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Alpine Treeline and Climate Warming: A Multiscale Study of Pattern and Process in Southwest Yukon

by

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ABSTRACT

The boundary between forest and tundra in mountainous areas, alpine treeline, is expected to advance as climate warming continues and change is likely to be pronounced in northern latitudes. I studied the white spruce (*Picea glauca* (Moench) Voss) treeline in the Kluane region of southwest Yukon, Canada, with the objectives of: (i) characterizing its responses to past climate change, and (ii) assessing the influence of different environmental variables on spruce growth and treeline dynamics. Four investigations were conducted, each employing fundamentally different methodologies and occupying distinct levels within a hierarchical, scale-based, analytical framework. At the landscape scale, I mapped spruce distribution and abundance from a QuickBird2 multispectral satellite image. Decision tree analysis was used to characterize relationships with topoclimatic variables. Results demonstrated the primary role of temperature in limiting spruce distribution, but also identified substantial fine-scale variability. At the population level, dendroecology was used to reconstruct recent dynamics of spruce and grayleaf willow (*Salix glauca* L.). Evidence of a rapid increase in treeline elevation or spruce density during the early-mid 20th century was found. There was a significant correlation between recruitment and reconstructed summer temperatures, indicating that climate was the cause of change. Comparison of aerial photographs from 1947 and 1989 verified stand reconstructions and showed that the change was widespread. At the organism level, I warmed 40 young spruce at treeline for 4-years using open-top chambers. Individuals responded positively to the treatment in both growth and physiology. There were also significant differences between individuals growing on north and south aspects.

Collectively, my results suggest a significant potential for subarctic alpine treeline to advance in response to future climate warming. However, the rate, pattern, and timing of advance will be contingent on heterogeneity of environmental variables at finer scales, especially direct solar radiation and permafrost distribution.

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CHAPTER 1

Introduction: A Hierarchical Framework for Study of the Forest-Tundra Ecotone

"Biological processes have many dimensions and need to be studied on different levels if they are to appear as anything other than impossibly complex."
Robert O'Neill (1987)

INTRODUCTION

This dissertation presents the results of research undertaken on alpine treeline and its dynamics in the Kluane region of southwest Yukon, Canada. Two fundamental research objectives were addressed: (i) characterization of treeline response(s) to past climate change and variability in the region, and (ii) assessment of the influence of various physical and biological factors on tree growth and treeline dynamics. Four scientific investigations were conducted to meet these objectives, each employing fundamentally different methodologies and each occupying a distinct level within a hierarchical, scale-based, analytical framework. These were: (i) treeline stand reconstruction using dendrochronology, (ii) assessment of treeline change over the last half century using sequential aerial photography, (iii) high resolution mapping and analysis of conifer distribution and abundance at the forest-tundra ecotone, and (iv) experimental warming of conifer seedlings at treeline. Chapters 2, 3, 4 and 5 of this dissertation present these components in their entirety. The final chapter (6) provides a synthesis of these results within the context of scale and hierarchy theory.

This introductory chapter is intended to provide the background necessary for understanding the rationale for the research which was undertaken and, importantly, how it was carried out. It begins with a brief overview of forest-tundra ecotones and their significance in arctic and alpine regions and introduces the Kluane region of southwest Yukon as the study area. It presents the overall methodological framework used to conduct the research and briefly introduces each of the four investigations which were undertaken.

TREELINE AND THE FOREST-TUNDRA ECOTONE

At their most fundamental level, ecotones are defined as the transitional areas between adjacent ecosystems (Risser 1995). The term is most commonly applied to transitions between homogenous vegetation types that coincide with steep environmental gradients (Kent *et al.* 1997). However, Gosz (1993) argued that it can be applied at any scale, ranging from the transition between local plant communities to the transition between global biomes. A corollary of this scale-independent definition is that the dynamics and causes of ecotones also vary with scale (Table 1-1).

The transition from forest to tundra in arctic and alpine regions is one of the best known, and most studied, of all naturally occurring ecotones. Its most conspicuous feature is known as treeline: the boundary coinciding with the uppermost altitude or latitude of individuals typical of a tree growth form, defined here as individuals having one clearly dominant stem, generally taller than wide, and tall enough to have its crown coupled with prevailing atmospheric conditions (generally more than 2 m). While treeline itself is often not a discrete or abrupt "line" on the landscape, it spans a shorter distance than the entire forest-tundra ecotone and it is often used as an indicator of the entire transition.

Numerous explanations for the existence of treeline have been proposed. These include structure-related factors such as frost damage, winter desiccation, and mechanical damage by wind, snow, and ice; growth-related factors such as limited seed development, germination, and recruitment in low temperatues; a negative balance between photosynthesis and respiration as a result of short growing seasons; and combinations thereof (Wardle 1971, Tranquillini 1979, Stevens & Fox 1991, Sveinbjornsson 2000). Körner (1998) conducted an extensive review of the literature and concluded that while many of these factors may be locally important, they cannot offer a universal explanation for treeline. He proposed a growth limitation hypothesis whereby low temperatures prevent tissue synthesis from matching the minimum requirements for growth. Thus, while the mechanisms are still not fully agreed upon, it is generally accepted that factors associated with low temperatures are the most fundamental cause of forest-tundra ecotones in arctic and alpine environments.

The physiological effects of low temperatures may be the dominant force controlling the *potential* limits of tree growth in alpine and arctic environments, but the *actual* position of treeline is the product of a complex interaction of physical and biological factors operating at a variety of scales (Holtmeier and Broll 2005) (Figure 1-1). These include terrain attributes such as aspect and slope (Brown 1994), edaphic variables such as soil type and moisture (Malanson *et al.* 2002), physical disturbance processes such as fire, avalanches, and rock slides (Daniels and Veblen 2003), and biological processes such as competition and herbivory (Cairns and Moen 2004). Furthermore, the importance of these other variables, as well as the strength of their interactions, undoubtedly varies from region to region and over time.

The literature on alpine and arctic treeline is so extensive that a multitude of terminologies for identical features exists. The result, in the words of Löve (1970), is that "utter confusion reigns" and it is necessary to define any potentially confusing terminology. Throughout this thesis I use the term forest-tundra ecotone to refer to the entire zone of transition between the two vegetation types. Additional terms that are used with specific reference to subzones within the ecotone, along with synonyms commonly found in the literature, are defined in Table 1-2 and illustrated in Figure 1-1.

CLIMATE CHANGE AND FOREST-TUNDRA DYNAMICS

A consistent prediction of global change research is that climate warming will be greatest in Arctic and subarctic regions, and recent evidence supports this prediction (ACIA 2004, Hinzman *et al.* 2005). Impacts in mountainous areas are also expected to be marked, though perhaps more complex, because of the climatic diversity that results from topographic variation (Beniston 2003, Huber *et al.* 2005). The potential ecological impacts of climate change in these biomes has been the subject of many studies and one of the most common hypotheses is that the forest-tundra ecotone will undergo a significant change in structure and position as a result (e.g. Sveinbjornsson 1992, Grace *et al.* 2002). The rationale for this hypothesis extends from the relationship between thermal regime and the ecotone's position (Jobbágy and Jackson 2000, Körner and Paulsen 2004) and the aforementioned critical role that temperature plays in controlling the reproduction, establishment and growth of tree species in this environment. Thus, as temperature continues to warm, treeline is expected to shift, and there is abundant evidence of more advanced treeline position during warmer periods of the mid-Holocene to support this axiom (e.g. MacDonald *et al.* 2000, Payette *et al.* 2002).

Widespread shifts and changes to forest-tundra ecotones could have important consequences for the Earth's climate system in terms of surface albedo, carbon and nutrient cycling, and hydrological cycling (Chapin *et al.* 2000). Changes are also likely to have significant effects at local and regional scales with respect to habitat change and biodiversity. The potential for an upward and northward movement of species across altitudinal and latitudinal gradients has received a great deal of attention and observations suggest these shifts are already occurring (Hickling *et al.* 2006). Models of future ecological change have been developed at several scales, ranging from regional to global and species-based to biome-based (e.g. Kaplan *et al.* 2003, Moen *et al.* 2004). The general conclusion of these studies is that as the forest-tundra ecotone advances upslope, alpine tundra will become increasingly fragmented and the extent of arctic tundra will shrink as the ecotone advances northward.

There have been numerous studies to investigate changes at latitudinal treeline in northern Canada, Alaska, Russia, and Scandinavia in response to recent climate change and variability over the past 150 years, and analogous studies have been carried out at alpine treeline in mountainous regions around the globe. However, the changes reported in these studies vary considerably in type and extent. In some regions, trees have invaded tundra, extending the altitudinal or latitudinal limit of tree species (e.g. Suarez *et al.* 1999, Lloyd and Fastie 2003). The extent of the ecotone has changed in other areas not by the establishment of new individuals but, rather, a change from stunted, low-growing individuals (i.e. krummholz) to upright growth forms (i.e. trees) (e.g. Lescop-Sinclair and Payette 1995). Other studies have revealed increases in stand density across the treeline ecotone, but have not observed any consequential extension of its limit (e.g. Szeicz and MacDonald 1995, MacDonald *et al.* 1998). In other areas, significant recent change has not been detected at all (e.g. Cullen *et al.* 2001, Cuevas 2002) and in still other regions, treeline occupies a position thought to be a relict of warmer periods prior to the Little Ice Age (e.g. Ives and Hansen-Bristow 1983). The extent and timing of these changes also varies considerably between locations, despite the fact that the majority of them are linked to a warming trend since the end of the Little Ice Age.

In light of this variability, it is evident that treeline dynamics are considerably more complex than the generalized hypotheses and models purport. While useful as a conceptual tool, projecting an altitudinal or latitudinal shift of n based on a temperature increase of x tends to over-simplify the process of treeline dynamics. An advance of treeline may be a very likely response to climate warming over long time periods or across large regions, but responses at finer temporal and spatial scales are more likely to be highly variable. There is also evidence to suggest that ecotones do not typically respond to climatic change in a direct fashion. Response lags are common (Figure 1-2) and the type and degree of response can vary across a region depending on more local variables (Kupfer and Cairns 1996, Dalen and Hofgaard 2005). Moreover, emphasis on treeline often ignores the transitional context of the forest-tundra ecotone. Unless all species exhibit an identical response to climate change, and unless responses are similar at all locations across the ecotone, it is probable that variables such as species composition, distribution, and abundance will also change. Consequently, in addition to –

or perhaps instead of – a change in treeline altitude or latitude, the structure and pattern of the entire forest-tundra ecotone is also likely to change.

SOUTHWEST YUKON: A SUBARCTIC ALPINE ENVIRONMENT

The Kluane region of southwest Yukon (Figure 1-3) offers a particularly useful locale for examining the forest-tundra ecotone. North America's highest mountain range, the St. Elias Mountains, dominate much of the landscape, and treeline is an altitudinal phenomenon here. However, the region is located at a high enough latitude that treeline is limited to elevations below 1500 m, meaning that the forest-tundra ecotone also spans some of the more gradual valley slopes and plateaus which exist in the lower, eastern parts of these mountains. In short, the low solar angle of northern latitudes combines with the extreme topographic variability to create a diverse array of environments within relatively short horizontal distances. Furthermore, southwest Yukon has experienced a significant warming trend since instrumental records began for the region (Zhang *et al.* 2000) and has seen some of the highest deviations from 30-year temperature normals of any region in Canada over the past decade (MSC 2005). This makes it a particularly useful locale for examining recent vegetation dynamics in response to climate change. Models predict that these climate trends will continue (Laprise *et al.* 2003), meaning that studies of treeline could have importance in forecasting future ecosystem responses to climate change.

The forest-tundra ecotone plays a critical role in defining the landscape structure of the Kluane region. Along with the periglacial environment which marks the terminus of the extensive permanent snow and ice, treeline is the most evident land cover transition in the region (Figure 1-3). It is also ecologically important, delineating the distribution of various habitats and, in turn, wildlife (Danby 1999). Shifts in the location or pattern of this ecotone are likely to have consequences for both subsistence human use and biodiversity conservation in the region, centred on Kluane National Park and Reserve and the adjacent Kluane Wildlife Sanctuary (see Danby and Slocombe 2005). Forecasts of these changes are critical for the development of adaptive planning and management strategies (Danby *et al.* 2003).

Vegetation Types

The major vegetation types in the Kluane region can be divided into three basic types: montane, subalpine, and alpine. Although definitions vary (cf. Douglas 1974), the subalpine zone in the Kluane region generally coincides with the forest-tundra ecotone. Plant community types within this zone vary greatly, as do their extent. At a regional scale, significant differences exist along a north-south gradient. In general, the subalpine zone becomes narrower, more distinct, and floristically less diverse with increasing latitude. This is mostly related to a gradual decline in precipitation and temperature (Theberge 1980). At finer scales, subalpine community composition in the region has been observed to vary with local gradients such as soil type, moisture, and topography (Douglas 1980).

White spruce (*Picea glauca*) is the dominant conifer in the Kluane region. It is a major component of the tree flora of the boreal forest of North America and grows under a wide range of climatic conditions (Figure 1-4). In northwestern North America, white spruce often grows in pure stands but it is also found in association with trembling aspen

(*Populus tremuloides*), white birch (*Betula papyrifera*), lodgepole pine (*Pinus contorta*) or balsam poplar (*Populus balsamifera*) (Nienstaedt and Zasada 1992). In northern limits of the boreal forest from Hudson's Bay to northwestern Alaska it is often found in association with black spruce (*Picea mariana*) and both species extend north to form the arctic treeline (Timoney 1988). However, with the exception of trembling aspen and balsam poplar, these other species are not found in any significant number in the Kluane region and white spruce exists in pure stands across the forest-tundra ecotone.

In the central and northern portions of the Kluane region, the focus of this study, white spruce forms both closed and open canopy stands in the low-elevation valley bottoms. Spruce density decreases with increasing altitude and an open forest canopy is ubiquitous at the lower end of the forest-tundra ecotone (the *open forest* zone). Between 1250 and 1350 m the spruce canopy is discontinuous and the crowns of individuals generally do not overlap (the *woodland* zone). Only occasional spruce are found above 1400 m and these are typically short, stunted, krummholz-type growth forms (the *shrubland* zone). Tall deciduous shrubs span the entire length of the forest-tundra ecotone. Dwarf birch (*Betula glandulosa*) and gray-leaf willow (*Salix glauca*) are the two dominant species, often forming a dense layer over one metre tall in spruce canopy openings and in the shrubland zone. Other shrub-forming species of willow include *S. arbusculoides*, *S. lanata*, and *S. planifolia.*

Aspect plays an important role in determining local characteristics of the forest-tundra ecotone. Treeline is typically 50 to 150 m higher on the warmer and drier south-facing slopes than it is on equivalent north-facing slopes. Green alder (*Alnus crispa*) can be locally common on north-facing slopes but is generally absent on south-facing slopes.

Various feathermosses and sedges (*Carex* spp.), along with *Ledum palustre*, typify the forest-tundra ground layer on north-facing slopes. Common dwarf shrubs on south-facing slopes include *Potentilla fruticosa, Arctostaphylos uva-ursi* and *Vaccinium uliginosum*, though species composition varies with drainage (see Birks 1977, for a detailed floristic account of the region).

The northern portion of the Kluane region, specifically the area between the Donjek and Duke rivers, was chosen as the focus of this study for several reasons. First, the treeline ecotone occurs on a wide range of grades and aspects here – from steep, well drained slopes to large, gently sloping plateaus. This permitted an examination of the influence of terrain characteristics on treeline and its dynamics without the confounding effect of different climatic regimes. Second, as mentioned above, the area's forests are dominated almost exclusively by white spruce. This eliminates the influence of interspecific competition or differential response to climate among treeline conifers observed elsewhere (e.g. Laroque *et al.* 2001). Finally, large natural disturbance events are infrequent in this part of the region. Theberge *et al.* (1986) describe portions of the montane forest in the Shakwak Trench as "fire mosaics" but found limited evidence of fire in the subalpine zone or in the confined creek valleys of the chosen study area, and I found no evidence of fire anywhere near my fieldwork locations. The area has not been affected by the extensive spruce bark beetle (*Dendroctonus rufipennis*) infestation in southern portions of the region and there is no historical evidence of past infestations (Berg and Henry 2003). Total annual snowfall is not significant enough in the northern portion of the Kluane Ranges to trigger stand clearing avalanches. Similarly, rainfall is generally not significant enough to cause the soil saturation required for major slope failures. Although placer mining has been widespread in the area's major creeks, these activities have had no impact on the forest-tundra ecotone. And while some limited hard-rock mining and exploration has occurred, these areas were removed from all consideration in this study. The relative absence of these types of disturbances meant that I could reduce the number of variables that needed to be considered when interpreting results and, therefore, focus more exclusively on the climate-treeline relationship.

OBJECTIVES AND METHODOLOGIES

At its inception, the objectives of this research project were to spatially model the response of the forest-tundra ecotone in the southwest Yukon to projected climate warming and, in turn, assess the impacts of this regional landcover change on biodiversity. However, predictions of landscape and habitat change are only as good as the level of understanding they are built on (Hobbs 1994) and it soon became evident that if a reliable forecast of change for southwest Yukon was to be achieved, the following questions first needed answering:

1. How has the forest-tundra ecotone in the Kluane region responded to climatic change and variability in the recent past?
2. To what extent are the physiological effects of low temperatures mediated by other factors to limit and constrain spruce growth and, therefore, control treeline dynamics in the Kluane region?

Answering these questions became the goal of this study and the original objectives served as the overall research rationale. However, as described previously, the concept of an ecotone can be applied to multiple scales of observation and the variables which structure ecosystems, their boundaries, and their dynamics vary significantly with scale

(O'Neill *et al.* 1986; recall Table 1-1). If these comprehensive goals were to be achieved then explicit consideration of scale was necessary.

Ecological Scale and Hierarchy Theory

Over the last two decades there has been an increasing awareness that the characteristics of ecological systems, be they related to the behaviour ("process") or expression ("pattern") of these systems, are heavily contingent on the scale at which the system is observed (O'Neill *et al.* 1986, Wiens 1989, Levin 1992, Allen and Hoekstra 1992, Peterson and Parker 1998, Schneider 2002). Schneider (1998) formulated six axioms that have emerged from this growing recognition of the importance of scale:

1. spatial and temporal patterns of ecological phenomena depend on the scale of analysis;
2. experimental results cannot be directly extrapolated to larger scales;
3. biological interactions with the environment occur at multiple scales;
4. population processes do not occur at scales convenient for investigation;
5. environmental problems arise through propagation of effects across scales;
6. there is no single or "characteristic" scale for ecological research.

This last axiom was emphasized by Levin (1992) who asserted "there is no single or 'correct' scale on which to describe populations or ecosystems" (pg. 1944) and is complementary to the notion of scale as a filter, as advocated by Hay *et al.* (2001) who define scale as "the window of perception, the filter, or measuring tool with which a system is viewed and quantified" (pg. 473).

Hierarchy theory[1] can be used to conceptualize the relationship between processes occurring at multiple ecological scales and offers a useful heuristic for organizing the complexity of ecosystems (O'Neill *et al.* 1987, Allen & Hoekstra 1992). A basic premise of hierarchy theory is that many systems, including ecological systems, are hierarchically structured (O'Neill *et al.* 1989). This means that any given system is comprised of smaller interacting systems and is itself a component of a larger system. The behaviour of each system is limited by the potential behaviour of its component systems (*bottom-up controls*) and constrained by the properties of the system(s) it is itself a part of (*top-down controls*) (Figure 1-5). Each level within the hierarchy operates at a distinct scale of time and space, meaning that certain patterns and processes are more important at a particular scale of observation than others. Hierarchy theory allows simplification of complex, multiscale systems by permitting the observer to focus on a single hierarchical level (and, therefore, a particular subset of processes and patterns), while simultaneously considering the influence of the adjacent upper and lower levels in the hierarchy (Parker and Pickett 1998).

A Hierarchical Framework for the Study of Treeline

Hierarchy theory lends itself naturally to the study of ecosystems and their boundaries, and I used it as a foundation for the study of the forest-tundra ecotone in southwest Yukon. Some researchers have considered scale in the study of forest-tundra ecotones and interpretation of treeline dynamics (Bian and Walsh 1993, Didier and Brun 1998,

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[1] Hierarchy theory is not a scientific theory in the conventional sense of the term but, rather, a metatheory, defined by O'Neill (1987) as "an underlying structure within which scientific theories are developed" (pg. 422).

Holtmeier and Broll 2005). Fewer have examined the forest-tundra within the explicit context of hierarchy theory (Brown *et al.* 1994, Resler 2006). I undertook four separate investigations, each conducted at a distinct scale, to address the research questions. These were:

1. Reconstruction of recent forest-tundra ecotone dynamics using dendroecology;
2. Assessment of the pattern of ecotone change using repeat photography;
3. Mapping and distribution modeling of white spruce using remote sensing, GIS, and classification and regression trees.
4. Experimental warming of white spruce seedlings at treeline;

These investigations were tailored to fit within a hierarchical framework (Figure 1-6), thereby allowing me to simultaneously consider questions related to cross-scale influences and pattern-process interactions.

Several important elements emerged from using the hierarchical framework. First, as outlined below, the methods and data used in the four investigations were exclusive of each other. This is a critical, but often ignored, necessity of multiscale investigations. Phillips (1999) explored this concept at length and concluded that because "fundamental system-level behaviours vary with scale or resolution...different methodologies are often appropriate or necessary at different scales" (pg. 758). An extension of using different methods for each investigation was the use of different scientific approaches at each scale of observation. In general, an experimental approach was used at the organism level of organization, while descriptive and predictive approaches were most prominent at the stand/slope and landscape scales, respectively. In turn, the hierarchical framework facilitated examination of both ecological pattern and process. Process was investigated at finer scales while pattern was investigated at coarser scales. Elements of both were evident at the stand/slope scale which acted as the focal scale of the hierarchy.

STUDY COMPONENTS AND THESIS OUTLINE

The following subsections describe each of the four components. With the exception of the experimental warming, the investigations are centred on a 1000 km^2 section of the Kluane Ranges that extends from the Duke River northwest to the Donjek River. The experimental warming was carried out on the east side of Kluane Lake for logistical reasons related to accessibility.

Dendroecological Stand Analysis

Dendrochronology is the study of tree rings using a suite of techniques to date them precisely to their exact calendar year of formation. Missing and extra growth rings may occur in increment cores and stem cross-sections, and samples may have been dead for an unknown period of time. This makes it impossible to assign calendar dates to individual rings simply by counting them. Dendrochronology uses annual variation in the width of growth rings to accurately date samples. In turn, this information can be used to date specific events and address questions regarding variables such as past climates (*dendroclimatology*) and earth surface processes (*dendrogeomorphology*). Thus, *dendroecology* is the use of dendrochronological techniques in the study of ecosystems and their dynamics.

Dendroecology has been used extensively in the study of both altitudinal and latitudinal treeline dynamics at a variety of time scales (see Graumlich and Brubaker

1996). In many recent studies (e.g. Szeicz and MacDonald 1995, Lloyd and Fastie 2003) the basic approach has been to age trees sampled within plots located at different altitudes or latitudes spanning the forest-tundra ecotone. Age structures are then developed for each plot and are statistically analyzed to assess whether densities have increased, decreased, or remained constant. Data are also compared to values from corresponding higher or lower altitudes/latitudes to determine whether or not treeline has advanced, receded, or remained constant.

