park, Montana, Alftine et al. (2003) identified snow as the most important factor in a feedback process ultimately linked to but not correlated with the Pacific Decadal Oscillation (PDO). The authors document tree establishment beginning in 1940 with a spike in the 1970s and early 1980s followed by a sudden decline in establishment rate. The PDO index is negative beginning in 1940 and then switches in 1977 to a positive signal and remains so till present. The authors hypothesized that the initial seedling establishment was driven by the negative phase of the PDO that caused an increase in snowfall in the park (Selkowitz et al., 2002), which provided insulation and moisture for trees in the dry environment of the eastern slope of the Continental Divide. A change to a slightly favorable (more mesic) climate initiated seedling establishment that then improved conditions in the ATE and caused further tree establishment. Once the conditions became less favorable in the early 1900s, the positive effects of an environment modified by trees were unable to counteract unfavorable climatic conditions and feedback ceased.

Bekker (2005) linked the spatial pattern of older trees to establishment of younger trees in Glacier National Park, Montana; during the period 1700-1850 nearly all trees established within five m of existing trees. In Northern Montana, Resler and Tomback (2008) concluded that whitebark pine stems were significant initiators of tree island formation. Forty-nine percent of multi-species tree islands were initiated by whitebark pine, indicating that establishment within the ATE can be dependent upon a specific tree species.

While most research views feedback mechanisms as largely positive, Körner (1998) argued that the shade and cooler air and soil temperatures caused by mature trees inhibit the carbon uptake of nearby seedlings which causes seedling mortality and reduced establishment. Thus a negative feedback mechanism is created in which mature trees prevent increases in the elevation and density of the present ATE.

To understand the factors that drive change within the ATE it is important to acknowledge the role that feedback mechanisms play in the spatial and temporal patterning of trees. While most site-specific parameters have little temporal variation, feedback processes, similar to climate, vary substantially through time (Alftine et al., 2003). Feedback mechanisms affect both the relative impact other site conditions have on establishment and the impact of climate variables. The role feedback plays in establishment patterns will vary both temporally and spatially (Bekker, 2005). The dynamic quality of feedbacks can decouple the response of tree establishment to climate. If feedback mechanisms create protected sites during periods of deteriorated climate, establishment levels may remain at levels more typical of a favorable climate. If all protected sites become occupied a subsequent period of ameliorating climate will have lower establishment rates than would be expected. This results from the loss of protected sites which occurred during poor climatic conditions (Malanson et al., 2009).

2.6 Conclusion: The Research Question.

There are two dominant perspectives concerning the controls on patterns of tree establishment within the ATE: i) fine-scale ecologic and geologic site conditions; and ii) coarse-scale climate drivers. In cases where the ATE has undergone change, the first perspective predicts a spatially-variable response of tree establishment (e.g. Moir et al., 1999; Germino et al., 2002; Resler et al., 2005; Danby and Hik, 2007a), while the second perspective predicts a more ubiquitous response (e.g. Magee and Antos, 1992; Suarez et al., 1999; Kullman, 2002; Lloyd and Fastie, 2003). If geologic and ecologic aspects within the ATE control tree establishment, then spatial establishment patterns should reflect those fine-scale processes, while tree establishment through time should be relatively consistent. If climatic conditions are the main driver of change within the ATE, then tree establishment will not reflect the underlying spatial patterns of the landscape, but tree establishment through time should be episodic and correlate with climate changes.

I position my research in the context of a rising treeline and ask whether change in the ATE is driven by ecologic and geologic conditions at the components level or by climate shifts acting at the constraints level. Strong spatial patterning in tree establishment relating to

environmental data collected at the study site will imply the former, while strong temporal patterning and episodic establishment that correlates with climate records will imply the latter.

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3.1 Introduction.

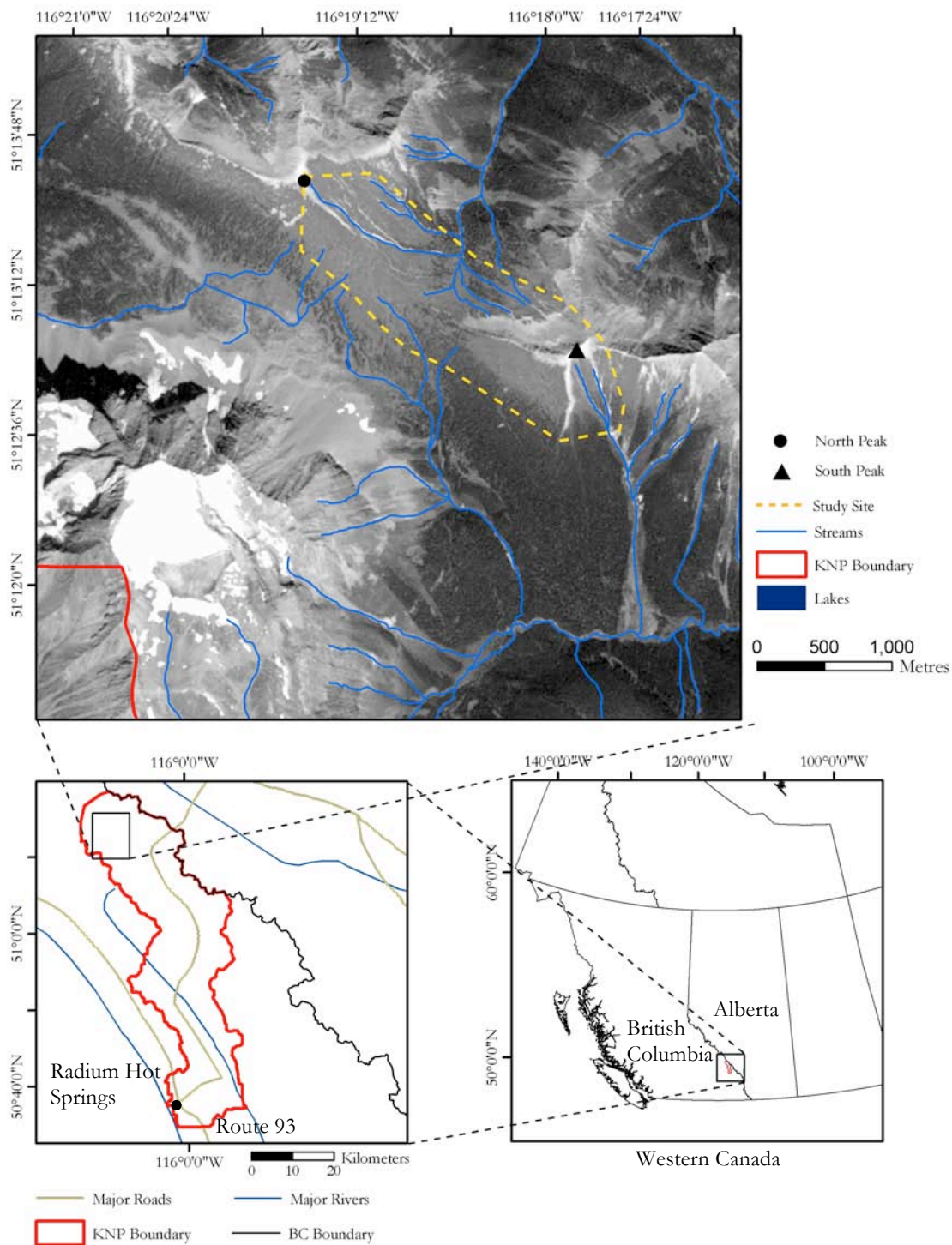
This chapter first describes the rationale for choosing the area around Goodsir Pass, located in Kootenay National Park, B.C., as the site for a detailed study of ATE change. Secondly, the geomorphology, climate, vegetation, and human influence on the area are described. Lastly, the Holocene history of the ATE in the region around Goodsir Pass is discussed.

3.2 Study Site Location and Selection.

This study was conducted at a remote site in northwestern Kootenay National Park in the southern Canadian Rocky Mountains. The study site is centred on a low saddle 0.5 km northeast of Goodsir Pass (51° 13' 10" N, 116° 18' 56" W, 2267 m asl) and extends 1.25 km to the NW, 0.3 km to the SW, 1.75 km to the SE, and 0.75 km to the NE and in doing so includes two low mountains; one to the north (51° 13' 37" N, 116° 19' 38" W, 2452 m asl), and one to the east (53° 12' 56" N, 116° 17' 49" W, 2502 m asl) of Goodsir Pass (Figure 3.1). The study site is thirteen km northwest of the Paint Pots trailhead along Highway 93 (the nearest road) and lies north and east of a hiking trail leading from the Helmet Falls campground into Yoho National Park.

The potential for changes to occur in the ATE may be determined in large part by the ecological and geological context and history of the site the ATE occupies (Holtmeier, 2003). Thus, the choice of a study site is likely to influence the results and conclusions of any study examining the ATE. Goodsir Pass was chosen as a study site because, unlike many ATEs in the Canadian Rocky Mountains, the ATE in Goodsir Pass has the potential to rise or shrink without being constrained by major terrain features, such as talus or cliffs. The variety in tree species, aspect, slope steepness, and snow depth present around the Pass provides an ideal template upon which to measure the relative importance for tree establishment of these differences in geography both to one another and to the effects of a changing climate.

Figure 3.1. Map showing the location of the study site. Orthophotograph 082N009 provided courtesy of the Crown Registry and Geographic Base Branch of Geo BC. (Government of British Columbia, 2008)



Two analyses led to the choice of Goodsir Pass as a significant and suitable location for a detailed field study of ATE change. First, repeat photography, over a ninety-year span, recording ATE change in the southern Canadian Rocky Mountains, the southern Alps of New Zealand, and the Scandes Mountains of Norway, shows the increased elevation of the ATE in Goodsir Pass to be globally significant (Roush, unpublished photo-pairs). The magnitude of the expansion of the ATE in Goodsir Pass is matched by only one other site in the Canadian Rocky Mountains near Mt. Assinaboine and by five sites in the northern Scandes Mountains. However, the Norwegian ATE range expansion likely resulted from a reduction in grazing rather than a climate shift (Hofgaard, 1997). The photograph that identified Goodsir Pass as the location of significant changes in the ATE is held by the Whyte Museum of the Canadian Rockies and was taken in 1923 by Byron Harmon and repeated in 2003 by myself (Figure 3.2). In the repeated photo-pair the dramatic upslope movement of the ATE is clearly evident.

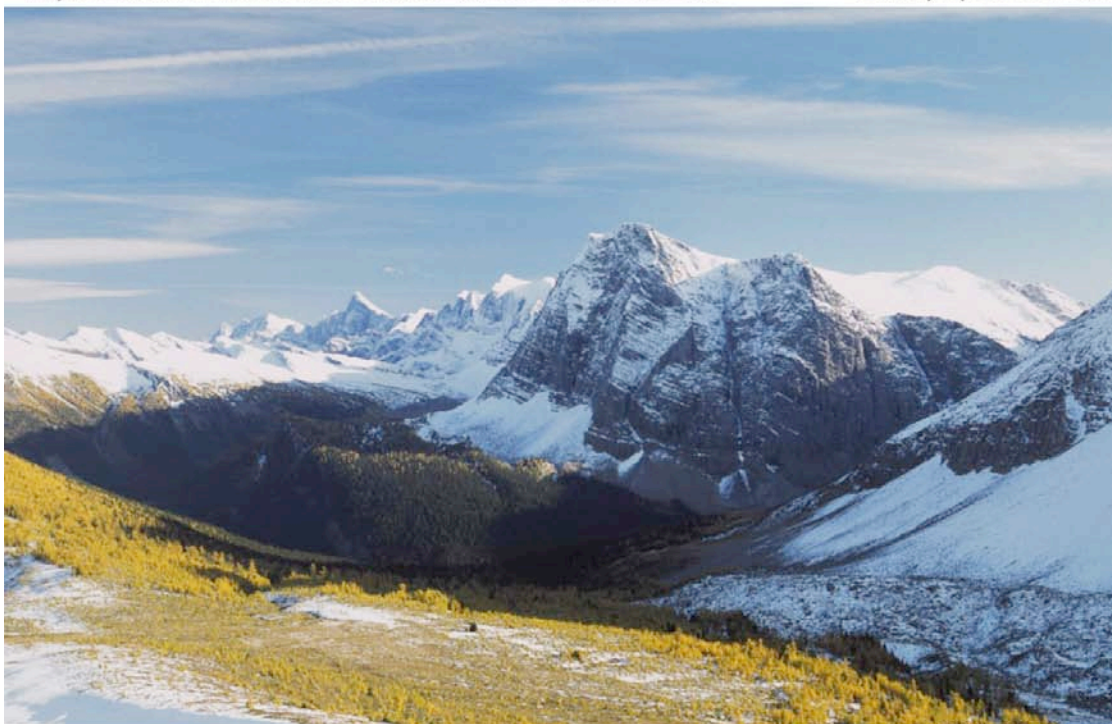
A GIS analysis using ecological land classification data (Achuff et al., 1984) and stand age data (Masters, 1990) for Kootenay National Park identified the area around Goodsir Pass as one of the few locations in the park with ecological characteristics suitable for a study of a minimally-disturbed ATE dominated by subalpine larch (*Larix lyallii* Parl.). The analysis was performed using ArcGIS software (ESRI, 2002) and located all areas in the park classified as a subalpine larch ecotype and having or lying adjacent and uphill to an area having a stand origin date of 1750 or earlier. These areas were found only in the northern portion of the park and were concentrated around Goodsir Pass in the upper reaches of the Helmet and Ottetail drainages (Figure 3.3). The site characteristics and results of the two analyses serve to pinpoint Goodsir Pass as a globally-relevant and locally-suitable location for a study of ATE dynamics.

Figure 3.2. Repeated photo-pair looking across Goodsir Pass, Kootenay National Park, B.C. and showing part of the study area. Note the large amount of subalpine larch establishment (visible as the bright yellow in the lower image) that has occurred in the period between when the two images were taken.



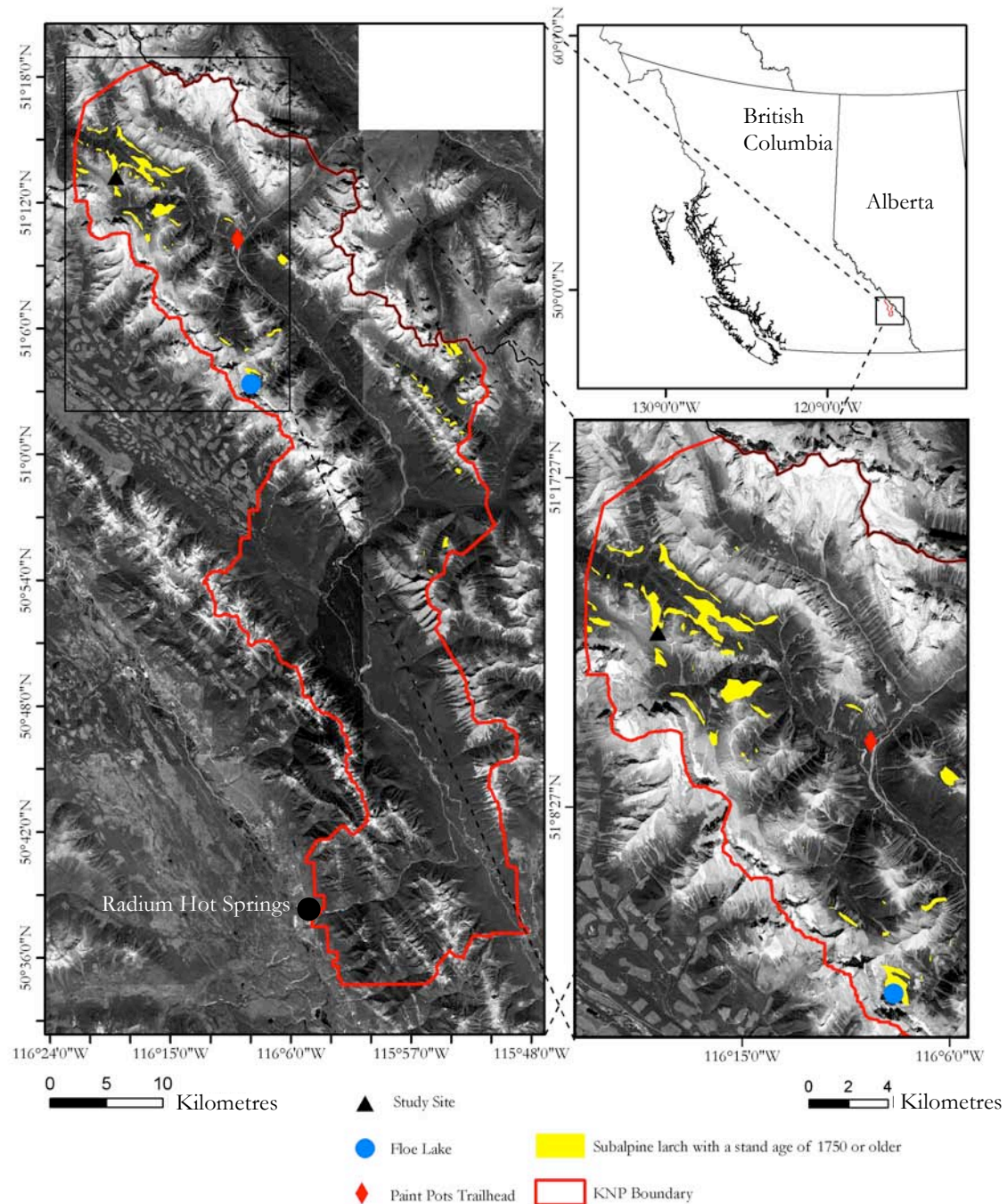
Whyte Museum of the Canadian Rockies WMCR - V263/ NA - 370

1923 by Byron Harmon



2004 by W. Roush

Figure 3.3. Undisturbed larch dominated ATE sites in Kootenay National Park, B.C. identified using a GIS analysis using stand age data (Masters, 1990) and ecological land classifications (Achuff et al., 1984). A detail of the area around the study site is shown in the lower right, and a reference map is shown in the upper right. Orthophotographs 082J012, 082J013, 082K009, 082K016, 082N009, and 082O004 provided courtesy of the Crown Registry and Geographic Base Branch of Geo BC. (Government of British Columbia, 2008)



3.3 Characteristics.

3.3.1 Geology and Geomorphology.

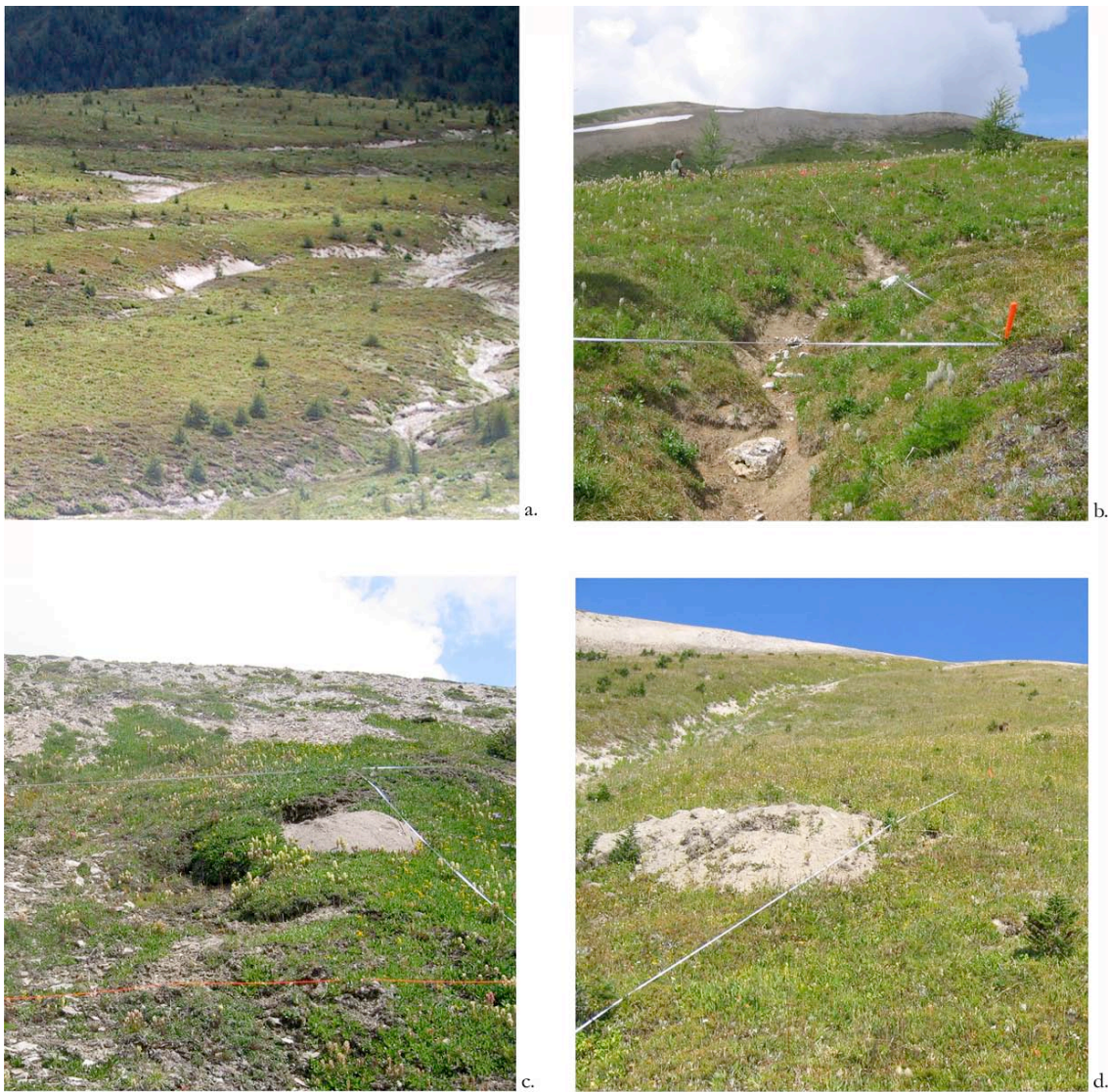
Goodsir Pass is located within the Western Main Ranges of the Canadian Rocky Mountains (Achuff et al., 1984). Immediately west of Goodsir Pass lies the Rockwall, a nearly unbroken fifty km long wall of shale and limestone, approximately one thousand m high. Mildly metamorphosed clay-rich shales of the Chancellor formation underlie most of the study site except where the Ottertail Limestone formation is found along the western boundary (Achuff et al., 1984; Gadd, 1995). Like most of the Main Ranges, the low hills to the north and south of Goodsir Pass dip to the southwest and have steep cliffy northeasterly slopes. The effect of Pleistocene glaciation on the landscape is minimally apparent. No obvious signs exist except for deep clay rich soils, a kame terrace on the slopes below the ATE, and erratics scattered along the western boundary of the site.

Ephemeral stream channels, hummocks, burrowing by Columbian ground-squirrels (*Spermophilus columbianus*) and grizzly bear (*Ursus arctos*) digs create extensive micro-topography, at scales ranging from several centimeters to tens of metres (Figure 3.4). Deep (one to two m) weakly-calcareous brunisols cover the study-site and exposures of the underlying shale are visible only in the upper portions of the study site (above 2400 m asl) where high winds and low biological productivity have prevented soil development.

3.3.2 Climate.

As no long-term weather station exists in close proximity to Goodsir Pass a precise description of the local climate regime is not possible. Kootenay National Park is located within a continental macroclimate and experiences long cold winters and cool summers. Though drier than the ranges to the west, the location of Kootenay National Park immediately west of the continental divide causes it to have generally moister conditions than areas on the eastern slope of the Canadian Rocky Mountains. The study area is located in the subalpine zone, and therefore likely has a mean annual temperature of close to 0 °C and receives over half its precipitation in the form of snow (Achuff et al., 1984). Within the ATE, continuous snow cover persists on the ground past the end of May and significant snowstorms can occur as early as the first week of September (personal observation).

Figure 3.4. Examples of topography in the study site. Ephemeral stream channels (a and b); burrowing by Columbian ground-squirrels (c); and grizzly bear digs (d) (photographs by W. Roush).



3.3.3 Vegetation.

The ATE in Goodsir Pass fits Holtmeier and Broll's (2005) climatic treeline category. The ATE is anchored in a forest dominated by subalpine fir and Engelmann spruce at 2100 m asl and transitions through a band of forest dominated by subalpine larch at 2200 m asl. The ecotone is composed of a subalpine meadow with scattered subalpine fir, Engelmann spruce and subalpine larch trees ranging in density from one hundred trees ha^{-1} to five thousand

trees ha⁻¹ and ending in the alpine zone at the ridge and peak tops at 2425 m. asl, which is dominated by bare ground and extensive patches of *Dryas* sp.

Meadow vegetation is a mix of shrubby and perennial herbaceous vegetation. The dominant shrubby species include *Cassiope tetragona*, *Phyllodoce empetriformis*, and small amounts of *Vaccinium caespitosum*. The dominant herbaceous plants include *Castilleja rhexifolia*, other *Castilleja* sp., *Anemone occidentalis*, *Silene acaulis*, *Valerian sitchensis*, *Anemone parviflora*, and *Arnica mollis*. Stand age maps of the area show the last stand-replacing disturbance of the surrounding lower elevation forest took place before 1700 (Masters, 1990). However, the size structure of the band of subalpine larch at the base of the ecotone is reminiscent of a post-fire population structure. A dense even-sized forest is interspersed with very old trees, some of which have fire and lightning strikes caused scars. Tree physiognomy within the ATE is almost exclusively of an upright nature (no krummholz were found in the study plots) and shows no evidence of recent dieback.

3.3.4 Human History.

Little is known about the specifics of early human use and occupation of the study area. Kootenay National Park lies within the historical territory of Ktunaxa (Ktunaxa Nation, 2008). The Kootenay and Vermillion Valleys were frequently used by the Ktunaxa as well as the Nakoda and Niitsítapi or Blackfoot First Nations peoples, as an east-west travel route between the Columbia Valley and the plains east of Banff (Hahn, 2000). Streams from the Goodsir Pass area drain into the Vermillion River about fifteen km southeast of the pass. At this confluence lies the Paint Pots, which has been a long-term site of low intensity ochre mining by the Ktunaxa, Stoneys, Blackfeet and Euro-Canadian settlers (Parks Canada, 2008). This cultural site and the travel route may have increased human activity in the area but specific uses of the ATE west of the ochre beds and valley are unknown.

Historical photographs taken by the Dominion Land Survey in 1904 and 1906 (Mountain Legacy Project, 2007) indicate at least limited travel in the area during the historical period. Surveyors made the first ascents of Helmet Mountain, Sharp Mountain and Limestone Peak to take these images, and the mountains were first named by Euro-Canadians in 1900 (Birrell, 2008), which implies that the area was not used by settlers prior to this time. Park

designation in 1920 has ensured that no large scale mining, grazing or forestry has taken place in or near Goodsir Pass.

The first detailed written documentation of human use in the area comes from the inaugural bulletin of the *Trail Riders of the Canadian Rockies*.^{*} The Bulletin describes a guided horse-pack trip in the summer of 1923 that traveled from Paint Pots up Tumbling Creek, along the Rock Wall and through Goodsir Pass to Lake O'hara in Yoho National Park^{**}. The riders were apparently so smitten with the scenery that they decided to form the *Trail Riders of the Canadian Rockies* in order to undertake similar rides each summer and provide others with the opportunity to view the scenic terrain (Anonymous, 1924). For the following three years a party of over one hundred riders retraced the original route. Photographs in the bulletins of the *Trail Riders of the Canadian Rockies* show fairly intensive use of the subalpine environment in Goodsir Pass as a result of these trips, including grazing (Anonymous, 1925a) and large camps (Anonymous, 1925b). The overall impact of these activities, however, was likely quite low because of their short duration. Accounts in the bulletin describing the trail ride of 1925 indicate minimal use of the area by Euro-Canadians and hints at the possibility that the Ktunaxa (known as the Kootenay Indians at the time) used it more extensively. One passage describes the cutting of a new trail from Paint Pots up Tumbling Creek to Wolverine Pass (immediately south of Goodsir Pass) (Figure 3.3) and mentions that prior to the trail ride “only straggling parties of hunters, trappers and Indians had attempted to get through the heavy timber.” While the club was camped in Goodsir Pass,

“Old Chief Louis Arbel of the Kootenay, arrived just before the sing-song as the first evening camp broke up. He will have traveled 400 miles to attend the ride and return home. Pointing to his own 2,500-mile badge, he told the riders that he was glad that the first big party to travel the land of his fathers should be members of his own organization.” (Anonymous 1925b: 4-5)

The somewhat remote location of Goodsir Pass relative to the main east/west Ktunaxa travel route in the Vermillion Valley makes it unlikely that the Ktunaxa used the ATE in

^{*} The Trail Riders of the Canadian Rockies is a non-profit riding club founded in 1923 which organizes a yearly three to seven day ride through the Rockies. Initially, many of the club's rides were similar to the annual camps of the Canadian Alpine Club, and involved hundreds of people camped in a series of locations and culminated in a party held for two or more nights in the same camp.

^{**} One of the members of this expedition was Byron Harmon whose 1923 photograph taken on this trip was part of the impetus for this study.

Goodsir Pass intensively. Intentional burning of the ATE by aboriginal people in southeastern British Columbia has not been specifically documented; however, oral interviews of Ktunaxa elders indicate that they used fire intentionally throughout their historical lands, though the burning was largely limited to lower elevation forests (Barrett and Arno, 1982). Evidence that regular aboriginal burning occurred in higher elevation landscapes is less well documented throughout the North-American West in general and British Columbia in particular. Writing on the use of fire by aboriginal people to manage food resources across British Columbia, Turner (1994) documents accounts describing how ‘mountain-sides’ were burnt for berries and records a references to Coquahalla Pass as a higher elevation site of aboriginal burning.

A detailed account of higher elevation burning by First Nations and early settlers in Jasper National Park is given in an interview with Edward Wilson Moberly, a descendent of Iroquois and Euro-Canadians (Murphy and Moberly, 2007). Moberly does not specifically reference the treeline but refers many times to burning in meadows, on land for growing hay, and to improve hunting habitat for sheep and deer. Four specific references are made to burning at higher elevations most often in conjunction with sheep habitat. Two descriptions by Edward Moberly in particular give a strong indication that fires set by First Nations burnt into the ATE; he mentions that

“they burn the sheep range - sheep feeding grounds - keep them clean. But then - there they start on the bottom...at the right time- and it burns up to the rocks and then stops,” and also that “to burn off the sheep ranges- feeding grounds- we have to do it pretty high. Now, you go way up- pretty near the top of the ridge- even if you find the grass- the grass don’t get thick enough, so they can’t burn that- so they leave that alone. They [sheep] keep that pretty cleaned anyway.”

(Murphy and Moberly, 2007: 144-145)

Whether the Ktunaxa or other first nations intentionally and regularly used fire in the ATE of Kootenay National Park is unknown. If they did so historically it is likely that the practice would have diminished or stopped during the 1600s and 1700s as a result of declining population following smallpox and other epidemics (Kay et al., 1996). Fire, regardless of ignition, likely plays a significant role in maintaining subalpine meadows throughout the North-American West (Agee and Smith, 1984; Butler, 1986). However, the historical images

of Goodsir Pass show no evidence of significant fire events one hundred years ago and other than fire scars on mature trees, no other direct evidence for fire is apparent in the landscape.

3.4 Holocene Climate and Alpine Treeline Ecotone Fluctuations Near Goodsir Pass.

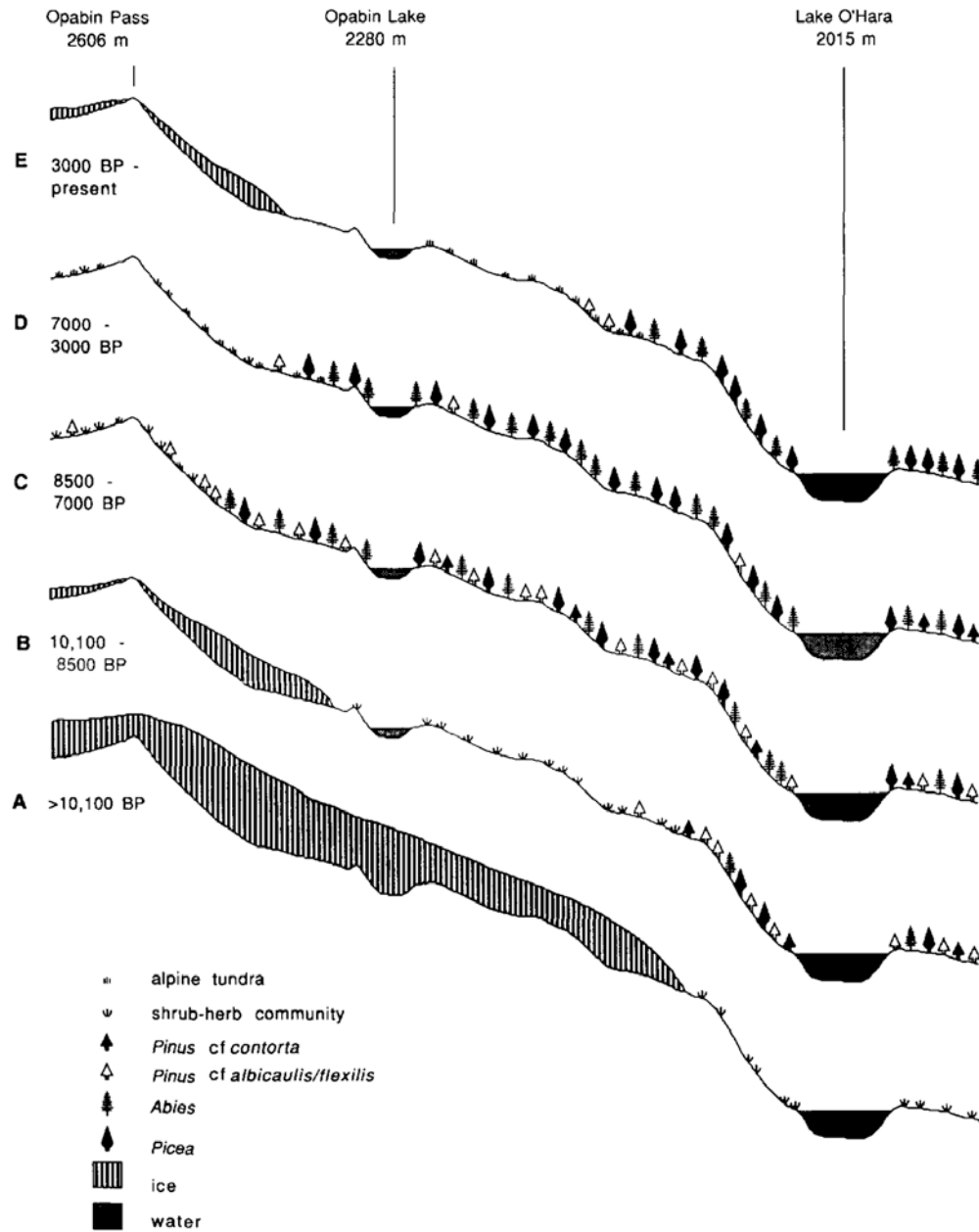
Fluctuations in the elevation of the ATE during the Holocene are not documented specifically for the Goodsir Pass area. However, a detailed pollen and macrofossil reconstruction of ATE elevation from 10,100 years B.P. to present is available for Lake O'Hara in Yoho National Park, thirty-five km to the northwest (Reasoner and Hickman, 1989) (Figure 3.5). Prior to 10,100 years B.P. ATE elevation was significantly lower. In the Lake O'Hara area, glacial ice extended down to ca. 2100 m asl and the upper limit of the ATE was likely no higher than 2000 m asl (Table 3.1). During the period 10,100-8,500 years B.P. the ice retreated and trees began to occupy the area around Lake O'Hara (m asl 2015). By 8,500 years B.P. the margin of the ATE reached an elevation about ninety m higher than present in response to warming temperatures which continued until 7,000 years B.P. During this time the subalpine forest was made up largely of Whitebark Pine (*Pinus albicaulis*), and *Picea* and *Abies* species (Reasoner and Hickman, 1989).

Table 3.1. Summary of ATE fluctuations during the Holocene at Lake O'Hara, Yoho N.P. located thirty-five km north of the study site at Goodsir Pass. Adapted from Reasoner and Hickman (1989).

Period (years B.P.)	Upper limit of the ATE	Climate
Before 10,100	2,000m	Cold.
10,100-7,000	2390m or 90m higher than present.	Warming.
7,000-3,000	Reduction in ATE density. Gradual decline in elevation from 2390 to 2280m.	Warm; becoming drier.
3,000- present	Further decline in elevation. Lowest elevation of the ATE elevation during the Holocene occurs at 1,000 B.P.	Cooling.

From 7,000 to 3,000 years B.P. the climate remained warm and likely became drier. The elevation of the ATE gradually declined and the forest around Lake O'Hara decreased in density. This mid-Holocene decrease in the elevation of the ATE near Lake O'Hara

Figure 3.5. History of the position of the ATE during the Holocene at Lake O'Hara, B.C., located 35 km north of the study site at Goodsir Pass. Though *Larix lyallii* likely was part of the historical vegetation in the ATE, and certainly is present in the ATE today, it is not shown in this figure because its pollen is indistinguishable from *Pseudotsuga menziesii* pollen. (Reasoner and Hickman, 1989:307).



corresponds well with a similar decrease in ATE elevation recorded in both Watchtower Basin in Jasper National Park, and in Wilcox Pass near the Columbia Icefields, Alberta (Kearney and Luckman, 1983; Beaudoin, 1986). Throughout the Canadian Rocky Mountains

ATEs likely reached their highest elevations (~two hundred m higher than present) sometime between 9,000 and 4,500 years B.P., though the timing varies with location (Kearney and Luckman, 1983).

Following 3,000 years B.P. forest species composition at Lake O'Hara reached similar characteristics to the subalpine forest of today and the elevation of the ATE reached a minimum elevation around 1,000 years B.P. (Reasoner and Hickman, 1989). These dates correspond well with the record from Wilcox Pass, which registers a minimum ATE elevation at 1,020 years B.P. (Beaudoin, 1986), and data from Watchtower Basin that indicates ATE elevation was similar to present between 3,000 and 1,600 years B.P. (Kearney and Luckman, 1983).

From 1,600 years B.P. to present ATE elevations in the Canadian Rockies may have fluctuated quite dramatically but were generally lower than at present, with a few brief exceptions. Beaudoin (1986) reports a brief reversal of the general lowering trend of the ATE around 430 years B.P. in which the ATE elevation may have been as high as it was during the mid-Holocene. Kearney and Luckman (1983) report a similar reversal around 500 years B.P. as well as one at 1,000 years B.P. from their pollen record in Watchtower Basin and estimate that the lowest ATE elevation occurred after 500 years B.P.

3.5 Conclusion.

Several characteristics combine to make the area around Goodsir Pass especially well-suited to conducting an analysis of the spatial and temporal changes in the ATE. First, minimal direct human modification to the ecology has occurred in the area. Second, historical photographs provide a snapshot of conditions in the area over one hundred years ago. Lastly, variation in topography and tree species allow for an examination of how diversity in local conditions may differentially affect change in the ATE.

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Data for this project can be divided into three categories: field data collected *in situ* at the study site in Kootenay National Park; image-based data derived from digital analysis of repeated oblique photo-pairs; and background and historical climate data compiled and edited from external sources. The data collection and analysis for this study were designed to assess changes occurring in the ATE at multiple scales. Field data were collected in an intensive manner from a single location within the landscape. These data allow for a detailed analysis of the impact that ecologic and geomorphologic site-specific influences have on vegetation changes in the ATE. Image data were collected extensively across a large portion of the southern Canadian Rocky Mountains, and allow for a less detailed but broader examination of vegetation change in the ATE. Specifically, these images were used to determine whether the type and magnitude of change in Goodsir Pass has occurred in a similar manner across a large portion of the landscape. Climate data allow results from the field data to be compared with the climate record to determine if similar patterns exist between the two time series: tree establishment and variability in temperature and precipitation.

4.1 DATA COLLECTION.

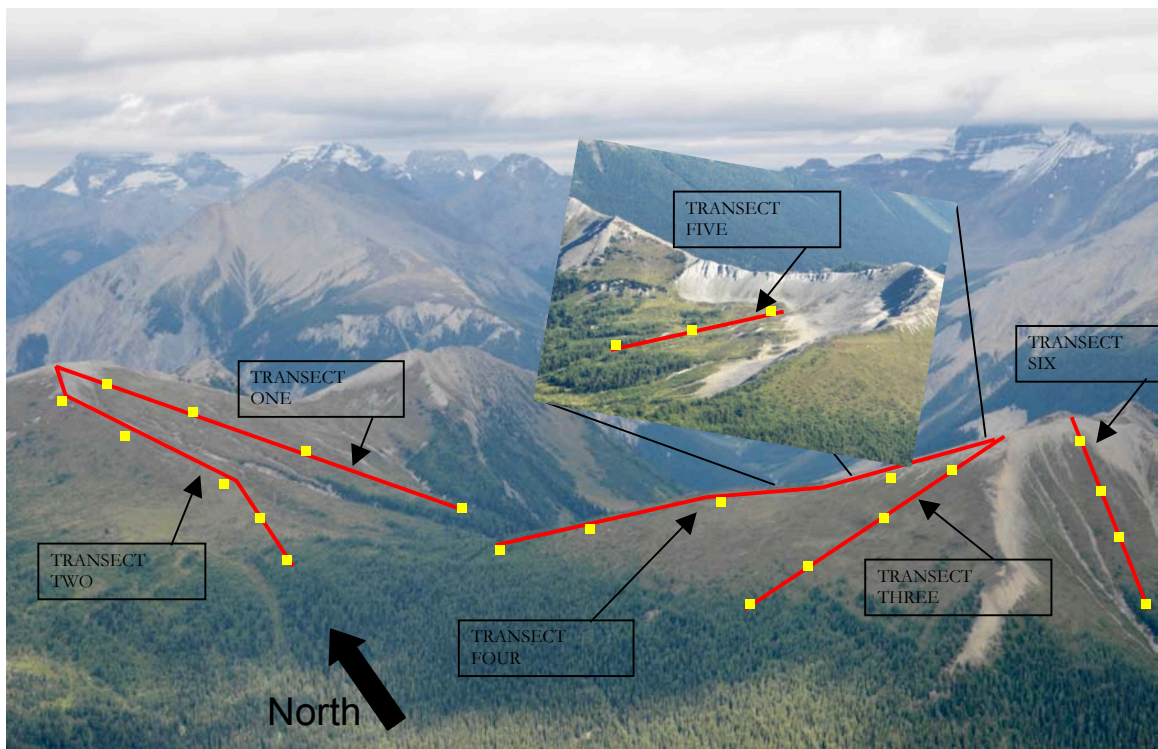
4.1.1 Collection of Field Data.

The majority of the field data were collected from July 15th to August 31st, 2006. Collection of snow depth and snow water equivalent (SWE) data occurred in May 2007 and May 2008. The collection of field data had two goals: to determine the spatial and temporal patterns of tree establishment and to document ecologic and topographic site-specific conditions. Intensive sampling of plots within the study site provided basal tree cores, detailed field observations of individual trees and their surroundings, and snow depth and SWE samples.

A transect and plot study design was used to obtain the data. This approach was used because it allowed information to be collected from throughout the study site over varying ecologic and topographic conditions. Vertical transects were used to answer questions

regarding vertical movement of the ATE. Rather than sampling the entire transect, data were collected in sample plots because the length of the transition zone from forest to alpine (i.e. the full extent of the ATE) covered approximately 150-200 m vertically and varied significantly in distance on the ground due to differences in slope steepness. Thus, while continuous sampling over the entire length of a transect would have yielded a more complete data record it was not logistically feasible. Plot size was based on tree density and ensured that a minimum of thirty trees were sampled from each plot.

Figure 4.1. Overview of the study site, in Goodsir Pass, B.C., in the Canadian Rocky Mountains. The figure shows transects in red lines and plot locations as yellow blocks. Transect Five is hidden from view in this image and shown in the inset (photographs by W. Roush).



An initial reconnaissance and assessment of the study site took place prior to the collection of field data. This work included repeat photography of the study site, observations of tree location in the landscape, and a brief sampling of tree density. This information contributed to decisions about the scale and location of the transects and plots that create the skeleton around which the data collection process was built. The layout and scale of transects and plots within the study site were determined in a structured, non-random fashion designed to

minimize subjectivity while providing the maximum ability to answer the research questions (Figure 4.1).

Field research was collected on a daily basis by the author and one field assistant and was based from the Helmet Creek Patrol Cabin at the headwaters of Helmet Creek, approximately a four km hike away from the study site (Figure 4.2). Food and field gear were transported to the cabin both on foot and by helicopter flights provided courtesy of Kootenay National Park. Collection of data and tree cores for each plot took approximately one day.

Figure 4.2. The Helmet Creek Patrol Cabin in May (photograph by W. Roush).



4.1.1.1 Transect location and character.

Six transects start from the alpine summits of two low peaks east of Goodsir Pass and run through the ATE into mature forest. Transect locations were chosen to provide a range of aspects, exposure (affected by whether a transect was located on or off a ridge), and slope

steepness (Figure 4.1). Due to the pronounced southwesterly dip slope of the underlying geology, north- and east-facing slopes were composed of cliffs, which made it impossible to establish transects on these aspects. With the exception of two transects that follow ridgelines, transects run directly down the fall line of the mountain faces.

Transect One starts from the northerly peak at a point located at $51^{\circ} 13' 38.078''$ N, $116^{\circ} 19' 31.315''$ W and an elevation of 2479 m asl. Transect One runs at a bearing* of 124° down a gentle slope punctuated by small steep gullies created by ephemeral stream beds and ends in a tongue of mature forest which reaches up the edge of one of the deeper gullies. Transect Two begins at the same point as Transect One and follows the southwest ridge of the northerly peak at bearings ranging from 133° to 152° **. The first of three plots are located along the west side of the minimally exposed ridge, which fades into flatter ground between the two peaks. At this point (the lower right corner of the third plot: $51^{\circ} 13' 23.391''$ N, $116^{\circ} 19' 16.322''$ W) the transect heads farther downslope towards mature forest at a bearing of 154° passing two more plots. Transect Three starts from a point located at $51^{\circ} 12' 55.652''$ N, $116^{\circ} 17' 49.156''$ W and an elevation of 2518 m asl on the southerly peak and runs down a broad, steep slope at a bearing of 225° punctuated by a number of rolls and swales that create localized zones of steeper and gentler slopes. Transect Four begins at the same point as Transect Three and follows the northwest ridge of the southerly peak at bearings ranging from 230° to 270° . Plots are located to the west of the ridge. In the winter of 2007, large (two to ten m) cornices were observed on the east side of the ridge, while in the winter of 2008 deep (three to four m) deposits of snow formed in the lee of vegetation in the lower half of the transect on the west side of the ridge. Transect Five begins from a point located at $51^{\circ} 13' 5.518''$ N, $116^{\circ} 17' 53.387''$ W at 2359 m asl immediately below the summit of the southerly peak at the base of a talus in a northwest-facing basin and runs at a bearing of 292° . Transect Five contains only 3 plots. Transect Six begins at the same point as Transect Three and runs down a steep slope paralleling a shallow gully at a bearing of 162° . With the exception of transects 2 and 5, four plots were established at equal elevational increments

* Compass bearings were adjusted to true north using a declination of 18 degrees east.

** Both Transect Two and Transect Four follow ridgelines and as such do not have a consistent bearing throughout their length. At each plot location a local bearing was established for the transect and the plot (90° from the transect) based on the local bearing which the ridgeline took at that location.

along each transect. The bottom plot anchored each transect at the very lower boundary of the ATE at the edge of the mature forest environment.

4.1.1.2 Plot location and size.

Plots are situated along each of the six transects at vertical increments of fifty m. Thus, each plot lies within an ecotone zone common to all transects. All plots within an ecotone zone are not at the same elevation but can be grouped into elevation categories. The top plot was located by running a measuring tape along the transect bearing and locating the lower left corner of the plot twenty m past the first tree within ten m of the measuring tape.

Subsequent plot locations were established by running a measuring tape along the transect bearing and measuring the elevation every twenty m. Each of these locations had the potential to become the lower left corner of a plot. The location closest in elevation to the point fifty m lower than the last plot was selected. Thus, plots can be classified either by transect (one through six) or by ecotone zone. The five ecotone zones are defined by elevation; moving upwards these are referred to as forest (2201 m asl), forest edge (2275 m asl), lower subalpine (2323 m asl), upper subalpine (2373 m asl) and alpine (2424 m asl).

Two types of plots were established in the study site: those along ridges, and those located on the faces of the two peaks. Plots on the faces (Transects One, Three, Five, and Six) are twenty by twenty m unless less than thirty trees were found within the plot, in which case the plot was expanded in ten m increments perpendicular to the transect to yield plot dimensions up to twenty by sixty m. Plots along the ridges (Transects Two and Four) begin at the edge of the ridge and run for fifty m toward the face, perpendicular to the local bearing of the ridge. The width of the plots located on ridges was determined by tree density and ranges from two to twenty-four m. A thirty-five cm section of rebar marks the lower left corner of each plot as a permanent marker. Table 4.1 summarizes the location and dimensions of all plots.

4.1.1.3 Environmental data.

Elevation, aspect, and slope steepness were recorded for each plot. Elevation for each plot was measured using a Thommen altimeter calibrated each morning and afternoon to a

known elevation two hours distant and seven hundred m lower from all plots. The morning and afternoon measurement were then averaged. Aspect was determined with a compass.

Table 4.1. Size, location and elevation of plots within the study site.

Transect	Plot	Plot Dimensions	Transect Bearing	Elevation (m asl)	Easting (m) (zone 11)	Northing (m) (zone 11)
1	Start		124	2479	547017	5675312
1	A	20x20	124	2426	547132	5675248
1	B	20x40	124	2380	547361	5675100
1	C	20x30	124	2321	547737	5674878
1	D	20x20	124	2271	547928	5674755
2	Start		NA	2476	547018	5675312
2	A	10x50	332	2449	547015	5675202
2	B	15x50	310	2397	547163	5675029
2	C	10x50	312	2352	547402	5674824
2	D	20x40	154	2300	547469	5674621
2	E	20x20	154	2234	547829	5674071
3	Start		225	2518	549101	5674020
3	A	20x40	225	2464	548948	5673880
3	B	20x60	225	2414	548873	5673807
3	C	20x60	225	2355	548785	5673719
3	D	20x20	225	2308	548729	5673645
4	Start		NA	2520	549101	5674021
4	A	24x50	60	2450	548835	5673971
4	B	8x50	107	2404	548601	5674059
4	C	8x50	103	2349	548397	5674111
4	D	2x50	134	2299	548198	5674201
5	Start		322	2359	549016	5674324
5	A	20x20	322	2357	548995	5674327
5	B	20x20	322	2317	548835	5674392
5	C	20x20	322	2278	548557	5674501
6	Start		162	2522	549090	5674015
6	A	20x20	162	2472	549119	5673929
6	B	20x40	162	2424	549148	5673846
6	C	20x50	162	2377	549177	5673763
6	D	20x40	162	2324	549214	5673665

Slope angle was calculated using a clinometer to determine the slope of measuring tapes laid along the two vertical axes of each plot; these values were averaged. During data collection each plot was further divided into five by five m quadrats. Within each quadrat the percent of ground cover occupied by bare ground, herbaceous plants, shrubby plants, mosses and lichens, and tree canopy cover was recorded. Percent cover was estimated by a visual examination and was approximated to the nearest 20%. In cases where a ground cover type was present, but only at very low concentrations, it was noted simply as present and given a value of less than 10%.

Within each plot, trees were visually inspected for branches flagged in a dominant direction as an indication of local wind patterns. Four twenty cm deep soil samples were extracted in each plot at the corners of a ten by ten m square centred on the plot centre; these samples were then visually examined on site for signs of charcoal. Additionally, two one m deep soil pits were dug within the study area and were examined for charcoal.

To measure year-end snow depth and SWE, all plots were marked with a three m high wooden stakes attached to a thirty-five cm piece of rebar guyed with wire. All plots were sampled in May 2007, and most during May 2008, but high avalanche danger prevented data collection within all plots along Transect Six and the lowest plot of Transect Three. Snow depth and SWE were sampled at the corners of each five by five m quadrat and the values averaged to determine the depth and SWE for each quadrat. During the 2007 field season snow depth and SWE were calculated using a U.S. Federal Snow Sampler and followed the B.C. Ministry of Environment guidelines for snow sampling (Province of British Columbia, 1981).

Snow depth was measured using an avalanche probe during the May 2008 field season. SWE was collected at four points within each twenty by twenty m plot, and snow density values were used to calculate SWE for the four quadrats closest to each SWE sampling point. While this method is slightly less accurate than that used in 2007, it saved considerable time in the field. 2007 data showed the study site snow density to vary by a mean of only $4.8\% \pm 2.7\%$ water content within plots, thus the limited SWE sampling in 2008 still provides detailed and accurate data. Previous research also validates the use of this

method by showing that snow density is much more homogeneous than depth (Erxleben et al., 2002) and variations are likely to be small and distributed more randomly in space than depth (Anderton et al., 2004). Often a simple linear regression explains the relationship between total snow depth and SWE, as a function of snow density (Elder, 1995; Elder et al., 1998; Balk and Elder, 2000). This relationship is particularly true during the spring melt period when the snowpack has reached an isothermal state (Elder et al., 1991; Anderton et al., 2004).

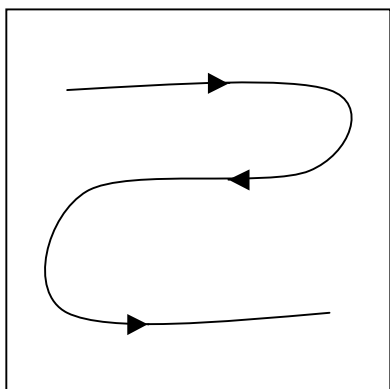
Snow depth and SWE were collected over a three-week period each year. To compensate for the melt that occurred during this period, daily snow depths at four points were measured at 51° 13' 00" N, 116° 18' 40" W at 2271 m asl in the saddle between the two peaks within the study site (Figure 3.1). Total snow loss or gain from the initial sampling date (May 4th in 2007 and May 3rd in 2008) was then applied to the snow-depth values obtained on each subsequent day. Because the snowpack had become isothermal in both years before sampling occurred, and due to the similarity in snow density values throughout the study area, a similar correction was applied to the SWE values for each sampled point using local snow density to calculate the missing SWE. One to three plots were sampled each day and with the exception of two plots, all plots were sampled on the same date or one day earlier in 2008 as they were in 2007.

4.1.1.4 Dendroecological data.

Efforts were made to locate all trees within each of the plots. This was accomplished by laying out measuring tapes to mark the boundaries of each quadrat. Two individuals then examined the ground in each quadrat by making three horizontal passes through each quadrat (Figure 4.3). No distinction was made between trees, sapling and seedlings. Because of the great variability in the height to growth ratio for trees in the ATE, a size-based categorization system is not useful. Thus, all individuals of any tree species were sampled, regardless of size. For each tree the following data were recorded: species, diameter at breast height (DBH), tree height, crown dimension, number of stems, presence of cones, tree health, regeneration substrate, microtopography, and soil moisture.

Each tree was given a unique number and cored or collected to determine the year in which it established. Trees with diameters greater than ca. five cm were cored to pith as close as possible to the root crown. While coring trees, the highest priority was placed on obtaining a core that intersected the root collar. Where possible a second core was taken perpendicular to the slope direction, and where possible, a full diameter core was extracted. When it was not possible to core a tree, either the tree was uprooted and the root collar collected, or the number of branch nodes was counted (only young trees with clearly defined whorls were sampled by this method).

Figure 4.3. Pattern used to search each five by five m quadrat for trees.



Tree height was determined using a measuring stick if the tree was under two m and with a clinometer if greater than two m in height. Crown dimension was established with a measuring stick laid parallel and perpendicular to the aspect of the slope where the tree was growing. Tree health was recorded using a subjective scale (Table 4.2).

Table 4.2. Metrics used to measure tree health.

Health Index	Metrics
0; Dead	Dead
1; Barely alive	Barely Alive; likely to be dead soon; two or more health problems.
2; Stunted or ill	Marginal in appearance, often with an obvious health problem or extremely stunted growth; few branches/needles.
3; Average	Growing well for a tree living in the ATE, but might be classified as slightly stunted or deformed for a tree growing at a lower elevation (e.g. topped with vigorous growth on lower branches).
4; Healthy	Nothing wrong physically; good growth; many branches; some long branches or nodes.
5; Vigorous	Vigorous bushy growth; long shoots; full and many branches.

Regeneration substrate was established by categorizing the dominant substrate located within ten cm of the tree base. The categories used were shrubs, herbs, lichens/mosses, bare mineral soil, soil covered by needles, rocky ground; and wood.

The microtopography at each tree was described to determine whether trees had established in a sheltered, neutral, or exposed location. Sheltered locations were defined as small depressions in which the ground within twenty-five cm of the tree rose by at least twenty-five cm on at least one side of the tree. Exposed locations constituted hummocks, ledges or slight topographic highs in which the ground dropped by twenty-five cm or more within twenty-five cm of the tree on at least one side of the tree. Neutral locations are defined as those where there was no significant change in topography within twenty-five cm of the tree. Soil moisture was classified as either mesic or xeric and was determined by physical examination of the soil texture and moisture at the base of the tree.