Like these other studies, the intent of this investigation was to identify periods and rates of establishment, recruitment, and growth of a tree species (*Picea glauca*) at altitudinal treeline and to relate these variables to past climatic change. However, unlike most other studies, this study also examined these trends in one of two dominant shrub genera in the ecotone (*Salix* spp.). This is particularly significant given the nearly exclusive emphasis other studies place on the tree component of alpine and arctic treelines. Yet shrubs often form a key component of forest-tundra ecotones, especially in the subarctic. They play critical roles in nutrient cycling of these systems and exert significant influence on community composition (Anthelme *et al.* 2003). Recent shrub expansion has been documented in some arctic and alpine areas and continued expansion is expected to have significant effects on ecosystem function (Sturm *et al.* 2001). Inclusion of the shrub component in studies of treeline is therefore important for a fuller understanding of past dynamics and, in turn, potential future change.

Six locales representative of a different slope-aspect combination were chosen for sampling purposes in 2001 and 2002. A transect was established across the ecotone and a variable area sampling approach (Kent & Coker 1992) was used to collect samples from the open forest, woodland, and shrubland zones. In total, 600 spruce plus an additional 113 clones and 55 dead individuals were measured and sampled at 12 locations. Nine hundred willows were measured and sectioned at 18 locations. Cores and disks were sanded and polished and annual rings were counted, measured and cross-dated using standard dendrochronological techniques (Stokes and Smiley 1968). Static age distributions spanning the period 1940-2000 were developed for each willow plot. Stem density was reconstructed for each spruce plot spanning the period 1600-2000. This investigation is presented in its entirety in Chapter 2.

Sequential Aerial Photography

Repeat and sequential photography have been used extensively in studies of vegetation change, particularly with respect to assessing the changing abundance, cover and composition of tree and shrub species (e.g. Mast *et al.* 1997; Allen and Breshears, 1998; Tape *et al.*, 2006; Zier and Baker, 2006). Strictly speaking, repeat photography is limited to instances where new photographs are obtained from the same location and perspective as the original for the specific purpose of the study (e.g. Pickard, 2002). On the other hand, sequential photography takes advantage of existing photographs and frequently includes more than two time-steps (e.g. Fensham and Fairfax 2002). Repeat photography typically utilizes ground-based photography while sequential photography most often utilizes vertical aerial photography. Techniques and approaches vary greatly, ranging from purely qualitative comparisons to highly quantitative analyses utilizing complex digital image transformations and spatial analysis. However, the basic premise is the same: to identify changes in the landscape and relate these to changes in land use, climate, natural disturbance, or some other combination of environmental drivers (Rogers *et al.*, 1984).

Ground-level repeat photography has been used to document some recent treeline change. By its very nature this has mostly been carried out at fine scales, examining individual locations or even the growth of individual trees (e.g. Kullman, 1987; Vale, 1987; Rochefort and Peterson 1996; Munroe, 2003). Fewer published studies have utilized vertical aerial photography to examine treeline change across larger areas (Scott *et al.* 1987; Klasner and Fagre 2002). This is due largely to the more recent advent of aerial photography and, therefore, an inability to observe changes prior to the mid-1900s, as well as the small scale of early aerial photography in remote areas, which can preclude detection of all but extensive changes in forest density or distribution (Rhemtulla *et al.*, 2002).

For this study I used sequential aerial photography to examine the pattern and extent of treeline change in the Kluane Ranges, southwest Yukon.[2] I hypothesized that any changes indicated by the dendroecological data over the past half century should be partly visible when comparing the earliest aerial photographs of the region (1947 and 1948) with those most recently acquired at a similar scale (1989). Specific objectives of the sequential photography investigation included: (i) characterizing the extent and pattern of change in tree density and distribution evident from the photographs, (ii) determining the extent to which the dendroecological data are representative of the entire

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[2] Consideration was initially given to supplementing this 40 year record with older ground-level perspective photography. However, a search of the photographic collection at the Yukon Territorial Archives in Whitehorse yielded no photographs which were actually usable for a long-term analysis of change. Many of the first available photographs from the region are of subjects taken in the Shakwak Valley and have little value in a study of treeline dynamics. There were some potentially usable photographs available from dates prior to 1940, but the photo locations were unknown.

landscape, and (iii) refining a technique for quantifying treeline change that could be applied to other regions where only small-scale historical aerial photography is available. Digital photogrammetry, including orthorectification and on-screen interpretation, was supplemented by stereoscopic inspection of the original prints. Qualitative assessment of change across nine image pairs was accompanied by quantitative analysis of changes in spruce density and elevation using 1 hectare plots and 100-metre-wide elevational belt transects, respectively, superimposed on the orthorectified images. This investigation is presented in its entirety in Chapter 3.

Mapping and Distribution Modeling

Species distribution modeling is a method used to statistically relate the observed occurrence of a species at multiple sites to the prevailing environmental conditions at those sites (Guisan and Thuiller 2005). The approach is equally applicable to the distribution of vegetation and habitat types (Guisan and Zimmermann 2000) and models are frequently used to map the probability of occurrence and predict distribution (Franklin 1995). Species data can be simple presence, presence-absence, or abundance, and is typically obtained from field sampling, opportunistic observations, or range distribution maps (Guisan and Thuiller 2005). Environmental predictor variables can be measured in the field but are increasingly derived from maps and datasets within a geographical information system (GIS) (Franklin *et al.* 2000). There are several published studies of the application of distribution modelling and other related spatial analytical techniques at alpine treeline for the purpose of either exploring topoclimatic influences on treeline vegetation or predictively mapping treeline vegetation (e.g. Brown 1994, Baker and Weisberg 1995, Kjallgren and Kullman 1998, Horsch 2003).

For this investigation I used a QuickBird multispectral image to map the distribution of spruce in a 64 km^2 area of the Quill Creek watershed in the northwest Kluane Ranges. Using this 2.4 m resolution map as input, I developed a map of spruce abundance and presence/absence at 16 m resolution. These data were spatially matched to the coverage of several topoclimatic variables which I derived from a 16 m digital elevation model (DEM) of the area, as well as thematic coverage of geology, rock cover, and non-spruce NDVI. Classification and regression trees were used to quantify the relationship between spruce presence/absence and abundance with these variables. These decision trees, as well as results from an evaluation assessment, shed light on the specific role of the various attributes in regulating the distribution of spruce in the region and, in turn, their influence on the forest-tundra ecotone. This investigation is presented in its entirety in Chapter 4.

Experimental Warming

In situ temperature manipulation has become a common technique in assessing the effects of climate warming on alpine and arctic plants and plant communities (Arft *et al.* 1999, Walker *et al.* 2006). Various approaches have been used to achieve warming, including active devices such as overhead infrared heaters and subsurface soil warming, and passive devices such as open-top chambers (OTCs). The common approach associated with these techniques is to elevate temperatures, measure biological and ecological responses, and compare these results with identical measurements obtained from unwarmed plots. Commonly measured response variables include phenology, growth, and species composition (Henry and Molau 1997, Hollister *et al.* 2005). There are some inherent drawbacks to the technique, most notably an inability to completely isolate the effects of elevated temperatures from other unwanted effects such as temperature extremes, and altered wind, light and moisture regimes (Marion *et al.* 1997). Nevertheless, its simplicity combined with the value of a controlled experimental approach (see Ford 2000) has made it a useful and popular tool.

I used passive OTCs to experimentally warm 40 naturally established white spruce seedlings at two opposing alpine treelines east of Kluane Lake. My objectives were to quantify the effect of increased temperatures on (i) primary and secondary growth and (ii) rates and efficiency of photosynthesis. My goal was to test the hypothesis that a slight increase in temperature in such a marginal environment will result in a significant difference in growth, presumably leading to faster recruitment into the tree population and, in turn, treeline advance. The overarching rationale for the study was related to global climate change and the prediction of vegetation response. However, the approach also permited an assessment of more fundamental questions related to the existence of alpine treeline and the specific role of temperature on tree growth and distribution at high altitudes.

Large seedlings (25-50 cm tall) were used because they were small enough to be easily managed within an OTC experimental warming and large enough that growth could be easily measured. More importantly, however, growth as a seedling and sapling, rather than establishment, appears to be the most critical period for individuals at alpine treeline, particularly as they extend above the thermal boundary layer near the ground

(Paulsen *et al.* 2000, Smith *et al.* 2003). Above these heights the plant becomes increasingly coupled to the thermal and radiative conditions of the open atmosphere and decoupled from the shelter and warmth associated with the ground. If temperature is the most prominent variable controlling potential treeline (or *climatic* treeline) then future climate warming is likely to increase its altitude by allowing seedlings to surpass this warm layer with fewer adverse effects.

Twenty treatment seedlings, each paired with a control, were located on a north aspect and 20 treatment-control pairs were located on a south aspect. Half of the chambers were removed during the winter season, thereby creating a second treatment level (i.e. year-round warming and summer-only warming). Environmental variables measured included temperature, humidity, precipitation, and snow depth. Seedling response to warming was quantified by measuring annual increments of vertical and lateral growth and root collar diameter. Annual assessments of needle and bud damage were also made and physiological measurements, including gas exchange and chlorophyll fluorescence, were obtained at the conclusion of the experiment. This investigation is presented in its entirety in Chapter 5.

Synthesis

Methods used in each of these investigations have been used elsewhere, and many have been tested successfully in forest-tundra environments. However, their integration and application to altitudinal treeline within a single region makes this study unique and results yielded new knowledge in determining how northern mountain ecosystems respond to climatic change. In addition, by utilizing a multiscale approach this research project contributes to the growing recognition of scaled influences in ecological systems. From a regional perspective, it is anticipated that the data collected and relationships derived from each investigation will be used in modeling future landscape change in the southwest Yukon. In turn, this model will be used to facilitate a prediction of how subalpine habitat change could affect landcover and wildlife habitat across the region.

This thesis concludes with a sixth chapter that highlights this significance and some of these potential applications. In addition to summarizing the results and main conclusions from each of the component investigations, this final chapter explores their linkages within the context of scale and hierarchy theory, and identifies potential areas for future research on subarctic alpine treelines and their dynamics.

Table 1-1 An ecotone hierarchy based on the sequence suggested by Gosz (1993). In this example, ecotones exist within other ecotones, with each changing at different rates and being influenced by a suite of factors that vary with scale.

Hierarchy Level	**Probable Constraints**
Biome Ecotone	Climate × topography
Landscape Ecotone	Climate × topography × geology × soils × human land use
Patch Ecotone	Weather × Soil characteristics × biological vectors × species interactions × disturbance × microtopography × microclimatology × human land use
Plant Community Ecotone	Interspecies interactions × intraspecies interactions × physiological controls × population genetics × disturbance × microtopography × microclimatology

Table 1-2. Examples of synonyms for terms used to describe the transition from forest to tundra, as well as zones within the transition (see Figure 1-1 for a diagrammatic representation).

Terminology	Defined here as:	Common synonyms
Forest-Tundra Ecotone	The transition from forest to tundra vegetation in mountainous (alpine) and high latitude (arctic) environments.	• Timberline zone • Treeline zone • Subalpine zone • Forest-tundra transition
Open Forest	Spruce canopy cover >25%. Mountain-slope forests in the Kluane region rarely surpass 50% canopy cover and so this is referred to as "open-forest" rather than the more generic "forest".	• Subalpine forest • Forest-alpine
Woodland	Spruce canopy cover 10-25%. The canopies of individual trees, or distinct groupings of trees, generally do not overlap	• Patch forest • Parkland • Kampfzone
Shrubland	Spruce canopy cover 0-10%. Some areas may have no spruce, but have a thick canopy of tall deciduous shrubs.	• Krummholz zone • Shrub zone • Kampfzone
Timberline	The upper limit of the open forest zone.	• Forest limit • Forest line
Treeline	The upper limit of the woodland zone. Spruce taller than 2 m and of greater height than breadth (i.e. tree architecture) are typically not found above this altitude/latitude.	• Timberline
Shrubline	Upper limit of the shrubland zone. Generally coincides with the upper limit of spruce distribution	• Scrub line • Tree species limit • Krummholz limit

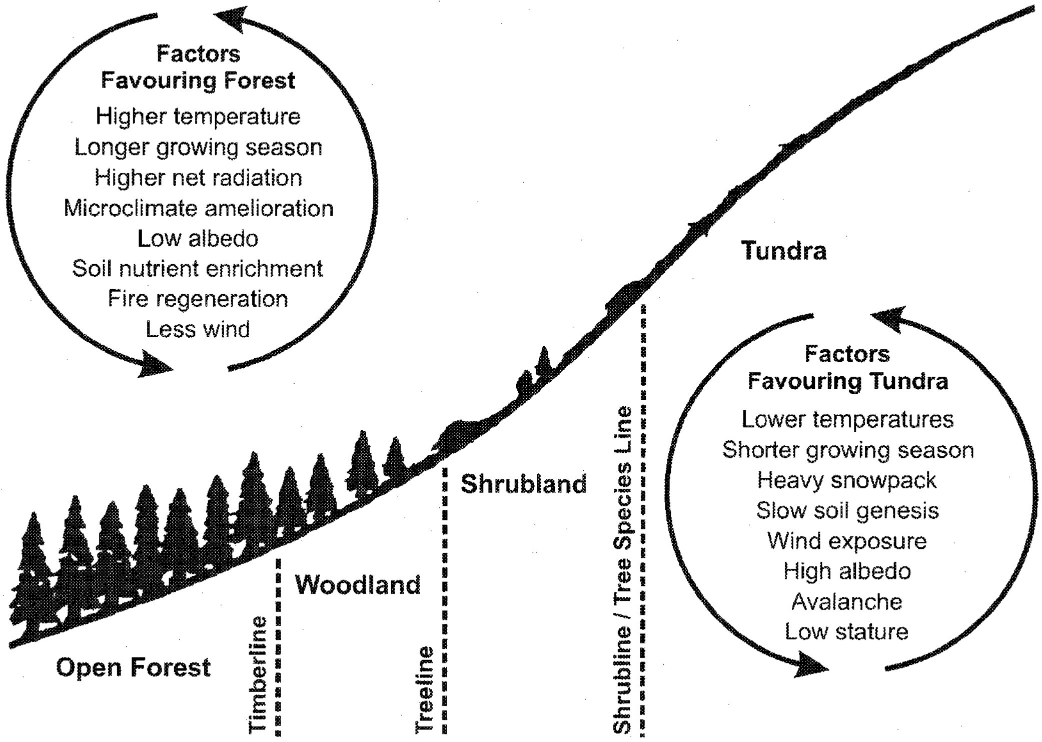


Figure 1-1. The forest-tundra ecotone as a tension zone between factors favouring forest and those favouring tundra (after Walsh 2001). The relative importance of different variables will vary with respect to alpine or arctic regions, though temperature and growing season are considered the most important in each environment. Subzone terminology follows the Alaskan Vegetation Classification (Viereck *et al.* 1992). Boundary terminology follows Bell (1999).

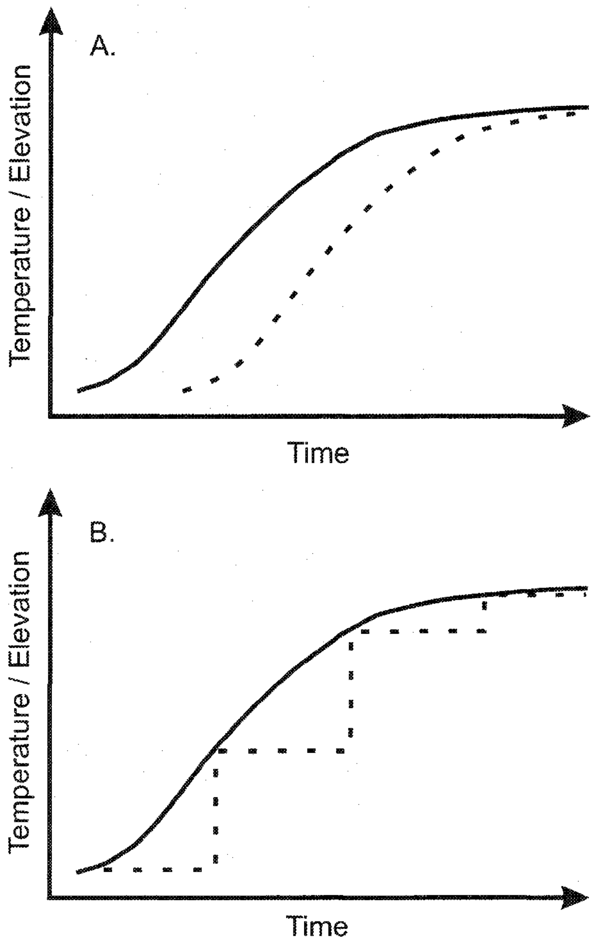


Figure 1-2. Potential scenarios of upslope (alpine treeline) or northward (arctic treeline) movement of forest-tundra ecotones to illustrate the notion of response lags (after Kupfer and Cairns 1996). Solid lines represent change in temperature, dashed lines represent the altitudinal or latitudinal response of treeline. (A) Gradual response with a time lag. (B) Rapid change at treeline as a result of threshold responses. In either scenario, treeline may or may not attain climatic equilibrium.

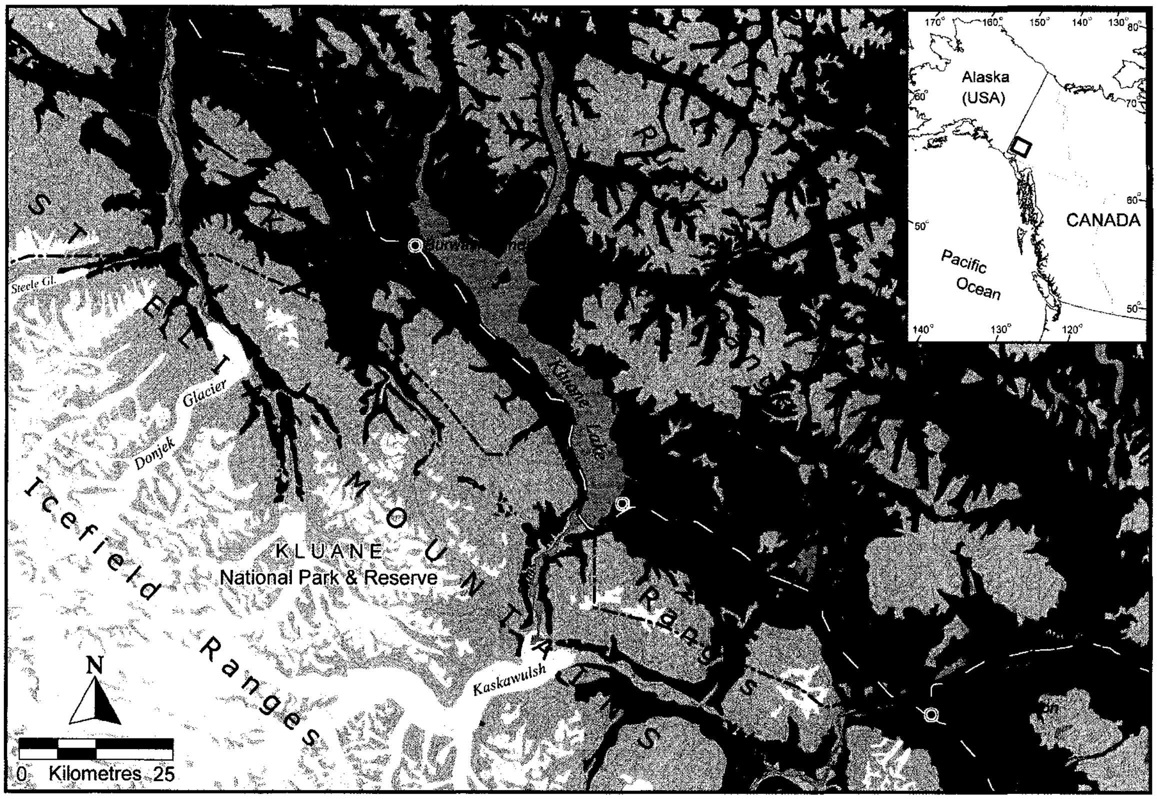
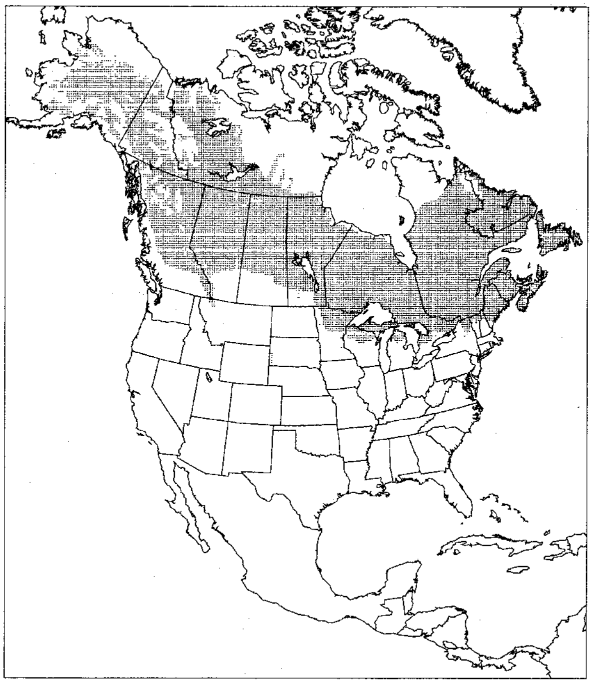
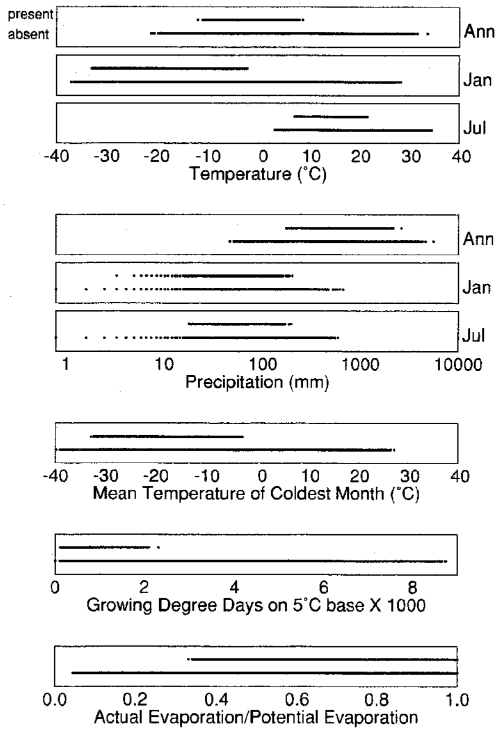


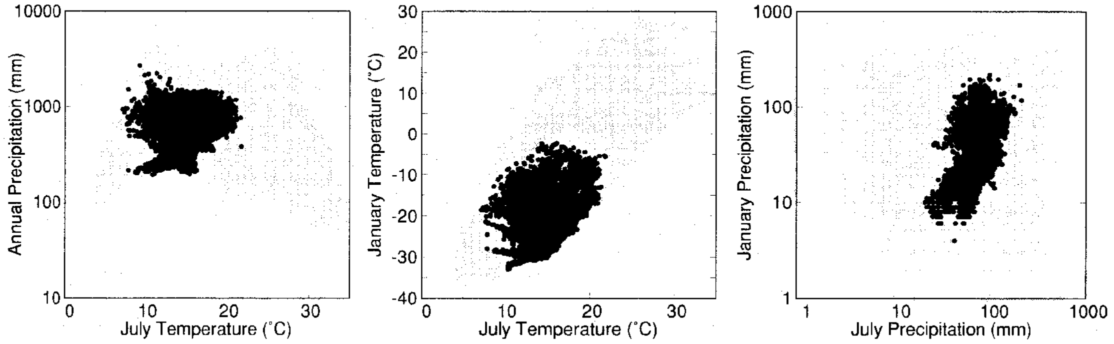
Figure 1-3. Central and northern portions of the Kluane Region, southwest Yukon. Major land cover types include glaciers (white), forest (green) and upland shrubland and tundra (tan).