4.1.2 Collection of Image-Based Data.

Repeat photography is a powerful tool for analyzing landscape changes (Roush, et al., 2007). Throughout western North America repeat photography has been used to document and analyze landscape changes in forest, mountain, alpine, and desert ecosystems (e.g. Rogers, 1982; Gruell, 1983; Klett et al., 1984; Baars et al., 1994; Vale and Vale, 1994; Webb, 1996; Fielder et al., 1999; Butler and DeChano, 2001; Klasner and Fagre, 2002; Rhemtulla et al., 2002; Munroe, 2003; Klett, 2004). The first detailed topographic maps of the mountainous regions of Western Canada were made using photographic surveying techniques and the images created during this effort constitute an extraordinarily comprehensive and detailed record of the landscape as it existed 60 to 120 years ago (MacLaren et al., 2005). The Mountain Legacy Project (2007) is systematically repeating these images to document and analyze the changes that have occurred in the landscape in the interval of time between when the historical and modern images were taken. This thesis, similar to several other studies conducted in Jasper, Kootenay, and Waterton Lakes national parks that examine changes in vegetation over the past century, used many of the photo-pairs generated by the project and was conducted within the larger research initiative of the Mountain Legacy Project.

In this study historical images were used to create a more complete and contextual picture of change in the ATE. Two types of image-based data were collected for this study; both consist of historical and modern images. The first focuses solely on the study site and helps to establish the context of change that may have occurred in the ATE, as well as provide a window into past conditions at the site. The second type of image-based data broadens the geographical scope of the research and allows for a regional analysis of changes in the ATE of the southern Canadian Rocky Mountains.

4.1.2.1 Ground-based Repeat Photography of the Study Site.

Four historical images of the study site were obtained from archives, the location from which they were originally taken determined, and a modern photograph taken to document changes in the ATE of the study site.

Byron Harmon took one of the historical photographs in the summer of 1923. The original (WMCR - V263/ NA – 370) is held the Whyte Museum of the Canadian Rockies. The photo-point of the Harmon image is located at the summit of the northern peak within the study site at $51^{\circ} 13' 37''$ N, $116^{\circ} 19' 38''$ W (Figure 3.1). While working for the Dominion Land Survey, A.O. Wheeler took the other three images in 1906; the original glass plate negatives (e008406868; e008406869; e008292123) are currently held by the Library and Archives Canada in Ottawa. Two were taken from the summit of Sharp Mountain ($51^{\circ} 12' 26''$ N, $116^{\circ} 20' 42''$ W) and one from the summit of Limestone Peak ($51^{\circ} 11' 01''$ N, $116^{\circ} 17' 57''$ W). A modern version of the Harmon photograph was taken in September 2004 using a Pentax67II medium format film camera. High resolution scans were obtained for both the original and repeated images for on-screen assessment. Modern photographs of the Wheeler images were taken in August 2007 using a Hasselblad H3D digital medium format camera. High resolution scans of either negatives or album prints were obtained of the historical images for on-screen comparison with the fifty mega-byte digital files created by the H3D camera.

Locating Historical Photo-positions.

To locate the sites of the historical photographs, the title or prominent landmarks in the photograph was used to find the general area on a topographic map. An eighteen by twenty-

two cm print of the historical images served as a guide to determine the location of the photo-point. In the field, intersections of ridgelines and permanent foreground objects, such as boulders, were used to find the general area (roughly fifty m²) in which the historical photograph was taken. To determine the precise location of the photo-point a ruler was used to find lines of equal perspective and proportionate length in the historical photograph and the present landscape. Given the amount of change that occurs in ridgeline intersections when moving only small distances, photo-points were determined to within ca. ten m using only background features. When prominent foreground features were present as well it was possible to locate photo-points to within less than one m. Superimposed vertical and horizontal centre-lines on the historical images ensured that the repeated images matched the bearing and tilt of the historical camera.

4.1.2.2 Regional Ground-based Repeat Photography.

To broaden the scope of the research, a regional analysis of changes in the ATE of the southern Canadian Rocky Mountains was carried out using repeated photo-pairs from Waterton Lakes, Jasper, and Kootenay national parks. The goal was to examine how both aspect and location within a regional landscape affected the type of change occurring in the ATE. While affording a less detailed view of the magnitude and local-scale variation of ATE change, this analysis provides the larger context within which the more detailed dendroecological study takes place.

Photo-pairs were obtained from the website of the Mountain Legacy Project (2007). These photo-pairs were generated from historical images taken by the Dominion Land Survey and repeated by the Mountain Legacy Project. Table 4.3 summarizes relevant information for these photo-pairs. Of the 1,327 photo-pairs viewed online, 69 photo-pairs were selected for further analysis, and downloaded at a resolution of one thousand dpi. Images were selected based on the following criteria: the ATE was a clearly defined and recognizable landscape feature; the ATE was non-orographic and had the potential to move vertically; no signs of past fire were visible in the ATE; and the ATE was located at a medium distance (0.25 to 2.5 km) from the photo-point.

Table 4.3. Dates in which repeated images were first taken and later repeated and the number of photo-pairs generated for each national park (N.P.).

	Jasper N.P.	Kootenay N.P.	Waterton Lakes N.P.	Total
Year historical images were taken.	1915	1922	1914	
Year repeated images were taken.	1997-1999	2006	2004-2005	
Range of years.	82	84	90	
Photo-pairs reviewed.	770	234	323	1327
Photo-pairs selected.	25	19	25	69
ATE segments analyzed.	35	34	35	104

4.1.3 Collection of Historical Climate and Ring Width Data.

Historical climate data were obtained from direct instrumental records proximate to the study site, tree-ring based climate reconstructions, and synoptic climate indices created by other researchers. Temperature and precipitation records for Banff, Alberta were obtained from Environment Canada's Adjusted Historical Canadian Climate Database (Vincent and Gullet, 1999). The record from Banff includes monthly mean, maximum, and minimum temperatures from 1895-2007, and monthly rain, snow and total precipitation from 1895-1995. Data were corrected to account for errors arising from changes in site exposure, location, instrumentation, observer, and observing program (Vincent and Gullet, 1999).

May 1st snow depth and SWE data were obtained from B.C. Hydro snow courses at Floe Lake (range 1969-2005, 2025 m asl and twenty-two km distant from the study site) and Marble Canyon (range 1947-2003, 1,500 m asl and fourteen km distant from the study site) (Government of British Columbia, 2007). Non-local climate indices used for analysis include annual Pacific Decadal Oscillation (PDO) (Mantua, 2004); and a record of reconstructed summer temperatures based on tree rings from the Columbia Icefield (located near the boundary of Jasper and Banff National Parks 133 km to the north and at an elevation of 2200 m asl) (Luckman et al., 1997). *Larix hyalii* ring-width indices from Wolverine Pass (2200 m asl and nine km southwest of the study site) and Floe Lake (2025 m asl and twenty-two km southwest of the study site) (Colenutt, 2000) were also obtained to compare with establishment patterns of subalpine larch in Goodsir Pass.

Growing season climate normals (1961 and 1990) were obtained for the ATE environments of Jasper, Kootenay and Waterton Lakes national parks to describe differences in regional

climate regimes. Climate normals were derived by inputting spatial data from two ATE locations* in each park into the climate modeling program ClimateBC (Wang et al., 2006), which generates scale-free climate data for Western Canada by applying interpolation techniques and elevation adjustments to existing climate records.

4.2 Data Analysis.

4.2.1 Analysis of Environmental and Dendroecological Data.

4.2.1.1 Determining Establishment Dates.

Mounted tree cores and basal cross sections were belt sanded using six hundred grit sand paper. Establishment dates were determined by examination of tree rings through a stereo microscope. During this process samples with extremely narrow rings were further sanded with three thousand grit sand paper. All samples were counted twice and where discrepancies between counts occurred the sample was counted a third time and the oldest establishment date was used. If the pith was absent, age was determined by extrapolating the number of rings to the pith based on the estimated distance of the last ring from the pith (Stokes and Smiley, 1968).

The high variability in growth patterns of trees in the ATE prevented the construction of a robust tree-ring chronology suitable for cross-dating. Marker years of extremely low growth identified by Colenutt (2000) from *Larix lyallii* chronologies collected at Wolverine Pass and Floe Lake were used to adjust establishment dates where a pattern of two or more marker years were visible.

For the samples not cored at the root collar, an age-height regression analysis was used to determine tree age at core height. With the exception of three larch trees all cores were taken at thirty cm or lower. A regression analysis was performed for each species using trees thirty cm or shorter. An additional regression was performed using larch trees 70 to 130 cm

* Locations and elevations are: Waterton Lakes National Park 49° 02' 56" N, 114° 59' 13" W. & 49° 13' 33" N, 114° 04' 43" W., Elevation 2200 m asl; Kootenay National Park 50° 59' 35" N, 116° 06' 08" W. & 50° 54' 06" N, 116° 11' 10" W., Elevation 2300 m asl; and Jasper National Park 53° 09' 38" N, 118° 13' 05" W. & 52° 57' 10" N, 118° 15' 45" W., Elevation 2100 m asl.

in height to determine the age to core height for the three larch samples taken in that height range. Table 4.4 summarizes the regression analysis.

Table 4.4. Regression equations used to calculate the ages of trees not cored at the root collar. y = years a tree takes to grow to height, x .

Species / height (cm)	Regression	R ²	# of individuals used to calculate regression
<i>Picea engelmannii</i> / 0-30	$y = 0.9473x$	$R^2 = 0.0283$	81
<i>Abies lasiocarpa</i> / 0-30	$y = 1.2163x$	$R^2 = 0.1231$	39
<i>Larix lyalli</i> / 0-30	$y = 1.0243x$	$R^2 = -0.242$	72
<i>Larix lyalli</i> / 70-130	$y = 0.4313x$	$R^2 = 0.2009$	40

4.2.1.2 Establishing the Presence and Rate of an Altitudinal Increase in the Alpine Treeline Ecotone.

To corroborate the photographic evidence of shifts in the ATE revealed from the repeated photo-pairs, two statistical analyses were carried out using SPSS 15.0 (SPSS Inc., 2007). In the first instance, the earliest date of establishment for each plot was determined and a mean establishment date for all plots within each ecotone zone calculated. A Shapiro-Wilks test was used to test the data for normality and a one-way ANOVA was employed to test for significant differences between mean earliest establishment dates among ecotone zones. While this approach does not provide much insight into when the tree population as a whole moved into the present day ATE, it does help determine when trees were first able to establish at progressively higher altitudes. Secondly, a Mann-Whitney test was used to assess whether the mean establishment dates for each ecotone zone differed significantly from each other.

To assess the details of vegetation change in the ATE two further characteristics of tree establishment relative to elevation were described: changes in tree density and changes in the upward rate of establishment. Density for each plot was reconstructed through time, and the decade in which tree density first reached one hundred trees ha^{-1} was noted. One hundred trees ha^{-1} is an arbitrary unit but is meant to distinguish between isolated tree establishment beyond the forest (an event that can occur during periods when the elevation of the ATE is static) and a true shift in the elevation of the ATE. It corresponds to the minimum tree density found in the study site during the collection of field data. Data from

dead trees were not used due to the difficulty in obtaining accurate cross-dated establishment dates for dead individuals. Additionally, the relatively low number of dead individuals found in the study-site and the high percent of seedlings in the ATE population (of which dead individuals do not persist in the exposed environment of the ATE) diminishes the importance and practicality of using dead individuals in this calculation. Though individual trees that established and then died will not be recorded in the establishment record, deviations from a steady increase in density through time will indicate changes in establishment patterns (Lloyd and Fastie, 2003).

Rates of change in the elevation of the ATE were determined using the mean establishment date and mean elevation of all plots within an ecotone zone. The vertical distance between ecotone zones was divided by the difference in the mean establishment dates in each zone to obtain an upward rate of advance for the ATE. Because this calculation uses mean establishment dates, very high rates of advance can be calculated; however, these rates are not for individual trees but rather the mean age of trees at a certain elevation. Because mean tree ages do not actually exist in the ATE, these methods of describing ATE advance are used only i) to determine whether an advance has occurred, and ii) to describe in basic terms the timing and character of that advance. There is not a specific line that can be identified in the ATE to measure the exact elevation of the treeline. Thus, it is not possible to measure a precise rate of advance during a certain time period. Rather the rates give a general sense of the periods during which tree populations expanded upwards and whether they did so episodically or continuously.

4.2.1.3 Examining the Effects of Historical Climate Trends on Tree Establishment.

It is difficult to assess the accuracy of tree establishment data obtained from tree cores. Errors are introduced when cores have missing rings and false rings, and when cores miss the pith or the root collar. Missing rings create an erroneously young population, while false rings create an erroneously old population. Errors due to missing the pith or wrongly estimating the height of the root collar relative to the increment borer at pith contact are likely to estimate trees as older and younger than they actually are. Missing rings are more common in subalpine larch than in Engelmann spruce or subalpine fir (Colenutt and

Luckman, 1991; 1995), which may bias the data towards a younger than actual subalpine larch population structure. While the establishment date associated with any individual tree is suspect, the number of trees recorded in a population as establishing in any one year is likely to be quite accurate as errors from surrounding years will compensate for errors associated with any one individual year. Because of these small but likely errors, and because successful seed production (Holtmeier and Broll, 2005) and tree establishment (Cui and Smith, 1991; Jakubos and Romme, 1993; Holtmeier and Broll, 2005) in the ATE depend on favourable conditions over more than one year, tree establishment and climatic data were grouped into five-year periods for analysis. However, these establishment classes are arbitrary, and so the data were also analyzed on an annual basis. Analysis of these data focused on the period 1800-2005: prior to 1800 very few trees had established. Half of the period is covered by instrumental climate records (1895 to 2005), while ring-width data (Colenutt, 2000) and reconstructed temperatures (Luckman et al., 1997) cover the entire period.

Pearson correlation analysis was used to investigate the relationship between local instrumental, regional reconstructed, and synoptic climate variability and the timing of tree establishment. Establishment data were summed for each five-year period, and climate data were averaged for the same five-year period. Establishment for each tree species was compared with monthly March-October mean, minimum, and maximum temperatures and annual monthly snow and rain values for the AHCCD Banff climate station (Vincent and Gullet, 1999). The effect of snow depth on establishment was investigated by comparing establishment patterns and May 1st SWE from B.C. Hydro Snow Pillows located at Marble Canyon and Floe Lake. To extend the climate data further back in time, two synoptic data sets were included in the analysis: reconstructed summer temperatures at the Columbia Icefield (Luckman et al., 1997) and the Pacific Decadal Oscillation (Mantua, 2004). Subalpine larch ring-width data from Floe Lake and Wolverine Pass were also included to test whether establishment patterns correlate with annual growth of trees in a nearby ATE. Climate variables were selected on the assumption that seed production, germination, and establishment are affected most by summer temperatures, length of the growing season, and the timing and type of precipitation. Winter temperatures (November-February) were not examined because the deep snowpack in Goodsir Pass (one to three m) covers and insulates

seedlings, thereby severely limiting the variability of winter temperatures experienced by seedlings.

4.2.1.4 Examining the Effects of the Local Environment on Tree Location and Character.

Three sets of analyses were undertaken to assess the influence that site-specific conditions have on tree establishment patterns and character. The first examined the relationship between establishment patterns and site-specific variables at the meso-scale: the quadrat and plot level (five to fifty m). The second examined the effect of the same meso-scale variables on tree health. The third examined the interaction of patterns at the meso- and micro-scales on tree establishment.

Impact of Site-specific Variables at the Meso-scale on Tree Establishment.

To examine the extent to which site-specific variables determine the spatial pattern of tree establishment, quadrats were categorized according to whether or not establishment had occurred. A binomial logistical regression was used to identify which of the site-specific variables (altitude, aspect, slope steepness, % bare ground, % shrub cover, % herb cover, % moss and lichen cover; and mean two-year SWE) most accurately predict whether tree establishment will occur within a given quadrat.

Impact of Site-specific Variables at the Meso-scale on Tree Health.

To determine the effect of site-specific variables on tree health all trees were grouped by their health class (0 to 5) (Table 4.2). A Kruskal-Wallis test was used to compare the ranked means of the site-specific variables against the tree-health data (SPSS Inc., 2007). For example, this analysis allowed a determination of whether the ranked mean ground cover or elevation of all the quadrats containing the healthiest trees was higher than the ranked mean ground cover or elevation of all the quadrats containing the least healthy trees.

Interaction between Microtopography and Snow Depth.

To determine whether the effect of microtopography on tree establishment was influenced by snow depth, a one-way ANOVA was used to test for significant differences between the mean snow depth around trees growing in either sheltered, neutral or exposed micro-

topographical sites. This analysis was performed on a subset of the total trees. Trees in the lowest plot of each transect were excluded because of the additional sheltering effect of the surrounding forest. Trees older than forty years were excluded because of the chance that a tree will modify its proximate microtopography over time (Holtmeier and Broll, 1992; Resler et al., 2005).

4.2.2 Analysis of Image Data.

4.2.2.1 Analysis of Repeated Photo-Pairs of the Study Site.

The repeated photo-pairs of the study site were used primarily to locate and select the study site. The Byron Harmon photo-pair was taken during a larger repeat-photography project that examined changes in treeline density and elevation in the southern Canadian Rocky Mountains, the Southern Alps of New Zealand, and the Scands mountains in Norway. Photo-pairs generated from the Dominion Land Survey extended the visual record of the site an additional two decades. The repeated photo-pairs were used as a visual reference and historical benchmark during the planning and execution of the field work and during the analysis of the environmental, dendroecological, and climate data collected for this study.

4.2.2.2 Analysis of Regional Photo-Pairs.

Analysis of the one thousand DPI photo-pairs was carried out by visually assessing the images on a dual screen display that allowed for simultaneous viewing of both the historical and modern images. The goal of this analysis was to compare the type and magnitude of change within the ATE as a function of aspect and regional landscape location.

Unlike a landslide or fire, the ATE is a continuous or semi-continuous spatial landscape element, which makes it difficult to measure change in discrete events. Therefore, within each photograph, segments of the ATE were defined by locating contiguous slopes of constant aspect not bisected by major gullies, debris paths, or ridges. In total, 104 segments of the ATE were analyzed. ATE segments were marked in GoogleEarth™ (Google Inc., 2007) to ensure that no spatial overlap occurred in the analysis. The aspect of each ATE segment was determined using GoogleEarth™. Analysis of individual photo-pairs focused on the type and direction of change but not the magnitude to ensure that the analytical

comparison between photo-pairs was objective and consistent. To determine the ubiquity or magnitude of a certain type of change in the ATE, the number of segments in which that change occurred was used as a metric.

For each segment of ATE, the photo-pair was visually compared on-screen and the type of change present in the ATE was recorded. Change within the ATE was categorized into five types: i) an altitudinal change in the upper limit of the ATE; ii) an altitudinal change in the upper limit of krummholz; iii) an altitudinal change in the upper limit of upright trees; iv) a change in growth form of the trees between either krummholz or upright trees; and v) a change in the density of trees. These data were aggregated and the percent of the ATE segments, having the same aspect or regional landscape position, that had changed was calculated.

4.3 Summary.

In this study I am concerned with change in the ATE and I attempt to determine whether that change is driven by site-specific ecologic and geologic conditions or climatic variability. Fundamentally this is a question about scale. Climate occurs at large scales, while ecologic and geologic conditions occur at smaller ones. The methods outlined in this chapter are designed to determine the scale at which processes that influence ATE dynamics operate and whether patterns and processes at one scale influence those at another. The field data collected in this study help to answer questions about change at smaller scales. When the field data is compared with historical climate data, questions about change at larger scales are addressed. The analysis of repeated images from the three mountain parks is designed to determine whether changes in the ATE are ubiquitous in magnitude and character at a very large scale, and provides a context in which to place the detailed study from Goodsir Pass.

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This chapter presents results from the fieldwork and data analysis described in the previous chapter. The first section presents relevant climate data, including the instrumental record and reconstructions of past climate. The second section describes results pertaining to data collected in the field. This section first describes the temporal variability in establishment patterns of the three tree species found in Goodsir Pass. Secondly, the rate and character of change in the elevation and density of the ATE is presented. This is followed by an exploration of the relationship between tree establishment and the climate records. Lastly, results from analysis of the spatial variability of establishment as it relates to site-specific conditions are presented. The final section of this chapter describes results from the analysis of repeated photographs taken in Jasper, Kootenay and Waterton Lakes national parks.

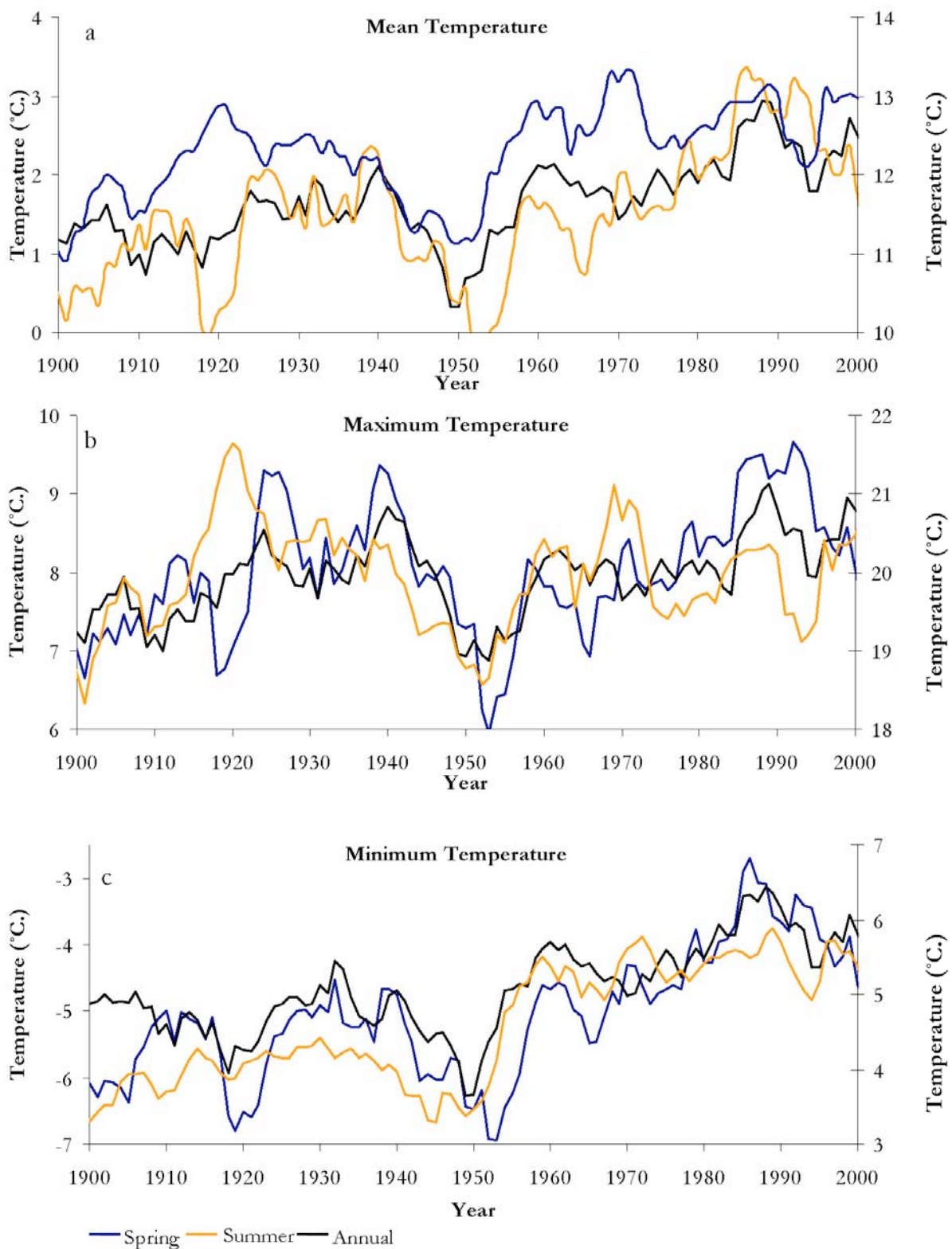
5.1 Climate Data.

5.1.1 Local Instrumental Climate Record.

Mean, minimum, and maximum air temperature records from the Banff AHCCD record show a gradual warming trend over the past century (Figure 5.1). Temperatures rose ca. 1 to 2 °C during the first four decades of the century then dropped in the 1940s and early 1950s to similar or slightly cooler (0.5 to 1 °C) temperatures as those that existed in the early 1900s. A rapid increase (ca. 2 °C in five to ten years) in temperatures followed during the late 1950s. Another less pronounced rise (ca. 1 °C in ten years) in temperature occurred during the 1980s.

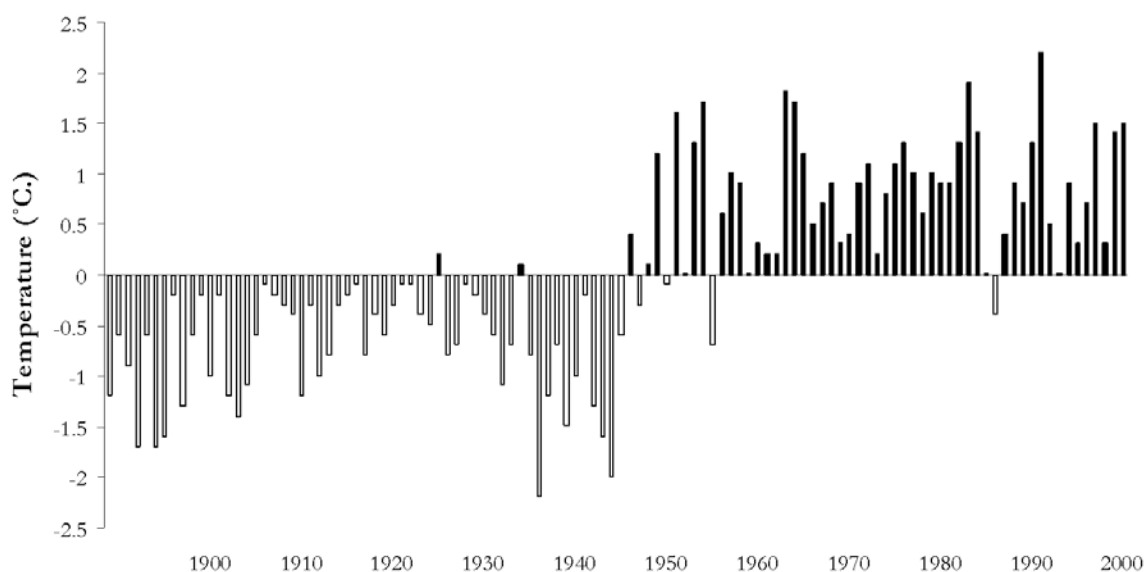
The pattern of repeated warm and cool periods is similar for mean, maximum and minimum temperatures, however, it is most pronounced for minimum temperatures, which show the most dramatic increase (1 to 2 °C) in spring (March to May), summer (June to August), and annual temperatures over the last century. Minimum summer temperatures in particular show a significant and consistent difference between the first half of the century and the latter half. The warmer temperatures present in the latter half of the century are particularly evident when the minimum summer temperature anomaly is examined (Figure 5.2); during

Figure 5.1. Mean, maximum and minimum temperatures from the Banff Adjusted Historical Canadian Climate Data station. The left-hand axis shows spring and annual temperatures and the right-hand axis shows summer temperatures.



the first half of the twentieth century, minimum summer temperatures ranged between 3 and 4 °C, while during the second half of the century minimum summer temperatures ranged between 5 and 6 °C (Figure 5.1).

Figure 5.2. Minimum summer temperature anomaly from the 1895-2000 mean for the Banff Adjusted Historical Canadian Climate Data station.



Precipitation records from the Banff AHCCD record show high inter-annual variability but no consistent trend over the one hundred year period of record (Figure 5.3). Examining snow and rain records separately reveals some decadal patterning. During the first four decades of the twentieth century and during the 1980s and 1990s snowfall was generally less (~100 to 225 yearly mm of moisture) than during the late 1960s and 1970s when annual total snow values range between ~200 and 300 mm of moisture (Figure 5.3). Annual rainfall shows a different pattern. The periods 1900-1920 and 1980 onwards have more years in which annual rainfall was greater than 350 mm than does the period 1920-1980 (Figure 5.3). The limited records from the Flow Lake and Marble Canyon snow courses show a trend similar to the AHCCD data for the latter half of the century (Figure 5.4).

Figure PP. Annual rain, snow and total precipitation at the Banff AHCCD station. The solid line shows the five year running mean, blue diamonds show annual totals.

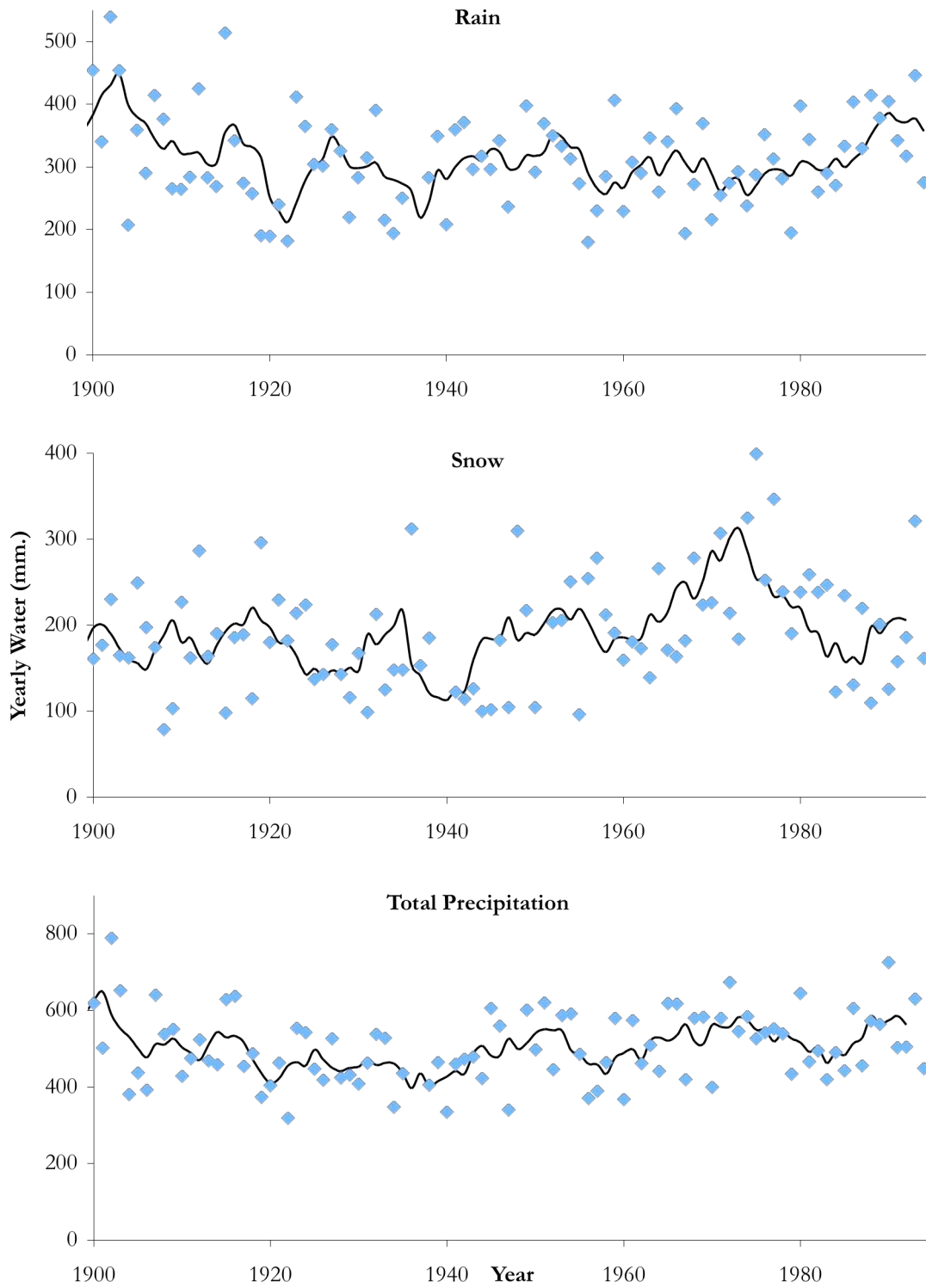


Figure 5.4. Snow water equivalent (SWE) at Marble Canyon, B.C., on May 1st, 1947 to 2003. Marble Canyon is located fourteen km southeast of Goodsir Pass. The dashed line shows mean SWE for the period 1947-2003 and the solid line shows a five-year running mean.

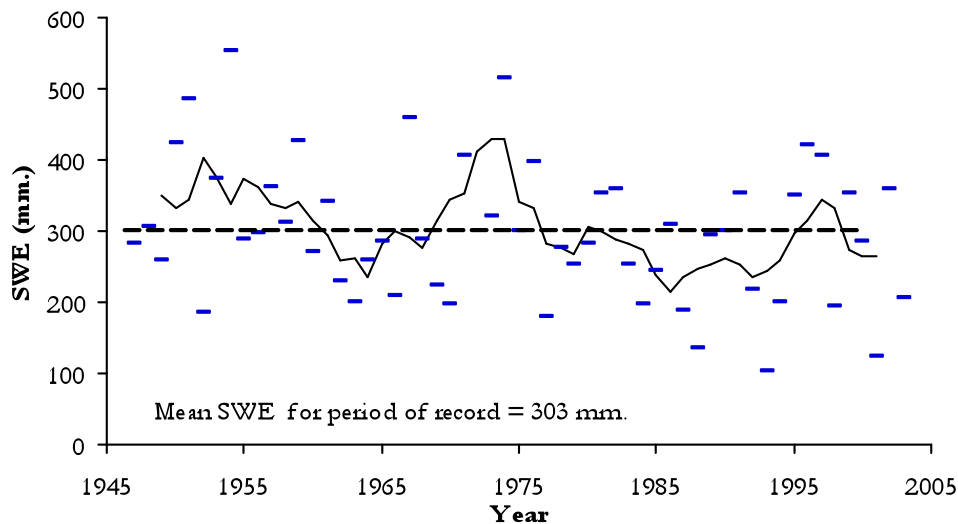
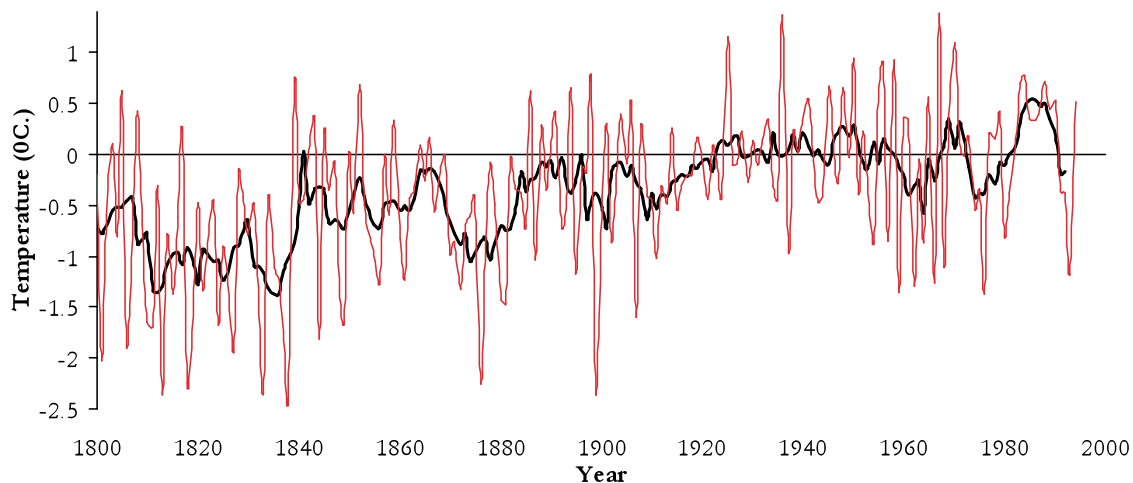


Figure 5.5. Tree-ring-based reconstructed of maximum summer temperature anomalies in Sunwapta Pass, Alberta (adapted from Luckman et al., 1997). The thin red line shows annual data, the thick black line shows the five-year running average.



5.1.2 Reconstructed Climate Records and Synoptic Climate Records.

Luckman et al. (1997) reconstructed mean summer air temperatures from tree-ring widths and late-wood ring density collected in the ATE of Sunwapta Pass in Jasper National Park. This record shows cool temperatures (-1.5 to -0.5 °C) during the early nineteenth century and a continued warming of summer temperatures beginning in the late 1800s to the present conditions (-0.5 to 0.5 °C) (Figure 5.5). The cool period during the 1940s shown in the

instrumental record from Banff is not well represented in the reconstructed temperature data.

The PDO index shows two cycles in the past century. Cool conditions were present from the beginning of the century until 1924 and again between 1947 and 1976, while warmer conditions prevailed between 1925 and 1946 and from 1977 until the mid 1990s (Mantua, 2004).

5.2 Dendroecological and Environmental Data.

5.2.1 Accuracy of Establishment Dates.

As previously noted it is not possible either to guarantee complete accuracy in determining establishment dates or to know the exact error that accompanies the data. However, the main goal of this study was to determine establishment dates and every effort was made to minimize errors in the data. Of the 917 tree-core samples collected the innermost ring was visible in 799. Of the 118 samples that were corrected, only 29 samples corrected pith dates by more than ten years. Of 986 dated individuals, 718 had establishment dates calculated from cores taken at the root collar, cross sections, or node counted trees. A further 181 samples were within five cm of the root collar and only nineteen trees were cored at a height of over ten cm above the root collar.

Results and analysis of tree establishment focus on the period 1800-2006 as only 16 of 984 dated trees established prior to 1800; these trees were all larch. Larch is the dominant species (58.5% of trees) in the ATE in Goodsir pass, while subalpine fir (22.8% of trees) and Engelmann spruce (18.7% of trees) comprise the remainder of the population. Dead trees make up 4.3% (44 out of 1030) of trees found in the study plots. Of these thirty-one were found in the lowest plot of each transect.

Because trees that establish and then die are not recorded in the establishment record of this study, the word 'establishment' refers to trees that established and then survived in the environment to the present day. Recording only those trees that established and survived creates obstacles to determining which time periods produced high numbers of seedlings,

but not to determining which time periods produced high numbers of seedlings that were able to survive into the present. The disappearance of dead trees from the establishment record will lead to a systematic underestimation of tree density and establishment numbers as time before the present increases (Lloyd and Fastie, 2003).

5.2.2 Temporal Establishment Variability.

Tree establishment in the ATE of Goodsir Pass over the past 200 years occurred in an episodic pattern that varies by species (Figure 5.6). Only the larch population registers more than one establishment pulse, with locally greater establishment rates seen in the 1840s, 1930s, and 1980s. Fir establishment begins very abruptly in the early 1960s and then tapers off by the 1990s, while continuous spruce establishment begins in the late 1940s and increases gradually to a peak in the late 1980s.

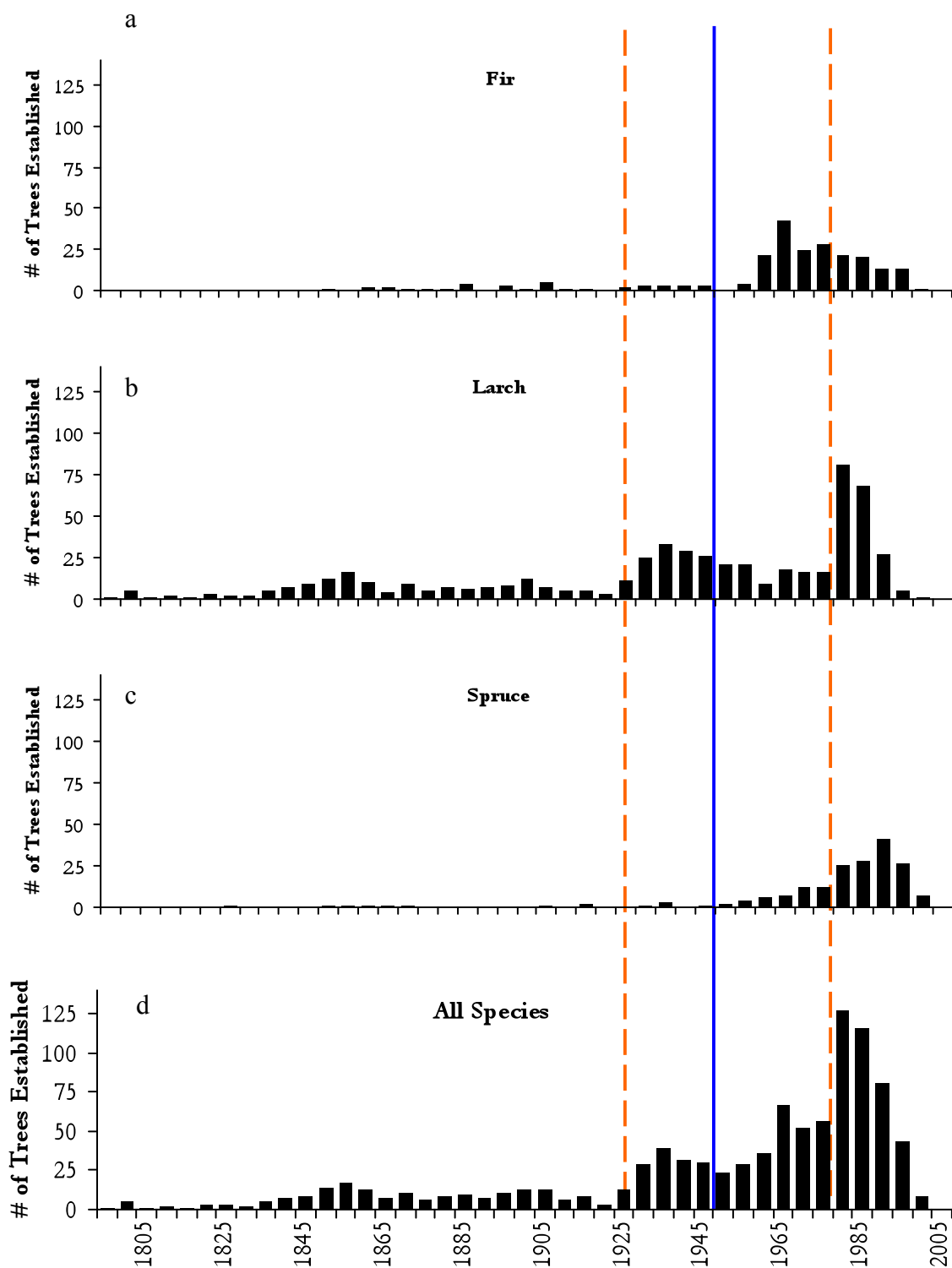
5.2.2.1 Fir Establishment Variability.

Fir establishment began in 1849 and occurred at very low levels (< 0.4 trees per year) until 1960, when establishment rates increased ten-fold to four trees per year. This high level of establishment continued until 1985 after which moderate levels of establishment persisted for another decade. Almost no fir establishment has taken place in the last decade (Figure 5.6).

5.2.2.2 Larch Establishment Variability.

Larch establishment occurred continuously over the 200-year record, but was concentrated in three pulses of establishment, each one containing greater numbers of surviving trees than the last (Figure 5.6). The oldest larch sampled in this study established in 1396; however, the next recorded larch to establish did not do so for nearly another three hundred years in 1667.

Figure 5.6. Tree establishment in five-year age classes of fir, larch, and spruce in Goodsir Pass. Orange dashed lines show the shift to the warm phase of the PDO and the blue solid line shows the shift to the cool phase of the PDO.



Establishment of surviving larch remained at very low levels (<0.5 trees per year) until 1830. Establishment of surviving trees increased to nearly two trees per year for the period 1830-1860, but then tapered off again to slightly more than one tree per year until 1924. A second pulse of larch establishment (mean rate of five trees per year) began in 1925 and lasted until ca. 1956. Following this, establishment decreased by 50% to 2.6 trees per year until 1976. The third and most intense pulse of larch establishment occurred from 1977 to 1986, during which establishment reached a mean of over fifteen trees per year. The next decade, 1987-1996, saw establishment decline nearly five-fold to 3.7 trees per year and only one larch established after 1997.

5.2.2.3 Spruce Establishment Variability.

Spruce establishment began in 1825 but was sporadic and occurred at very low levels (ca. 0.1 tree per year) until 1949 (Figure 5.6). Beginning in 1950, spruce establishment rates gradually increased to a peak of nine trees per year for the five-year period 1986-1990. Since then, spruce establishment declined to 3.6 trees per year.

5.2.3 Changes in the Elevation, Density, and Rate of Upward Advance of Trees in the Alpine Treeline Ecotone of Goodsir Pass.

The ATE in Goodsir Pass has increased in both elevation and density. Trees established earliest at lower elevations and the upward rate of advance of the entire tree population in Goodsir Pass has increased through time as the ATE moved to progressively higher elevations. However, changes in the elevation and density of each tree species occurred at different times and at different rates. As mentioned previously the study design created five ecotone zones defined by elevation; these zones are used to describe changes in the elevation of the ATE and are defined as follows: forest (2201 m asl), forest edge (2275 m asl), lower subalpine (2323 m asl), upper subalpine (2373 m asl) and alpine (2424 m asl).

5.2.3.1 Earliest Establishment as a Function of Elevation.

The oldest trees to establish and survive at all elevations were subalpine larch (Figure 5.7). This difference is especially notable at the lower edge of the ecotone. The oldest surviving larch trees began establishing at the forest edge in the 1700s, while fir and spruce did not do so until the late 1800s and early 1900s respectively. At lower elevations (2275-2323 m asl)

early fir establishment dates preceded those of spruce, while the reverse occurred at higher elevations (2373-2424 m asl). While early larch and fir establishment moved to progressively higher elevations in a roughly linear fashion, early spruce establishment occurred synchronously throughout the middle elevations (2323-2373 m asl) of the study site (Figure 5.7).

Figure 5.7. Mean earliest establishment dates of trees growing in four different zones: alpine (2424 m asl), upper subalpine (2373 m asl), lower subalpine (2323 m asl) and forest edge (2275 m asl) of the ATE in Goodsir Pass, B.C.

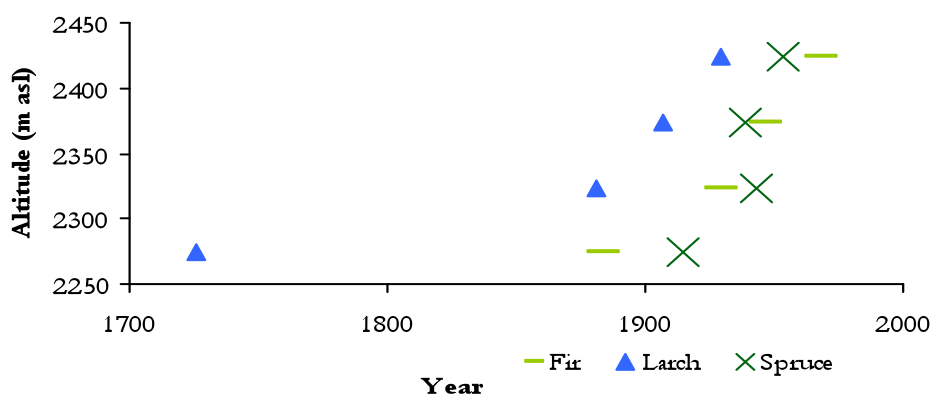


Table 5.1. Statistically homogenous means, generated by a one-way ANOVA, of the earliest establishment dates in each plot compared by ecotone zone of the ATE in Goodsir Pass, B.C. Columns below each species indicate means that are statistically similar. Thus each column represents a separate population of the earliest trees to establish in the ATE as differentiated by elevation.

Ecotone Zone (m asl)	Statistically Homogenous Means						
	Subalpine Fir		Alpine Larch		Engelmann Spruce	All Three Species	
Forest Edge (2275)	1883.8		1726.0		1914.7	1726.0	
Lower Subalpine (2323)	1929	1929	1880.8	1880.8	1942.8	1870.8	1870.8
Upper Subalpine (2373)	1946.6	1946.6	1906.7	1906.7	1938.8		1906.3
Alpine (2424)		1967.8		1929.4	1953.6		1921.4
Sig.	0.079	0.398	0.05	0.873	0.5	0.138	0.855

Results from the one-way ANOVA comparing the means of the earliest establishment dates in each ecotone zone show statistically homogenous means (Table 5.1). Mean earliest establishment dates for spruce at all elevations are statistically similar. Mean earliest establishment dates for fir and larch fall into two homogenous sets. The lower and upper

subalpine ecotone zones occupy both sets, while the forest edge and alpine bands differ significantly. Homogenous means for the three species combined also fall into two sets though they are slightly more differentiated than the sets for fir and larch; only mean earliest establishment dates in the lower subalpine are common to both sets (Table 5.1).

5.2.3.2 Total Establishment as a Function of Elevation.

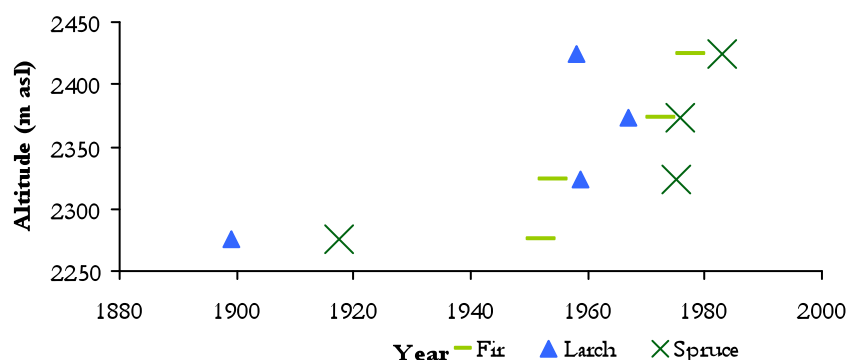
Tree establishment within each ecotone zone of the ATE in Goodsir Pass occurred asynchronously. In general, tree establishment occurred first at lower elevations and moved to higher elevations as indicated by progressively later mean establishment dates (Figure 5.8). This trend is clearly expressed for the tree population as a whole but individual species show significant variation (Table 5.2).

Figure 5.8 shows how establishment at different elevations varies in its timing as a function of tree species. Mean establishment dates of fir trees show a period of establishment occurring in the lower part of the ATE prior to 1960 and a subsequent period of establishment occurring at higher elevations in the 1970s. Mean establishment dates for larch populations at the forest edge occurred prior to 1900, while nearly synchronous establishment occurred at higher elevations from 1958-1967. At the forest edge a mean spruce establishment date of 1917 is followed by much later, and nearly synchronous, mean establishment dates in the lower and upper subalpine zones in 1975, and in the alpine zone in 1983.

The mean establishment date within each ecotone zone was calculated and a Mann-Whitney test of significant differences between those means describe where ecologically-relevant boundaries may lie along an elevation gradient (Table 5.2). Mean fir establishment dates at the forest edge and in the lower subalpine are statistically similar, and differ significantly from mean establishment dates in the upper two ecotone zones. Mean larch establishment dates in the forest and at the forest edge are statistically different from one another as well as all other populations of larch. However, mean establishment dates for the upper three ecotone zones of the study site are all statistically similar. Mean establishment dates for the lower subalpine even indicate a slightly younger tree population than exists higher in the ecotone. The mean spruce establishment dates of the upper three ecotone zones in the study

site are all statistically similar, differing by only eight years. The mean establishment date at the forest edge population is statistically different from the other three spruce populations.

Figure 5.8. Mean establishment dates of trees growing in four different zones: alpine (2424 m asl), upper subalpine (2373 m asl), lower subalpine (2323 m asl) and forest edge (2275 m asl) of the ATE in Goodsir Pass, B.C.



5.2.3.3 Changes in Tree Density through Time.

Similar to the patterns seen in the mean earliest establishment dates and the mean total establishment dates, tree density increased in lower portions of the ATE prior to upper elevations when all trees species are considered in aggregate. However, populations of individual species exhibit variations from this trend (Figure 5.9). Fir density increased from ca. two trees ha^{-1} to ca. fifty trees ha^{-1} in the forest edge and lower subalpine portions of the ATE from 1850 to 1900 and subsequently increased at a rate of ca. twenty trees ha^{-1} per decade during the twentieth century. In the upper subalpine and alpine areas of the ATE increases in fir density did not begin until the 1930s. From 1930 to 1960 fir density increased by ca. 2.5 trees ha^{-1} per decade in the upper subalpine, and from 1960 to 2000 rates of density increase jumped to ca. 25 to 50 trees ha^{-1} per decade in both the upper subalpine and alpine zones (Figure 5.9).

Larch density in the forest ecotone zone increased rapidly from ca. 200 trees ha^{-1} in the 1850s to over 2500 trees ha^{-1} by the 1900s, but the rate of increase in density declined to a lower rate of ca. 85 trees ha^{-1} per decade until present. The density of larch at the forest

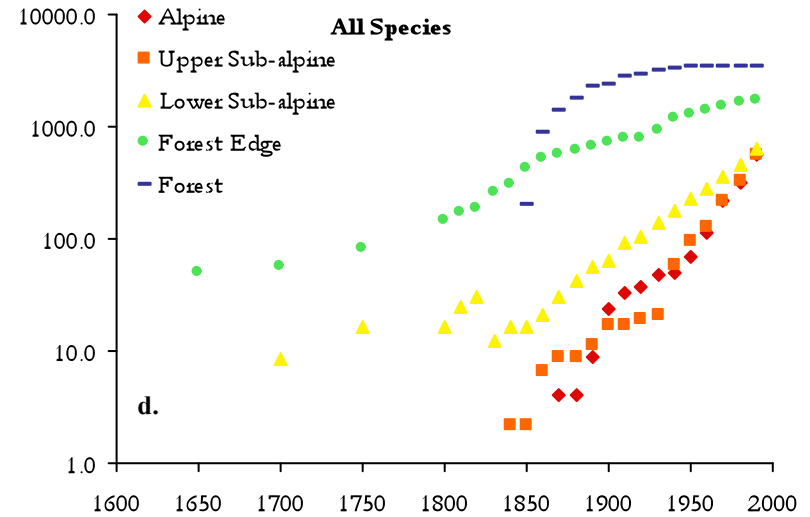
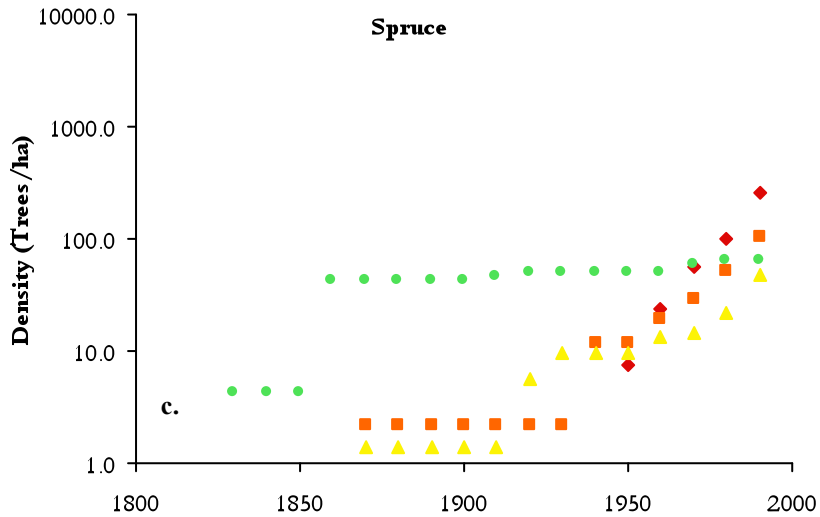
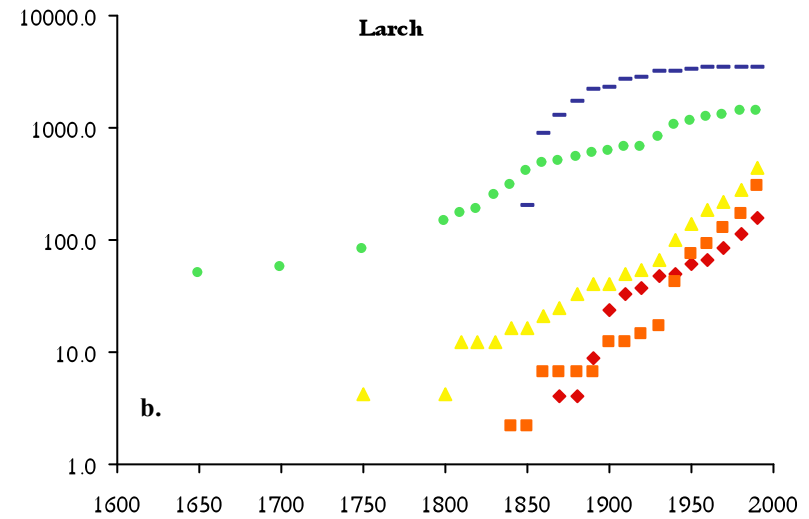
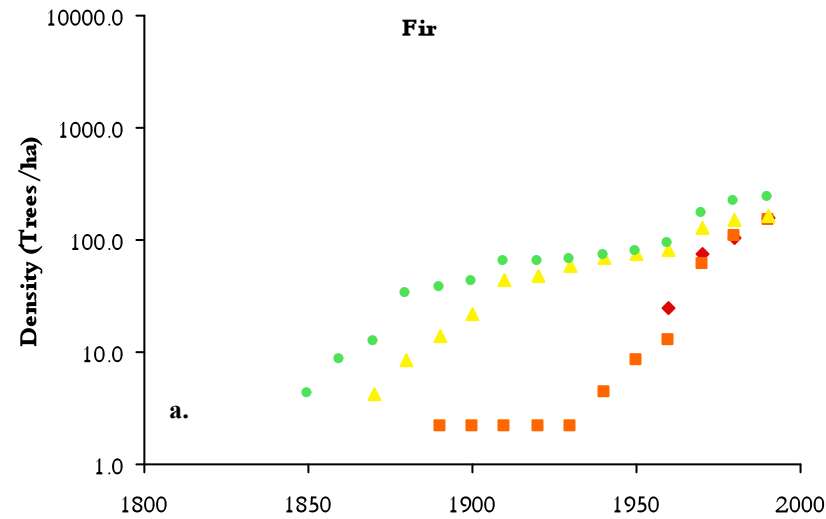
Table 5.2. Statistically homogenous means ($P < 0.025$) of the mean establishment dates in each plot compared by ecotone zone. Homogenous means were generated by comparing results from individual Mann-Whitney tests between each ecotone zone. The forest ecotone zone consisted of only one plot and contained only larch trees and thus is not shown for the fir or spruce populations.