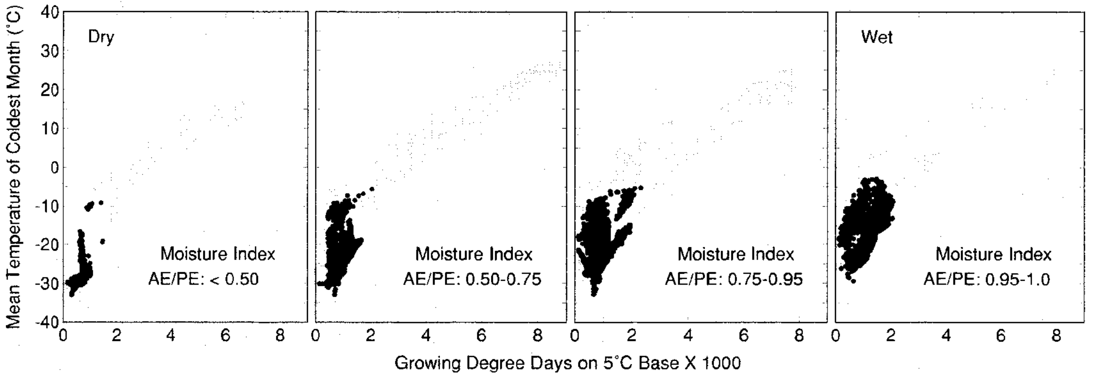
Figure 1-4 (next page). Distribution and "climate space" of white spruce in North America based on the relationship between distribution and climate. Top left: Modern distribution. Top right: Univariate plots of presence and absence relative to single climatic parameters. Upper line illustrates climate values where the species is present; lower line where it is absent. Middle: Bivariate plots between climatic variables. Gray dots represent absence, black dots presence. Bottom: Relationship between growing degree days (5°C base) and mean temperature of the coldest month. Each box represents one quartile of the moisture conditions in North America, from the driest quarter of all 25km^2 grid cells (left) to the wettest (right). Reproduced from Thompson *et al.* (1999).

Picea glauca









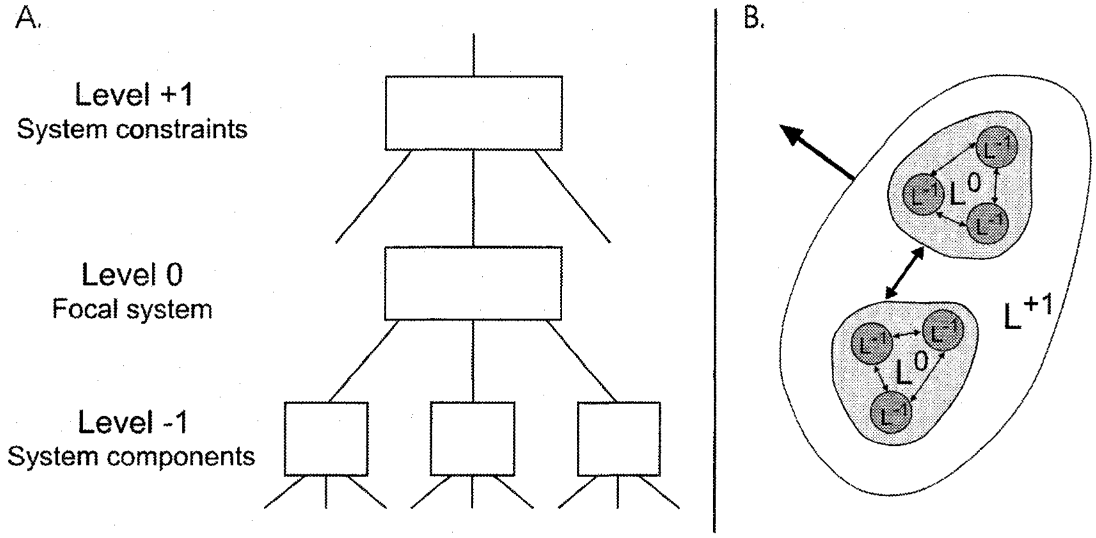


Figure 1-5. Relationships between levels in a hierarchical system. Hierarchy theory addresses issues of scale by permitting the observer to focus on a single phenomenon and a single time-space scale (Level 0). However, understanding of phenomenon at the focal level is dependent on explicit reference to the adjacent upper (+1) and lower (-1) levels within the hierarchy. (A) The behaviour of Level 0 appears to be constrained, bounded, and controlled by the higher level and can be mechanistically explained by interactions among lower level components. Levels higher than +1 operate at scales too coarse to be seen at the focal level and can typically be ignored, while levels lower than -1 operate at scales that are too fine to appear as anything but "background noise". A (left, redrawn from O'Neill, 1988) is a formalized hierarchy while B (right) illustrates a more realistic nested hierarchy (based on Allen and Hoekstra, 1992).

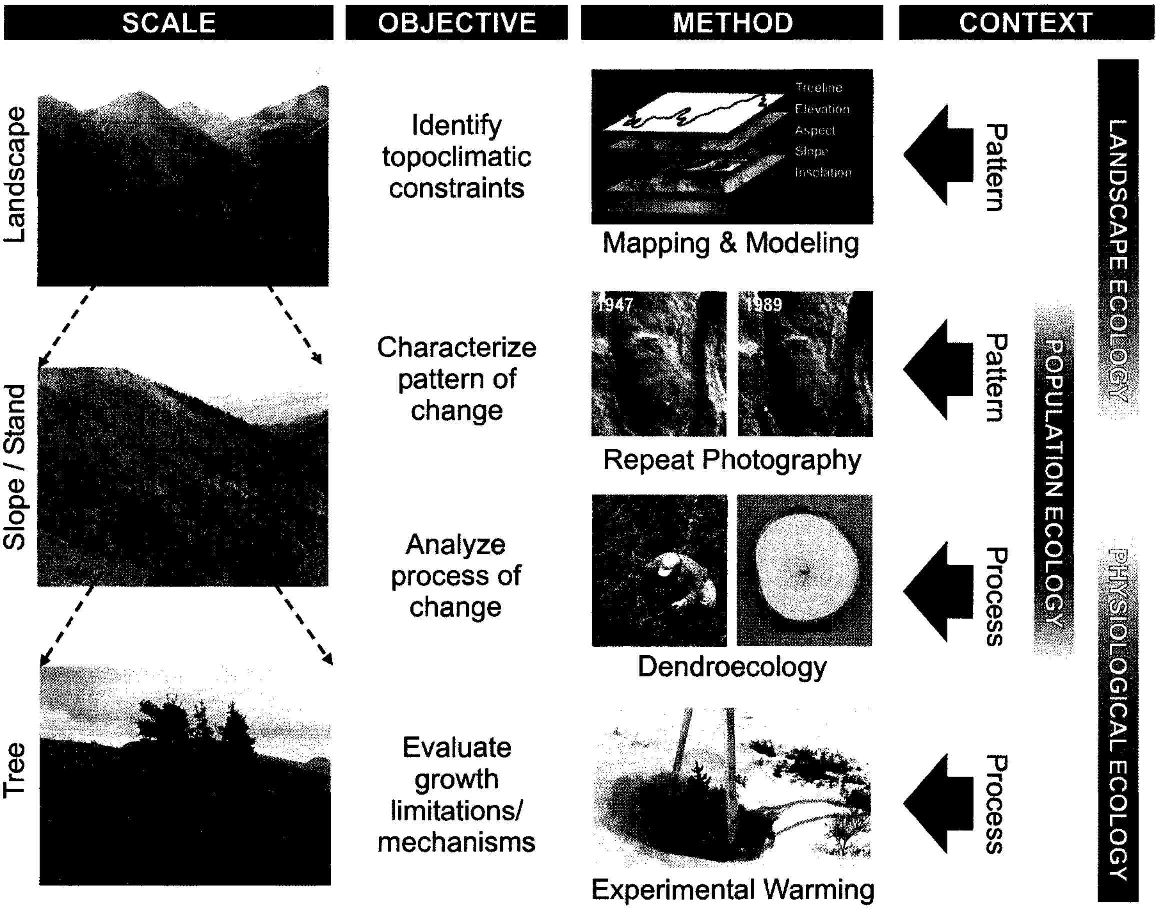


Figure 1-6. Hierarchical framework for studying the forest-tundra ecotone. Within the context of the entire research project, Level 0 in the hierarchy is the stand/slope scale, while the tree scale is Level -1 and the landscape scale is Level +1. However, when considered independently, the scale of each individual investigation also constitutes a Level 0 investigation. For example, within the experimental warming the tree scale becomes Level 0, while the leaf scale is Level -1 and the stand/slope scale is Level +1.

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CHAPTER 2

Variability, Contingency, and Rapid Change in Recent Subarctic Alpine Treeline Dynamics [1]

INTRODUCTION

Recent evidence supports the prediction that climate warming and subsequent effects will be greatest in Arctic and subarctic regions (ACIA 2004, Hinzman *et al.* 2005). Impacts in mountainous areas are also expected to be marked, although perhaps more complex because of the climatic diversity resulting from topographic variation (Beniston 2003, Huber *et al.* 2005). The potential ecological effects of climate change in these biomes have been the subject of many studies. One of the more consistent predictions is that the boundary between forest and tundra zones, hereafter referred to as treeline, will undergo a significant change in structure and position (Grace *et al.* 2002). The rationale for this prediction extends from the relationship between thermal regime and the position of treeline (Jobbágy and Jackson 2000, Körner and Paulsen 2004) and the critical role that temperature plays in controlling the reproduction, establishment and growth of trees in this environment (see Tranquillini 1979, Körner 1998). Thus, as temperatures continue to increase, treeline is expected to shift, and there is abundant supporting evidence of more advanced treelines during warmer periods of the mid-Holocene (e.g. MacDonald *et al.* 2000, Payette *et al.* 2002).

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Numerous studies have investigated treeline responses to climate change over the past 150 years. In some regions, trees have invaded tundra, extending the altitudinal or latitudinal limit of tree species (e.g. Suarez *et al.* 1999, Kullman 2002, Lloyd and Fastie 2003). In other areas, a shift from stunted, low-growing individuals (i.e. krummholz) to upright growth forms (i.e. trees) has been observed (e.g. Lescop-Sinclair and Payette 1995). Other studies have observed an increase in stand density across the forest-tundra ecotone but have not observed any consequential extension of the upper limit (e.g. Szeicz and MacDonald 1995a, MacDonald *et al.* 1998, Klasner and Fagre 2002). There have been no significant changes in some areas (e.g. Butler *et al.* 1994, Cullen *et al.* 2001, Cuevas 2002) and in other areas treeline occupies a position thought to be a relic of past climatic conditions (e.g. Hansen-Bristow and Ives 1984). This variability is mediated by species-specific traits and environmental conditions at multiple scales (Holtmeier and Broll 2005). Additional studies, particularly those attempting to identify these mediating factors, are therefore required to improve our understanding of climate-treeline relationships and are critical for accurate forecasts of landscape change.

Treelines in mountainous areas of the subarctic exhibit characteristics typical of both alpine and arctic treelines. Low solar angles combine with topographic variability to create a diverse array of ecotonal environments within relatively short horizontal distances. Southwest Yukon is particularly useful for examining treeline dynamics in this environment. The region has experienced a significant warming trend since instrumental records began (Zhang *et al.* 2000) and some of the highest deviations from normal temperature of any region in Canada during the past decade (MSC 2005). Models of future climate change predict that these trends will continue (Laprise *et al.* 2003). Studies of past treeline dynamics in this region should have utility in forecasting treeline response to the present, and anticipated future, warming trend.

The objectives of this investigation were: (i) to identify periods and rates of establishment and mortality of woody vegetation across the forest-tundra ecotone at several topographically different sites in southwest Yukon, (ii) to interpret these data in terms of structural and elevational change of the ecotone at each site, (iii) to explore relationships between these changes and climate, and (iv) to examine the variability between sites and identify any causes thereof. I used dendrochronological techniques to obtain data relevant to the dominant tree species, white spruce (*Picea glauca* (Moench) Voss), but also examined trends in willow (*Salix* spp.) which, along with birch (*Betula* spp.), is one of two dominant shrub genera. Tall shrubs often form a key structural component of forest-tundra ecotones, play critical roles in nutrient cycling of these systems and exert significant influence on community composition (Anthelme *et al.* 2003). Recent shrub expansion has been documented in some arctic and alpine areas and continued expansion is expected to have significant effects on ecosystem function (Sturm *et al.* 2001). Still, few studies have examined shrub dynamics in a forest-tundra environment.

METHODS

Study Area

I conducted this study in the northern section of the Kluane Ranges of the St. Elias Mountains (Figure 2-1). This area was chosen because the forest-tundra ecotone occurs on a wide range of grades and aspects here, allowing for an examination of the influence of terrain characteristics on treeline dynamics without the confounding effect of different climatic regimes. In addition, large natural disturbance events such as fire, insect infestations, slope failure, and avalanches are relatively infrequent at treeline in this area. Population changes observed in stand reconstructions are therefore more likely to be a response to climatic change than to other external influences.

The ecotone generally extends from 1200 to 1400 m elevation. Spruce forests thin with increasing altitude, and an open canopy prevails at the lower end of the ecotone (the "open-forest" zone). By 1300 m the canopy is discontinuous and the crowns of individual trees generally do not overlap (the "woodland" zone) (Figure 2-2). Only occasional spruce are found above 1400 m and these are typically short, krummholz-type growth forms. Aspect plays an important role in ecotone structure and composition, with treeline typically 50 to 150 m higher on drier south-facing slopes than on the more mesic north-facing slopes. Deciduous shrubs span the entire length of the ecotone. Dwarf birch (*Betula glandulosa* Michx.) and gray-leaf willow (*Salix glauca* L.) are the two dominant species, frequently forming a dense layer over one metre high (Birks 1977).

Field Methods

Spruce and willows were sampled from six sites during July 2001 and 2002 (Figure 2-1). I stratified sampling with the primary objective of incorporating the differences related to aspect. Three north-facing and three south-facing sites were selected. Each grouping was comprised of a gentle, moderate and steep grade to facilitate capture of any variation related to inclination. All locations were identified *a priori* using a 30m digital elevation model developed by the Yukon Territorial Government. I established three sampling points along an altitudinal transect at each site. The lowermost point (C) was located near the upper edge of open-forest. The middle point (B) was located near the upper edge of the woodland. The uppermost point (A) was located in the shrubland at an approximately equidistant elevation above point B (see Figure 2-2). Circular sampling plots were established at each point using the nearest individual method (Kent & Coker 1992). Plot areas varied with the objective of including the 50 individuals nearest the sampling point.

Spruce was sampled at points B and C on each of the six transects (i.e. 12 plots total). Low densities in the shrubland zone precluded sampling at point A. The height and diameter of each individual was measured. Vegetative clones and standing dead trees were also sampled. Individuals were considered clones if a vegetative connection existed with another stem (Szeicz and MacDonald 1995a). Stems were either sectioned (n=645) or cored (n=123) as close to the root crown as possible. Intact samples could not be obtained from two dead individuals due to severe rot. Only individuals taller than 0.5 m were included in sampling. Shorter individuals were classified as seedlings and were counted but not sectioned.

Willows were measured and sampled at all three points on each of the six transects (i.e. 18 plots total). As for spruce, willow plots included the 50 genets closest to the sampling point. The largest ramet from each genet was sectioned, based on the assumption that it was among the oldest of all living ramets and its age would provide a minimum year of establishment. Sections were obtained at ground level if the plant was growing directly in soil, or below adventitious roots when growing in moss. Presence or absence of dead stems on each genet was noted. Individuals less than 25 cm were not sampled. This size class was super-abundant and its inclusion would have come at the exclusion of older age classes, yielding virtually no information related to the establishment history of willow in a given zone. All shrub-forming species were included in sampling, though more than 90 percent were *Salix glauca*.

Laboratory Methods

Spruce samples were air-dried and sanded to a high polish. Annual rings were counted and measured using one of two techniques. Samples with ring boundaries easily distinguishable to the naked eye (n=283) were dated using a WinDendro digital image measurement system (Regent Instruments Inc., Quebec, QC). Remaining samples were dated using a stereomicroscope and Velmex sliding stage micrometer with digital encoder (Velmex Inc., Bloomfield, New York). Samples were cross-dated with the aid of CDendro (Cybis Elektronik & Data, Saltsjöbaden, Sweden) and COFECHA (Laboratory of Tree-Ring Research, University of Arizona, Tucson) software programs.

Twenty-three spruce could not be completely aged due to rotten piths. These came from large, older trees and elimination of these samples from analysis would have skewed data towards younger age structures. I therefore estimated the establishment date of these individuals using age-diameter regressions constructed from other individuals sampled at the same site. Estimated ages ranged from 10 to 131 years ($\bar{x} = 49$) greater than the total number of intact rings in the samples. None of the estimates yielded establishment dates earlier than the oldest intact sample from each plot.

Two adjustments were applied to inner ring dates after cross-dating. First, in instances where coring missed the pith, the number of rings to the pith was estimated geometrically in WinDendro. Second, the number of years for trees to reach coring height was estimated and subtracted from inner ring dates of core samples. Values of 2.5 cm yr^{-1} and 2.0 cm yr^{-1} for individuals on south and north-facing slopes, respectively, were used (see Chapter 5). The error introduced by these two adjustments is minimal since only 24 cores had missing ring estimates greater than 10, and 90% of all cores were obtained within 30 cm of the ground surface.

Outer ring dates of dead spruce were adjusted to account for loss due to weathering. Cross-dating indicated that all individuals with mortality after 1950 had at least some trace of bark. For all other individuals (n=41), I used an adjustment based on an estimated weathering rate of one ring per decade (Szeicz and MacDonald 1995a). While there is no definitive way of assessing the accuracy of this adjustment, it had little effect on the overall distribution of mortality events because of the 10-year age classes used in the analysis (see below).

Willow sections were air dried and sanded, but annual rings proved difficult to discern under the stereomicroscope. Stems were therefore sectioned to 25 μm using a sledge microtome. Sections were suspended in water and examined under the stereomicroscope using a transmitted light source. Annual rings were counted but not measured. Visual cross-dating was carried out using iteratively identified pointer years. No age adjustments were necessary since all willows were sectioned at the soil surface.

Data Analysis

Spruce and willow characteristics measured at the plot and individual level were analyzed using nested mixed-model ANOVAs to compare differences between aspect and zone. Stem data for willow and spruce required log transformation to achieve normality and homoscedasticity. All statistical analyses were carried out using SPSS 12.0.2 (SPSS Inc., Chicago, Illinois).

Two general approaches were used to examine spruce age data. First, age-structures of living trees in the 12 plots were constructed by grouping data into decadal age-class frequency distributions. Comparison of open-forest and woodland age distributions provided insight into whether or not treeline advanced or remained stable, since an advance should be indicated by younger spruce in the woodland zone. Three statistical tests were used to aid my evaluation: (i) age distributions within the open-forest and woodland at each site were compared using a Kolmogorov-Smirnov test, (ii) median age of each plot was compared using a Mann-Whitney U test , and (iii) mean age of the five oldest living individuals in each plot was compared using a Mann-Whitney U test.

The second approach was based on reconstruction of stand density over time, a more dynamical approach that incorporates data from dead individuals. A slow but steady rate of increase would be expected as individuals die and decompose, while a significant deviation from a steady increase would be indicative of a sudden change in recruitment (Lloyd & Fastie 2003). In contrast to the static age distributions the density reconstructions excluded the sapling size class (i.e. 0.5-1.3 m) to avoid the potentially more rapid decomposition of dead individuals in this size class. I determined the decade in which a population density of 50 trees ha^{-1}, the approximate density of adult spruce at treeline, was attained and a Wilcoxon Signed Ranks test was used to compare the open-forest and woodland zones.

Pearson correlation analysis was used to examine relationships between regional and synoptic climate and spruce density at treeline. Changes in the density of genets during each decade were quantified for each plot and correlated with four reconstructed climate variables: (1) average June-July temperature for northwestern Canada (Szeicz and MacDonald 1995b); (2) summer-weighted Arctic temperature anomalies (Overpeck *et al.* 1998); (3) June-August Palmer drought severity index (PDSI) for southwest Yukon (Cook *et al.* 2004); and (4) annual Pacific Decadal Oscillation (PDO) (D'Arrigo *et al.* 2001). Successful recruitment may be related to climate beyond a forward window of 10 years, so changes in density were also compared to averages over 20, 30, 40 and 50 year periods (Szeicz and MacDonald 1995a).

Age-structures of the 18 willow plots were derived by grouping data into five-year age-class frequency distributions. I compared age structures of each plot to distributions predicted by a negative exponential function and a power function (see Balogh and Grigal 1988). Deviations are likely indicative of a change in the pattern of the population's recruitment and/or survival during a given time period (Hett and Loucks 1976). Regression coefficients obtained when fitting the models to the age-class data were used to identify such deviations, and regression residuals indicated when they occurred. Standardized Z-scores were calculated to facilitate comparison of residuals between plots (see Bégin and Payette 1991). Because sampling did not include individual stems shorter than 25 cm, the 1990-95 and 1995-2000 age classes are likely under-represented in the data and only individuals dated earlier than 1990 were included in the analysis.

RESULTS

Spruce Stand Characteristics

Spruce diameter and height was significantly greater on south aspects ($F_{1,6.3} = 37.25$, P=0.001; $F_{1,6.0} = 33.11$, P=0.001; respectively), and in the open forest ($F_{1,6.3} = 23.67$, P=0.002; $F_{1,6.0} = 20.21$, P=0.004; respectively) (Table 2-1). Spruce density was greater on north aspects ($F_{1,8} = 5.29$, P=0.050), though the differences in stature resulted in comparable canopy cover. With the exception of Site 6, density of living trees was at least twice as high in the open-forest. Density of seedlings and standing dead individuals varied greatly. Although north-facing slopes had significantly higher densities of each ($F_{1,8} = 12.2$, P=0.008; $F_{1,8} = 10.2$, P=0.013, respectively), there was no significant difference between woodland and open-forest.

There was no evidence to suggest that vegetative regeneration of spruce was more prevalent in woodland than in open-forest, either in terms of the absolute number of vegetative stems or in the number of genets with multiple stems. In fact, there was a tendency for higher vegetative regeneration in the open-forest ($F_{1,8} = 5.0$, P=0.055). Individuals on north-facing slopes had a significantly greater propensity for vegetative regeneration regardless of elevation ($F_{1,8} = 7.6$, P=0.025).

Spruce Age Structures and Density Reconstructions

Age distributions from each of the 12 spruce plots illustrate considerable differences between the six sites (Figure 2-3). Some plots contained individuals older than 400 years, while other plots, and even entire transects, contained few or even no individuals older than 100 years. Stands on north-facing slopes were generally older than those on south-facing slopes and trees in woodland plots were generally younger than those in open-forest plots. These two trends were not obvious when comparing the mean age of trees in each plot (Table 2-1), but became apparent when the spread and distribution of the data were considered. For example, the age of the oldest individuals in each plot was significantly greater on north-facing slopes (*t*-test: t_{58}=-3.2, P=0.002) than on south-facing slopes, while a significantly greater proportion of individuals date to recent decades (i.e. 1960-1990) in the woodland than in the open-forest at each site (paired *t*-test: t_5=-3.7, P=0.014).