Ecotone Zone (m asl)	Statistically Homogenous Means											
	Subalpine Fir		Alpine Larch		Engelmann Spruce		All Species					
Forest (2201)			1887					1886				
Forest Edge (2275)	1952			1899			1917		1909			
Lower Subalpine (2323)	1954				1959		1975			1959		
Upper Subalpine (2373)		1972			1967		1976				1970	
Alpine (2424)		1978			1958		1983					1976

Table 5.3. Upward advance rates (m/year) of the ATE in Goodsir Pass. Rates are calculated by dividing the difference in altitude between ecotone zones by the difference in mean establishment date for all trees within adjacent ecotone zones. Rates of advance are given between ecotone zones and vary in their period of advance by species. Advance of the larch ATE is not given incrementally upwards through the study site because mean establishment dates indicate that larch establishment occurred synchronously in all three upper ecotone zone.

Ecotone Zone / Elevation (m asl)	Increase in ATE Elevation	Rates of upward ATE advance (m/year) / (Period of Advance)			
		All Trees	Fir	Larch	Spruce
Upper Subalpine – Alpine / 2373 - 2424	51	8.50 / (1970-1976)	8.50 / (1972-1978)		7.29 / (1976-1983)
Lower Subalpine – Upper Subalpine / 2323 - 2373	50	4.55 / (1959-1970)	2.78 / (1954-1972)		50 / (1975-1976)
Forest Edge – Lower Subalpine / 2275 - 2323	48	0.96 / (1909-1959)	24 / (1952)-1954)		0.83 / (1917-1975)
Forest Edge – Alpine / 2275 - 2424	149	2.22 / (1909-1976)	5.73 / (1952-1978)	2.53 / (1899-1958)	2.26 / (1917-1983)

Figure 5.9. Change in tree density in the ATE of Goodsir Pass, B.C. Each figure shows decadal increases in mean density at five elevation zones in the study site. Density in the forest zone is not shown for fir and spruce trees as no trees of these species established there. Density is shown on a log-scale.



edge has increased at relatively consistent levels of ca. 25 to 100 trees ha⁻¹ per decade from 1800 until present with the exception of the period 1920 to 1940 when rates jumped to ca. 200 to 250 trees ha⁻¹ per decade. In the subalpine and alpine (2323 to 2424 m asl) sections of the ecotone, larch density has steadily increased starting ca. 1880 at rates of ca. twelve to fifty trees ha⁻¹ per decade. A notable exception to this is the period 1980 to 1990 when density in the lower and upper subalpine increased by 125 to 150 trees ha⁻¹ per decade (Figure 5.9).

Changes in spruce density occurred in a similar manner to changes in fir density except that the elevational division between the lower ATE (which experiences an early rapid increase in density followed by low rates into the present) and the upper ATE (which underwent a later sustained increase in density) is fifty m lower for spruce than it is for fir (Figure 5.9).

While densities of both spruce and fir were originally differentiated by altitude, they are now similar (ca. one hundred to two hundred trees ha⁻¹) at all elevations. Larch densities, however, have remained largely stratified by elevation through time, although densities in the upper portion of the ATE have converged (Figure 5.9).

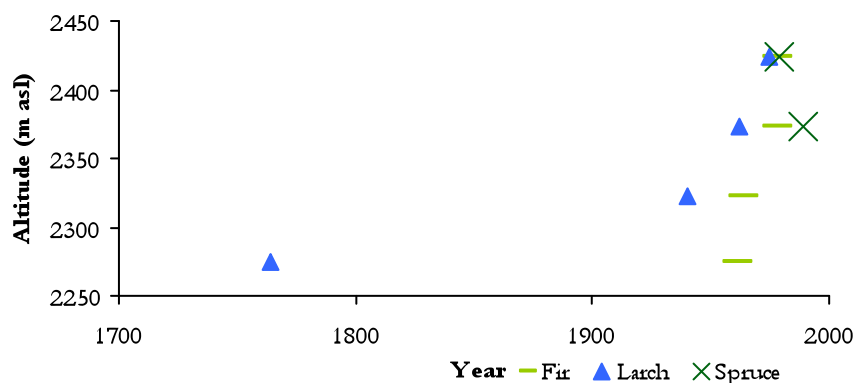
The change in density through time described above is also evident in Figure 5.10, which identifies the year in which tree density reached one hundred trees ha⁻¹. Larch populations are the first to reach this density at all elevations and do so earlier at lower elevations. Fir also reaches this threshold density first at lower elevations and later at higher elevations. Again, the distinction in the timing of establishment between the upper and lower portions of the ecotone is evident. The threshold density is reached at the forest edge and in the lower subalpine in the early 1960s, and in the upper subalpine and alpine just prior to 1980. Unlike larch and fir, spruce density first reaches one hundred trees ha⁻¹ in the alpine zone and does so ten years later in the upper subalpine. Spruce density never exceeds one hundred trees ha⁻¹ in the lower portion of the ATE (Figure 5.10).

5.2.3.4 Rates of Upward Advance of the Alpine Treeline Ecotone.

The ATE in Goodsir Pass moved upwards in elevation at an average rate of 2.22 m per year over a seventy-year period beginning in the early 1900s (Table 5.3). Rates of ATE advance

between different zones of the ATE are higher in the upper part of the ecotone. Trees established at increasingly higher elevations in the area between the forest edge and the lower subalpine at a rate of just under one m per year. This rate increased to 4.55 m per year in the area between the lower subalpine and upper subalpine and to an even greater 8.5 m per year in the area between the upper subalpine and alpine. Rates of advance for individual species are more variable than for the tree population in the ATE as a whole.

Figure 5.10. Year in which tree density reached one hundred trees ha^{-1} in four different zones: alpine (2424 m asl), upper subalpine (2373 m asl), lower subalpine (2323 m asl) and forest edge (2275 m asl) of the ATE in Goodsir Pass, B.C. Spruce density has surpassed one hundred trees ha^{-1} only in the upper portion of the ecotone.



An upward shift in the elevation of the fir ecotone did not begin until the middle of the twentieth century, but then did so very quickly, at a rate of twenty-four m per year between the forest edge and lower subalpine. This rate decreased to slightly less than 3 m per year as trees populated the middle elevations of the ATE and then increased again to 8.5 m per year in the upper portion of the ATE (Table 5.3).

Larch trees expanded upward from the forest edge to all higher portions of the ecotone in a synchronous manner as is evident from the very similar mean establishment dates for larch in the three upper ecotone zones (Table 5.2). This rapid advance results in the calculation of a single rate of upward advance through the entire ecotone of 2.53 m per year. Larch upward expansion into previously un-treed areas occurred earlier than the expansion of fir and spruce (Figure 5.8).

Rates of spruce advance into higher portions of the ecotone occurred slowly between the forest edge and lower subalpine (less than one m per year). Trees established nearly simultaneously in the middle portion of the ecotone (Figure 5.8) at a high rate (fifty m per year) of upwards expansion, which then slowed to just over seven m per year as trees established in the alpine zone (Table 5.3).

5.2.4 Relationship between Tree Establishment and Climate Variability.

5.2.4.1 Five-Year Establishment Age Classes.

Pearson's correlation coefficients between five-year establishment age classes and five-year climate averages identify several climate parameters that are significantly correlated with establishment patterns of the tree species in Goodsir Pass. Only March and October mean and maximum temperature values are correlated with tree establishment of all species (Table 5.4). The patterns for individual species are less consistent. Establishment patterns of fir and spruce are significantly correlated ($P \leq 0.05$) with May-September monthly minimum temperatures, a period that encompasses the entire period during which tree growth is likely. (Alexander and Shepard, 1990; Arno, 1990; Holtmeier, 2003) (Table 5.4). Larch establishment is only correlated significantly ($P \leq 0.05$) with March minimum temperatures.

Mean monthly precipitation totals (rain, snow, and total precipitation) generally are not significantly correlated with tree establishment. The only months that do correlate are April and May and do so only with fir and spruce establishment (Table 5.4). May 1st SWE, the PDO, and Colenutt's (2000) *L. lyallii* ring-width indices from Wolverine Pass are not correlated with tree establishment for any species (Table 5.4). *L. lyallii* ring-width indices from Floe Lake are significantly correlated ($P \leq 0.01$) with fir and larch establishment. Reconstructed summer temperatures from the Columbia Icefield (Luckman et al., 1997) are significantly correlated ($P \leq 0.05$) with all tree species though more so with larch and spruce than with fir.

Table 6.1. Selected upward shifts of ATEs in the past two hundred years. While not an exhaustive list, the table displays a majority of studies concerned with ATE dynamics that calculate an upward rate of advance or shift in elevation of the ecotone. The first six studies did not give a clearly defined period during which an upward shift was recorded and thus no rate can be calculated. All rates are likely not to be directly comparable due to differences in how the ATE was defined and how rates of change and upward shifts were calculated.

Location	Authors (year of study)	Species	Upward Shift (m)	Period (year)	Rate (m per year)
Alaska Range, AK	Lloyd and Fastie (2003)	<i>Picea glauca</i>	14-29	The period of record is not clearly defined.	No rate calculated.
White Mountains, AK	Lloyd and Fastie (2003)	<i>Picea glauca</i>	30		
Western Alaska	Suarez et al. (1999)	<i>Picea glauca</i>	122		
South Island, New Zealand	Cullen et al. (2001)	<i>Nothofagus menziesii</i>	5		
Northern Patagonia	Daniels and Veblen (2004)	<i>Nothofagus pumilio</i>	0		
South Island, New Zealand	Wardle & Coleman (1992)	<i>Nothofagus menziesii</i> & <i>Nothofagus solandri</i>	7-9		
Swiss Alps	Hattenschwiler & Körner (1995)	<i>Pinus sylvestris</i> - <i>Pinus cembra</i>	0	1981-1992	0
Glacier N.P., Montana	Bekker (2005)	<i>Picea engelmannii</i> , <i>Pinus contorta</i> , & <i>Abies lasiocarpa</i>	7-16	1800-1980	0.28-0.62
Northwestern Canada	Szeicz & MacDonald (1995)	<i>Picea glauca</i>	5	1850-1990	0.04
Sunwapta Pass, Alberta	Luckman and Kavanagh (2000)	<i>Picea engelmannii</i> & <i>Abies lasiocarpa</i>	145	1700-1994	0.5
Uinta Mountains, UT	Munroe (2003)	<i>Picea engelmannii</i> & <i>Abies lasiocarpa</i>	61-183	1870-2001	0.5-1.4
South-west Yukon	Danby and Hik (2007)	<i>Picea glauca</i>	65-85	1920-2005	0.8-1.0
Scands Mountains, Sweden	Kullman (2000)	<i>Betula pubescens</i> , <i>Pinus sylvestris</i> , & <i>Picea abies</i>	100-130	1915-1999	1.2-1.5
Scands Mountains, Sweden	Kullman (2001)	<i>Betula pubescens</i> , <i>Pinus sylvestris</i> , & <i>Picea abies</i>	100-165	1915-2000	1.2-1.9
Kootenay NP, B.C.	This study	<i>Larix lyallii</i> , <i>Picea engelmannii</i> , & <i>Abies lasiocarpa</i>	149	1909-1976	2.2-5.7

5.2.4.2 Annual Establishment Age Classes.

Pearson correlations between annual establishment and climate show significant correlations similar to the five-year establishment age classes. May through August monthly minimum temperatures are significantly correlated ($P \leq 0.01$) with fir and spruce establishment. Both Colenutt's (2000) *L. hyalii* ring widths and Luckman et al.'s (1997) reconstructed summer temperatures from the Columbia Icefield area are significantly correlated ($P \leq 0.05$) with all tree species. Similar to the five-year climate averages, correlations of annual climate values of monthly mean and maximum temperatures and all monthly precipitation values are infrequent and do not occur during the period when tree growth is expected.

5.2.5 Spatial Variability of Tree Establishment.

5.2.5.1 Quadrat-Level Predictors of Tree Establishment.

The binomial regression analysis generates a model that predicts whether establishment will occur in a given quadrat based on seven independent environmental variables (altitude, slope steepness, % bare ground, % shrub cover, % herb cover, % moss and lichen cover; and mean two-year SWE). It identifies which of the variables are significant in predicting establishment and the degree to which an increase in an independent variable affects the likelihood that establishment will occur in a quadrat. The model also assesses its own effectiveness in predicting establishment.

Hosmer and Lemeshow chi-squared values were not significant for any of the models, which indicates that all models fit the data well (Table 5.5). Models generated by the binomial regression analysis do not predict either fir or spruce establishment any better than a random choice would (Table 5.5). Despite this, all environmental variables were identified as significant predictors of fir establishment ($P \leq 0.01$). Significant predictors ($P \leq 0.01$) of spruce establishment included the percent of a quadrat occupied by bare ground, shrubs, and herbs and the SWE. The analysis did produce models that predicted establishment of both larch and all three species in aggregate better than a random choice would (Table 5.5).

Table 5.5. Results of a binomial regression that models the impact of quadrat-level environmental variables on tree establishment. The upper left table in each series shows the effectiveness of the model in estimating whether establishment will occur in a particular quadrat. To be effective, the model must predict correctly more often than the blind estimation. The blind estimation is the percent of cells that would be correctly predicted to have or not to have establishment if a coin toss was used to predict establishment. The Hosmer and Lemeshow significance value assesses the model's goodness of fit. Non-significant values indicate the model is a good fit. The lower table in each set gives the model results. The odds ratio for each independent variable shows the factor by which the odds of establishment occurring in a quadrat changes for a one-unit increase in the independent variable. Units of increase are: Altitude: 100 m; Slope: 1 degree steeper; Bare Ground, Shrubs, Herbs, and Moss and Lichen: 1% greater coverage of the quadrat; 2 yr. SWE: 1 cm. Bold values are significant * for $P \leq 0.05$; ** for $P \leq 0.01$.

a. FIR		Percentage Correct		Blind Estimation					
No Establishment		98.7		78.5		Hosmer and Lemeshow Significance Value = 0.362			
Establishment		10.5		21.5					
Overall Percentage		79.7							
Variable	Altitude	Slope	Bare Ground	Shrubs	Herbs	Moss/Lichen	2 yr SWE	Constant	
B	-0.798	0.099	-0.063	-0.060	-0.057	-0.048	-0.019	23.087	
S.E.	0.302	0.018	0.016	0.014	0.014	0.018	0.006	7.435	
Odds ratio	0.450**	1.104**	0.939**	0.942**	0.945**	0.954**	0.981**	1.06 E¹⁰ **	

b. LARCH		Percentage Correct		Blind Estimation					
No Establishment		80.8		55.2		Hosmer and Lemeshow Significance Value = 0.504			
Establishment		62.0		44.8					
Overall Percentage		72.4							
Variable	Altitude	Slope	Bare Ground	Shrubs	Herbs	Moss/Lichen	2 yr SWE	Constant	
B	-1.694	-0.057	-0.011	0.001	-0.011	0.017	-0.005	41.451	
S.E.	0.281	0.014	0.013	0.011	0.011	0.011	0.006	6.839	
Odds ratio	0.184**	0.944**	0.989	1.001	0.989	1.017	0.995	1.01 E¹⁹ **	

c. SPRUCE		Percentage Correct		Blind Estimation					
No Establishment		97.2		79.9		Hosmer and Lemeshow Significance Value = 0.756			
Establishment		19.0		20.1					
Overall Percentage		81.4							
Variable	Altitude	Slope	Bare Ground	Shrubs	Herbs	Moss/Lichen	2 yr SWE	Constant	
B	0.559	0.035	-0.060	-0.054	-0.062	-0.026	-0.019	-8.068	
S.E.	0.368	0.020	0.016	0.014	0.014	0.016	0.007	8.884	
Odds ratio	1.749	1.036	0.942**	0.947**	0.940**	0.974	0.981**	0	

d. ALL SPECIES		Percentage Correct		Blind Estimation					
No Establishment		35.0		37.7		Hosmer and Lemeshow Significance Value = 0.233			
Establishment		86.1		62.3					
Overall Percentage		66.8							
Variable	Altitude	Slope	Bare Ground	Shrubs	Herbs	Moss/Lichen	2 yr SWE	Constant	
B	-1.085	-0.010	-0.029	-0.017	-0.026	0.006	-0.013	29.353	
S.E.	0.262	0.014	0.013	0.012	0.011	0.011	0.005	6.410	
Odds ratio	0.338**	0.990	0.971*	0.984	0.974*	1.006	0.987*	5.59 E¹² **	

Increases in altitude and slope both reduce the chance that larch establishment will occur, although altitude does so to a much greater degree. For every one hundred m increase in elevation the chance of larch establishment taking place is 0.18 times the chance that larch establishment would occur at the original elevation. In contrast, a slope steepness increase of one degree means that larch establishment is only 0.944 times as likely (Table 5.5).

Increases in elevation, the percent of ground cover occupied by both bare ground and herbs and the amount of SWE all reduce the chance of a tree of any species from establishing in a given quadrat. Again the impact of elevation is greatest and causes establishment to be 0.338 times as likely for every one hundred m increase compared with odds ratios of 0.971, 0.974, and 0.987 for increases of bare ground, herb cover, and SWE (Table 5.5).

5.2.5.2 Impacts of Quadrat-Level Conditions on Tree Health.

Tree health shows few significant variations as a function of the four site-specific variables: elevation, aspect, slope steepness and snow depth (Table 5.6). Dead trees were found at statistically significant lower elevations than any other trees except for those that were classified as barely alive. Mean elevation is highest for trees of average health. No significant differences exist among the mean elevation of trees that were barely alive, stunted or ill, healthy, or vigorous. Trees of all health categories were found on statistically similar aspects. The relationship between slope steepness and tree health exhibits the clearest trend. In general the healthiest trees are found on steeper slopes. However, all trees except for those that are dead or barely alive are found on slopes with statistically similar mean values. Mean snow depth is lowest around trees of average health and increases both as tree health improves and declines. Significant differences exist between mean snow depths around trees classified as stunted or ill and average and mean snow depths around dead and vigorous trees (Table 5.6).

5.2.5.3 Interaction between Microtopography and Snow Water Equivalence.

The mean SWE around fir and spruce trees growing in micro-shelters is significantly less than the mean SWE around fir and spruce trees growing on exposed ground ($P = 0.005$ and $P = 0.031$ respectively) (Figure 5.11). The mean SWE around larch trees in micro-shelters is also less than that around larch trees growing on exposed ground though not significantly so (Figure 5.11). The mean SWE around trees of all species growing in micro-shelters is

significantly less than the mean SWE around trees of all species growing on exposed or level ground (Figure 5.11). Mean SWE is greatest around Larch trees and least around spruce trees, and significant differences exist between the mean SWE around all species ($P < 0.001$).

Table 5.6. The impact of four site-specific variables on tree health in the ATE of Goodsir Pass, B.C. The table shows sets of homogeneous ranked means (displayed in columns underneath each site-specific variable) generated by a Kruskal-Wallis test. The table allows for an assessment of whether trees of a given health tended to be found in environments distinct from those in which trees of a different given health were found.

Tree Health	Statistically Homogenous Means								
	Altitude (m asl)		Aspect (degrees)	Slope steepness (degrees)		Snow Depth (cm.)			
Vigorous growth		2320		197			18.4		193
Healthy		2330		199			18.1	185	185
Average			2350	201			18.9		168
Stunted or ill		2334	2334	201		17.32	17.32		178
Barely alive	2308	2308		183	14.7	14.7		181	181
Dead	2273			206	13.2				195

5.3 Ground Based Repeat Photography of the Study Site.

While the ground-based repeat photography of the study site initially was used to locate an ATE that has increased in elevation, the resulting photo-pairs also reveal important details concerning the magnitude and character of change in the ATE of Goodsir Pass. The four photo-pairs allow for a visual assessment of the area from three different angles and visually support results obtained from the more detailed dendroecological data.

Photo-pairs produced from historical images taken in 1906 by A.O. Wheeler show the entire study site in eastern and northern views (Figures 5.12, 5.13, and 5.14). The photo-pairs show a significant increase in the density of trees, particularly evident in the lower portion of transect two (Figures 4.1 and 5.13) and clear upward movement of the ATE elevation most noticeable across the entire face on which transect three is located (Figures 4.1 and 5.14). The entire forest at and immediately below the ATE was far more open and consisted of larger trees (indicating an older age structure) in the historical landscape than exists in the modern landscape.

The photo-pair produced from the historical image taken in 1923 by Byron Harmon (Figure 3.2) gives a view southwest looking down the length of transect two (Figure 4.1). As in the Wheeler photo-pairs the substantial increase in tree density is clear. While the extreme oblique view of the study site landscape in this images makes it challenging to assess the exact type and magnitude of the change, the complete change from an open alpine environment to a treed landscape is immediately obvious. Additionally, the repeated image was taken in late September when needles on the subalpine larch trees change to a gold colour. The dominance of larch trees growing at higher elevations in the ecotone is especially striking in this image, though a band of lighter green trees (presumably subalpine larch) is also visible growing at the upper extent of the forest in the modern images of the Wheeler photo-pairs (Figures 5.12 and 5.13).

Figure 5.11. The graphs show the mean snow water equivalent present around trees growing on three different types of microtopography. Only trees in the middle and upper portion of the ATE in Goodsir Pass, B.C., are included. Letters indicate statistically different means for each population of trees. Hollow columns show mean snow depths for all trees.

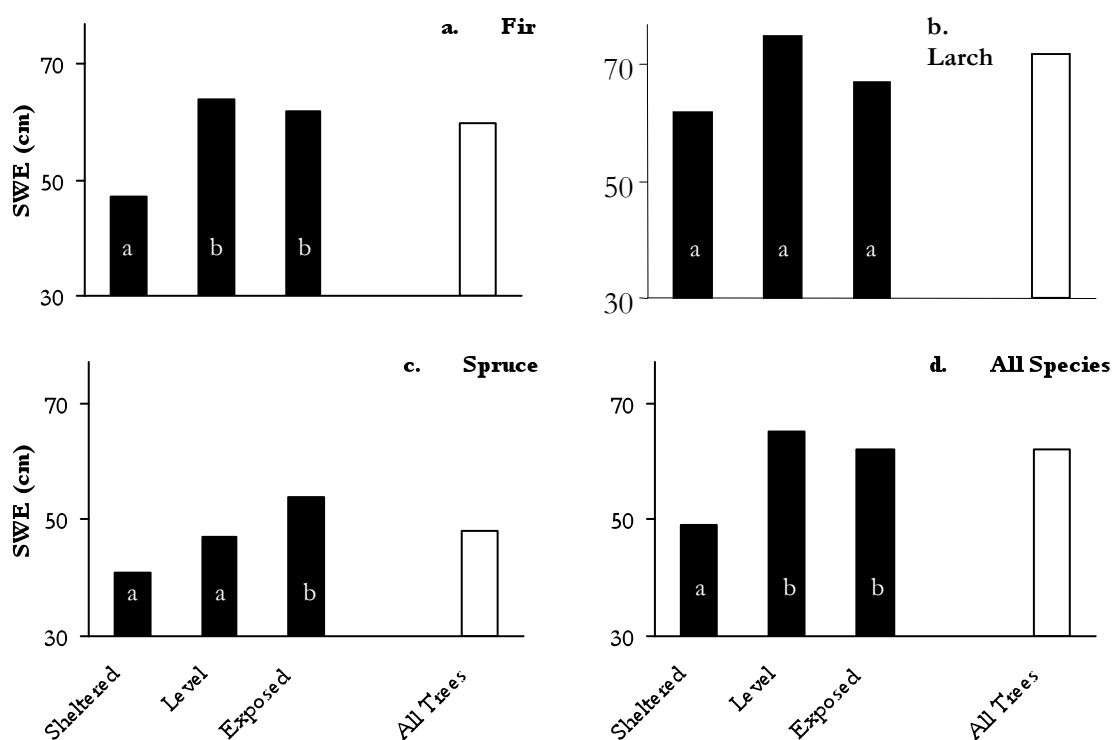


Figure 5.12. Repeat photo-pair showing the study site in a view east from the summit of Mt. Sharp, B.C. Note the increase in density and elevation of the ATE in the foreground of the image. Densely spaced trees are now growing to the ridge-top in the 2007 image.



Library and Archives Canada. e008406868

1906. by A.O. Wheeler



Mountain Legacy Project. Sharp Mt. view East

2007. by W. Roush

Figure 5.13. Repeat photo-pair showing the study site in a view southeast from the summit of Mt Sharp, B.C. Note the large increase in tree density in the lower portions of the ecotone at the bottom of the photograph, and in the basin in the centre of the image.



Library and Archives Canada. e008406869

1906. by A.O. Wheeler



Mountain Legacy Project. Sharp Mt. view Southeast

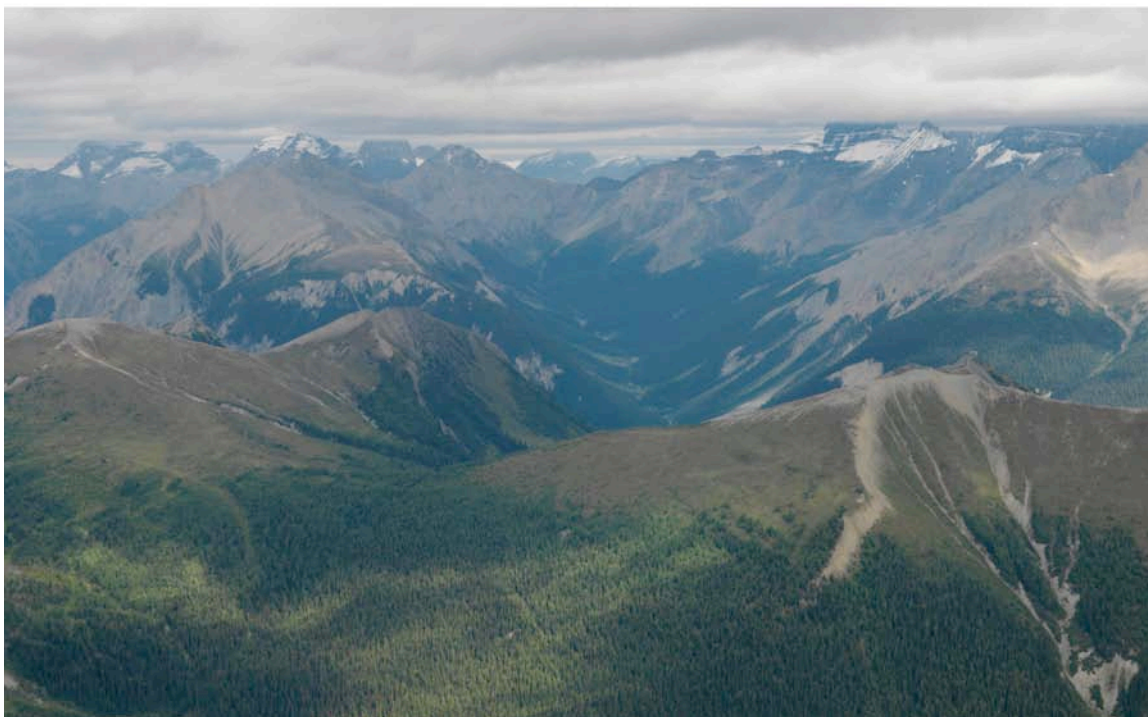
2007. by W. Roush

Figure 5.14. Repeat photo-pair showing the study site in a view north from the summit of Limestone Peak, B.C. Note the increase in tree density in the lower left portion of the image and the increase in the upper limit of the ecotone on the slope in the centre of the image and up the ridge in the lower right of the images.



Library and Archives Canada. e008292123

1906. by A.O. Wheeler



Mountain Legacy Project. Limestone Peak Mt. view Northeast

2007. by W. Roush

5.4 Regional Ground-Based Repeat Photography.

Photo-pairs produced by regional repeat photography surveys were categorized by aspect and location within the southern Canadian Rocky Mountains (i.e. National Park). The differing landscape characteristics of each park dictated which photo-pairs were suitable for analysis; this resulted in an unequal number of ATE segments for each aspect within each park. To control for this inconsistency in the data, the results presented show the number of ATE segments in which a type of ATE change occurred as a percent of the segments analyzed, rather than an absolute number of segments.