Differences in the dynamics of woodland and open-forest populations are evident at three of the six sites. Sites 1, 2, and 3 are characterized by younger populations in the woodland zone, while no real differences exist at Sites 4, 5 and 6. The more recent and contracted timing of recruitment differentiates woodland from open-forest at the first three sites. Differences at the latter three sites are related more to stand structure (i.e. density or tree size) (Table 2-2).

Many plots exhibited a considerable recruitment pulse during the second quarter of the 20th century. This is most evident in the open-forest and woodland at Sites 1, 5, and 6, but is also evident in the woodland at Sites 2 and 3 and the open-forest at Site 4. For instance, at Site 1, 46% of all woodland and 45% of all open-forest spruce established during the period from 1920-1950. Distinct periods of mortality are also evident, though synchrony between sites is not pronounced (Figure 2-4).

Density reconstructions (Figure 2-5) indicate that the threshold of 50 stems ha^{-1} was reached significantly earlier in open-forest than in woodland plots (Wilcoxon Signed Ranks test, Z=-2.03, P=0.042). Tree density in open-forest at sites 1, 4, and 6 nearly doubled as a result of the 1920-1950 cohort. Density in the north-facing woodland plots 2B and 6B also doubled as a result of this cohort and density in the south-facing woodland plots 1B and 3B nearly tripled. Site 5 warrants special attention as the changes observed in both the open-forest and woodland plots are exceptional. Apart from two individuals, all trees sampled at this site established after 1910.

Willow Stand Characteristics

The general characteristics of the 18 willow plots are presented in Table 2-3. Density of willow genets increased with elevation ($F_{1,12} = 6.5$, P=0.012), averaging 2800 ha^{-1}, 3500 ha^{-1}, and 5300 ha^{-1} in the open-forest, woodland, and shrubland, respectively. There were no differences in density related to aspect, though field observations indicate that genets on south-facing slopes had a higher number of stems per individual. Willows were generally taller on south-facing slopes ($F_{1,12} = 6.43$, P=0.026) but there was no significant difference between zones ($F_{1,12} = 0.314$, P=0.737). Average diameter did not vary significantly with zone or aspect. However, the maximum for each measure tended to decrease with elevation, and tended to be greater on south-facing slopes (Table 2-3).

Willow Age Structures

Willow age distributions (Figure 2-6) indicate that shrubland plots were typically the youngest in terms of maximum ages, though this difference was not statistically significant ($F_{2,12} = 3.16$, P=0.079). No similar trends were evident with respect to mean age (Table 2-3). Of the three south-facing slopes, Site 5 had the youngest mean and maximum stem ages at each elevation. Site 2 had the oldest mean and maximum age at each elevation among the three north-facing slopes.

The negative exponential function modelled willow age distributions significantly better than the power function (paired *t*-test: t_{17}=6.77, P<0.001). Model agreement was generally high, with r^2 values averaging 0.71 (Figure 2-6). Shrubland, woodland, and open-forest populations were served equally well by the model. Populations on south-facing slopes tended to exhibit better fit than those on north-facing slopes, although this was influenced heavily by low r^2 values at Site 2 where irregular or random age distributions were exhibited.

Standardized regression residuals were pooled in several ways to identify common and/or divergent patterns in population dynamics. Pooling of residuals from all 18 plots yielded no definite trends. When examined on a site-by-site basis, there was little agreement between plots on any of the three south-facing slopes. Plots on north-facing slopes were in greater agreement, with residual curves from Site 6 overlapping remarkably well. Examination of residuals on an elevation basis yielded no regionally common signal when all six transects were considered together. However, a common positive deviation from model predictions followed by a strongly negative deviation was evident at all three elevations on north-facing slopes during the 1980s.

Spruce Recruitment-Climate Relationships

Significant positive correlations between changes in stand density and June-July temperature reconstructions and summer temperature anomalies were found at all sites except Site 2 (Table 2-4). On south aspects these correlations were generally present only in the woodland zone. On north aspects there were no consistent patterns with respect to elevation. No one single window of temperature averaging consistently performed best, though 50-year and 30-year forward means commonly yielded the highest correlations. There were few significant correlations with reconstructions of PDO or PDSI, and these did not exhibit trends with respect to site, aspect or elevation.

DISCUSSION

Spruce Population Dynamics

The results indicate that the forest-tundra ecotone in the southwest Yukon study area advanced rapidly or underwent a significant increase in density during the 20th century. However, the change was neither ubiquitous nor uniform in pattern. South-facing slopes experienced a rapid advance in white spruce distribution during the early-mid 20th century. A minimum 80% of all spruce in woodland plots established after 1900. Dynamics at lower elevations in the open-forest varied. Some areas experienced little change. Others experienced a slow colonization of spruce during the 19th century followed by a rapid increase in density in the early-mid 20th century. Finally, evidence from the Burwash Uplands suggests that only occasional, possibly krummholz-type, spruce were present in the current open-forest prior to 1920.

North-facing slopes experienced very different, and more variable, change. Instead of an advance in tree-forming spruce, these areas underwent increases in the population density of spruce in either the woodland or open-forest zones. Individuals older than 350 years were found in the woodland and open-forest zones at two sites, demonstrating a long history of establishment. Density reconstructions indicate that significant stand infilling began in the early-mid 20th century. The steep, north facing slope did not have as long an establishment history. Both the open-forest and woodland date to approximately 1800. But while spruce dynamics in the open-forest have been stable since the mid 19th century, the woodland zone experienced the rapid infilling observed at the other sites.

Trends in establishment and mortality related to slope inclination were far less evident. The one noteworthy trend was related to gentle slopes where both the woodland and open-forest plots had very similar age structures. Additionally, the rates of change in stem density in the woodland and open-forest at the two sites were nearly identical over the past four centuries.

Differences in aspect appear to be partly related to the differential occurrence of permafrost. Random shallow test pits (<60 cm) dug during August 2002 confirmed the presence of ground-ice across the treeline ecotone on north aspects while permafrost was not encountered in shallow pits dug at treeline on south aspects. Suarez *et al.* (1999) also found differences in ecotone dynamics due to permafrost in northwestern Alaska where an advance of treeline was observed on all sites except those with a shallow active layer. Lescop-Sinclair and Payette (1995) demonstrated an advance of the black spruce (*Picea mariana*) treeline in the extensive-discontinuous permafrost of northern Quebec not by establishment of new individuals but by changing growth form of pre-established individuals. Individuals in the woodland zone of the study area were present at low densities on north aspects prior to 1900, and it is possible that they underwent a similar change from krummholz growth forms to trees. If true, one could also argue that, in addition to infilling, the treeline has also advanced on these slopes in the last two centuries. However, in the absence of stem analysis of these older individuals it is impossible to evaluate this possibility.

The changes observed at each site result from the nearly ubiquitous recruitment pulse between 1920 and 1950. Recruitment continued at some of the sites, specifically south-facing woodland areas and the gently sloping north-facing woodland plot, where a significantly greater proportion of individuals date to recent decades (i.e. 1960-1990). This is indicative of more recent infilling of these stands. Recruitment rates declined at other sites after 1950, despite its continuance at sites with lower densities, suggesting that these stands attained at least a temporary equilibrium or upper density threshold (but see discussion below).

Vegetative regeneration typically increases with altitude as seed production declines and damage that triggers vegetative regeneration increases (Holtmeier 2003). I did not observe such a difference and attribute this to the fact that many of the vegetative stems in the open-forest date to when these trees occupied a higher position in the ecotone. The rapid expansion of trees and subsequent woodland recruitment indicates that sexual reproduction has not been problematic in this zone and that the population has not had to rely on vegetative regeneration. The greater propensity for vegetative regeneration on north-facing slopes is explained by the widespread presence of a thick moss layer on these slopes and the greater capacity for the development of adventitious roots in this environment.

Willow Population Dynamics

The fit of the negative exponential model with willow population data supports the view that *Salix*, at least in tall shrub form, have a constant probability of death throughout their lifespan and that their abundance is controlled by regeneration, not mortality (Balogh and Grigal 1988). Age structures at Site 2, particularly in the open-forest, are a notable exception and may be related to the lower elevation or higher density of spruce.

Previous studies of boreal shrub dynamics have illustrated renewal synchrony among populations in response to events such as herbivore dynamics (Ericson *et al.* 1992) and periodic disturbance (Bégin and Payette 1991). The general agreement in model residuals between populations on north-facing slopes is suggestive of such synchrony, but the mechanism is unknown. The lack of residual agreement between populations on south aspects suggests that the mechanism is either absent or unimportant on these slopes.

Interpretation of shrub advance is limited by the relatively short lifespan of willow stems when compared to the possible, but largely undeterminable, age of the parent genet. Nevertheless, a recent upslope expansion of shrubs should be indicated by the absence of older individuals in plots from the shrubland zone, a disproportionately large number of individuals in the oldest age class (due to a rapid change), or a combination thereof. The results do not offer evidence of a widespread expansion but suggest it may have occurred at two of the six sites. Data from Site 4 best fits these indicators, with its oldest age class, 1970-75, comprising nearly 20% of all individuals. All plots at Site 5 also warrant discussion. As with spruce stands, there was an absence of older individuals and a relatively high proportion of younger stems in all three plots at this site. This could be indicative of more recent establishment, or simply a higher rate of turnover. The fact that the negative exponential model fits the data well is suggestive of higher turnover. However, there were no individual ramets greater than 40 years old while older individuals were present elsewhere. Given the rapid transformation of this area evident from the spruce data, I cannot rule out an advance, or at least significant population increase, of willow in this area.

The relatively short age-span of willow stems also limits an examination between shrub and spruce population dynamics. An interaction between these two ecotone components is undoubtedly important, but its specific nature and extent is unknown. It is likely that this relationship changes with elevation, and it is conceivable that spruce limit the growth and establishment of willows in the open-forest. In turn, willow can influence spruce establishment and seedling growth in the shrubland zone. There is evidence to suggest that these competitive relationships are density-dependent and vary significantly with aspect (Green and Hawkins 2005). Identifying the magnitude of these interactions and its influence on treeline dynamics is an important avenue for further work.

Treeline Ecotone Dynamics and Climate Change

The strongly positive correlations between recruitment and temperature reconstructions at most sites are indicative of the influence of temperature on spruce population dynamics in the forest-tundra ecotone. With one exception, increase in stand density on north aspects and advance of treeline on south aspects were significantly positively correlated to periods of above-average temperatures. The negative correlations in the forest zone at Site 2 are inconsistent with all other sites. Combined with the low elevation of this site and the timing and pattern of stand establishment the data suggest a rebound from an unknown disturbance or cessation of a pressure that had previously depressed treeline at this location.

The fact that multi-decade windows of forward temperature averaging performed better than the minimum 10-year window of analysis reinforces the idea that temperature influences recruitment as much as establishment. Low temperatures reduce seedling and sapling growth rates at treeline, extending the time between germination and maturation and increasing the risk of seedling mortality (see Chapter 5). Thus, favourable temperature regimes throughout these early life stages, not just at the time of establishment, are critical for successful recruitment (see also Wang *et al.* 2006).

The relationship between increases in the abundance and elevation of treeline spruce and periods of warmer temperatures is not unexpected. Yet, while summer temperatures increased gradually since the 1850s the increase in spruce density lagged and was abrupt at many sites. This is suggestive of a threshold response (Groffman *et al.* 2006) and implies that a critical temperature was surpassed, above which seedlings could more readily grow and survive to maturity. The reduction in recruitment following the 1950s could be related to a temperature decline from 1950 to 1980 and a drop in average long-term conditions below this threshold level. Individuals established during the recent warming period (i.e. 1980 to present) would not necessarily have been detected given that sampling excluded individuals <0.50 m. Alternatively, it is possible that recruitment slowed as a result of temperature-induced moisture stress. This appears to be responsible for recent reduction of secondary growth in some treeline white spruce (Wilmking and Juday 2005) as well as seedling survival (Black and Bliss 1980) and would partly explain the inconsistent correlations between density changes and PDO and PDSI since moisture availability, not just total precipitation, is responsible.

P. glauca seeds lose viability in the seedbank within 1-2 years (Nienstadt and Zasada 1990). Above treeline, seeds have low germination rates and germinants have low survival (Hobbie and Chapin 1998). Large or regular seed crops are therefore necessary for an advance of treeline (Holtmeier 2003). White spruce periodically undergo synchronous production of large seed crops (masts) at regional scales which are critical in establishment and regeneration dynamics (Peters *et al.* 2005). One or more of these events could have facilitated the episodic establishment in southwest Yukon. Juday *et al.* (2003) found a relationship between warm, dry summers and the occurrence of masts in Alaska the following year; conditions which are also conducive for forest fires. Alaska and Yukon experienced their most extensive fire year on record during 2004, followed by a large cone mast in 2005. The previous mast years on record in southwest Yukon were 1993 and 1998 (McAdam and Boutin 2003). Alaska's previous mast year was also 1998 (Figure 2-7), suggesting periodic synchrony between the two regions. Additionally, there is a significantly positive correlation between summer temperatures in interior Alaska (Fairbanks Airport, 64.8°N / 147.9°W) and southwest Yukon (Burwash Airport, 61.4°N / 139.1°W) ($r = 0.624$, $p<0.001$).

Our field observations indicate that the 2005 mast extended into the forest-tundra in southwest Yukon (Figure 2-8), confirming that treeline spruce are capable of synchronous masting. Still, a year of high seed production will not necessarily result in subsequent episodic recruitment in the forest-tundra ecotone. Sustained warmer temperatures and climatic stability are also necessary for successful germination and, more importantly, seedling growth (Hobbie and Chapin 1998). As illustrated in Figure 2-7, at least two mast years (1924 and 1940) fall within a sustained multi-year period of above average temperatures, indicating that such conditions existed during the second quarter of the 20th century. Although subsequent mast events occurred, annual summer temperatures were not elevated for a sustained period afterwards and therefore not conducive to seedling growth or survival.

CONCLUSION

While the pattern of change in the forest-tundra varied in southwest Yukon over the past two centuries, the differences between south and north-facing slopes and the widespread effect of the early-mid 20th century recruitment event are clearly evident. Szeicz and MacDonald (1995a) found evidence of a similar, though less pronounced, recruitment event at some, but not all, of their study sites in the Mackenzie Mountains, Northwest Territories. Overall though, their results point towards a gradual increase in stand density during the last century, heavily influenced by vegetative regeneration. Lloyd and Fastie (2003) examined recent white spruce dynamics in the mountains of interior Alaska and found evidence of treeline advance, as well as an increase in density of existing forests, at each of their study sites. These changes were characterized by either a gradual increase in density of the open-forest since the 1800s as well as in woodland stands since 1950, or a gradual increase in density in open-forest during the 1800s followed by a rapid treeline advance after 1950. In this study, I found that the most rapid change occurred from 1920-1950, when treeline advanced on south-facing slopes and woodland spruce densities increased on north-facing slopes. Thus, between the three studies, it is evident that the pattern, timing, and rate of ecotone change in the alpine subarctic of North America have been quite variable.

Periods of heightened recruitment as well as significant and rapid advance have been observed at subarctic treelines elsewhere during the 20th century (Payette and Filion 1986, Gervais and MacDonald 2000, Kullman 2002). The changes observed in southwest Yukon contribute to the growing body of evidence of these phenomena. The pattern and rate of change observed at some of the Yukon sites are particularly noteworthy because they are suggestive of a threshold response. The notion of inertia or slow gradual change followed by rapid change has gained increased attention in the literature, particularly with respect to ecosystem responses to global climate change (Chapin *et al.* 2004, Burkett *et al.* 2005). This type of lagged, nonlinear response to climate change has been hypothesized for treeline ecotones (Kupfer and Cairns 1996, Malanson 2001, Lloyd 2005) but few other studies have provided empirical evidence for it. Thus, the response of treeline to future warming may not necessarily be gradual (e.g. Slatyer and Noble 1992).

The study of treeline characteristics (e.g. vegetation pattern, species composition, etc.) in relation to local and landscape-scale variables is a longstanding theme (see review in Holtmeier 2003). That these differences are accentuated at higher latitudes because of lower solar angles is not new either (Dingman and Koutz 1972). However, studies of variation in ecological processes have been far less common. As demonstrated for other mountainous subarctic regions (Kullman 1979, Dalen and Hofgaard 2005), my results illustrate that population-level responses can vary significantly at regional, landscape and even local scales, and are partially contingent on terrain variability, landscape setting, and existing vegetation.

Table 2-1. *Picea glauca* characteristics in each sampling plot. F = Open-forest zone; W = Woodland zone. *Average of breast-height and root-crown diameters. **Origin presumed based on field evidence. ***Number of individuals with evidence of vegetative regeneration expressed as a proportion of the total number of individuals.

	South Aspects					
	Site 1		**Site 3**		**Site 5**	
	F	**W**	**F**	**W**	**F**	**W**
Elevation (m)	1308	1383	1315	1404	1222	1256
Slope (%)	27	35	12	17	5	2
Plot Area (m^2)	2307	6082	1320	3981	1493	3176
Genet Age (year est.)						
Mean	1898	1945	1798	1925	1946	1949
Std. Dev.	44.4	22.9	105.0	49.0	10.6	24.8
Maximum	1799	1895	1541	1747	1922	1854
Height (m)						
Mean	8.1	3.6	6.9	4.4	4.1	2.5
Std. Dev.	4.2	1.7	3.1	2.6	1.9	1.7
Maximum	18.0	6.5	14.6	9.2	10.2	8.3
Diameter* (cm)						
Mean	21.7	10.6	17.5	13.3	9.1	5.7
Std. Dev.	14.3	7.1	9.7	9.9	4.6	5.2
Maximum	49.8	25.5	41.2	40.4	21.5	28.4
Stem Density (ha^{-1})						
Seed origin**	217	82	379	126	335	157
Vegetative origin**	22	21	144	10	20	9
Dead	9	7	30	0	0	6
Seedlings	30	25	38	48	47	60
Vegetative Proportion***	0.06	0.06	0.16	0.02	0.02	0.06

	North Aspects					
	Site 2		**Site 4**		**Site 6**	
	F	**W**	**F**	**W**	**F**	**W**
Elevation (m)	1062	1109	1229	1264	1216	1246
Slope (%)	20	23	16	12	6	11
Plot Area (m^2)	254	1562	1182	2551	607	1063
Genet Age (year est.)						
Mean	1870	1913	1906	1867	1907	1919
Std. Dev.	47.0	38.2	66.6	92.2	65.3	75.6
Maximum	1793	1826	1711	1657	1699	1630
Height (m)						
Mean	2.9	1.8	2.7	2.3	2.2	1.8
Std. Dev.	2.0	1.0	2.1	1.3	1.7	1.1
Maximum	8.9	4.8	9.4	5.1	7.2	6.5
Diameter* (cm)						
Mean	6.6	4.0	6.1	6.1	5.1	4.8
Std. Dev.	5.4	2.7	5.5	4.3	4.9	5.1
Maximum	22.6	10.6	21.7	17.2	22.8	24.1
Stem Density (ha^{-1})						
Seed origin**	1969	320	423	196	824	470
Vegetative origin**	79	19	85	82	165	179
Dead	118	19	51	43	198	103
Seedlings	79	205	76	110	231	169
Vegetative Proportion***	0.04	0.04	0.10	0.22	0.14	0.10

Table 2-2. Results of age distribution statistical comparisons. Values represent P-values generated by each test in comparing woodland (b-plots) with open-forest (c-plots) age characteristics for each site. Bold text indicates comparisons where the null hypothesis was not rejected (i.e. not statistically different).

Comparison	Age Class Distribution (K-S test)	Median Age (M-W Test)	Establishment Date (M-W Test)
1B x 1C	Z=2.40; P<0.001	Z=-5.63; P<0.001	Z=-2.65; P=0.008
2B x 2C	Z=2.30; P<0.001	Z=-4.31; P<0.001	Z=-2.66; P=0.008
3B x 3C	Z=3.10; P<0.001	Z=-6.52; P<0.001	Z=-2.62; P=0.009
4B x 4C	**Z=1.20; P=0.112**	Z=-2.06; P=0.040	Z=-2.20; P=0.028
5B x 5C	Z=1.60; P=0.012	**Z=-1.52; P=0.129**	Z=-2.00; P=0.045
6B x 6C	Z=1.70; P=0.006	Z=-2.62; P=0.009	**Z=-0.63; P=0.530**

Table 2-3. Characteristics of *Salix* spp. sampled in each plot. F = Open-forest zone; W = Woodland zone; S = Shrubland zone. NR = Not recorded.

	South Aspects								
	Site 1			**Site 3**			**Site 5**		
	F	**W**	**S**	**F**	**W**	**S**	**F**	**W**	**S**
Elevation (m)	1308	1383	1457	1315	1404	1465	1222	1256	1270
Slope (%)	27	35	33	12	17	24	5	2	3
Plot Area (m^2)	135	137	101	224	110	135	177	158	68
Age (years)									
Mean	20.1	19.4	20.2	21.6	18.6	22.5	19.7	16.8	17.2
Std. Dev.	9.9	9.6	8.8	8.6	7.5	9.7	7.4	7.1	5.7
Maximum	53	46	43	55	35	43	43	34	31
Height (m)									
Mean	1.07	1.08	0.75	1.10	0.90	1.32	0.66	0.66	0.70
Std. Dev.	0.52	0.39	0.22	0.50	0.28	0.33	0.34	0.20	0.16
Maximum	2.90	1.90	1.35	2.35	1.45	1.95	1.55	1.10	1.15
Diameter (mm)									
Mean	12.4	13.7	12.4	12.8	11.6	16.5	9.1	10.0	9.7
Std. Dev.	5.7	5.5	3.2	5.3	3.5	4.2	3.8	3.2	2.5
Maximum	29.5	28.0	23.0	30.0	21.5	27.5	20	18.5	19.5
Genet Density (ha^{-1})	3710	3650	4940	2230	4530	3710	1740	3200	5460
Percent with dead ramets	NR	NR	NR	56	92	56	54	68	76

	North Aspects								
	Site 2			**Site 4**			**Site 6**		
	F	**W**	**S**	**F**	**W**	**S**	**F**	**W**	**S**
Elevation (m)	1062	1109	1198	1229	1264	1290	1216	1246	1283
Slope (%)	20	23	34	16	12	14	6	11	12
Plot Area (m^2)	103	201	109	260	111	75	287	156	92
Age (years)									
Mean	28.0	24.3	21.0	18.9	20.2	18.9	19.8	17.2	20.7
Std. Dev.	11.7	11.4	7.2	9.3	10.4	7.3	8.5	8.2	8.8
Maximum	48	50	35	51	46	33	37	33	43
Height (m)									
Mean	0.90	0.61	0.60	0.82	0.62	0.45	0.61	0.57	0.88
Std. Dev.	0.53	0.31	0.31	0.36	0.21	0.13	0.14	0.18	0.26
Maximum	2.45	1.35	1.60	2.10	1.20	0.90	0.90	1.10	1.50
Diameter (mm)									
Mean	14.5	11.0	11.3	12.8	11.7	8.5	11.4	11.0	12.7
Std. Dev.	7.4	4.5	5.4	4.9	3.9	1.7	3.2	2.8	3.0
Maximum	37.0	17.5	28.0	26.5	23.5	12.0	19.5	18.0	19.5
Genet Density (ha^{-1})	4860	2490	4570	1920	4500	6630	2830	3160	7360
Percent with dead ramets	NR	NR	NR	56	68	64	76	76	38

Table 2-4. Correlations between changes in stand density and reconstructed climate from 1800-1980. Cell values are Pearson correlation coefficients with proportional change in density. Values are followed by the length of forward average (in years) yielding the best correlation for each variable. Column variables: (A) Temperature (Szeicz and MacDonald 1995b); (B) Temperature (Overpeck *et al.* 1998); (C) PDO (D'Arrigo *et al.* 2001); (D) Drought (Cook *et al.* 2004). Only values associated with P≤ 0.10 are shown; P≤ 0.05 for bolded values, P≤ 0.01 for asterisked values. Sample size (n) varies with the age of the stand at each site. *W=woodland, F=Open forest

			Temperature		**PDO**	**PDSI**	
Aspect	**Site**	**Zone***	**A**	**B**	**C**	**D**	**n**
South	1	W	**0.777*** **(50 yr)**	**0.872*** **(30yr)**	–	–	10
		F	–	0.440 (50yr)	**0.592*** **(20yr)**	–	18
	3	W	**0.762*** **(50 yr)**	**0.860*** **(40yr)**	**0.493** **(10yr)**	–	18
		F	–	–	–	0.435 (50yr)	18
	5	W	**0.901*** **(50yr)**	**0.867*** **(10yr)**	–	-0.581 (50yr)	13
		F	–	**0.843** **(30yr)**	–	**-0.976*** **(20yr)**	6
North	2	W	–	0.433 (40yr)	**0.557** **(20yr)**	–	16
		F	**-0.612*** **(10yr)**	**-0.514** **(20yr)**	0.431 (30yr)	**0.524** **(50yr)**	18
	4	W	0.425 (40yr)	**0.599*** **(30yr)**	–	–	18
		F	**0.568** **(50yr)**	**0.693*** **(30yr)**	0.429 (10yr)	–	18
	6	W	**0.798*** **(50yr)**	**0.866*** **(30yr)**	–	-0.426 (50yr)	18
		F	–	**0.610*** **(40yr)**	**0.539** **(30yr)**	–	18

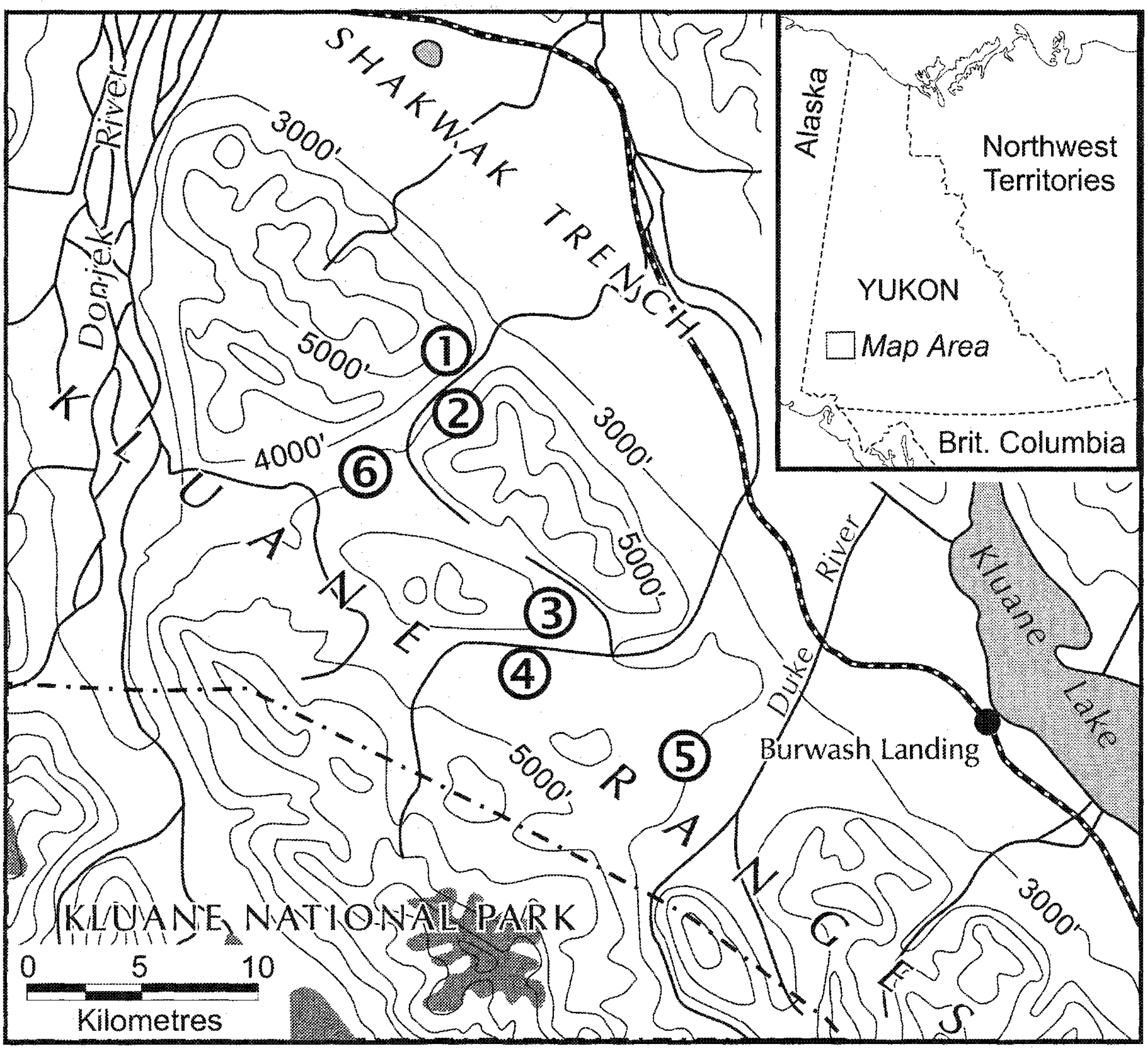

Figure 2-1. Location of the southwest Yukon study area (inset) and the six sampling sites in the northern section of the Kluane Ranges, Saint Elias Mountains. Site numbers correspond to the sampling transects described in the text. Contour interval 1000 feet (305 m).

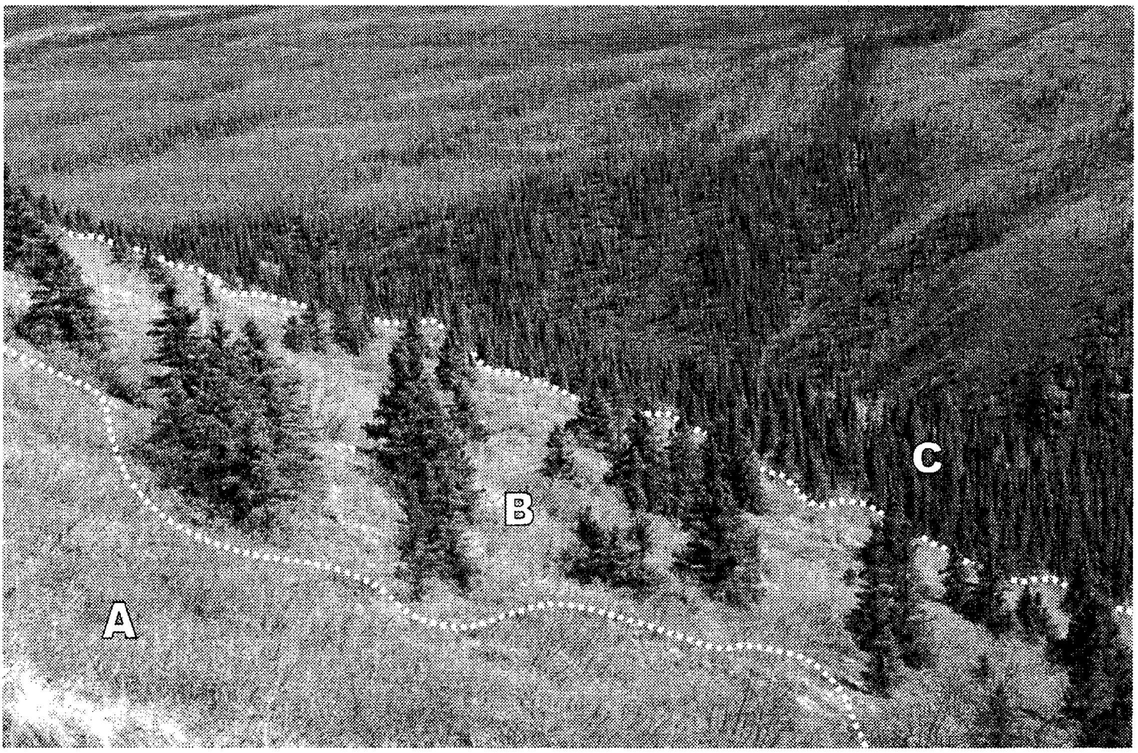

Figure 2-2. The forest-tundra ecotone on a steep, south-facing slope. Labels represent the shrubland (A), woodland (B), and open-forest (C) zones. The line dividing forest from woodland is referred to as the timberline and the line dividing woodland and shrubland is referred to as the treeline. Scattered spruce are present in the shrubland zone but are generally stunted and in a krummholz-type growth form.

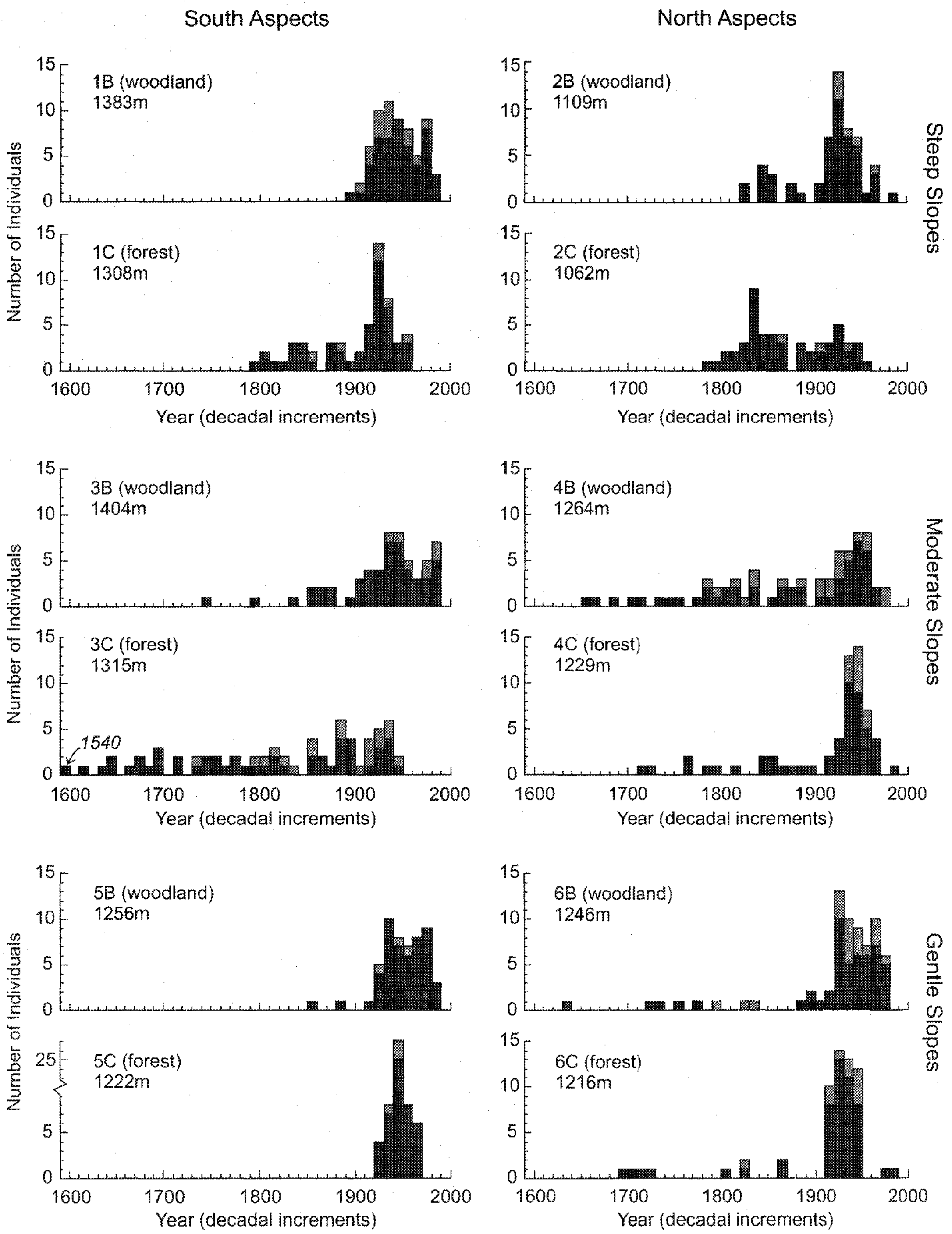

Figure 2-3. Age distribution of living individuals in spruce plots, divided into 10 year classes. Darker bars are for individuals of suspected seed origin, lighter bars are for confirmed vegetative origin. Note y-axis scale break for 5C.

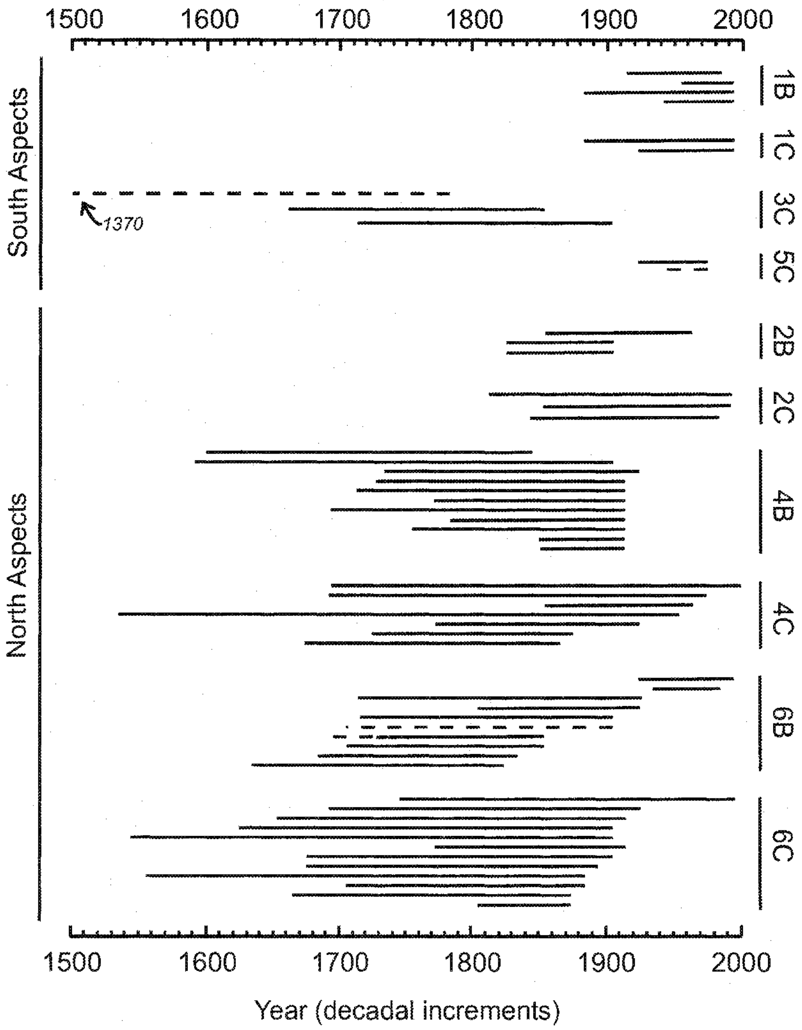

Figure 2-4. Ages of dead stems in each sampling plot. Solid horizontal lines represent life-spans of individual trees. Dashed horizontal lines are indicative of uncertainty in dating due to rotten piths, short ring-width series, or non-overlapping ring-width series. No dead individuals were located in plots 3B or 6B.

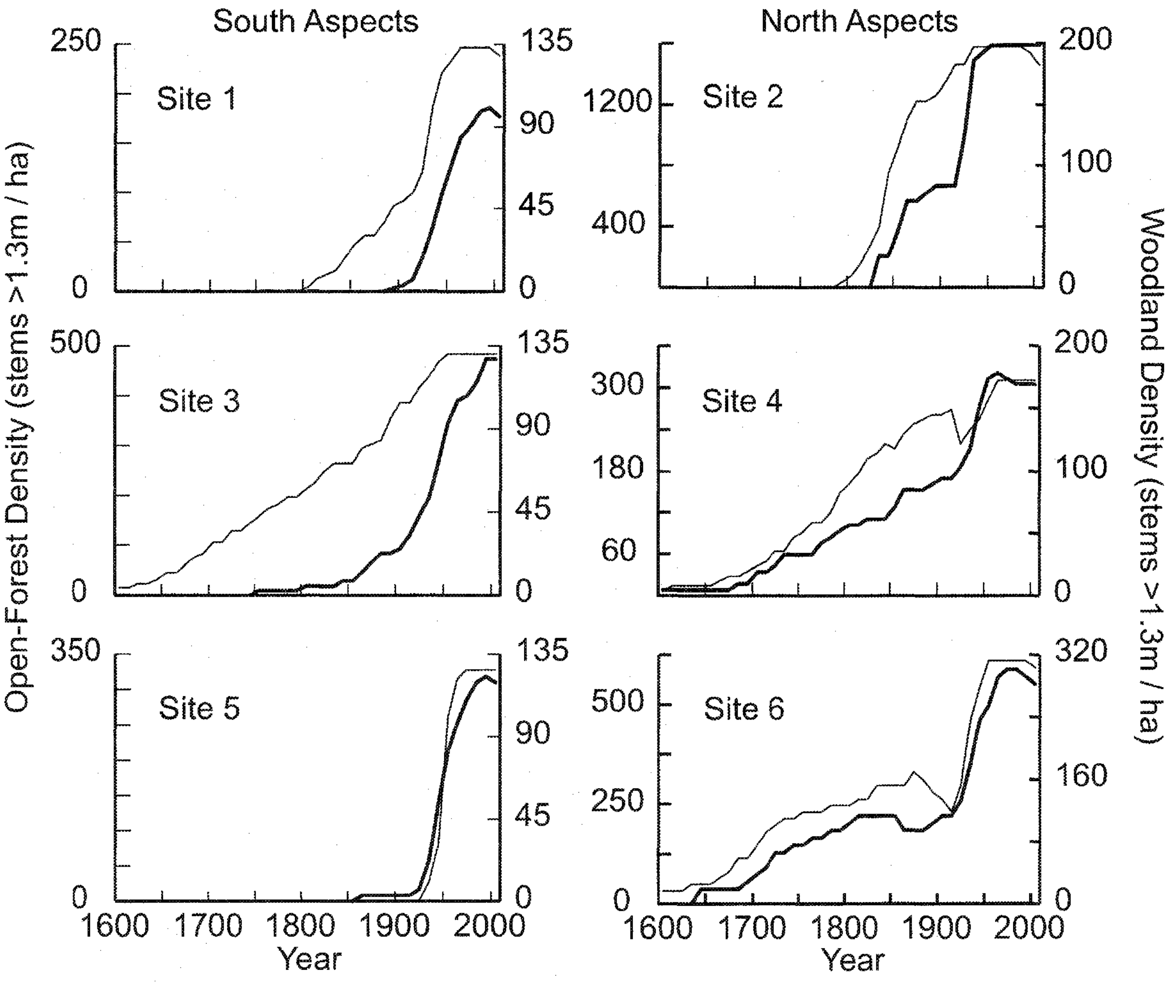

Figure 2-5. Spruce density reconstructions for individuals ≥1.30 m height, year 1600 to 2000. Data points represent density in the first year of a given decade based on changes in recruitment and mortality during the preceding decade. Heavy lines correspond to woodland density at each site, and are plotted against the right y-axis. Lighter lines correspond to open-forest density and are plotted against the left y-axis.

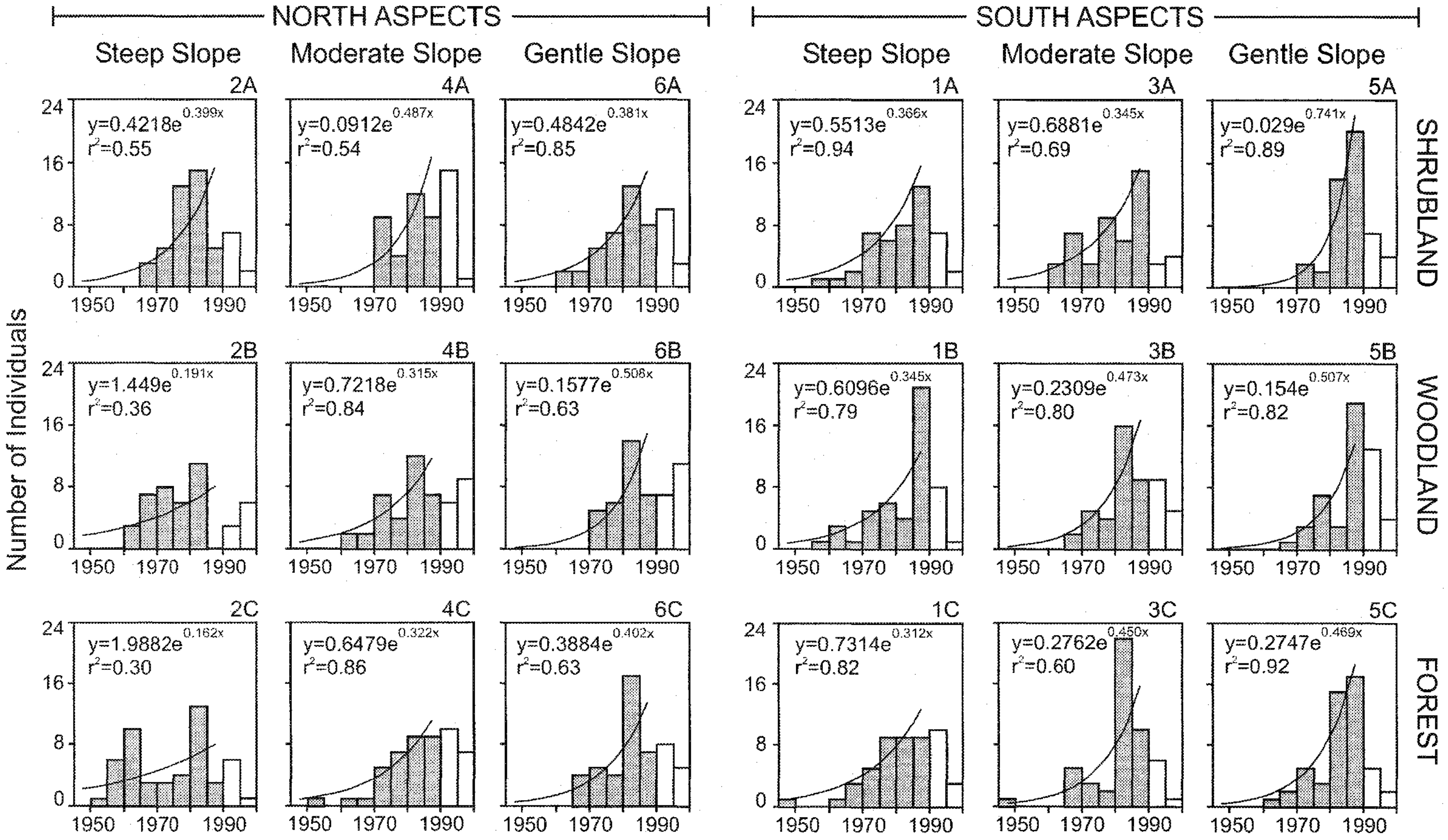

Figure 2-6. Age distribution of willow ramets sampled within each plot, grouped into 5-year age classes (all vertical bars). Negative exponential models were fit to each distribution (equations and curves). Individuals established after 1990 (open bars) were not used in model fitting (see methods section). Regression coefficients provide a measure of fit between model and data.