5.4.1 Changes in the Alpine Treeline Ecotone Relative to Landscape Position.

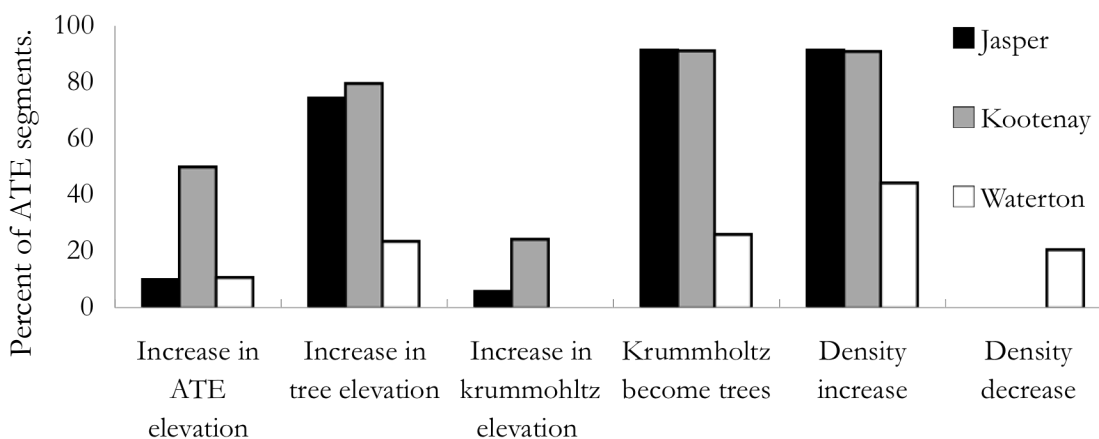
Classifying ATE segments based on the park in which they are located reveals a number of patterns (5.15). The greatest amount of change in the ATE occurred in Jasper and Kootenay national parks where 74% (twenty-six of thirty-five) and 79% (twenty-seven of thirty-four) of ATE segments respectively showed an increase in the altitude of upright trees. Increases in tree density and changes in tree form from krummholz to upright trees were observed in 91% (thirty-one of thirty-four) of ATE segments in these two parks. Increase in the elevational extent of the ATE was less common in all three parks but occurred most commonly in Kootenay National Park (50% (seventeen of thirty-four) of segments). Observed changes in the ATE of Waterton Lakes National Park were typically a quarter to half that observed in the two northern parks. Waterton Lakes National Park was the only park where a decrease in tree density in the ATE was observed (Figure 5.15). In no park did upright trees change to krummholz.

5.4.2 Changes in the Alpine Treeline Ecotone Relative to Aspect.

Patterns of change in the physiognomy and position of trees in the ATE are less pronounced when ATE segments are classified by aspect (Figure 5.16). Change within ATE segments of the same aspect in Jasper and Kootenay national parks show a similar pattern. In both cases the altitude of upright trees increased the most on east and west aspects, and trees on north-facing slopes experienced the least amount of change from krummholz to upright trees. However, these are isolated cases and no single aspect has a consistent, region-wide effect on any of the other types of change within the ATE. In Waterton Lakes National Park, the greatest percent of ATE segments showing an increase in tree altitude and tree density was

observed on northern and western aspects. Decreases in tree density occurred only in Waterton Lakes National Park (21% (seven of thirty-four) of segments), was most pronounced on eastern slopes (50% (2 of 4) of segments), and did not occur at all on northern aspects (Figure 5.16). 12% (four of thirty-four) of ATE segments in the park showed no change. Only eight photo-pairs showed northern and eastern aspects in both Kootenay and Waterton Lakes national parks. Due to the low sample size, results for these aspects may be less representative of actual conditions in the landscape.

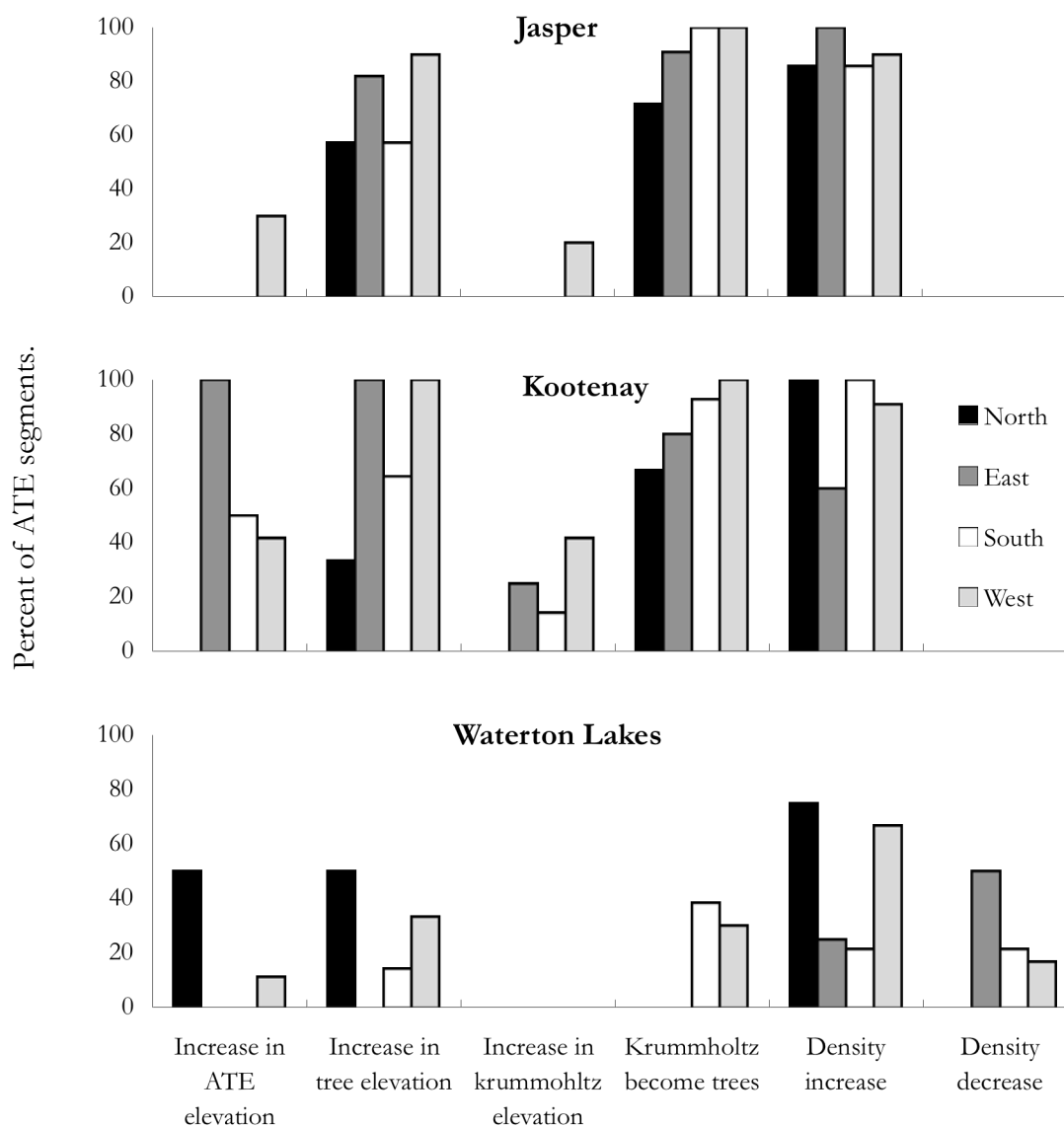
Figure 5.15. Percent of ATE segments that underwent a change in ATE elevation and character in Jasper, Kootenay, and Waterton Lakes national parks. A total of 104 segments were analyzed: 35 each from Jasper and Waterton Lakes national parks, and 34 segments from Kootenay National Park.



5.5 Summary.

Taken as a whole, the results presented in this chapter form a picture of change in the ATE. Along with repeated photo-pairs of the study site and the history of the study area (described in chapter three), the climate data presented in section one of this chapter set the scene and provide the backdrop against which the ATE dynamics of the past two centuries take place. A general warming trend of air temperatures throughout the past century (most pronounced for minimum temperatures), high interannual variation in precipitation amounts, and a rough correspondence in most climate records indicating a cooler period in the mid nineteenth century and a warmer period from 1980 onwards constitute the most salient results.

Figure 5.16. Percent of ATE segments, classified by aspect, that experienced a change in ATE elevation and character in Jasper, Kootenay, and Waterton Lakes national parks.



The second section and the bulk of this chapter focused on the timing, magnitude and nature of change within the ATE and presented results from analyses that attempt to identify drivers behind these changes. Four themes emerge. The first describes the temporal variability in tree establishment and indicates an episodic pattern of establishment that varies by species. Larch began establishing in significant numbers in the early 1800s, well before either spruce or fir, which only established in significant numbers beginning in the late 1940s and early 1960s respectively. The second theme indicates that the timing and rate of increase

in both ATE elevation and density vary markedly by species. The third and fourth themes address possible causes of change within the ATE. Correlations between climate and establishment values are most pronounced for minimum air temperatures and fir and spruce establishment patterns, as well as reconstructed temperatures and larch and spruce establishment. Lastly, analyses concerning the impact of site-specific variables on the location and character of tree establishment indicate that site-specific conditions influence larch establishment more than spruce or fir and that site-specific variables have an ambiguous impact on tree health. The most salient result of this fourth theme centres upon interaction between site-specific variables acting at two scales; the impact of microtopography on the location of tree establishment was shown to be related to SWE.

The third section places the more detailed study of the ATE in Goodsir Pass in the context of ATE change throughout the southern Canadian Rocky Mountains. Here results point to the importance of landscape position over aspect in determining the magnitude and nature of change within the ATE.

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Significant changes have occurred within the ATE of the southern Canadian Rocky Mountains over the past two centuries. While these changes are not continuous either in time or space, they are, with little exception directionally biased towards a denser and higher ATE. While finding specific causes is challenging, several climatic shifts and environmental conditions are likely drivers of a number of the observed changes in the ATE. These drivers vary in their impact depending on the scale at which they operate and on how they interact with other drivers at different scales. Lastly, response to these drivers varies among tree species.

The main objectives of this study were: i) to build upon the visual evidence of an upward shift in the ATE of Goodsir Pass, by determining the timing and rate of that advance; ii) to identify likely drivers of this change; and, iii) to contextualize the research in Goodsir Pass by comparing it to changes that have occurred in the ATE at three other locations in the southern Canadian Rocky Mountains. This chapter addresses these objectives and concludes by synthesizing the discussion into two broad themes: the first theme examines whether spatial or temporal patterning is more dominant in tree establishment in Goodsir Pass. The second theme describes how coarse-scale geo-climatic patterns change the importance that fine-scale patterns of topography have on the process of tree establishment.

The interpretations of the results presented in Chapter Five lead to four significant conclusions. First, the amount and rate of upward movement of the ATE in Goodsir Pass is globally significant. Second, temporal patterns of tree establishment are more pronounced than spatial patterns indicating that the ATE is influenced more strongly by factors at the constraints level than the components level. Third, the change that has occurred in Goodsir Pass is not anomalous for the southern Canadian Rocky Mountains; however it is of a greater magnitude than is seen in either Jasper or Waterton Lakes national parks. Lastly, coarse-scale landscape patterns often determine the relative importance that finer-scaled patterns will have on processes of change in the ATE.

6.1 Substantial Evidence for an Upward Shift of the Alpine Treeline Ecotone in Goodsir Pass.

Quantifying an upward shift in the ATE is surprisingly difficult. In his comprehensive description of treeline ecotones, Holtmeier (2003) devotes several pages to the difficulties of identifying and describing this ecological process. In addition to the difficulties caused by various definitions of what is considered to be the limit of the ecotone, change in the ATE can take a variety of forms including changes in tree position, density, form and composition (Weisberg and Baker, 1995). A change in the elevation of the uppermost tree in the ATE is the simplest way to describe an upward shift; however, this metric focuses on a single individual rather than the tree population as a whole. Using mean age as a metric helps to quantify change at a population level, but details in time become lost. Reconstructing tree density allows for a comprehensive view of change through time and acknowledges that significant change can occur in the ecotone without a shift in the position of the highest trees. Thus, a comprehensive assessment of a changing ATE requires a variety of metrics that examine both the type and rates of change.

An upslope advance of the ATE will create a pattern of decreasing stand age with elevation (Lloyd and Fastie, 2003). Mean establishment dates in upper portions of the ecotone will be more recent than those in the lower portions. Steady recruitment will be indicated by progressively more recent mean establishment dates at higher elevations in the ecotone, while episodic establishment will be expressed in significant differences in stand age between some elevations but not all. I found unequivocal evidence for upslope advance of the ATE in Goodsir Pass. Mean establishment dates of both the oldest trees and all trees at lower elevations preceded mean establishment dates for trees growing at higher elevations.

Mean establishment dates of the oldest trees within each ecotone zone provide an indication of when conditions began to allow isolated establishment at higher elevations. Results of an ANOVA specify which means are statistically similar. Four statistically different means are possible (one for each ecotone zone) and the fewer means that are statistically different, the less likely that early establishment in the ecotone was constrained by elevation. The results of the ANOVA (Table 5.1) indicate that early establishment was minimally influenced by an elevation gradient. A significant difference in the timing of early fir and larch establishment

only occurs between the forest edge and alpine ecotone zones. Early establishment of spruce is not differentiated by elevation. This lack of well-differentiated means implies that early establishment took place throughout the ecotone and had only a slight spatial relationship with elevation.

Total establishment shows more stratification by elevation. In aggregate the entire tree population is significantly younger at each fifty m increase in altitude. However, individual species have a more homogenous age distribution and only belong to two or three separate populations rather than five (Table 5.2). This observation suggests that the ATE as a whole has moved up in a somewhat continual manner, while individual species have done so in an episodic pattern. The design of this study allowed for trees to be grouped into five ecotone zones based on elevation. However, for individual species, the ATE consists of a lower portion in which establishment occurred earlier in the twentieth century and an upper portion in which trees established after 1950. This division is less temporally distinct for subalpine fir than it is for the other two species. As Bekker (2005) points out, a lack of a significant difference in mean establishment dates between upper and lower sections of an ATE may result from ongoing establishment throughout the entire ecotone. As a result, mean establishment dates will tend to converge, thereby causing the populations to become statistically similar despite a real difference in the timing of initial establishment.

Upslope advance of the ATE is not the only possible explanation for an age structure that decreases with elevation (Lloyd and Fastie, 2003). If tree mortality increases at higher elevations, the population in the upper ATE would experience a high turnover resulting in a younger population structure at higher elevations. If this were the case at Goodsir Pass, dead trees and seedlings should be common at higher elevations; however, I found very few dead trees throughout the entire study site (4.3% of all trees), and 70% of dead trees were found in the lowest plot of each transect. Therefore, I conclude that an upslope advance of the ATE is the cause of the decreased age structure at higher elevations.

6.1.1 An Upward Shift of Hemispheric Significance.

Upward shifts of the ATE have been hypothesized as a response to warming trends over the past century (Hessl and Baker, 1997; Holtmeier, 2003); however, specific examples are less

common than expected (Wieser, 2007). Several studies specifically looking for an upward advance found little to no change in the ATE of the European alps (Hattenschwiler and Körner, 1995), Scandinavia (Dalen and Hofgaard, 2005), New Zealand (Cullen et al., 2001) and the North-American Rockies (Butler et al., 1994), while others posit that responses to climate changes will be greatly delayed (Kullman, 1993). These findings suggest that in many locations the ecological inertia of a static ATE counteracts any warming trends that might otherwise cause an upward shift of the ecotone. Site-specific conditions and processes that have been ongoing for hundreds or even thousands of years help to maintain what Grace et al. (2002) call a “conservative” ecotone.

In contrast, a number of more recent studies have found significant directional changes within the ATE; however, the majority of change has taken place within rather than beyond the ecotone (Klasner and Fagre, 2002; Roush et al., 2007) and in associated subalpine meadow complexes (Jakubos and Romme, 1993) instead of a true elevational increase in the upper ATE margin. Dramatic meadow infilling and densification of the ATE has been reported throughout North America (Brink, 1959; Franklin et al., 1971). In general, this process has occurred rapidly and episodically, often in response to climatic variability (Rochefort et al., 1994; Hessel and Baker, 1997; Millar et al., 2004). In the more maritime climates of the Pacific Northwest this phenomenon is common and extensive (Magee and Antos, 1992; Woodward et al., 1995; Rochefort and Peterson, 1996).

Reports of true upward advances of the ATE are less common, and many authors attribute the change to non-climatic drivers. In the European Alps and parts of Scandinavia, the upward expansion of the ATE is due to a cessation of grazing and logging within the ATE (Hofgaard, 1997; Holtmeier, 2003, Tømmervik, 2004). Notable exceptions to this are found in research from Scandinavia that shows rapid upward advances of both the ATE (Kullman, 2002) and lower-elevation thermophilic species (Kullman, 2008) and in research from Alaska where upward migration of trees has occurred on scales of hundreds of metres (Lloyd et al., 2003). In instances of both infilling (Roush et al., 2007) and upward advance (Lloyd and Fastie, 2003) ubiquitous change of the ATE has been observed over large areas with minimal to no direct human impact. This ubiquitous change provides strong evidence for a

climatically driven response of the ATE that is similar in many ways to the results documented in Goodsir Pass.

Upward shifts of the ATE have been observed in northern North America since the late 1970s. Cooper (1986) observed white spruce establishing hundreds of vertical metres beyond the forest limit in the Arrigetch Peaks, Alaska, and Daly and Shankman (1985) documented newly established trees in the alpine zone on Niwot Ridge, Colorado. In both cases, the researchers were unable to determine with certainty whether the ecotone had shifted upwards or isolated individuals were establishing but not surviving over the long-term at higher elevations. In Goodsir Pass, both the large numbers of trees and the presence of larger (one to two m tall) and older (fifty to eighty years) trees in the middle portion of the ecotone, and in an area well beyond the historical forest limit, indicate that the establishment represents an upward shift of the ecotone rather than instances of isolated establishment at higher elevations.

In the Canadian Rocky Mountains and the northern American Rocky Mountains, impacts of humans on the ATE have been less intense relative to ATEs in the Old World (Gadd, 1996). Here upward shifts in the ATE similar to what I observed in Goodsir Pass are occurring. Danby and Hik (2007) in the southeastern Yukon and Luckman and Kavanagh (1998) in Sunwapta Pass, Alberta both documented substantial tree establishment occurring beyond historical (past 300 years) limits of the ecotone. In both instances, the amount of change was dependent on aspect: upward shifts occurred predominately on south-facing slopes. The ubiquity of the change in Goodsir Pass, regardless of aspect, likely differs from these two studies as a result of strong differences in stress the trees in each of these studies face. In the Yukon, permafrost on north-facing slopes limited tree establishment (Danby and Hik, 2007). Similarly, in Sunwapta Pass the micro-climatic differences between the north- and south-facing sites are extreme, and cause trees growing on north facing slopes to have greatly reduced annual growth and increased physical damage (Luckman and Kavanagh, 1998).

Table 5.4. Pearson correlations between five-year climate averages and five-year establishment age classes. Bold values are significant. * = $P < 0.05$; ** = $P < 0.01$. Temperature values run from 2005-1900 n = twenty-two. Precipitation values run from 1990-1900; n = nineteen. Other periods of record are given in the tables.

a. Mean Temperature	March	April	May	June	July	August	September	October
All Species	0.467*	0.226	0.358	0.377	-0.002	0.301	0.272	0.468*
Fir	0.240	0.048	0.154	0.380	0.132	0.389	0.258	0.514*
Larch	0.337	0.121	0.293	0.142	-0.100	0.061	0.087	0.400
Spruce	0.569**	0.417	0.405	0.497*	0.037	0.403	0.404	0.183

b. Maximum Temperature	March	April	May	June	July	August	September	October
All Species	0.571**	0.128	0.077	0.207	-0.332	0.086	0.123	0.529*
Fir	0.275	-0.109	-0.165	0.200	-0.193	0.135	0.122	0.453*
Larch	0.432	0.140	0.206	0.080	-0.219	-0.012	-0.026	0.506*
Spruce	0.658**	0.243	0.034	0.269	-0.404	0.137	0.285	0.226

c. Minimum Temperature	March	April	May	June	July	August	September	October
All Species	0.644**	0.554**	0.657**	0.632**	0.618**	0.613**	0.536*	0.411
Fir	0.380	0.399	0.519*	0.608**	0.646**	0.699**	0.479*	0.564**
Larch	0.476*	0.282	0.393	0.302	0.293	0.231	0.318	0.286
Spruce	0.691**	0.743**	0.732**	0.725**	0.662**	0.702**	0.546*	0.147

d.	Rain	January	February	March	April	May	June	July	August	September	October	November	December
All Species		0.367	0.098	0.205	0.322	0.206	-0.156	0.081	-0.201	0.034	-0.352	-0.229	0.180
Fir		0.234	0.013	-0.138	0.156	0.032	-0.191	0.037	-0.277	0.147	-0.113	-0.091	-0.016
Larch		0.267	0.159	0.430	0.160	0.228	-0.114	-0.060	-0.208	-0.020	-0.326	-0.339	0.369
Spruce		0.410	0.005	0.015	0.541*	0.198	-0.078	0.317	0.043	-0.015	-0.386	-0.009	-0.081

e.	Snow	January	February	March	April	May	June	July	August	September	October	November	December
All Species		-0.181	0.076	0.001	0.163	0.183	-0.016	-0.233	-0.298	0.115	0.329	0.353	0.330
Fir		0.151	0.331	0.062	0.516*	0.263	-0.054	-0.222	-0.176	0.164	0.247	0.498*	0.316
Larch		-0.393	-0.062	-0.042	-0.103	0.010	0.045	-0.182	-0.368	0.029	0.232	0.076	0.274
Spruce		-0.021	-0.007	0.013	0.138	0.267	-0.070	-0.159	-0.080	0.128	0.340	0.424	0.196

f. Total Precipitation	January	February	March	April	May	June	July	August	September	October	November	December
All Species	-0.129	0.110	0.038	0.267	0.258	-0.155	0.076	-0.206	0.072	0.015	0.220	0.363
Fir	0.181	0.349	0.034	0.471*	0.164	-0.194	0.033	-0.279	0.187	0.119	0.404	0.311
Larch	-0.353	-0.014	0.037	-0.011	0.184	-0.106	-0.065	-0.215	-0.006	-0.045	-0.068	0.346
Spruce	0.035	-0.006	0.015	0.343	0.297	-0.084	0.315	0.040	0.034	0.000	0.371	0.178

g.	<u>May 1st SWE</u>		<u><i>L. lyalli</i> Ring-Widths Colenutt (2000)</u>		<u>Synoptic Climate</u>	
	Marble Canyon	Floe Lake	Wolverine Pass	Floe Lake	Instrumental PDO Mantua (2004)	Reconstructed Summer Temperatures Luckman et al. (1997)
All Species	-0.415	-0.487	0.223	0.489**	0.256	0.570**
Fir	-0.097	0.158	0.245	0.504**	-0.138	0.397*
Larch	-0.272	-0.612	0.309	0.450**	0.371	0.556**
Spruce	-0.583	-0.210	-0.087	0.260	0.256	0.423**
Period / n	1950-2000 / 11	1970-2000 / 7	1800-1995 / 40	1800-1990 / 39	1900-2005 / 22	1800-1995 / 40

Few studies calculate rates of increase in elevation of the ATE and often differences in methods make it difficult to compare among studies. Table 6.1 places the results of this study in the context of other twentieth century shifts of the ATE and identifies the rate of ATE rise in Goodsir Pass as the most rapid on record. Kullman (2000, 2001) documents comparable, but not greater rates in the Scands Mountains in Sweden. The rates of ATE advance (2.2 m per year) recorded in Goodsir Pass are twice that of any rates previously documented in North America. Luckman and Kavanagh (1998) documented upward shifts of a similar magnitude on south-facing slopes in Sunwapta Pass, Alberta, but the process of advance took three times as long. Similarly, Munroe (2003) used repeated photographs to show an upslope shift of between 60 m and 180 m on western and northern slopes in the Uinta Mountains, Utah, though a lack of *in situ* data makes the accuracy of these results difficult to judge.

6.1.2 Episodic Species-Specific Change in the Elevation and Density of Trees.

Examining changes in tree density through time and rates of upward advance calculated from mean establishment dates provide two additional perspectives from which to catalogue the shifts in the ATE. Reconstruction of tree density has been used by a number of authors to describe changes in ATEs (e.g. Lloyd and Fastie, 2003; Danby and Hik, 2007), though in most cases differences in density are examined only between the forest and a single point in the ecotone.

I reconstructed tree density at each of the five ecotone zones (two at the upper edge of the forest and three at consecutively higher points through the ecotone). Results from these reconstructions underscore how the density of individual species has changed in markedly different ways. Many studies examine changes in the elevation and density of the ATE regardless of species. Researchers conduct work in ATEs populated by only one species, lump species together, or choose to sample only one species. Exceptions to this include: Woodward et al. (1995); Luckman and Kavanagh (1998); and Resler and Tomback (2008). While this grouping of species creates a summary of change, species are likely to respond individually because of fine-scaled, site-specific ecological and environmental variations (Cole, 1985). A species-level analysis provides data that allow for a more detailed portrayal of ATE composition and pattern.

The reconstruction of density illustrates that many of the trends observed in overall tree establishment reflect the dominance of larch in the ecotone (Figure 5.9). Viewing each species separately reveals marked differences in the establishment patterns of each species. Most notable is that the stratification of fir and spruce tree density (higher densities at lower elevations and lower densities at higher elevations) disappeared by ca. 1970, while larch density remains stratified by elevation into the present. Two conclusions emerge. Through time, elevation has consistently influenced larch establishment, while its impact on spruce and fir establishment has waned. Results from the binomial regression also support this conclusion showing that an increase in elevation of one hundred m causes larch establishment to be 0.18 times as likely. Secondly, drivers of spruce and fir establishment have changed through time more dramatically than have drivers of larch establishment. A continuation of this pattern and the high density of larch at the forest edge will lead to species stratification in the ATE. A dense band of larch will populate the lower portions of the ecotone, while more open mixed species stands will establish at higher elevations.

Few studies exist in the region with which to compare the temporal patterns of ATE advance in this study. In the ATE of Sunwapta Pass an upward advance of Engelmann spruce and subalpine fir occurred over the past one hundred years (Luckman and Kavanagh, 1998) with an establishment pulse recorded between 1965-1973 (Kearney, 1982). These changes roughly match the pattern in Goodsir Pass of limited establishment of these two species prior to 1950, and significant establishment in the past fifty years. The earlier onset of establishment recorded in Goodsir Pass may be the result of a larger sample that captured older establishment patterns or, establishment may have been a response to a slightly more pronounced mid-century shift to warmer minimum summer temperatures in the area around Banff, Alberta than the area around Jasper, Alberta (Kearney, 1982).

6.1.2.1 Dissecting Rates of Change in the Alpine Treeline Ecotone.

While appearing to offer a precise yearly metric of change, upward advance rates as calculated from mean establishment dates actually provide a summary of change that integrates changes in both the density and altitude of trees. Due to the numerous ways in which the ATE can change and the inability to determine a precise ecological line that marks ATE elevation, calculating a true rate is not possible. Similar to Lenoir et al.'s (2008) analysis

of changes in a species' optimum elevation, calculating rates of upward advance of the ATE based on mean establishment dates produces information more relevant to the entire population instead of individuals living at the spatial edges.

Greater rates of advance will be produced when tree establishment occurs more frequently at progressively higher elevations in the ATE. Large amounts of establishment throughout the ATE is indicative of an increase in density but not upward movement and thus does not produce high rates of upward advance of the ecotone. Mortality of older trees at lower elevations would produce an erroneously low rate, while mortality of older trees at higher elevations would produce an erroneously high rate. Due to the very high ratio of live to dead trees neither of these scenarios is likely to be the case in Goodsir Pass. The extremely high rates of advance of fir between the forest edge and the lower subalpine, advance of spruce between the lower and upper subalpine zones, and the synchronous establishment of larch in the upper three elevation zones indicate that impacts of elevation on tree establishment have not changed through time for species in these areas of the ecotone (Table 5.3).