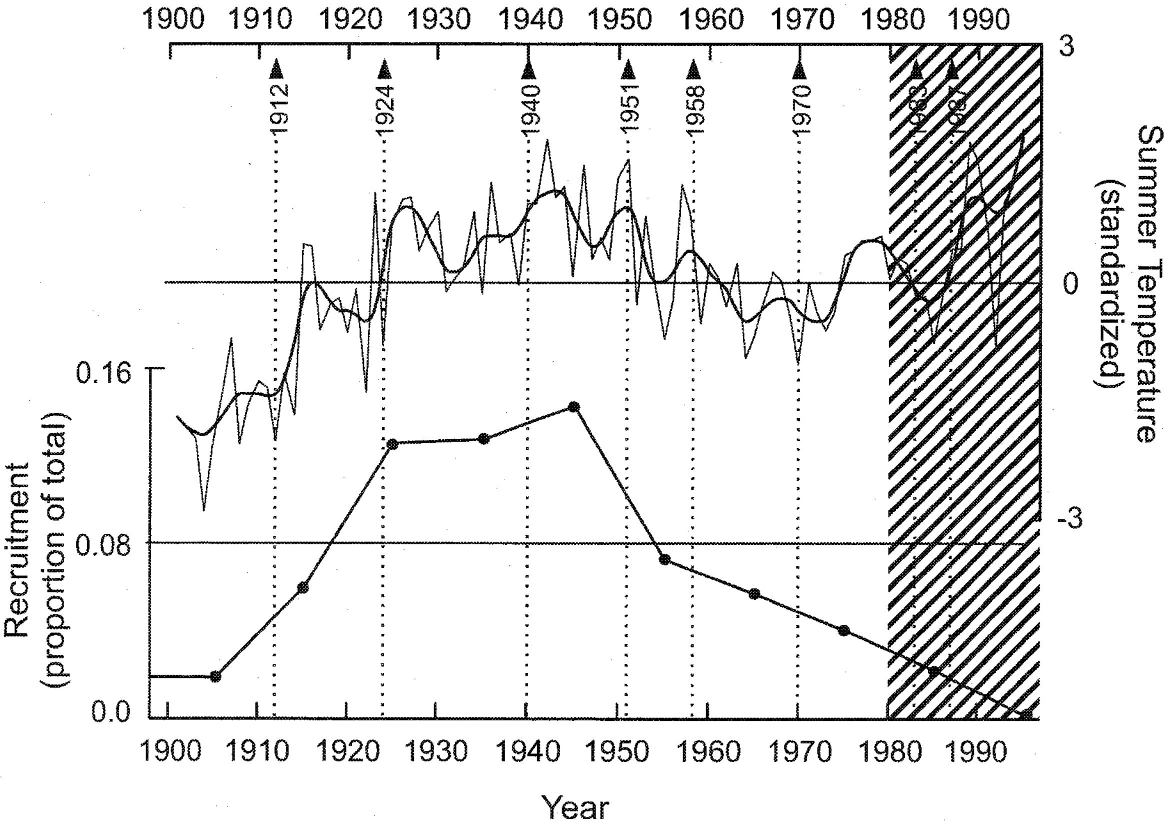

Figure 2-7. Relationship between forest-tundra dynamics, spruce masting, and climatic change during the 20th century. Bottom: Proportion of the total number of stems sampled in this study that established themselves in the noted decade. Top: Average May-September temperatures for the area bounded by 141°W/61°N and 138°W/62°N, from New *et al.* (2000). The thin line is the raw data standardized over the 95 year period. The thick line is the same data fitted with a compound smoothing filter. Vertical lines indicate white spruce mast years in Alaska from Juday *et al.* (2003). Masts after 1957 are based on observational data. Masts prior to 1957 are inferred from a combination of climate and ring-width data. Low recruitment since 1980 is partly a function of sampling, which excluded individuals less than 50 cm in height (indicated by hatching at right). In combination the three data sets illustrate that the recruitment pulse during the second quarter of the 20th century fell within a period of sustained above-average temperatures coinciding with two mast events.

Figure 2-8. Example of a krummholz-type white spruce above treeline, with abundant ovulate and pollen cones during the 2005 spruce mast. Tape measure is extended to 1.0 m. Photo taken June 23, 2005.

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CHAPTER 3

Evidence of Recent Treeline Dynamics in Southwest Yukon from Aerial Photographs [1]

INTRODUCTION

The boundary between forest and tundra zones, hereafter referred to as treeline, is expected to change in structure and position with continued climate warming (Grace *et al.* 2002). A host of studies have documented recent changes in the growth, density or distribution of high altitude and latitude forests in response to 20th century warming using dendroecological techniques (e.g. Lescop-Sinclair and Payette 1995, Szeicz and MacDonald 1995, Lloyd and Fastie 2003). Ground-level repeat photography has also been used to document these changes. By its very nature this has mostly been carried out at fine scales, examining change at individual locations or even the growth of individual trees (e.g. Kullman, 1987; Vale, 1987; Rochefort and Peterson 1996; Luckman and Kavanagh, 2000; Munroe, 2003; Kullman, 2005). Fewer published studies have utilized vertical aerial photography to examine treeline change across larger areas (Scott *et al.* 1987; Klasner and Fagre 2002). This is due largely to the more recent advent of aerial photography and, therefore, an inability to observe changes prior to the mid-1900s, as well as the small scale of early aerial photography in remote areas, which can preclude detection of all but extensive changes in forest density or distribution (Rhemtulla *et al.*, 2002).

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[1] A version of this chapter has been submitted for publication in *Arctic*.

In this study I used sequential vertical aerial photography to examine the pattern and extent of treeline change in the northern section of the Kluane Ranges, southwest Yukon. This region has experienced a significant warming trend since instrumental records began (Zhang *et al.* 2000) and therefore provides a useful locale for examining treeline response to climate change. Moreover, results from an extensive dendroecological investigation in the area (Chapter 2) indicate a period of rapid change in spruce distribution and density from 1920 to 1950 coinciding with a period of above average temperatures. Given this timeframe, as well as the degree of change inferred, I hypothesized that these changes should be partly visible when comparing the earliest aerial photographs of the region (1947 and 1948) with those most recently acquired at a similar scale (1989). Specific objectives of this investigation included: (i) characterizing the extent and pattern of change in spruce density and distribution evident from the photographs, (ii) determining the extent to which the dendroecological data are representative of the entire landscape, and (iii) refining a technique for quantifying treeline change that could be applied to other regions where only small-scale historical aerial photography is available.

MATERIALS AND METHODS

Study Area

The area examined is bounded by the Duke and Donjek Rivers in the northern section of the Kluane Ranges of the St. Elias Mountains (Figure 3-1). White spruce (*Picea glauca*) is the only conifer of note in the region, forming closed-canopy stands in valley bottoms. Density thins with increasing altitude, and an open canopy prevails at the lower end of the ecotone. At 1300 m the spruce canopy is discontinuous and the crowns of individuals generally do not overlap. Only occasional spruce are found above 1400 m and these are typically short, krummholz-type growth forms. Aspect has an important influence on ecotone structure and community composition. Treeline, defined as the upper limit of individuals typical of a tree growth form, is typically 50 to 150 m higher on drier south-facing slopes than on the cooler and more mesic north-facing slopes (Figure 3-2). Natural disturbances such as fires and avalanches are rare at treeline in this area, meaning that changes observed through photographic comparison are more likely to be a response to climatic change than to other influences.

Orthorectification

The earliest aerial photographs available for the area (1947 & 1948, ca. 1:40,000), as well as the most recent of comparable scale (1989, ca. 1:57,500) were identified from the Yukon Energy, Mines and Resources air photo database (Whitehorse, Yukon) and prints were acquired from the National Air Photo Library of Canada (Table 3-1). I selected nine areas for detailed examination based on image illumination and clarity (Figure 3-1). Prints were scanned at 1000 dpi using an Epson 1560 large-format flatbed scanner and saved in tagged interchange file format (TIFF). The images were orthorectified to the UTM (Zone 7) projection using rigorous models in PCI Orthoengine (PCI Inc., Richmond Hill, Ontario). Thirty metre resolution digital elevation models (DEMs) generated by the Yukon Territorial Government (YTG) were used as elevation input. I experimented with nearest neighbour, bilinear, and cubic convolution resampling at a variety of output resolutions. Bilinear resampling with 1.0 m pixel spacing was chosen.

This product maintained the ability to identify the individual spruce observable in the original images while optimizing file size and processing time.

Orthorectification began by processing the six photographs from 1989 to create a georeference control. Camera-specific calibration information, including lens length, distortion, and spacing of fiducial coordinates, was used to parameterize the model. All 1989 photos were taken on the same flight path and I incorporated 90 tie-points to connect overlapping portions. Coordinates for 28 ground control points (GCPs) were obtained in the field with a Garmin 12XL handheld GPS receiver (Garmin International Inc., Olathe, Kansas). An additional 39 GCP coordinates were obtained from features identified from the Natural Resources Canada 1:50,000 National Topographic Database (NTDB, 2nd edition) vector map coverages. The overall root mean square (RMS) registration error for these images was 15.7 m (x-axis) and 11.1 m (y-axis).

The 1947/48 images were individually registered to these orthoimages. However, camera calibration data were not available for these early photographs. Lens distortion was assumed to be zero and fiducial measurements were obtained by manual measurements of the photographic prints. As a result, RMS error was inflated for each of these early orthoimages relative to the 1989 images. To help remedy this situation, I re-rectified the 1989 images individually using the same set of GCPs used to process the 1947/48 images. Although this slightly increased RMS error, image-to-image comparison indicated that by registering the 1989 photos to the 1947/48 photos I was able to reduce the relative positional error (i.e. improve alignment) between photo pairs.

Analysis

Automated classification of panchromatic aerial photography for the purpose of vegetation change detection has been applied successfully to large scale photography (i.e. ≤1:20,000) (Carmel and Kadmon, 1998; Kadmon and Harari-Kremer, 1999) but becomes increasingly problematic at smaller scales. For example, pixel-based image classification schemes based only on gray values can fail because of reduced variation in brightness between vegetation types, particularly in older photographs (Fensham *et al.*, 2002). Shadows are also problematic for automated pixel-based classification of panchromatic images (Hutchinson *et al.*, 2000). Experience is growing with object-based classification (Laliberte *et al.*, 2004), but poor contrast in the 1947/48 photographs limited its possible application only to the 1989 images, and scale remained an issue. For these reasons I opted for user-based interpretation of the digital images rather than automated classification.

Change at treeline from 1947/48 to 1989 was first assessed through a qualitative comparison of images. This was accomplished through the flicker and swipe visualization techniques within PCI Focus (PCI Inc., Richmond Hill, Ontario) and provided an indication of the type and extent of change across the landscape. Subsequent to this assessment I quantified stem density and maximum spruce elevation at random locations to provide a more rigorous analysis of change.

Using ArcGIS (ESRI, Redlands, California), random points were generated along a linear representation of treeline derived from YTG Forest Resource Inventory (FRI) maps. Points were separated by a minimum 200 m and confined to areas where the image was clear enough to distinguish individual trees. In total, 104 points were generated. A one hectare “virtual plot” was overlaid on the orthophotos immediately upslope of each random point. The position of several plots was adjusted slightly to minimize differences between images. Individual spruce were identified and marked within each plot. For each pairing of plots, the 1989 plot was examined first, with corresponding individuals identified in the 1947/8 plot. The original photographic stereo pairs were used to aid image interpretation. The number of individuals in each plot was tallied to yield an estimate of spruce density in each year.

Change in the elevation of spruce was analyzed by extending a 100 m wide belt-transect directly upslope from 100 of the random sample points. The three uppermost spruce in each belt on the 1947/48 and 1989 images were identified and marked. The original photographic stereo-pairs were again used to aid interpretation of the digital orthophotos. The elevation of each data point was obtained from the DEM, resampled to 5 m resolution using a cubic convolution. The positions of spruce identified in the 1947/48 images were located and marked in the 1989 images and elevations were determined from these adjusted positions. This prevented any errors that would be introduced by the differences in image registration. The three elevations from each time step were then averaged to yield a single value for each belt transect. My decision to measure maximum spruce elevation rather than treeline elevation was based on the fact that the delineation of treeline would be subject to discrepancies between timesteps (Armand, 1992).

A one-way repeated-measures analysis of variance (RMANOVA) was used to analyze the density and maximum elevation data. Net solar radiation was used as the between-subjects factor. This is an important variable controlling soil temperature and vegetation composition in mountainous regions of the subarctic (Dingman and Koutz, 1974) and plays an important role in treeline structure and position in the study area. Using the 30 m DEM, I modeled net radiation across the study area for the summer solstice with the terrain analysis module of SAGA GIS (Göttingen University, Germany). Two levels were used for the ANOVA model; areas receiving <7.0 kWh m^{-2} were classified as low solar radiation areas, those ≥7.0 kWh m^{-2} were classified as high solar radiation areas. Although this is an arbitrary threshold, areas of high solar radiation generally corresponded to slopes with southerly aspects while low radiation areas generally corresponded to more northerly aspects.

RESULTS

Initial inspection of the photographic prints with the naked eye suggested little change from 1947/48 to 1989. However, magnification of the prints under a stereoscope and subsequent on-screen comparison of the digital orthophotos at 100% resolution revealed that change was widespread throughout the study area. The degree of change varied significantly, ranging from areas where no change was evident to areas where rapid, large-scale landscape transformation had occurred.

An increase in the overall canopy cover of individual spruce was the most common type of change observed (Figure 3-3A). Canopy closure increased in most areas of woodland and open forest, even in areas where there was little or no evidence of new individuals. An increase in stand density resulting from the recruitment of new individuals was the next most common change evident between the photo pairs (Figure 3-3B). Though it was evident at a number of sites, advance in the elevation of treeline

(Figure 3-3C), as well as recruitment of scattered new individuals above treeline, was limited in comparison with changes in canopy cover and density.

The most extensive change was observed on the Burwash Uplands. Large portions of its southern and eastern slopes underwent a transformation from shrub tundra, with only scattered individuals above treeline, to woodland vegetation. At lower elevations it was apparent that areas of woodland vegetation in 1947/48 had become open forest by 1989 (Figure 3-4). Significant change was also observed at the heads of several creek valleys throughout the study area where spruce advance along the creek drainage was observed (Figure 3-5).

The quantitative analyses of plot and transect-based spruce counts support these observations. Density of spruce increased significantly over the 40 year period ($F_{1,102}$ = 65.056, $P<0.001$), from an average of 21.3 ha^{-1} in 1947/48 to 30.3 ha^{-1} in 1989 (Figure 3-6). The difference in the upper elevation of spruce was also statistically significant ($F_{1,98}$ = 23.745, $P<0.001$), increasing from an average of 1396 m in 1947/48 to 1406 m in 1989 (Figure 3-6). RMANOVA results indicate that the density of spruce did not vary significantly with solar insolation, but that the average upper elevation of spruce was more than 90 m higher on slopes with high insolation than on slopes with low insolation (Table 3-2 and Figure 3-6). However, the absence of any significant within-subjects interactions indicates that the amount of change did not vary between the two levels of solar insolation (Table 3-2).

Despite the statistically significant changes, the net differences in density and elevation (i.e. 1989 minus 1947/48 values) were not normally distributed (Figure 3-7). Nearly two-thirds of all sites experienced no change in uppermost spruce elevation (n=61). Where it was observed, the extent of change varied greatly. The distribution of differences in density was less, though still positively, skewed. As visual inspection of the photographs indicated, the sites with the largest increases in density were located on the Burwash Uplands. The eight plots located in this area experienced an average 840% increase in spruce density from 1947/48 to 1989. Spatial clustering of change was not evident in any other part of the study area.

DISCUSSION

Treeline Dynamics

MacDonald *et al.* (1998) identified three possible responses of treeline to a warming climate: (1) increased growth of individual trees, (2) increased population density of trees at treeline, and (3) expansion of the distribution of trees (i.e. invasion into tundra). My results indicate that each of these responses occurred in southwest Yukon during the 20th century, but that the frequency of occurrence declined in this order. Additionally, the extent and type of change evident from the photographic pairs varied across the landscape.

The larger canopies of individual spruce relocated in the 1989 photographs indicated a net growth since 1947/48. The growth of spruce was not unexpected, but a noticeable increase in the overall size of treeline individuals was not a certainty from the outset. Slow growth rates combine with mechanical damage at high elevations and latitudes to limit increases in the size of tree canopies, especially in isolated individuals above treeline (Holtmeier, 2003). So, while this result would be expected for individuals at lower elevations, the observed change in the size of individuals at and, especially, above treeline is noteworthy. Significant net growth of individuals has been observed in several ground-level repeat photography studies and appears to have been the most consistent type of change evident at treelines worldwide during the 20th century (e.g. Vale, 1987; Kullman 1987). Indeed, growth at latitudinal treeline in parts of northern Quebec has been so significant and widespread that treeline has advanced because of a shift from stunted individuals (i.e. krummholz) to upright growth forms (i.e. trees), rather than through establishment of new individuals (Lescop-Sinclair and Payette 1995).

The growth of pre-existing individuals likely contributed to the significant increase in spruce density observed. Given the small scale of the photographs it is probable that many spruce were not identifiable in the 1947/48 photographs but in the intervening years grew to a size that could be detected by 1989. Rather than a result of widespread change in growth form from krummholz to tree, this is more likely the result of small individuals maturing into trees since then. The 1947/48 photos were taken at the end of the rapid period of establishment identified in my dendroecological studies and my height and diameter measurements from these individuals suggests that it would have taken 2-3 decades before attaining a size that could be detected in the photographs. This is supported by the fact that density calculations from the aerial photographs were approximately half of that measured on the ground for south-facing slopes, and approximately one-tenth of that for north-facing slopes. In essence, only larger individuals were discernable in the photographs. In turn, this explains the lack of significant effect of insolation on density in the ANOVA model, which contradicts the significant difference detected through ground-level measurements.

Though statistically significant, changes in the uppermost position of spruce were considerably less prevalent than changes in density. Changes in treeline elevation may have been more substantial but difficulties consistently delineating a boundary precluded use of a metric to test this. The effect of solar insolation on elevation was anticipated and concurs with observations from other subarctic alpine regions (e.g. Dingman and Koutz, 1974; Viereck, 1979). The lack of interaction between insolation and elevation change is attributable to the relatively small differences which were measured.

These results are in agreement with dendroecological data from southwest Yukon. Based on stem analysis of individuals in the southern portion of the Kluane Ranges, Ayotte (2002) concluded that spruce at and above treeline have increased in overall size since the early 1950s and presented evidence of a growth release from stunted forms. My dendroecological results (Chapter 2) indicate a significant increase in density in the second quarter of the 20th century and a gradual in-filling of the forest-tundra ecotone since. Finally, with respect to elevation, the dendroecological data indicate that treeline advance occurred mainly during the second quarter of the 20th century (i.e. in the 25 years prior to the first set of photographs). Ages of "outpost" trees and krummholz well above treeline indicate that a large proportion of these individuals – equivalent to those identified here in the virtual belt transects – also established at this time (Figure 3-8).

Assessment of Methodology

Overall, the combination of manual interpretation with digital image transformation was successful. Manual interpretation allowed me to take advantage of characteristics such as texture, shape, and pattern when differentiating individual spruce from adjacent vegetation types and shadows and, when using the original photographic prints, an ability to exploit the vertical dimension by way of stereoscopic viewing. Image digitization allowed for continuous adjustment of contrast and brightness values. This was particularly important for the early photographs which, despite being a larger scale, were of poorer clarity and contrast. Digitization also permitted the use of various filters, such as edge detection algorithms, to supplement on-screen interpretation of features. I was able to quantify change by using the virtual plot and transect overlays. But this would not have been possible without orthorectification to remove distortion and permit standardized measurements across the images.

There were, however, several difficulties encountered during the study that require mention. They did not result in significant error, but are important caveats to consider, especially if the approach is to be applied elsewhere in similar environments. Small photographic scale was the root cause of most of these difficulties and proved problematic during image interpretation. For example, an inability to resolve small spruce in the photographs means that the differences I observed were applicable only to individuals above a certain size. My field data suggests that this was less problematic on south-facing slopes than on north-facing slopes where individual spruce are much smaller. In addition, there were several instances when a spruce was identified in the 1989 image, but its presence or absence in the earlier image was uncertain. In these instances I erred on the side of caution, tagging the location as a spruce so as not to over-estimate the degree of change. It is possible then, that this lead to an underestimation of change and the results should be considered in this light.

Errors in rectification were significant relative to the resolution of the rectified images. Known sources of error were (1) spatial inaccuracies in the GCPs obtained from the NTDB (up to 40 metres difference on either axis between GPS and NTDB coordinates of the same feature), (2) the lack of camera and lens calibration information for the early photographs, and (3) inaccuracies in the DEM, which is mostly based on NTDB hypsography and therefore subject to the same error as the NTDB-derived GCPs. While the resulting positional error did not affect the results, it did present problems that required adjustments. This included slight shifting of plots and belt transects, relocating spruce from the 1947/48 images on the 1989 images for consistent elevation determination, and omitting peripheral areas on images where distortion and positional error was greatest.

One of the advantages of using sequential aerial photography over repeat ground-level photography is that the investigator is not limited to specific locations based on the availability of existing photographs, since aerial coverage is generally widespread. In turn, it is possible to assess the extent to which the observed changes reflect the entire study area and not just a single location. Still, my experience indicates that it is important to nest fine-scale field investigations within the sequential photography investigation, especially when using small-scale photography. This facilitates an evaluation of the resolving power of the photographs which is crucial for image interpretation. Equally important, this helps identify the mechanisms of change, a critical component of any such study.

It is often difficult for non-experts to interpret scientific figures that quantify landscape change through means such as spruce age histograms, lake sediment stratigraphies, or even change detection maps. Repeat and sequential photography are powerful tools for depicting landscape change and the images provide a visual record that is interpretable by anyone. These techniques need not be limited to qualitative assessments of change. As shown here, quantitative data, testable with inferential statistics, can be obtained from these images to provide the rigour and repeatability required of scientific investigations.

CONCLUSION

The potential ecological effects of climate change in arctic and alpine regions have been the subject of extensive study. One of the most common predictions is that continued global temperature increases will cause treeline to advance in elevation and latitude. Studies of past changes therefore have important value for forecasting the possible extent and pattern of treeline change. My comparison of aerial photographs of southwest Yukon from 1947 and 1948 with those taken in 1989 indicate significant changes in the spruce forest-shrub tundra transition. In decreasing order of occurrence these include (1) increased growth of individual spruce, (2) increased population density of spruce at treeline, and (3) an upward expansion of spruce distribution.

Many areas exhibited increased growth of individual spruce without an increase in stand density or an advance in spruce distribution. An increase in both growth and density occurred in most other areas. Increases in the elevational distribution of spruce were observed in comparatively fewer areas, though typically in combination with the other two types of change. The greatest changes were observed in the area of the Burwash Uplands in the southern portion of the study area which experienced a transformation from sparsely treed shrubland to woodland and open canopy forest. Other significant changes were observed along creek channels.

Given the absence of major natural disturbances or widespread land use change, I attribute these changes to climate. Dendrochronological evidence from the study area indicates that the most influential climatic period for treeline was the 25 years immediately prior to the first photographs. Temperatures were consistently above the 100-year average (Luckman *et al.*, 2002) and more than 40% of all treeline spruce date to this time (see Chapter 2). Without earlier photographs it is difficult to say what proportion of these spruce were actually visible in the 1947/48 photographs and it is probable that the change I observed in the photographs represents only part of the total amount of change during the 20th century.