That the rate of upward advance for the entire tree population increases at higher elevations suggests a non-linear response to the drivers of ATE change (Table 5.3). Chapin et al. (2004) suggest that at the upper margins of species' ranges sustained and gradual change in response to global warming is most likely, but several authors posit that the ATE will exhibit a non-linear response (Kupfer and Cairns 1996; Malanson 2001; Lloyd, 2005). In the southwest Yukon Danby and Hik (2007) observed what they hypothesize to be the beginning of a threshold response to warming. After finding that white spruce establishment patterns correlated most strongly with warmer temperatures thirty to fifty years prior to establishment they predicted that the response of the ATE to future warming may not be gradual. In Goodsir Pass, both the variability in rates of establishment for individual species and the dramatic increase in rates of establishment with increasing elevation for all species provide strong evidence for a non-linear response. Tree establishment appears to have crossed a threshold beyond which elevation no longer exerts a strong control on patterns of upward advance. Not only are trees establishing well beyond their historical range (one hundred to two hundred m higher), but this advance is also

accelerating and occurring through a series of rapid upward jumps rather than in a uniform manner.

6.1.3 An Incomplete Establishment Record.

As mentioned previously tree establishment only records individuals that established and survived to present. The implications of this are especially significant in the context of finding correlations between tree establishment and climate because climate conditions in the year of establishment will be diminished and correlations will reflect the diffuse impact of climate or other factors in all years since establishment. The high number of trees that have established within the past fifty years within the ATE can be explained in one of two ways: first, tree establishment and density are increasing; second, tree density in the ATE is relatively static but high mortality exists for younger trees and the majority of recently established trees will not persist in the ATE for very long. The almost complete lack of dead wood observed in the study site, and the low numbers of dead individuals found in the study plots, suggest that the modern tree population in the ATE of Goodsir Pass is undergoing low levels of mortality and thus the first explanation is more likely. Whether or not this was the case in the past is unknown, but establishment in the past fifty years likely reflects actual establishment with relative accuracy. Thus, while it may be problematic in this study to identify climate conditions (especially those further into the past) that produced conditions conducive to establishment, the historical images of the study site, low numbers of dead individuals recorded in the study site, and the current high numbers of young trees (\leq fifty years old) in the study site all provide conclusive evidence for tree establishment leading to a denser ATE with an increased elevation.

6.2 Drivers of Vegetation Change in the Alpine Treeline Ecotone.

6.2.1 Climate.

6.2.1.1 Minimum Temperature.

Results from the Pearson's correlation analysis emphasize the importance of minimum growing-season temperatures in driving tree establishment. With the exception of minimum temperatures, climate variables showed significant correlations with tree establishment in

only a few months (Table 5.4). When correlations occur in only a few months, the correlation analysis may not be a definitive indicator of climate influencing tree establishment due to the likely errors introduced into the analysis by the distance of climate stations to the study site, and the inaccuracies in establishment data due to individuals that established but did not survive to the present. However, the ubiquity and strength of the correlation between minimum temperatures and fir and spruce establishment patterns suggest that this climate variable does in fact influence tree establishment despite any inaccuracies in the data. Though investigators of ATE dynamics recognize the importance of minimum temperature in the ecotone (e.g. Moir et al., 1999), few have examined this climate variable for correlations with patterns of establishment in the ATE (exceptions include Kearney, 1982; Millar et al., 2004). While all temperature variables are derived from means, and therefore do not represent in-situ conditions directly, minimum temperatures may be more indicative than mean or maximum temperatures of actual climatic conditions that influence trees. In general, warmer summer temperatures and longer growing seasons drive change in the ATE throughout the temperate zone (Butler et al., 1994; Rochefort et al., 1994; Linderholm, 2002). Warmer minimum temperatures rather than mean or maximum temperatures play a significant role in reducing overnight freezing, cause earlier melt-out of snow-covered areas, and directly cause germination and growth during the growing season (Millar et al., 2004). Furthermore, seed germination and survival in the ATE are predominately controlled by low temperature thresholds rather than mean temperatures (Noble and Alexander, 1977).

Minimum temperatures give the best indications of the occurrence of mild frosts, which are possible at any time of the year in the ATE. In the Colorado Front Ranges, both subalpine fir and Engelmann spruce were severely damaged by summer frost events (Holtmeier, 2003). While frosts affects all trees, it has its greatest effect on seedlings, as a greater percent of their tissue may be damages by frosts (Sakai and Weiser, 1973; Alexander et al., 1990), and may impede regeneration in the ATE (Holtmeier, 2003). Minimum temperatures may also have a direct effect on whether germination occurs. Germination rates of *Larix* seeds are reduced when temperatures drop below 15 °C (Farmer, 1997). Subalpine fir and Engelmann spruce seeds do not persist in seed bank (Holtmeier, 2003); thus, successful germination occurs only when the subsequent growing seasons are sufficiently warm (Kearney, 1982).

The reason for the paucity of significant correlations between subalpine larch establishment and any temperature variable is not entirely clear. The subalpine larch population in Goodsir Pass is differentiated from the subalpine fir and Engelmann spruce populations in two ways. First, subalpine larch grows in a very narrow habitat niche (high elevations with cool temperatures and relatively moist soils) (Arno, 1990). The ATE encompasses nearly the entire range of subalpine larch rather than just the upper margin (as it does for subalpine fir and Engelmann spruce). Though the upper limits of the ecotone certainly can be considered the range margin of subalpine larch the ecotone in general is a typical and often the only habitat of the species (Arno and Habeck, 1972). Warming temperatures are expected to cause the most dramatic effect on the distribution of individuals at species' margins (Grabherr et al., 1994; Hickling et al., 2006). Hence, the ATE represents less of a margin for subalpine larch than it does for the other two species in this study, which means the impact of warming temperatures may be lessened.

The second way in which the subalpine larch population differs from the other two species is in an establishment pattern that has been considerable and continuous for the past two centuries in Goodsir Pass. In addition to high levels of establishment in the 1980s (common to all species) subalpine larch established in large numbers during the period 1930 to 1955 and locally high numbers in the period 1840-1860 (Figure 5.6). The dramatic switch from cooler to warmer minimum temperatures that occurred in the late 1940s (Figure 5.2) is roughly coincident with the shift from almost no establishment to high levels of subalpine fir and Engelmann spruce establishment that occurred in the later half of the twentieth century (Figure 5.6). In contrast, subalpine larch establishment was already at a relatively high level during the early part of the twentieth century, thus, the increase during the latter half of the century does not register as an equally dramatic shift.

The lack of correlations between subalpine larch and temperature records may then be a function both of the life history of the species and the temporal scale at which the analysis was conducted. Extending the time frame of observation often leads to different conclusions concerning the directional change of a system (Turner et al., 2001). While subalpine larch establishment has been occurring for two centuries, instrumental temperature records exist for only the latter half of this period. Thus, results showing a lack

of correlation between temperature and establishment over the past century may lead to the inaccurate conclusion that temperature played no role in subalpine larch establishment.

6.2.1.2 Synoptic Climate.

Proxy air temperature records allow the temporal scale of observation to be extended over the entire period of subalpine larch establishment. Luckman et al.'s (1997) reconstruction of summer temperatures from near the Columbia Icefield shows warmer periods in the mid 1800s, from the 1920s to the 1950s, the late 1960s, and the 1980s. Excluding the late 1960s all of these periods correspond with pulses of larch establishment in Goodsir Pass and imply that on a longer temporal scale subalpine larch establishment, like subalpine fir and Engelmann spruce, is responding to the overall warming trend occurring in the Canadian Rockies (Luckman, 1998).

It is also possible that larch establishment shows greater correlation with Luckman's (1997) proxy record than instrumental records because the reconstruction was built from trees sampled in the ATE. As Holtmeier (2003) points out, one of the problems facing predictions of ATE position is the use of valley bottom climate records to predict phenomena at higher elevations. The correlation between Colenutt's (2000) subalpine larch tree-ring chronology at Floe Lake and subalpine larch establishment in Goodsir Pass suggests that similar environmental factors drive both growth and establishment of larch trees growing in the ATE. Not only does Luckman et al.'s (1997) reconstruction represent summer temperatures, it is likely to reflect other factors influencing tree growth and establishment in the ATE. That the reconstruction is built from trees growing in the ATE also makes it more representative of factors influencing tree establishment in the ATE.

While no species showed a significant correlation with the PDO, both subalpine larch and Engelmann spruce establishment rates show dramatic increases immediately following the change from the negative to positive PDO phase (Figure 5.6). Major increases in the number of subalpine larch trees establishing coincide with both the 1924 and 1977 shift from the negative to positive phase of the PDO. In both cases, during the decades prior to the PDO phase change, establishment rates declined gradually, and then, with near perfect synchronicity, establishment rates increased by five times the previous rates as the PDO

shifted to its positive phase (Figure 5.6). Similarly, Engelmann spruce establishment doubled immediately following the 1977 shift to the positive phase of the PDO (Figure 5.6).

The lack of a significant Pearson's correlation between PDO and tree establishment but a high degree of synchrony between PDO phase changes and onset of establishment pulses dovetails with Alftine et al.'s (2003) work examining ATE response to PDO in Glacier National Park, Montana. The authors found no overall correlation between PDO and decadal scale establishment patterns of lodgepole pine (*Pinus contorta* var. *latifolia*), subalpine fir, Engelmann spruce, and whitebark pine; however, they note that the onset of establishment pulses coincides with switches to the negative phase of the PDO (the reverse of what I observed in Kootenay National Park). The authors attribute this relationship to increased snowfall during negative phases of the PDO (Selkowitz et al., 2002), which prevents winter desiccation and ice abrasion in the dry and windy continental environment present in their study site east of the continental divide. Similar to Glacier National Park, Montana, lower than average values of May 1st SWE at Marble Canyon (fourteen km southeast of the study site) become common following 1977 (Figure 5.4); however, the deep seasonal snowpack in Goodsir Pass reverses the relationship between snow and establishment. High snow years in dry environments like Glacier National Park, Montana favour establishment, while in Goodsir Pass, which typically experiences large seasonal snow packs, low snow years likely produce favorable establishment conditions as the ATE becomes snow free earlier in the year and lengthens the growing season (Rochefort et al., 1994).

Establishment of each of the three species in Goodsir Pass is correlated with at least two independent climate records that are separated in space from each other and are not sourced from the study site. This suggests that the relationship between establishment and climate, to the extent that it exists, is not spatial, and in turn supports the theory that change in the ATE is influenced by regional drivers. Were establishment records correlated with only one temperature record the argument could be made that the influence of climate is a localized driver of ATE change. The correlations with multiple climate records, sourced from separate locations within the southern Canadian Rocky Mountains, imply a regional, non-localized influence on tree establishment.

6.2.2 Site-Specific Environmental Variables.

The spatial patterning of tree establishment in the ATE of Goodsir Pass is less pronounced than temporal patterns. Site-specific conditions affect both initial establishment and tree health, but are likely not dominant factors in determining the position of trees within the ATE as other studies have documented (Minnich, 1984; Germino et al., 2002; Resler, 2006; Danby and Hik, 2007). Interactions among environmental conditions at more than one scale likely offer the best predictors of whether tree establishment will occur in a given location or not. Feedback mechanisms, extensively documented in other ATEs (Malanson et al., 2009), do not play a role in establishment patterns within the ATE of Goodsir Pass, likely because of the uniform edaphic conditions and deep seasonal snowpack.

6.2.2.1 Establishment Probability.

While all models produced by the binomial regression passed the Hosmer and Lemeshow goodness of fit test, the classification tables for subalpine fir and Engelmann spruce indicate an inability of those models to predict tree establishment based on environmental variables (Table 5.5). The poor predictive capability of the models indicates that the environmental variables measured in this study only weakly influence subalpine fir and Engelmann spruce establishment (Kinnear, 2007).

Results of the binomial regression show elevation and slope steepness to be significant predictors of subalpine larch establishment. Increases in both elevation and slope reduce the chance of establishment, although elevation is a stronger predictor. Trees growing on steep slopes are subject to greater environmental stress from the downslope movement of rock, soil and snow and may be drier due to more rapid water drainage (Malanson and Butler, 1986; Walsh et al., 1994; Holtmeier, 2003). Although two of the transects were located on slopes steep enough to produce avalanches, there was no evidence of landslides or avalanches in the study area. Most likely the negative impact of steep slopes is a result of gradual increases in stress that slightly reduce the overall chance for tree germination and survival. Trees are less able to establish in areas with active ground surfaces due to poor soil conditions and damage from debris movement (Malanson et al., 2009). Trees growing on steep slopes must also allocate greater carbon reserves to produce reaction wood. Both tree

cores and field observations provided evidence for this occurrence in the steeper areas of the study site.

For every one hundred m increase in elevation the chance of larch establishment occurring within the ATE of Goodsir Pass is 0.18 times as likely (Table 5.5). This result demonstrates a strong gradient through the ecotone, and is consistent with the similarly stratified density of larch. Elevation is a more complex environmental condition than most other site-specific variables. Environmental lapse rates cause a decrease of 0.65 °C for every one hundred m increase in elevation (Whiteman, 2000). This basic property of thermodynamics underlies the widespread hypothesis that predicts an upward shift of the ATE in response to warming temperatures (Grace et al., 2002; Holtmeier, 2003). Consequently, the decrease in the likelihood of establishment as a function of elevation indicates that the vegetation in the ATE is strongly controlled by temperature. While snow depth also varies along an altitudinal gradient (generally increasing with increasing elevation) (McKay and Gray, 1981) it does so in a far more variable manner than temperature due to the high degree of redistribution that occurs in mountainous areas (Hiemstra et al., 2002).

The strong effect of elevation on establishment probability is likely also a function of the study design, which anchored each transect at the edge of the montane forest. These lower-elevation plots have much greater tree density and likely have a strong influence on the output of the model because the model does not differentiate between upper and lower portions of the ecotone. Thus, there is an inconsistency between the results of the model and the mean establishment dates of ecotone zones, which indicate that establishment is proceeding uninfluenced by elevation in the upper portion of the ecotone. Many of the lower-elevation trees are older, and this inconsistency indicates that while elevation once played a role in determining establishment location (the artifact of which is still seen clearly in the models' output), it no longer has a significant impact on establishment as evidenced by the synchronous establishment of subalpine larch observed in the upper three ecotone zones.

Unlike subalpine fir and subalpine larch, the binomial regression models indicate that the probability of Engelmann spruce establishment was not significantly affected by elevation

(Table 5.5). A similar differentiation between species establishment patterns is revealed from calculations that identify the year in which tree density reached one hundred trees ha^{-1} . The density of Engelmann spruce in the lower portion of the ecotone never surpasses this threshold, while density of the species is highest (257 trees ha^{-1}) in the uppermost portion of the ecotone. This suggests a decoupling of Engelmann spruce establishment from the elevation/temperature gradient. There are two possible conclusions: i) one or several other site-specific conditions in the ATE create a strong enough environmental gradient that Engelmann spruce preferentially establishes at higher elevations, essentially overriding the environmental gradient created by elevation; or ii) the elevation range in which temperature limits spruce establishment has risen beyond the upper elevations of the ATE and no longer produces a strong gradient through the ecotone. The poor predictive power of the model in predicting tree establishment from any site-specific conditions makes the latter conclusion more likely. While it is possible that inter-species competition could also produce some of these spatial patterns the reduced role of competition in the ATE where abiotic factors are the main determinants of whether trees establish and survive (Holtmeier, 2003) makes this less likely.

The lack of any strong and significant relationship between the ground cover and tree establishment in Goodsir Pass may result from the relative uniformity of the ground cover. Most five by five m quadrats had a variety of ground cover. Thus, the scale at which data were collected may mask the effects of plant cover. Prior investigations have documented a wide range of impacts from surrounding vegetation on tree establishment in the ATE. Vascular plants in general (Moir et al., 1999) and herbaceous cover in particular (Magee and Antos, 1992) have been found to inhibit tree establishment likely because of competitive effects and an inability of young seedlings to reach mineral soil. In the Goodsir Pass area, the high amount of excavation by Columbian ground squirrels and grizzly bears may provide a consistent enough amount of exposed mineral soil so that dense or continuous ground cover in surrounding areas does not have an adverse effect on tree establishment (Figure 3.4). Surrounding vegetation has also been shown to protect seedlings in their first few years of growth by blocking sky exposure and limiting the negative impacts of both excessive daytime radiation and nighttime frosts during the growing season (Rocheffort and Peterson, 1996; Maher and Germino, 2006). The generally high rates of establishment in Goodsir Pass

indicate a favorable establishment environment. Animal activity provides enough micro-disturbance sites to expose mineral soil while the extensive herb and shrub cover protects seedlings from exposure once they have established (Germino et al., 2002). Additional benefits of the extensive herb/shrub cover may include slope stabilization and reduced soil moisture loss.

The lack of strong spatial patterning in tree establishment of the ATE in Goodsir Pass contradicts several other studies that found tree establishment to reflect patterns in snow depth (Minnich, 1984), soil geomorphology (Butler et al., 2004), bedrock structure (Butler et al., 2003), boulders (Resler et al., 2005), light availability, and soil pH, moisture and texture (Weisberg and Baker, 1995). This contradiction may arise either because different metrics were used in other studies to document spatial patterning or because the spatial patterning in the underlying geomorphologic features in Goodsir Pass was not pronounced enough to influence tree establishment.

6.2.2.2 Establishment Shelter at Two Scales.

The spatial patterns of tree establishment in Goodsir Pass may be most influenced as a result of the interactions among patterns and processes operating at different spatial scales. Many studies have examined the interactions among snow distribution, topography and vegetation (e.g. Walker et al., 1993; Walsh et al., 1994; Hiemstra et al., 2002; Winstral and Marks, 2002; Geddes et al., 2005) but few have directly addressed issues of scale in these relationships. Butler et al. (2007) discuss the impact of topography and geomorphology on the ATE at three different scales, but do not examine how patterns at one scale may affect those at another.

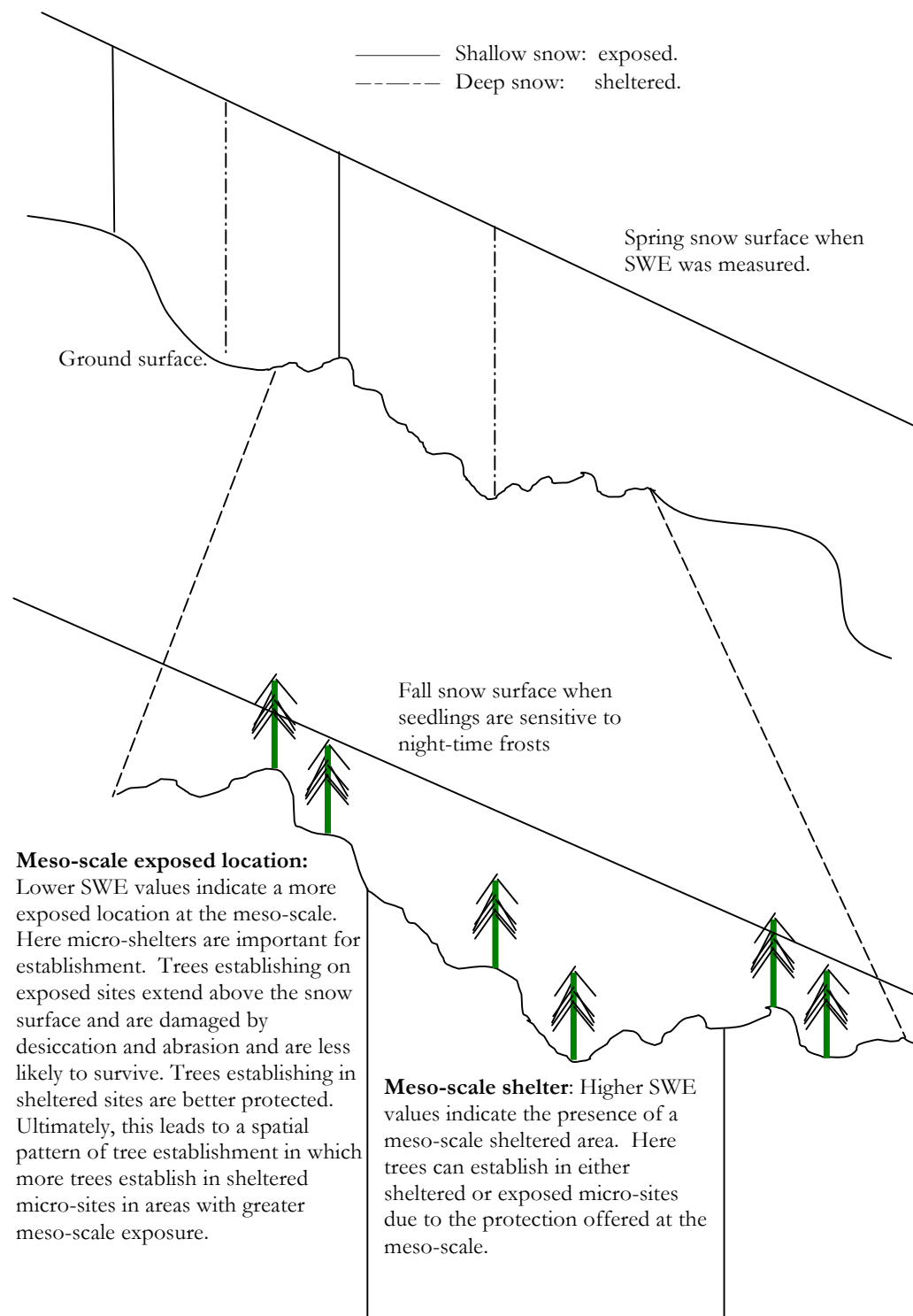
Deeper than normal values of SWE and snow depth are produced by two mechanisms: drifting and smoothing. Drifting occurs when topography and vegetation cause drifts in their lee (Pomeroy and Gray, 1995). Smoothing occurs in areas with large annual snowfall where there is a tendency for the snow surface to become flat and smooth, producing local zones of deeper snow in gully or trough features (Erickson et al., 2005). In Goodsir Pass, the trough and swale topography and the ephemeral stream gullies combined with a deep annual snowpack are likely to produce numerous areas of deeper snow that provide meso-

scale sheltered areas (Figure 6.1a). In the fall, these areas are more likely to accumulate drifted snow than topographic highs that remain exposed (Elder et al., 1991; Elder et al., 2000). These meso-scale shelters protect newly established seedlings from winter desiccation and exposure to cold nighttime temperatures. Seedlings without this protection undergo 25% greater mortality rates during exposed fall nights than do seedlings covered in snow (Germino et al., 2002).

Results from the ANOVA comparing mean SWE around trees that established in varying types of micro-sites show that SWE is greater around trees that established in exposed micro-sites than it is around trees that established in sheltered micro-sites. For Engelmann spruce and subalpine fir this difference is significant. I assume that locations where greater values of SWE were measured indicate the presence of meso-scale sheltered areas (Figure 6.1). Thus, in areas with deeper snow, the meso-scale shelter allows trees to establish in more exposed locations at the micro-scale. In contrast, in meso-scale exposed areas (less SWE) trees that establish in sheltered micro-sites are given protection in the fall not provided by the meso-scale landscape, while trees that establish on exposed micro-sites are less likely to survive. Further research, specifically targeting the difference in spatial establishment patterns as a function of meso-scale shelter is needed to address this hypothesis more thoroughly.

Two possibilities explain why larch establishment is not influenced as strongly by the interactions between meso- and micro-topography and associated SWE values throughout the winter. First, results show that subalpine larch trees established in areas with more snow than other species (Figure 5.11). Thus, larches are likely to be less dependent on micro-shelters than the other two species. Secondly, several traits make larch less vulnerable to winter desiccation than fir and spruce. Larch trees drop their needles in the fall and so have a greatly reduced surface area from which to lose moisture as a result of winter desiccation. In years when early snowfall occurs prior to sustained cold periods all species will be protected equally. However, in years without significant early season snow, the ability of larch to drop their needles will greatly reduce their mortality from desiccation. Additionally, larch trees grow very slowly until they are about twenty-five years old and allocate resources first to developing a deep and extensive root system (Arno, 1990). Their reduced stature and

Figure 6.1. The impact of meso-scale topography on the importance micro-scale topography plays in the spatial pattern of tree establishment. (a) Meso-scale shelter sites in the landscape are detected by differences in snow depth. (b) Meso-scale patterns of shelter then determine the relative impact that micro-scale shelters have on tree establishment.



ability to draw on deeper reserves of water both reduce the likelihood of mortality due to autumn nighttime exposure and winter desiccation.

6.2.2.3 Feedback Mechanisms.

Feedback mechanisms that clearly play a role in establishment in the xeric, rocky soils of the ATE in eastern Glacier National Park, Montana (Alfitine and Malanson, 2004; Geddes et al., 2005; Resler et al., 2005), do not appear to play a significant role in the ATE of Goodsir Pass. In Glacier National Park, Montana, trees are clearly associated in space with both other trees and locations in the environment that have been modified by other trees. While no explicit method in my research tested for the presence of feedback mechanisms, no spatial associations among trees were observed. Additionally, the absence of krummholz or tree clumps in the study area indicates that trees depend very little on one another for the development of favorable establishment sites. This observation contrasts with those of numerous multi-tree clumps in the ATE of Glacier National Park, Montana, in which whitebark pine trees serve as an initial colonizer and facilitate further establishment by other species (Resler and Tomback, 2008). The most pronounced feedback mechanisms within the ATE occur between tree establishment and the distribution of snow within the ecotone (Minnich, 1984; Geddes et al., 2005; Malanson et al., 2009). The deep and uniform snow cover within Goodsir Pass likely diminishes or eliminates this effect.

6.2.2.4 Effects of Site-Conditions on Tree Health.

Once a tree has established, site-specific variables appear to have little effect on tree health in Goodsir Pass. While statistical differences in mean values of site-specific variables do exist among trees of different health classes, trees were not obviously stratified or grouped in clumps corresponding to their health. Dead and barely-alive trees tend to be found at lower elevations likely as a result of the impacts of shading and competition, which occur only in the lower more densely-forested plots (Table 5.6). Conversely, the tendency for trees of only average health to be found at higher elevations likely reflects conditions that follow an altitudinal gradient. Greater exposure, reduced snow cover, lower temperatures, and less stable ground at higher elevations in the ATE reduce the number of healthy and vigorously growing trees found on average more frequently in the middle of the ecotone.

In contrast to some of the patterns observed in the regional repeat photography, aspect has no influence on the health of trees growing in the ATE of Goodsir Pass. In the northern hemisphere, southern aspects can cause reduced seedling survivorship because of increased sun exposure and moisture loss from needles and roots (Germino et al., 2002). Northern aspects also may reduce survivorship or prevent establishment outright due to permafrost (Danby and Hik, 2007), reduced sunlight and colder temperatures (Holtmeier, 2003). The lack of a response to aspect by trees in Goodsir Pass is likely a function of the minimal ecological differences between aspects in the study site. Furthermore, the southwest dip-slope of the underlying geology prevented the establishment of transects on the cliffy northeasterly aspects, which limits the ability of the study design to compare establishment on all aspects. While the upper limit of the ATE was lower along the one northwestern facing transect, the steep cliffs and active talus immediately above the highest plot on that transect makes it problematic to attribute this effect to aspect alone. Significant ecological differences do not exist among the different aspects in the Goodsir Pass region: permafrost is not present, and the sharp differentiation seen between northern and southern aspects in the more easterly ranges of the Rocky Mountains is not present immediately west of the continental divide (Gadd, 1996). Thus, not only was it difficult to assess the impact of all aspects on tree establishment, but the environmental differences between aspects also appear to be quite small.

Slope steepness has the most linear effect on tree health with a general trend towards healthier trees on steeper slopes (Table 5.6). However, only dead trees and those barely alive were on average found on slopes with significantly lower gradients than other healthier trees. Results from the binomial regression indicated that increased slope steepness increases the chance of establishment for larch. Thus, slope steepness may have opposing effects on establishment and continued tree survival.

It is difficult to explain why both dead trees and the healthiest trees were found growing in areas with significantly deeper snow. A Pearson's correlation showed that elevation is strongly negatively correlated with snow depth ($P < 0.001$). Thus, deep snow is more common in the forest and forest edge zones of the ecotone where forest population dynamics are expected to produce higher mortality rates of young trees, which is likely to

account for the link between dead trees and deep snow. The link between the healthiest trees and deep snow may be a result of the protection from desiccation and abrasion provided by a deep snow pack (Walsh and Kelly, 1990).

6.3 The Larger Context: Causes of Variability in Vegetation Dynamics in the Alpine Treeline Ecotone at Landscape Scales.

Results from regional repeat photography considerably broaden the scale of analysis concerning change in the ATE of the southern Canadian Rocky Mountains. Analysis of photo-pairs from Jasper, Kootenay, and Waterton Lakes national parks shows significant change occurring within the ATE over the past century. However, the majority of the change occurs within rather than beyond the historical boundaries of the ATE. Increases in tree density and changes in tree physiognomy from krummholz to upright trees occurred frequently and regardless of landscape location or aspect. The less frequent occurrence of an elevational expansion of the ATE implies that tree establishment beyond the historical ATE occurs under a narrower range of environmental conditions. Tree establishment within and beyond the ecotone, the capacity of trees to change from one form to another, and tree growth are all governed by varying sets of environmental variables (Tranquillini, 1979; Holtmeier, 2003).