Table 3-1. Characteristics of aerial photographs from each study area. Images from 1989 were initially used to generate an orthomosaic georeference control from which GCPs for rectification of 1947/48 photos were obtained (see text for details).

Map ID	**Name**	**Area (km^2)**	**Date**	**Photo Number**[1]	**RMSE (m)**[2]
A	Swede Johnson	31.4	1947/07/25	A11014-418	27.16
			1989/08/10	A27518-141	35.58
B	Nickel Creek	18.7	1947/07/25	A11002-386	19.77
			1989/08/10	A27518-82	19.44
C	Quill Ponds	31.8	1948/06/09	A11383-215	15.62
			1989/08/10	A27518-82	22.24
D	Maple Creek	25.1	1948/06/09	A11383-217	21.41
			1989/08/10	A27518-83	18.12
E	Quill Creek	17.8	1948/06/09	A11383-216	20.05
			1989/08/10	A27518-82	18.98
F	Tatamagouche	26.4	1947/07/25	A11002-418	17.20
			1989/08/10	A27518-74	15.83
G	Burwash Creek	19.4	1947/07/25	A11002-415	18.62
			1989/08/10	A27518-74	17.24
H	Burwash Uplands	39.4	1947/08/01	A11015-83	19.46
			1989/08/10	A27518-2	19.32
I	Squirrel Creek	46.7	1947/08/01	A11015-84	22.72
			1989/08/10	A27518-1	21.57

[1] Photo scales:
1947/48 = 1:40000 (Focal length = 152.40 mm, Flying altitude = 20000')
1989 = 1:57600 (Focal length = 152.86 mm, Flying altitude = 28800')

[2] Average RMSE = 20.6 m

Table 3-2. Results of repeated measures ANOVA on two metrics of treeline change. S=Solar insolation; Y=Year (repeated). [1]Values based on Wilks' lambda are reported.

	Spruce Density				**Maximum Spruce Elevation**			
Between Subjects	df	MS	F	P	df	MS	F	P
S	1	42.8	0.150	0.699	1	351849	23.75	**<0.001**
Error	102	285.1			98	14817		

Within Subjects[1]	F	N df	D df	P	F	N df	D df	P
Y	65.06	1	102	**<0.001**	14.52	1	98	**<0.001**
Y*S	2.32	1	102	0.131	0.93	1	98	0.339

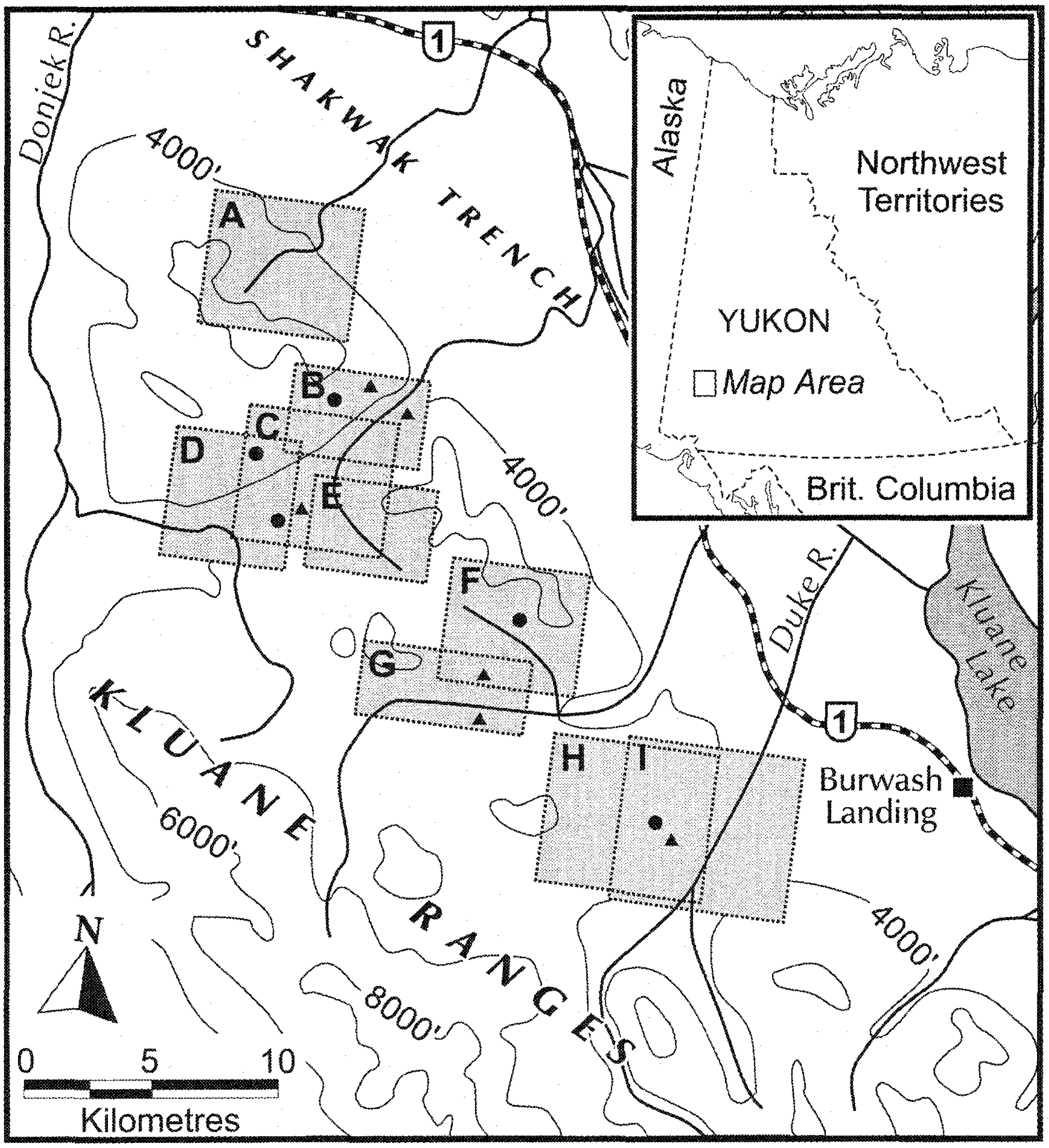


Figure 3-1. The southwest Yukon study area. Boxes demark areas from each of the nine photo pairs which were examined. Numeric labels (upper left of each box) correspond to photo details provided in Table 1. Solid circles denote the locations of aerial photographs shown in Figures 3, 4 and 5. Triangles denote locations of dendrochronological sampling.

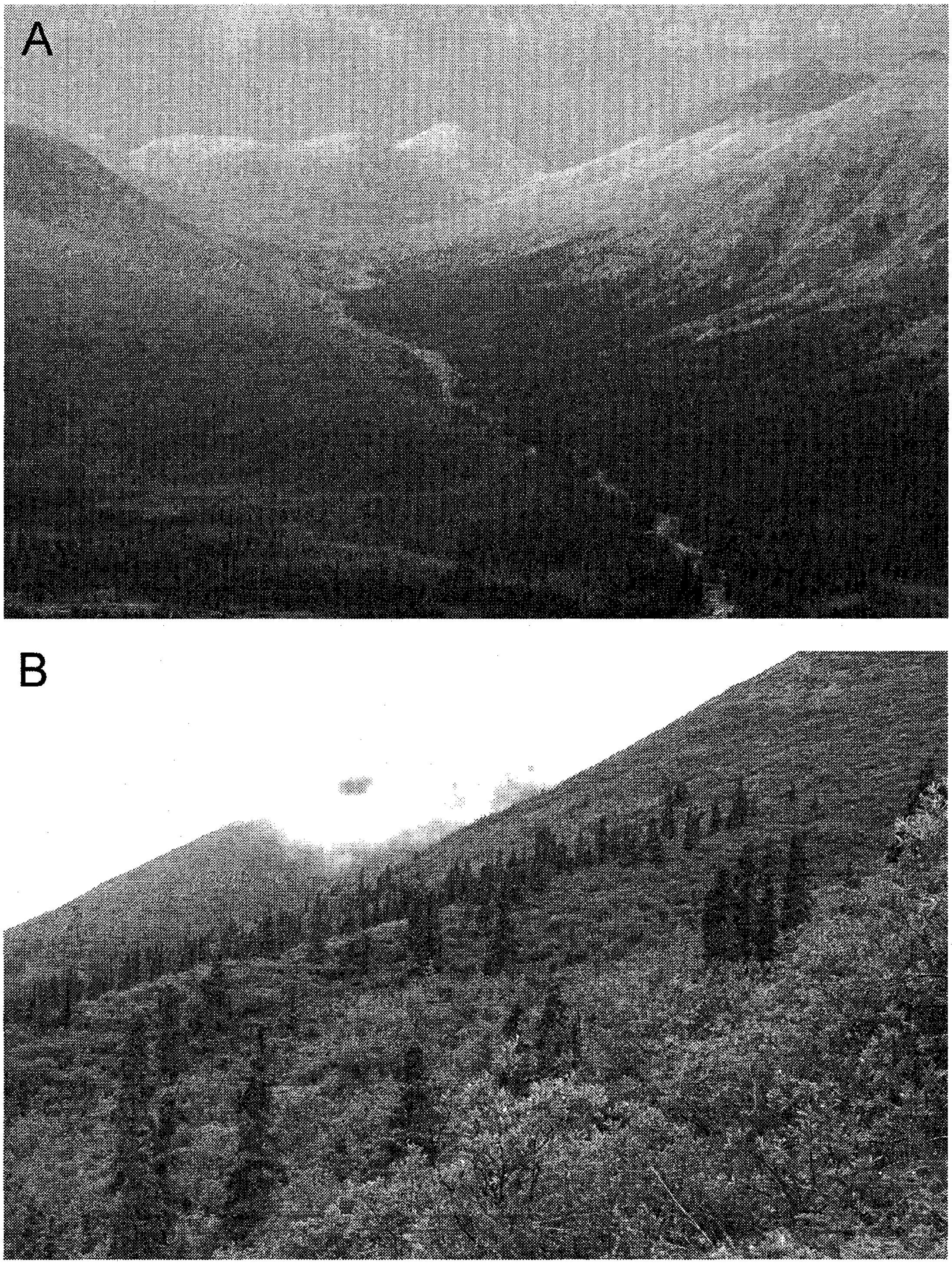
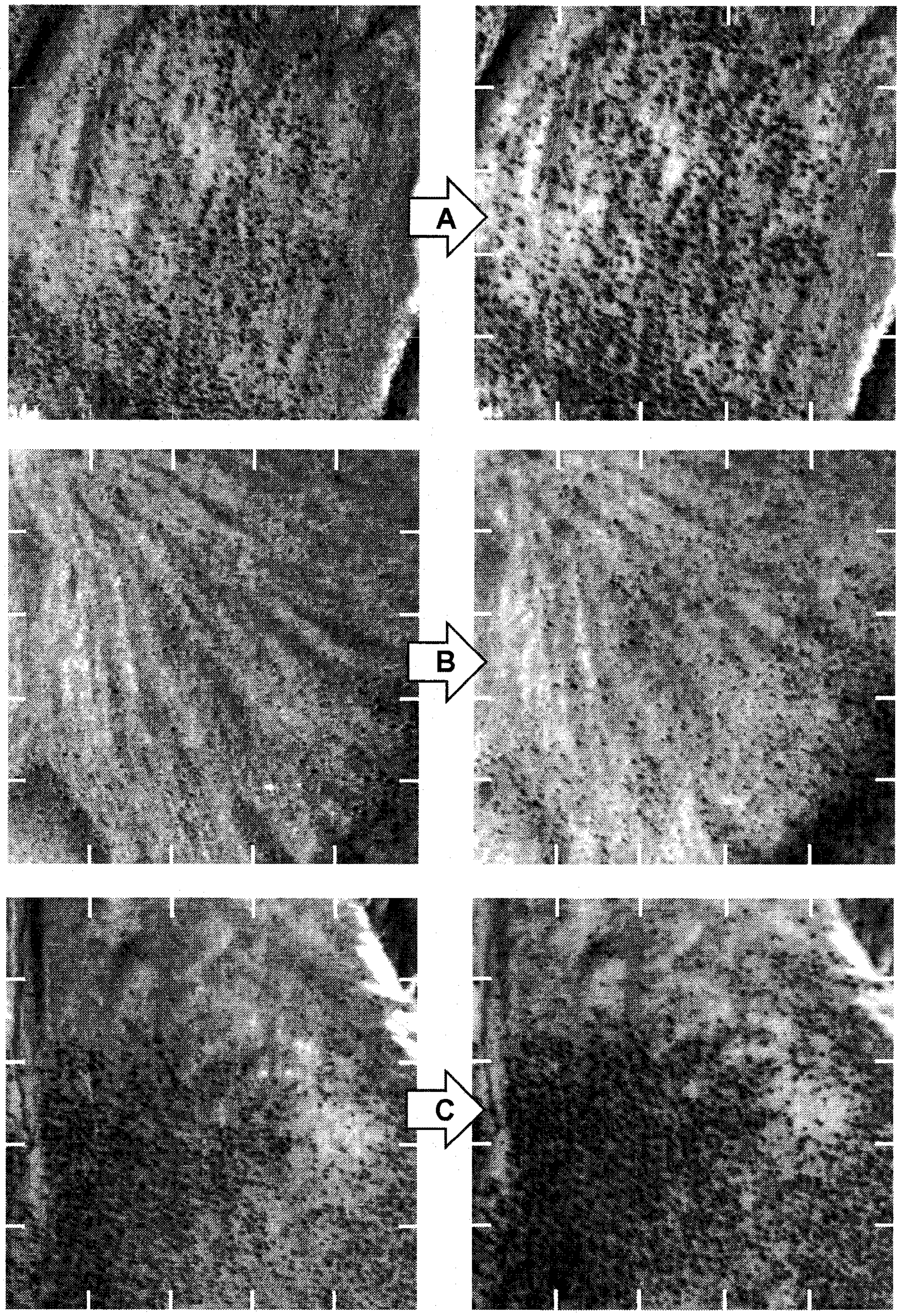


Figure 3-2. Treeline environments in the northern Kluane Ranges, Yukon. (A) Landscape-scale ground-level photograph viewing north illustrates the differences between southwest (right of creek) and northeast (left of creek) aspects. (B) Ground-level photograph of the forest-tundra ecotone on a southwest-facing slope.

Figure 3-3 (next page). Air-photo subsets from three locations (1947/48 on left, 1989 on right) illustrating the types of change observed at treeline. (A) Increase in the size of individual spruce canopies, but negligible change with respect to density or elevation of trees. (B) Increase in the density of spruce but no advance of treeline. (C) Advance in spruce distribution indicated by the establishment of new individuals upslope of treeline, combined with an increase in canopy size and spruce density in areas below treeline. All areas shown are 500 x 500 m. Individual spruce or clumps of spruce are identifiable as distinct dark spots. Slope runs from lower right to upper left in each photo.


A
B
C

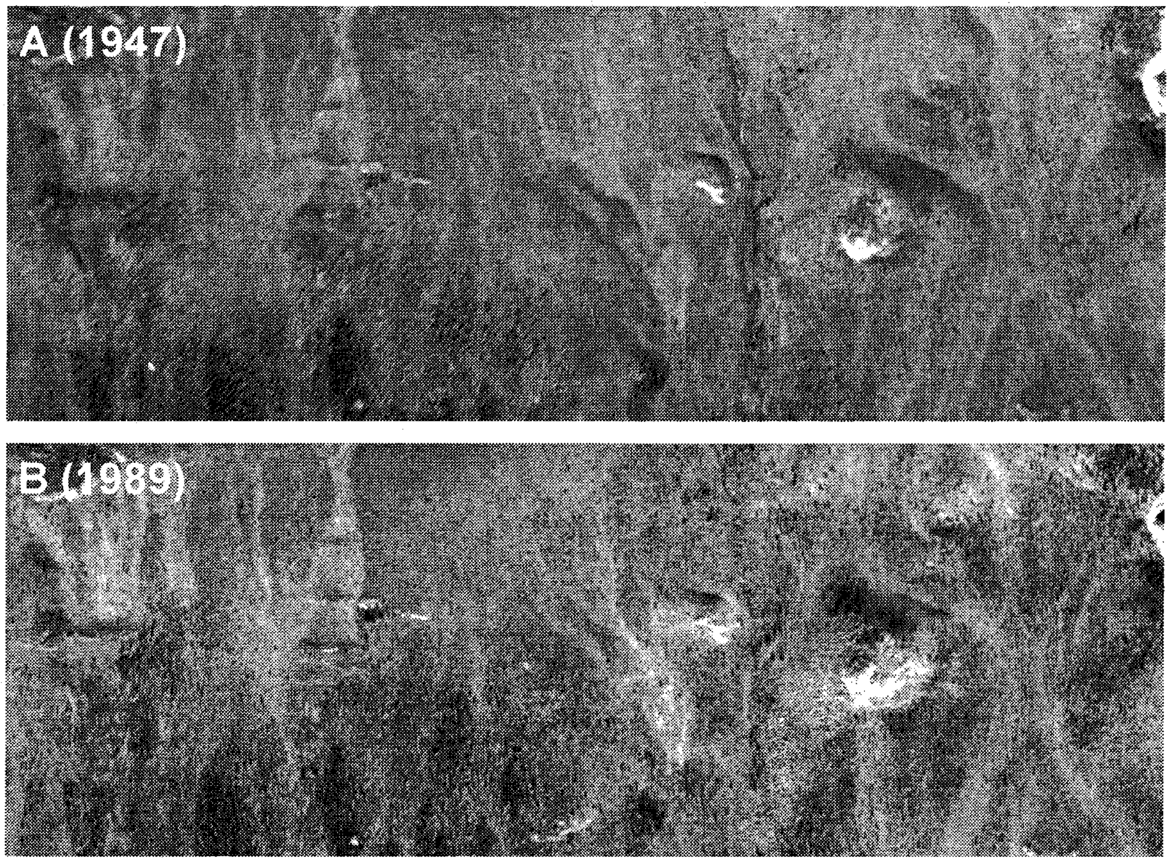


Figure 3-4. Treeline change on the Burwash Uplands, southwest Yukon. Individual spruce or clumps of spruce are identifiable as distinct dark spots against the lighter background of shrub tundra. Each photo measures 2500 m wide. Slope runs from the bottom to top of each image.

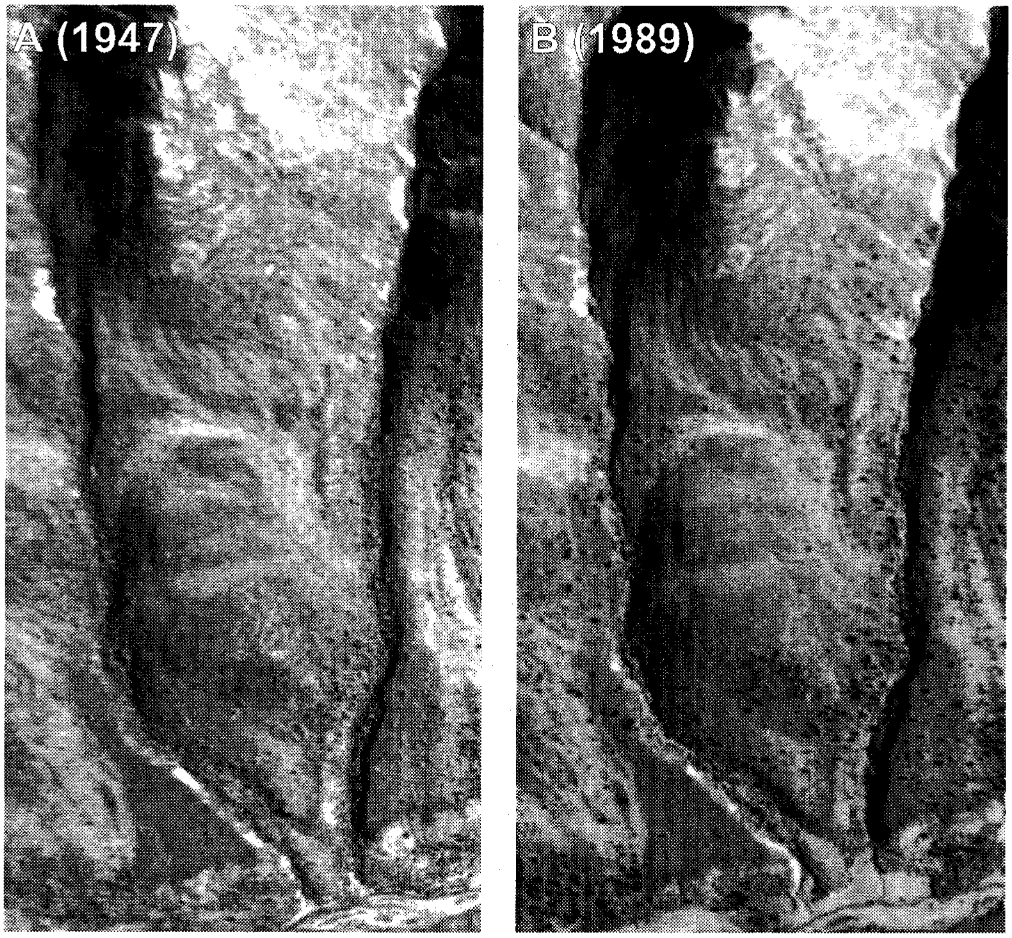


Figure 3-5. Changes in spruce distribution along two tributaries of Tatamagouche Creek, southwest Yukon. Photos measure 650 x 1250 m. Slope runs from the bottom to top of each image.

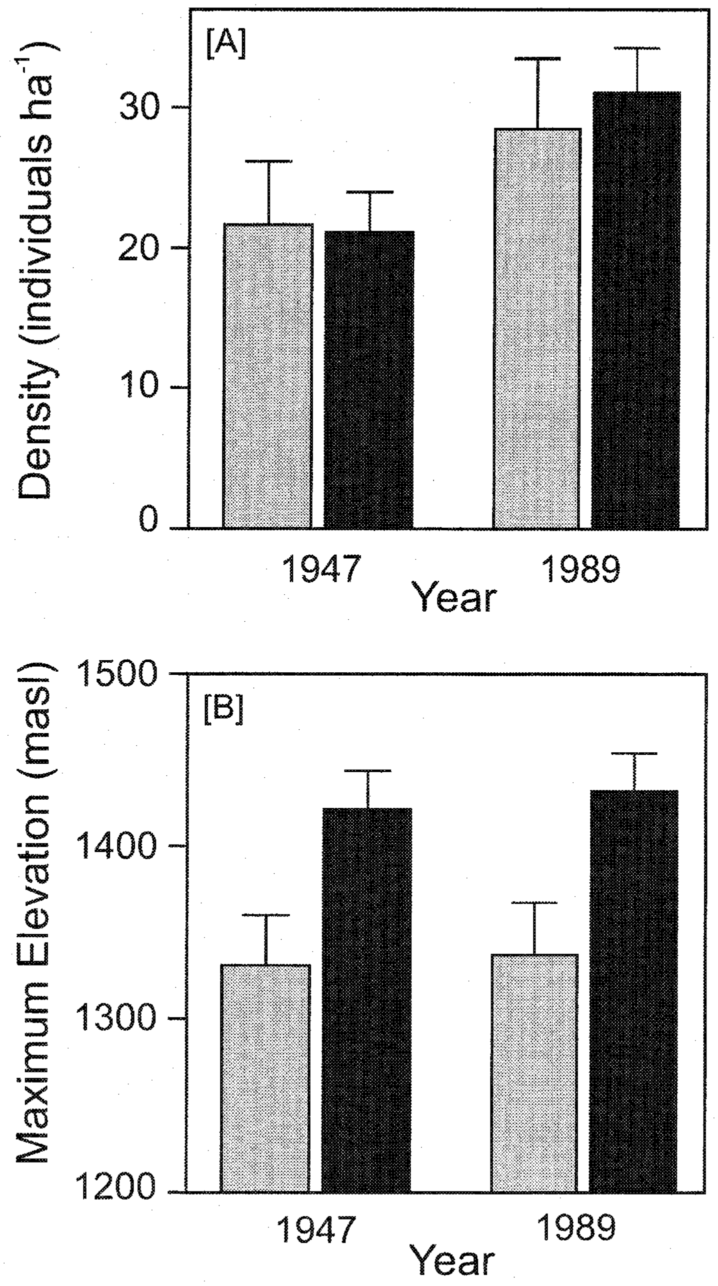


Figure 3-6. Average density [A] and upper elevation [B] of spruce in plots and belt transects superimposed on aerial photographs from 1947/48 and 1989. Light bars represent sites with low solar insolation (n=30 for [A], n=28 for [B]), dark bars represent sites with high solar insolation (n=74 for [A], n=72 for [B]). Error bars show 95% confidence intervals.