Results from analysis of the regional photo-pairs add a spatial component to the differentiation of factors affecting processes within the ATE. Specifically, the prevalence of change within rather than beyond the ecotone suggests that establishment beyond historical limits of the ATE is driven by a different set or magnitude of environmental variables than establishment within the ecotone. This predominance of change within rather than beyond the ecotone emphasizes the positive impact that surrounding trees have on later tree establishment (Germino et al., 2002) and fits predictions that tree density in the ATE is likely to increase before moving upslope (Klasner and Fagre, 2002).

Classification of ATE segments by aspect and park shows that the regional location of an ATE segment is more likely than its aspect to be a determinant of whether a particular type of change has occurred in the ecotone. A consistent pattern is evident in the type and location of change within the ecotone when ATE segments are arranged by park (Figure

5.15). Jasper and Kootenay national parks both show similar changes that indicate the elevation and density of the ATE have increased since the early part of the twentieth century, and that many of the trees have shifted from krummholz to an upright growth form. Far less change has occurred in Waterton Lakes National Park and some segments even show a reduction in tree density within the ATE. Less differentiation in the amount and type of change occurs in the ATE as a function of aspect. While ATE segments with westerly aspects have experienced greater change than easterly or southerly aspects, the differences are far less pronounced than those that exist among ATE segments within different parks. Other studies indicate landscape position is more likely to affect ATE change than the finer-scale details within that ATE. In the Pacific Northwest, Peterson et al. (2002) describe large-scale patterns of response in the subalpine forest due to climatic variation. In their study they found inter-regional differences in growth patterns to be more pronounced than inter-species differences; these results mirror my observations that found more pronounced differences in ATE change among parks than those that occurred among aspects.

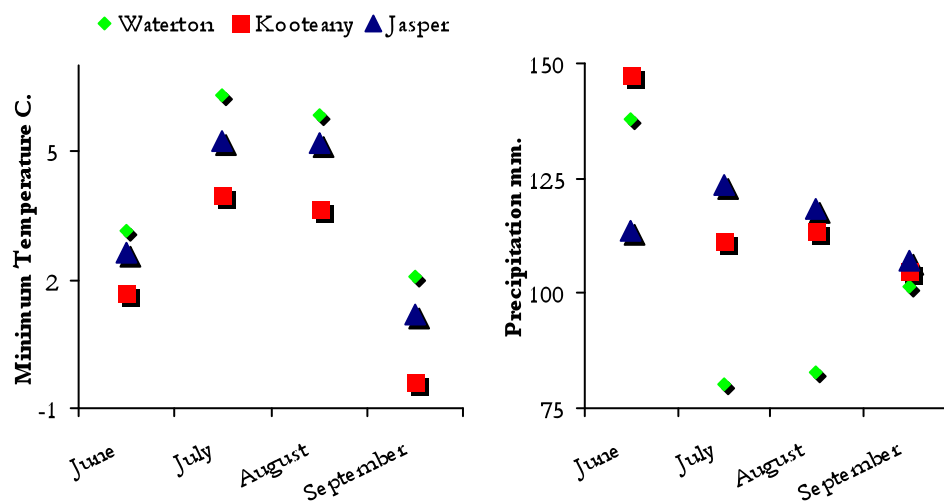
6.3.1 Probable Causes: Differences in Regional Climate and Geophysical Conditions.

Climate normals from each national park help to illustrate how the climate regimes of Kootenay and Jasper national parks are similar at coarse scales while the climate regime for Waterton Lakes National Park differs. Minimum growing-season temperatures (June-September) in Waterton Lakes National Park are on average 2 °C and 0.7 °C higher than in Kootenay and Jasper national parks respectively. Waterton Lakes National Park receives seventy-five and sixty mm less precipitation during the growing season than Kootenay and Jasper national parks respectively (Figure 6.2) (Wang et al., 2006). The cooler temperatures and greater precipitation in Kootenay and Jasper national parks create more mesic conditions while the warm dry summers coupled with frequent high winds in Waterton Lakes National Park produce more xeric conditions in the alpine and subalpine zones (Coen and Holland, 1976).

The differences in soil type in the ATE in the three parks show similar associations to climate normals. Subalpine soils in Waterton Lakes National Park are predominately

comprised of stony regosols and podisols, while at elevations above 2100 m asl poorly developed, extremely rocky soils and talus dominate (Coen and Holland, 1976). Alpine and subalpine soils in Kootenay and Jasper national parks are dominated by well-developed brunisols with significant quantities of fine regosols and podisols respectively (Holland and Coen, 1982; Achuff et al., 1984). Waterton Lakes National Park is characterized by frequent high winds (Coen and Holland, 1976), while wind velocities in Kootenay and Jasper national parks are light to moderate and calm periods in the alpine and subalpine are common (Holland and Coen, 1982; Achuff et al., 1984). Integration of soil type and development and macro-climate variables for the three parks allows for a general characterization of conditions found within the ATE (Table 6.2). The ATE in Waterton Lakes National Park is likely to be relatively xeric in nature with high rates of evapotranspiration while the ATE of Kootenay and Jasper national parks is mesic with relatively lower rates of evapotranspiration.

Figure 6.2. Growing season minimum temperature and precipitation normals (1961-2001) in the ATE for Waterton Lakes, Kootenay and Jasper National Parks (Wang et al., 2006).



Mesic conditions promote tree growth (Ettl and Peterson, 1995; Peterson et al., 2002) and increase the likelihood of establishment in the ATE (Brink, 1959; Franklin et al., 1971; Agee and Smith, 1984; Agee, 1993; Rochefort and Peterson, 1996). This relationship between edaphic conditions and tree establishment provides a compelling explanation of the widespread and diverse change in the ATEs of Kootenay and Jasper national parks and the limited change in Waterton Lakes National Park. Mesic conditions that promote tree

establishment in the ATE may occur in both time (Fonda and Bliss, 1969) and space (Weisberg and Baker, 1995). In the case of the former, temporal variations in climate interact with local conditions to produce a mesic environment. In other words, mesic periods determine spatial patterns of establishment. Both Rochefort et al. (1994) and Woodward et al. (1995) document increased establishment occurring in dry areas during wet periods and in wet areas during dry periods. By providing a generally favorable environment for establishment to occur, mesic ATEs mitigate the role of climate variability (Hessl and Baker, 1997). As such, certain areas will be the sites of nearly continual establishment while others may undergo very little change.

Table 6.2. Regional differences in soils and climate normals between Waterton Lakes, Kootenay, and Jasper national parks. Differences in June to September macro-climate variables (temperature and precipitation) and wind velocities are relative. Edaphic conditions represent a composite of the above categories.

Geo-climatic Conditions	Waterton Lakes	Kootenay	Jasper
Growing Season Temperature	Warm	Cool	Cool
Growing Season Precipitation	Dry	Moist	Moist
Wind Velocities	Extremely high	Light	Moderate
Soil Types (Dominant / Secondary)	Rock/ Stony Regosolic & Podsollic	Brunisolic/ Fine Regosolic	Brunisolic/ Fine Podisolic
Soil Development	Poorly developed	Well developed	Well developed
Edaphic Conditions	Xeric	Mesic	Mesic

Results from the analysis of regional photo-pairs demonstrate the importance of edaphic conditions in determining the spatial pattern of tree establishment. Furthermore, they suggest that this occurs at landscape-level spatial scales in addition to the more commonly documented meso- and micro-site scales (e.g. Malanson and Butler, 1994; Allen and Walsh, 1996; Butler et al., 2003; Walsh et al., 2003; Butler et al., 2004, Resler et al., 2005; Resler, 2006; Zeng and Malanson, 2006; Malanson et al., 2007; Zeng et al., 2007).

The most marked difference between patterns of change in the ATE of the two northerly parks is the greater percent of ATE segments in which the upper margin of the ecotone increased in elevation: 50% in Kootenay National Park and only 10% in Jasper National Park. In the context of other similarities this difference is initially puzzling. Given the similar geo-climatic characteristics of the two parks the most marked differences in the ATEs of the two parks is the complete lack of subalpine larch in Jasper National Park (Arno,

1990) and its relative prevalence in the ATE of Kootenay National Park (Achuff et al., 1984). While it was not possible to identify tree species in the repeated photo-pairs, the results from my research in Goodsir Pass indicate that the dramatic increase in the upper margin of the ecotone in Kootenay National Park may result from the prominence of subalpine larch within the ecotone.

Changes in the ATE observed within the two northerly parks mirror findings from the treeline ecotone at Sunwapta Pass (Luckman and Kavanagh, 2000), which is located roughly equidistant to the sites of repeat photography in the ATEs of Jasper and Kootenay national parks. Like the ATEs in Jasper and Kootenay national parks (Figure 5.16), northerly slopes in Sunwapta Pass show the least morphological change and little altitudinal increase in the upper margin of the ATE on a scale similar to that which would have been visible in the photo-pairs. Similarly, the pattern of tree establishment in Waterton Lakes National Park most closely resembles results from studies in adjacent Glacier National Park, Montana. Several repeat photography studies document increased tree density in the ATE but little or no upward movement in the position of the ATE (Butler et al., 1994; Klasner and Fagre, 2002; Roush et al., 2007). The similarity in research findings from Glacier National Park, Montana to patterns of change in the adjacent ATE of Waterton Lakes National Park and the similarity in research findings from Sunwapta Pass, situated half-way between Jasper and Kootenay national parks provide independent evidence that reinforces the importance of regional-scale drivers in determining the type and amount of change within the ATE.

6.3.2 Implications for Temporal Patterns of Establishment.

While it is not possible to determine the timing of the limited tree establishment and change in the ATE of Waterton Lakes National Park, research by Woodward et al. (1995) suggests that tree establishment may be driven by temporal patterns of mesic conditions. Given the xeric nature of Waterton Lakes National Park, establishment is most likely to have occurred during wet periods, when more mesic conditions existed. Conversely, in Kootenay and Jasper national parks, the dominant mesic nature of the region may have limited the importance of climate variability and encouraged continued establishment over the past century. Ongoing establishment is much more likely than limited sporadic establishment to produce the ubiquitous and dramatic changes in tree density and elevation seen in the ATEs

of the northerly two parks. The episodic pattern of subalpine larch establishment recorded in Goodsir Pass (which is predominately mesic) at first seems to counter this line of reasoning. However, while mesic site conditions do mitigate the role of climate variability (Hessl and Baker, 1997), a strong enough climate signal may cause fluctuations in an otherwise consistent establishment regime. The continuous low rates of subalpine larch establishment documented in Goodsir Pass may be a response to the mesic conditions of the area, while the pulses of high rates of establishment may be responding to climate variability.

6.3.3 Limitations of a Coarse-Scale Repeat-Photography Study.

As described earlier in this chapter, site-specific conditions including safe sites (Malanson et al., 2009), local-scale feedback mechanisms (Bekker, 2005) and geomorphology (Resler et al., 2005) often influence the spatial pattern of tree establishment and physiognomy within the ATE (Butler et al., 2007). At the coarse-scale of information derived from the regional photo-pairs, it is likely that the complex interactions or noise of these localized and overlapping environmental variables diminish the relative importance of aspect on ATE dynamics. At the scale of an individual tree this portion of the study has too coarse a grain to distinguish among these numerous factors. Additionally, aspect may be too general a proxy for site-specific factors driving ATE change, given the number and complexity of site-specific variables and the differences in how they affect ATE dynamics within the context of different regional landscape characteristics. Finally, results from Goodsir Pass indicate that aspect is the least influential site-specific variable on the health of trees within the ATE (Table 5.6).

The under-representation of northerly and easterly ATE segments in Kootenay and Waterton Lakes national parks decreases the explanatory power of some of my results. To remedy both this problem and the difficulty of classifying ATE segments within photo-pairs, future studies should identify ATE sites using topographic maps and aerial imagery prior to analysis of photo-pairs. By reversing the process of identification, ATE sites could be defined more rigorously. Examination of an equal number of all aspects coupled with the comprehensive nature of repeated photo-pairs from the Mountain Legacy Project would allow analysis based on a population rather than a sample.

6.4. Patterns and Scale.

Much of the research concerned with ATE dynamics has emphasized the interplay between site-specific conditions and climatic changes in driving change within the ecotone. At the outset of this project I proposed that strong spatial patterning of tree establishment suggests the importance of site-specific conditions while strong temporal patterning implies a climatic control. Results of this study indicate temporal patterning to be stronger. Results also indicate that the importance of site-specific conditions is dependent upon their larger-scale geo-climatic context. Both conclusions are discussed below.

6.4.1 Spatial and Temporal Patterning.

6.4.1.1 Spatial Patterning of Trees.

Spatial patterning of trees in the ATE of Goodsir Pass was measured in terms of both tree health and establishment. There is a lack of any clear pattern in the location of trees of varying health relative to the major environmental variables in Goodsir Pass. Spatial patterning of establishment does occur, but the poor predictive capability of the binomial regression models demonstrates the weak influence all site-specific variables (excluding elevation) have on determining the location of tree establishment within the ecotone. While elevation does appear to have some power in predicting tree establishment, it is far less than would be expected given the strong elevation gradient that creates the ecotone. Two results even indicate that establishment may be decoupled from altitude: i) spruce density is greater at higher elevations; and ii) while the earliest larch trees to establish at progressively higher elevations did so in a temporally consecutive fashion, mean larch establishment dates indicate that establishment throughout the entire upper three quarters of the ecotone occurred synchronously.

The decoupling of establishment from elevation may indicate a threshold response of establishment to climate. A threshold response occurs when a dramatic change occurs in a response variable as a result of only a small change in a causal variable. Bekker (2005) describes a threshold response of tree establishment in Glacier National Park, Montana that he attributed to climate conditions ameliorating sufficiently to allow far greater amounts of establishment than would ordinarily be permitted by site-specific conditions and processes.

The ubiquity, magnitude and lack of spatial patterning of tree establishment in Goodsir Pass suggest a similar set of climate-based drivers. Certainly, the pulses of increasing magnitude in subalpine larch establishment and the rapid increase of Engelmann spruce and subalpine fir establishment in the ecotone indicate that the ability of trees to establish has surpassed a threshold and is now occurring with far greater frequency than fifty to one hundred years ago.

6.4.1.2 Temporal Patterning.

There are a number of results that suggest that the temporal pattern of seedling establishment is linked to climate variability: the high degree of correlation between minimum growing season air temperatures and fir and spruce establishment, correlations between the establishment of all species and reconstructed summer temperatures (Luckman et al. 1997), and the correspondence of pulses in larch establishment to the warm phases of the PDO. While each line of evidence taken separately does not offer conclusive evidence for a link between climate and establishment patterns, the combined weight of evidence makes a convincing case for climatically-influenced tree establishment and adds to the significant body of literature that finds climate as a substantial driver of recent change within the ATE (Millar et al., 2004).

Because this was not an experimental study it is not possible to demonstrate causality conclusively; however, strong ecological reasoning underlies each of the three sets of results that link climate and establishment. First, mean monthly minimum temperatures best represent actual ecological conditions that influence survivorship of young trees (Millar et al., 2004). Second, Luckman et al.'s (1997) temperature reconstruction is better correlated with all three species than is the Banff record; this result is expected because the data are derived from the ATE. Like minimum temperatures, a temperature reconstruction based on tree ring-width data from the ATE better represents the climatic variables influencing establishment in the ATE than do valley bottom weather stations (Holtmeier, 2003). Lastly, changes in the PDO phases create alternating periods of more or less mesic conditions, which have a strong impact on the ability of trees to establish in the ATE (Woodward et al., 1995). These phase changes have been shown to occur synchronously with changes in tree growth and establishment in the ATE across the American West. More specifically, in dry

areas such as the eastern portion of Glacier National Park, Montana, tree establishment is positively correlated with the negative phase (Alftine et al., 2003), and in areas that receive high snow-fall such as the Cascade Mountains of Washington and Oregon, tree establishment is positively correlated with the positive phase (Peterson and Peterson, 2001; Peterson et al., 2002). This differential influence of PDO phases results from the increased snowfall during the negative phase of the PDO (Selkowitz et al., 2002). Thus, the two to three m snowpack present in Goodsir Pass suggests that tree establishment should increase during the positive phase of the PDO, which is what I observed.

6.4.2 Higher Levels of Influence: The Impact of Coarse-Scale Pattern on Fine-Scale Process.

Results from this study indicate that the importance of certain drivers of tree establishment is highly dependent on the regional context. Larger-scale climatic and environmental conditions determine whether ecological patterns at smaller scales (both meso and micro) influence the processes of establishment within the ATE.

6.4.2.1 The influence of Regional Context on Meso-scale Processes.

The impact of the regional context on meso-scale processes operating in the ATE is brought to light by considering the effect of aspect on vegetation change in the ATE. Aspect has a minimal effect on change within the ATE in the predominately mesic environments of Kootenay and Jasper national parks. In contrast, in Waterton Lakes National Park, aspect does affect the location of tree establishment; cool and wet northern and western aspects show the greatest amount of establishment activity while dry eastern aspects have experienced decreases in tree density. Aspect becomes important only given the regional more xeric context of the subalpine and alpine zones of Waterton Lakes National Park. Aspect plays no role in determining where trees establish in the mesic conditions present in Goodsir Pass. In other words, regional characteristics have a greater influence on the role aspect plays in determining the location of tree establishment than do the intrinsic attributes of aspect itself.

At large scales, the regional geo-climatic setting likely controls the occurrence, magnitude, and type of change in the ATE. Analysis of the regional repeated photo-pairs shows that the

results from Goodsir Pass are not a local anomaly; they are representative of the region and provide insights into the type and nature of change that might be found were other detailed studies to be undertaken in Kootenay National Park and, likely, Jasper National Park. Had the detailed dendroecological study in Goodsir Pass been conducted in Waterton Lakes National Park, it is likely that considerably lower rates of upward ecotone advance or increases in tree density would have been documented.

6.4.2.2 The influence of Regional Context on Micro-scale Processes.

The impact of the regional context on micro-scale processes operating in the ATE is brought to light by considering research from the eastern portion of Glacier National Park, Montana, which is geo-climatically very similar to Waterton Lakes National Park. Studies in Glacier National Park, Montana demonstrate the importance of numerous pedologic and geomorphologic features in determining the spatial pattern of tree establishment (Butler et al., 2003; Butler et al., 2004; Bekker, 2005; Resler et al., 2005). The dry conditions cause considerable micro-patterning of tree establishment. Conversely, the mesic conditions and deep, well-developed soils in Goodsir Pass diminish the importance of pedologic and geomorphologic features and there is little micro-spatial patterning of tree establishment.

6.4.2.3 The influence of Meso-scale Pattern on Micro-scale Processes.

It is not only pattern at the regional scale that influences finer-scaled processes. In Goodsir Pass the importance of tussock-formed micro-shelters in determining the pattern of establishment is highly dependent on their context within the larger landscape. A meso-scale topography with no relief would greatly enhance the importance of small hummocks in protecting young trees from desiccation. However, swale-and-trough meso-scale topography in the study site creates variability in the distribution of early season snow (Marsh, 1999), and, as a direct consequence, the importance of shelters at the micro-scale in Goodsir Pass increases on the exposed tops of the swales and decreases in sheltered bottoms of the troughs.

6.4.3 Conclusion.

While Butler et al. (2007) discuss how geomorphology can enhance or minimize the effect of climatic warming, I argue that the regional geo-climatic context plays the largest role in

determining not only the amount of change that will occur in the ATE in response to climatic changes, but also the relative impact that conditions at smaller scales will have on establishment patterns. I find that the ATE in Goodsir Pass is influenced predominately by variables at the constraint level. In a specific location where significant tree establishment has occurred, temporal variability of tree establishment in response to regional climate is more pronounced than spatial variability in response to site-specific variables, and on a regional scale, the spatial patterning and magnitude of tree establishment is ultimately a function of the broader ecologic and geo-climatic context.

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7.1 Conclusions.

I began this study with three main objectives.

- i. To quantify the magnitude, timing, rate, and type of change that has occurred over the past two centuries in the ATE of Goodsir Pass.
- ii. To establish whether these changes were driven by climate variability at the constraints level or were controlled by site-specific environmental variables at the components level.
- iii. To contextualize the results from the detailed study in Goodsir Pass by assessing, at a coarse scale, the magnitude and type of change that has occurred in the ATE of the southern Canadian Rocky Mountains over the past century.

Results from this study produced four main conclusions.

- i. The ATE in Goodsir Pass has increased substantially in both elevation and density and it has done so at a rate of change that is equal to or greater than other changes documented in the ATE around the globe.
- ii. Temporal patterns of tree establishment correlated to climate records are more pronounced than spatial patterns linked to environmental variables indicating that change in the ATE of Goodsir Pass is affected more by variables at the constraints level than by variables at the components level.
- iii. The repeated photographs from the three mountain parks show that the change seen in Goodsir Pass is not anomalous and exemplifies the most substantial type of change documented in the three national parks.
- iv. Throughout the southern Canadian Rocky Mountains the ecologic and geoclimatic setting exerts the greatest control on the occurrence and character of changes in the ATE at a specific location. Furthermore, the character of larger-scale topography influences the relative impact microtopography has on the spatial

pattern of tree establishment. Together these two interpretations indicate that coarse-scale landscape patterns may determine the relative importance that finer-scaled patterns will have on processes of change in the ATE.

The first three conclusions are primarily concerned with documenting and analyzing changes that have already occurred; however, the fourth conclusion has some theoretical implications (predominately within the field of landscape ecology) and may allow for predictions of future change. Specifically, the importance of fine-scale environmental conditions in the process of tree establishment is enhanced or diminished in direct relation to the context of the regional landscape, climate, and environmental conditions. As Turner et al. (2001:36) write:

“although the variables that influence a process may or may not change with scale, a shift in the relative importance of the variables or the perceived direction of a relationship often occurs when spatial or temporal scales are changed.” Applying this logic to the ATE means that predicting the specific pattern of tree position within the ATE at fine scales will require extensive knowledge of the edaphic conditions, microtopography, site history, tree species, and other site-specific conditions. However, at coarse scales it may be possible to predict whether or not change will occur in the ATE and possibly the magnitude of such change, simply by placing models of future climatic change in the regional context of the ecology, geomorphology and climate.

To conclude this thesis I return to the two broad themes on which most current research on ATE dynamics centres: one that finds notable change (increases in tree density and elevation) in the ATE as a result of recent climatic changes; and one that finds change in the ATE to be strongly controlled by site-specific ecologic and geomorphologic factors. The overarching goal of this study was to shed greater light on this dichotomy through an in-depth examination of an ATE that was known to have undergone significant change.

The similarities between several climate records and the temporal patterns of tree establishment in Goodsir Pass support the first line of reasoning. However, this study also escapes from the dichotomy of whether climate or site-specific conditions exert a greater influence on change in the ATE by demonstrating the importance of the regional context in determining whether change will occur and what will drive that change. Changes bearing the

mark of both climate and local conditions have certainly occurred, but in looking for ultimate causes of changes in the ATE, neither line of thinking is completely satisfactory. Rather, the ecologic, geo-climatic and anthropogenic context of the ecotone determines whether the ATE will be more strongly influenced by climatic changes or site specific conditions. A greater study and appreciation for the environmental circumstances of specific ATEs will allow for a more comprehensive and unified picture of how and why change may occur in the ATE.

7.2 Future Research.

Two interpretations from this study would benefit from additional research. First, the idea that the importance of micro-scale topography in the spatial pattern of tree establishment is determined by meso-scale topography requires targeted research in order to be substantiated more thoroughly. This conclusion is best seen as the beginning of a new hypothesis. As such, specific research is needed that asks if trees establish in greater numbers in sheltered micro-sites than on exposed micro-sites in areas with a shallow snowpack. Unlike this study, further research would need to document snow distribution during the fall when young trees benefit most from the protection of snow (Sakai and Wiser, 1973). Though past research points to the high interannual similarity in relative snow depths in the alpine and subalpine zones (Elder et al., 1991) it is unclear whether spatial variability in snow depth is the same in the fall and the spring (when snow depth was measured for this study).

The second interpretation that would benefit from additional study is my assertion that the environmental context or circumstances of the ATE are the greatest determinants of whether and how change will occur in the ATE. Two possibilities exist to investigate this idea further. First, a review of past studies documenting change in the ATE could categorize studied ecotones into several geo-climatic and ecological types and then ask if the occurrence and character of change was consistent within types. Secondly, the extensive collection of repeated images created by the Mountain Legacy Project could be used to generate new data concerning the occurrence and character of change within the ATE. A prior identification of ATE segments in the landscape and a classification of those segments based on their geo-climatic and ecological context, coupled with the comprehensive nature of the repeated photographs, would allow analysis of an entire population rather than just a sample. Though

of a coarser nature than many ecological studies, analysis of the repeated photographs allows for change to be assessed across an entire landscape, which is in marked contrast to nearly all other studies of the ATE that assess change at only one or a few sites.

7.3 Conservation and Restoration Implications.

While the goal of this study was not to develop conservation or management prescriptions for the ATE, my findings do have implications for both fields. Two considerations are most relevant. The first centres on the difference between the character of change that has occurred in the ATE and the character of change that is likely to occur in the ATE in the future. The second poses challenging logistical and ethical questions concerning the appropriate response to the changes seen in the ATE.

With respect to the first consideration, the change documented in this study does not constitute a wholesale shift from one ecosystem type to another as predicted for certain mountain ecosystems (Hall and Fagre, 2003). The previously un-treed area into which trees have established over the past two centuries still retains much of its tundra or alpine characteristics and species. This is due in large part to the long ecological gradient over which the ATE is located in Goodsir Pass. So far, the increase in tree density and elevation has not caused an extirpation of tundra species. However, if tree establishment continues at its present rate the ecotone is likely to occupy an increasingly narrow elevation band. In the area around Goodsir Pass this shrinking of the ATE will occur because the elevation at which trees are now able to establish is equal to the elevation of the mountain-tops; tundra species will have no higher terrain to which they can migrate. In other locations where mountain terrain extends beyond the increasing upper limit of tree establishment, cliffs, poorly developed soils, high rates of evapotranspiration, and talus are likely to limit migration of tundra species. Ongoing establishment within the ecotone will create both a denser ecotone and a higher lower boundary between the ATE and the forest.

Effects of climatic changes on the ATE and the alpine ecosystem in Goodsir Pass may have occurred so far in a 'grace period' in which the upward shifts of trees is permitted by the existing and wide gradient of the ATE. Continued warming, as a result of anthropogenic greenhouse gas emissions (Pachauri and Reisinger, 2007), may cause this 'grace period' to

close as the ecological gradient of the ATE narrows. It is likely that the ATE will become more abrupt as trees reach physical barriers or other limitations to establishment other than temperature at higher elevations. This shortening of the ecotone could result in the loss of certain alpine species or species assemblages. In Goodsir Pass the low elevation of local mountain-tops makes this scenario likely, which would result in a future landscape that contains no tundra ecosystem and possibly no ATE.

The second set of interpretations from this study that has significant conservation and restoration implications revolves around practicing ecological restoration in response to climatic changes. The changes I observed in the ATE are linked to increased temperatures, caused by anthropogenic greenhouse gas emissions (Pachauri and Reisinger, 2007). This, coupled with the substantial nature of past and likely future ecological changes in the ATE of Goodsir Pass, may be seen as an impetus for action by managers of Kootenay National Park. Other cases of human caused impacts to the park environment, such as fire suppression, declining populations of threatened species, and exotic plant invasion have resulted in significant restorative and conservative measures by the park management (Parks Canada, 2009).

Park land managers may not be able to address the changes I observed in the ATE near Goodsir Pass using the same methods employed by more traditional and targeted restoration actions. The diffuse nature of both the cause (climatic changes) and the resulting ecological shift (widespread increased tree establishment in the ATE and alpine ecosystems) creates new restoration and conservation challenges. First, the logistics of designing and executing feasible restorative actions for a landscape that is not only remote and fragile, but also undergoing change that is widespread, long term, and highly integrated into the normal ecological processes are obviously significant. *In-situ* restorative practices are difficult to imagine. Should trees in the ATE be removed to maintain an historical ecological character and preserve habitat for tundra species? This line of questioning quickly leads to more complex issues related to the inherent values we place on certain ecosystems, the services those ecosystems may provide for human populations, difficulties in defining historical baselines, and the likely inability to maintain historical ecosystems or species assemblages in the face of rapid climate change (Harris et al., 2006). Secondly, defining restoration or

conservation goals for ATEs impacted by climatic changes poses several ethical questions. Paramount in my mind is whether, in a fragile alpine landscape already undergoing impacts due to human actions, it is right to introduce additional restorative actions. Despite the impetus to fix a problem or positively direct the course of changes resulting from anthropogenic induced climatic changes, it may be preferable simply to leave the ATE alone. Widespread climate change guarantees that all ecosystems will bear the mark of human action. In light of the difficulties presented by practicing restoration in a remote landscape and the diffuse nature of the causes of and impacts to that landscape I assert that it is appropriate to preserve ecosystems where the initial impacts of climate change are not further complicated by additional human action on the landscape.

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