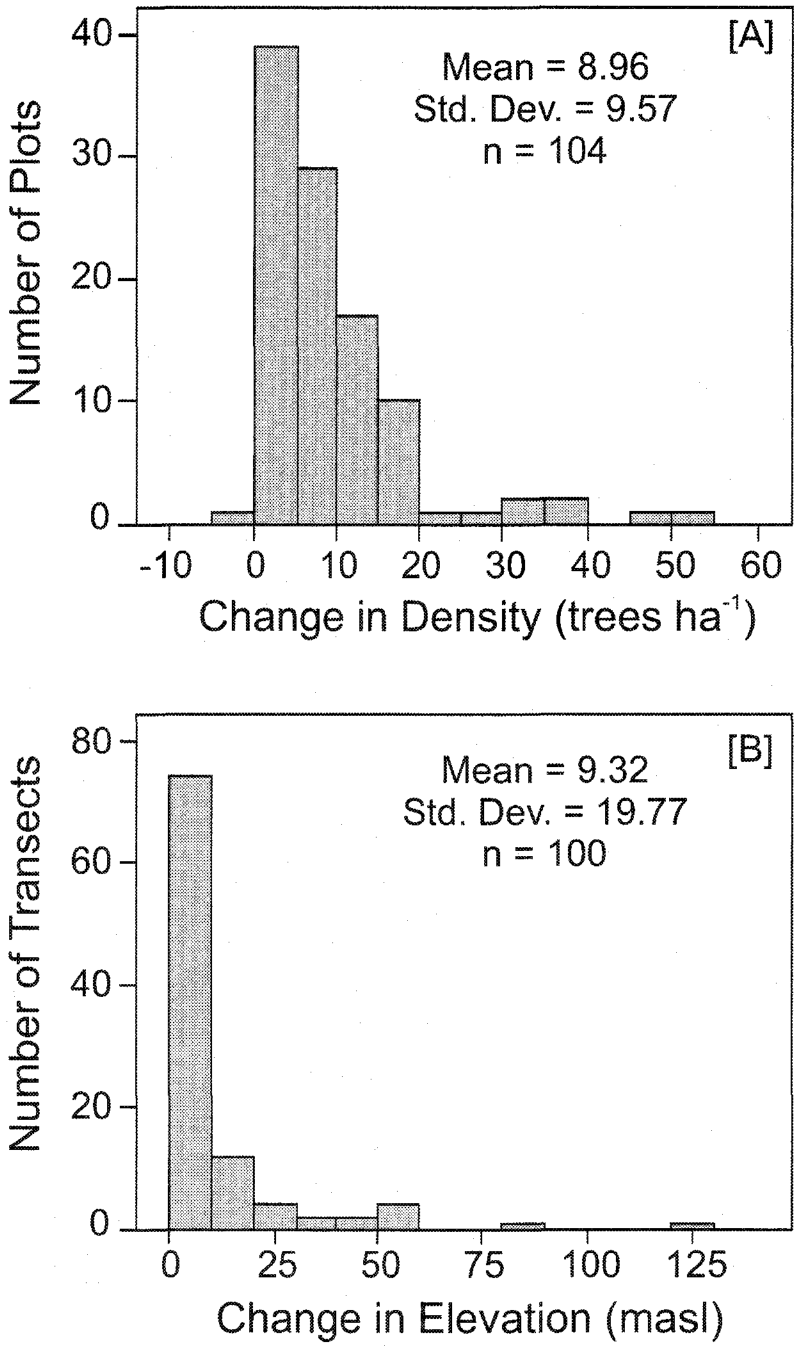


Figure 3-7. Frequency distributions of the change in spruce density [A] and the change in uppermost spruce elevation [B]. Changes in each plot [A] or belt transect [B] were calculated as the difference in the number of spruce identified in early (1947/48) and recent (1989) aerial photographs.

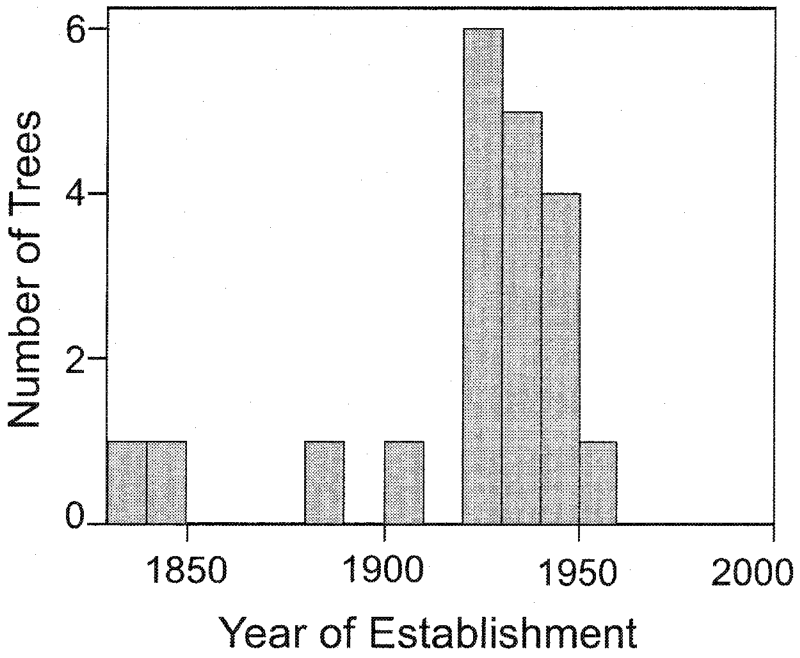


Figure 3-8. Age distribution of 20 living spruce randomly sampled above treeline in the shrubland zone at four locations in the study area (see Figure 3-1; 4 samples from each site).

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CHAPTER 4

Conifer Mapping and Distribution Modeling at a Subarctic Alpine Treeline

INTRODUCTION

The physiological effects of low temperature are generally considered to be the most prominent variables controlling the *potential* upper altitudinal limit of trees, known as treeline (Körner and Paulsen 2004). However, *actual* treeline is equally likely to be influenced by a range of variables operating at multiple scales including edaphic variables such as soil type, fertility, and moisture; snow accumulation; wind; disturbances such as fire, avalanches, and rock slides; and biological processes such as competition and herbivory (see Holtmeier 2003, and references therein). Many of these variables are controlled or influenced by terrain attributes such as aspect and slope which are significant correlates of tree growth and vegetation pattern at some alpine forest-tundra ecotones (Bunn *et al.* 2005). Identifying these additional environmental variables, or "regional modifiers" (Körner 1998), and assessing their relative significance is an important task in understanding forest-tundra dynamics and is critical for accurate forecasts of future change.

Species distribution modeling is a method used to relate the observed occurrence of a species at multiple sites to the prevailing environmental conditions at those sites (Guisan and Thuiller 2005). The approach is equally applicable to the distribution of vegetation and habitat types (Guisan and Zimmermann 2000) and models are frequently used to map the probability of occurrence and predict distribution (Franklin 1995). Species data can be simple presence, presence-absence, or abundance, and is typically obtained from field sampling or range distribution maps (Guisan and Thuiller 2005). Environmental predictor variables may be measured in the field but are increasingly derived from maps and datasets within a geographical information system (GIS) (Franklin *et al.* 2000).

There are several published studies of the application of habitat and species distribution modelling and other related spatial analytical techniques at alpine treeline (Brown 1994a, 1994b, Baker and Weisberg 1995, Allen & Walsh 1996, Baker and Weisberg 1997, Kjallgren and Kullman 1998, McGregor 1998, Cairns 2001, Horsch 2003). Collectively, this work has demonstrated the importance of elevation, and by extension temperature, in limiting the distribution of conifers. But it has also shown the relative importance of other variables, and that these differ among regions and even locally within the same region. For instance, based on a comparison of vegetation-topography relationships, Brown (1994a) concluded that factors such as snow cover, substrate, and disturbance frequency are significantly more important in limiting treeline elevation and vegetation pattern in Glacier National Park, Montana, than they are further south in Rocky Mountain National Park, Colorado. At a finer scale, Brown (1994b) found significant differences in treeline vegetation-topography relationships between adjacent subwatersheds in Glacier National Park attributable to variations in wind patterns resulting from different topographical settings.

Much of this previous work has been conducted in either the central Rocky Mountains of North America or the European Alps. There has been less research in alpine regions of the subarctic where the effects of climate warming have been the most pronounced and where marked change is predicted to continue (ACIA 2004). Forecasts of treeline dynamics in these regions based on results from temperate mountain systems where treeline occupies a much higher elevation, has a patchier vegetation pattern, and is biologically more diverse, is less than ideal. Moreover, there is a growing body of literature on recent dynamics of forest-tundra ecotones in subarctic-alpine regions (e.g. Szeicz and MacDonald 1995, Lloyd and Fastie 2003). Pairing data from these investigations with spatial analyses could prove useful in identifying pattern-process interactions in this environment.

Most previous studies have examined either landcover type or vegetation pattern at treeline, as opposed to species distribution *per se*. While insightful in its own right, this is a limitation of the spatial resolution of data used. Maps have typically been derived from aerial film photography and LANDSAT TM data. However, a newer group of satellite sensors, including IKONOS, QuickBird2, and Orbview3, now offer the opportunity for high resolution multispectral as well as panchromatic imaging. This has opened up an entirely new range of mapping precision that includes the ability to resolve individual trees and, in turn, greatly expands the ecological questions which can be addressed through their analysis (Wulder *et al.* 2004).

In this study I used decision tree analysis (DTA) to examine the relationship between (i) distribution and (ii) abundance of white spruce (*Picea glauca*) and several biophysical terrain variables for a 64 km^2 area of forest-tundra transition in the Kluane Ranges, southwest Yukon, Canada. Maps of distribution (in the form of presence/absence) and abundance (in the form of canopy cover) were generated by classifying a multispectral QuickBird2 image. Terrain variables were derived from a 16 m resolution digital elevation model (DEM). Field observations suggested that there is significant variation in the elevation of treeline as well as in the density of spruce at treeline and the central hypothesis was that this variation is partly controlled by terrain characteristics that vary at local to landscape scales. However, the extent of this influence, the specific factors responsible, and whether or not the factors are different for distribution and abundance, were unknown.

STUDY AREA

I conducted this study in the Quill Creek watershed in the northern section of the Kluane Ranges of the St. Elias Mountains. This study area was chosen for several reasons. First, the treeline ecotone occurs on a wide range of grades and aspects here – from steep, well drained slopes to gently sloping plateaus. This allowed for an examination of the influence of terrain characteristics on conifer distribution and abundance and treeline elevation without the confounding effect of different climatic regimes. Second, the area's forests are dominated almost exclusively by white spruce, allowing for species-level mapping and eliminating the influence of interspecific competition between conifers. Finally, large-scale disturbance events such as fire, insect infestation, avalanches, slope failure, and human activies are relatively infrequent across the forest-tundra ecotone in the area (see Chapter 1). In short, this means that landscape-scale disturbances have little effect on spruce distribution in this area and I could safely omit these from consideration as independent predictor variables.

The forest-tundra ecotone in the study area extends from approximately 1200 to 1400 metres. Spruce density thins with increasing altitude and an open canopy prevails at the lower end of the ecotone (the *open forest* zone). Between 1250 and 1350 m the spruce canopy is discontinuous and the crowns of individuals generally do not overlap (the *woodland* zone). Only occasional spruce are found above 1400 m and these are typically stunted growth forms (the *shrubland* zone). I refer to the division between forest and woodland as the timberline. The division between woodland and shrubland coincides with the upper limit of spruce typical of a tree growth form and is therefore referred to as the treeline. Deciduous shrubs become an increasingly important component of the vegetation with increasing altitude. Dwarf birch (*Betula glandulosa*) and gray-leaf willow (*Salix glauca*) are the two dominant species, frequently forming a dense layer over one metre tall in spruce canopy openings and in the shrubland zone (see Birks 1977, for a detailed floristic account of the region).

METHODS

Image Preprocessing

Standard ortho-ready QuickBird2 multispectral (2.4 m pixel) and panchromatic (0.60 m pixel) images were used to map spruce distribution and abundance (Figure 4-1). Cloud-free images from the summer were not available and images from early autumn (September 12, 2003, 13:30 PST) were used. The images covered 64 km^2 and encompassed the forest-tundra ecotone across a wide range of aspects and slope grades. ERDAS version 8.7 (Leica Geosystems, Atlanta, GA, USA) was used in image processing and classification. A Trimble GeoExplorer 2 (Trimble Navigation Ltd., Sunnyvale, CA, USA) global positioning receiver and data logger was used to record the locations of 16 ground control points (GCPs) throughout the study area for accurate spatial referencing of the image. An average of 181 position fixes (SD=68.1), taken every five seconds, were recorded for each GCP location. The points were post-processed for differential correction using data collected from a GeoExplorer 3 unit which simultaneously collected data from a surveyed location at the Arctic Institute of North America Kluane Lake Research Station, 75 km southeast of the study area. Post-processing reporting indicated an average horizontal precision of 1.85 m (SE ± 0.13m). Orthorectification of the images was carried out using the rational polynomial coefficient (RPC) approach (Toutin 2004). A 16 m digital elevation model (DEM) of the study area (see below), was used as elevation input. Total root mean square error (RMSE) was 2.92 m for the panchromatic image and 3.69 m for the multispectral image.

Topographic correction proceeded transformation of digital numbers to at-sensor radiance and was critical due to the rugged nature of the landscape and the low solar angle associated with the higher latitude and image date. The two-step topographic normalization approach of Civco (1989) was used. In the first step, a shaded relief image corresponding to the solar zenith and azimuth at the time of image acquisition was used to modify radiance data. The second step was a band-specific modification based on calibration factors derived from the image. Law and Nichol (2004) tested this approach on IKONOS multispectral data and found it performed better than the Lambertian-cosine or Minneart corrections, especially when image classification is to be undertaken. Some areas of over- and under-correction were obvious upon inspection of the corrected multispectral image. However, these were unavoidable due to the different resolutions of the imagery and the DEM.

Additional preprocessing steps included atmospheric correction and creation of a pan-sharpened image. Scene-based, band-specific, dark-object subtraction (DOS; Chavez 1988) was used for atmospheric correction. This step was not considered as critical as topographic correction since image-to-image comparison was not a component of this study (see Song *et al.* 2001). The corrected panchromatic and multispectral images were fused using the principal component analysis method to create a four-band 0.60 m resolution image (Zhang 2004). This was used to aid in classification of the multispectral image and accuracy assessment.

Image Classification and Spruce Mapping

The primary objective of image classification was to map the distribution of white spruce. The mid-September acquisition date proved both advantageous and disadvantageous in this regard. Leaf senescence was well underway by this time and spruce was readily distinguishable from all other vegetation. Derivation of the normalized difference vegetation index (NDVI) was particularly useful in this regard and it was added as a fifth layer in the image to improve classification (Li and Moon 2004). However, because of the low solar elevation at this time of year (32.2° at the time of acquisition), there was extensive shading in the image and shadows were ubiquitous in treed areas. Several attempts at a supervised classification of the image were unsuccessful because it was impossible to select homogenous training areas. This resulted in confusion between some vegetation classes, most notably between the spruce class and shaded shrub tundra located on north-facing slopes where topographic correction appeared inadequate. Inclusion of a tasseled cap transformation (Yarbrough *et al.* 2005) did not yield significant improvements.

To address these difficulties, I segmented the image into areas of above average and below average illumination based on the shaded-relief image. These were classified separately using an unsupervised classification. Elevation was included as a sixth image layer in the low-illumination subset to improve accuracy (Wulder *et al.* 2004). The ISODATA algorithm was used to group each image subset into 100 clusters. The pan-sharpened image was used to assist in assigning these clusters to a land cover class. From these initial 200 groupings, 24 clusters were classified as spruce. Eleven additional clusters were identified as "potentially" spruce and were placed into a pool of pixels which were classified again (Jiang *et al.* 2004). Clusters identified as spruce in this second round were added to the initial set, resulting in a binary map of spruce presence and absence. Approximately 8% of the image was topographically shaded and left unclassified.

The binary map was down-scaled to derive two 16 m resolution maps for use in distribution modelling. The first was a map of relative abundance. This was generated by casting a virtual net across the map and tallying the number of spruce pixels captured in each 16 x 16 m mesh based on the location of grid cell centres. This number was divided by the total number of pixels captured by each mesh, yielding a continuous map of percent spruce analogous to a map of canopy cover. This continuous data field was then transformed into a binary categorical field by recoding any pixel with values >0 as 1, but leaving all values =0 as 0, thereby yielding a 16 m resolution presence/absence map.

Classification accuracy of the 2.4 m binary map was assessed with 209 random points. Classification membership of each point was automatically determined within ERDAS. Actual presence or absence of spruce at that location was determined by inspecting the pan-sharpened image. Accuracy of the 16 m binary map was assumed to be at least equal to values obtained at 2.4 m and accuracy of the canopy map was a function of the initial classification.

Environmental Variables

Terrain variables for the study area were derived from a 16 m DEM produced by the Yukon Territorial Government (TYG) for the Canadian digital elevation data (CDED) database. This DEM was generated from contour intervals and stream networks in version 3 of the 1:50,000 National Topographic Database (NTDB) and is the most horizontally accurate DEM available (Matt Wilkie, YTG, pers. comm.). Slope grade and aspect are the two most common terrain attributes derived from DEMs and were calculated using SAGA GIS (Göttingen University, Germany). Slope was calculated in degrees and aspect as degrees clockwise from north. This circular measure required transformation to a linear scale and a measure of "southwestness" was derived (Miller 2005).

Direct solar radiation has a significant effect on local climate in mountainous subarctic regions. In addition to the direct resource gradient of light, direct radiation influences timing of snowmelt and the extent of daytime heating which, in turn, influences the distribution of permafrost (Pomeroy *et al.* 2003). The amount of direct solar radiation a slope receives is a function of its aspect, gradient, and surrounding topography and can therefore be estimated using a DEM. Potential direct solar radiation was calculated using the Solar Analyst extension (HEMI, Los Alamos, NM) for ArcView (ESRI, Redlands, CA) by totalling daily estimates of direct radiation at weekly intervals for each season (April-May, June-August, September-October, November-March). Estimates were calculated at hourly intervals during each day and summed to yield daily potential.

Winter snow accumulation and timing of melt can have both positive and negative effects on the growth of conifers at treeline (Geddes *et al.* 2005). Convex sites tend to be wind blown and accumulate less snow while snow tends to accumulate in topographically concave settings (Holtmeier 2003). Therefore, in the absence of detailed snow data, landscape curvature was considered a surrogate for snow distribution potential. Measures of plan and profile curvature were derived from the DEM and landscape curvature was classified according to the 9 categories in Table 4-1.

The distribution of moisture across the landscape is partly controlled by topography, and I used the topographic wetness index (TWI) as a measure of this effect (Beven and Kirkby 1979). Soil type and characteristics such as holding capacity clearly have an influence on this potential, but this type of data were not available. However, bedrock geology has been mapped for the area at a scale of 1:50,000 based on extensive field reconnaissance (Israel *et al.* 2005) and digital coverages were obtained from its authors.

Two independent variables were derived from the QuickBird2 multispectral image. The first, percent rock cover, was calculated in the same manner as the canopy cover map, but the input data used were the classes identified as rock or gravel during the initial unsupervised classifications. Areas near these features tend to have shallow soils and percent rock cover was used as a surrogate of soil availability and depth. The second variable was non-spruce NDVI, calculated as the average NDVI value for all non-spruce pixels in each 16 m mesh. NDVI is commonly used as an index of vegetation "greenness" or vigor and is correlated with aboveground biomass. Interactions with other vegetation including competition or facilitation may be an important factor influencing spruce distribution and canopy cover.

Despite its biological promise as an explanatory variable, I was unable to test this hypothesis since nonspruce NDVI was highly correlated with elevation. Inclusion of multiple correlated variables violates the assumption of independence and I therefore removed nonspruce NDVI from further consideration. Other highly correlated independent variables were the four seasonal estimates of direct solar radiation and southwestness. Potential direct radiation for June-August was chosen as the single variable from this group, leaving a total of seven variables used in model development (Table 4-2).

Spatial Sampling

Data points near to each other have a higher probability of being similar, known as spatial autocorrelation (Dale and Fortin 2002). Utilizing every case in the data set would therefore violate the statistical assumption of independence between cases and lead to biased results and incorrect conclusions (Segurado *et al.* 2006). Systematic sampling was used to reduce the level of spatial autocorrelation in the data (Cairns 2001). However, data sampling presents a tradeoff between maintaining a sufficiently large data set and minimizing autocorrelation. I used semivariogram and correllogram analysis of the spruce canopy map to determine the optimum sampling scale (Cablk *et al.* 2001). Seven 1 km^2 subsets of the map were used for analysis. These were distributed evenly across the map and positioned such that they spanned the full extent of the forest-tundra ecotone.

Moran's coefficient (I) was used as a measure of spatial autocorrelation. Values can range from +1 to -1, with high and low values indicating significantly positive and negative spatial autocorrelation. Zero represents complete spatial randomness in the dataset. Although results varied among the seven subsets, reductions in I declined slowly after a separation distance of approximately 200 m and a 12 pixel sampling lag (192 m, average $I \approx 0.15$) was chosen.

Initial sampling yielded a training data set of 1693 pixels within the mapped area. This was further reduced by removing pixels above 1750 m elevation, well above the altitude of spruce growth, and pixels falling within topographically cast shadows and water bodies. The final training data set contained 1437 samples. A validation data set was also generated (see below). This was sampled from the full raster data set at the same 12 pixel lag, but offset from the training data set by 6 pixels in the horizontal and vertical directions. The same refinements were placed on this data as for the training data, yielding a validation set of 1439 samples.

Model Development and Evaluation

A variety of computational methods have been used in species distribution modelling (Guisan and Zimmerman 2000). An increasing number of studies have compared the efficacy of these methods in a variety of settings (e.g. Franklin 1998, Thuiller *et al.* 2003, Miller 2005) including alpine treeline (Cairns 2001). Conclusions vary, suggesting that there is no one best technique for all circumstances. In this study, the rationale for model development was to aid in hypothesis testing, rather than prediction. Although decision tree analysis (DTA) is increasingly used for prediction, it is rooted in data mining and exploration and was chosen because it is particularly useful when (i) variables are suspected of interacting in a hierarchical fashion, and when (ii) relationships between the dependent and some independent variables are conditional on the values of other independent variables (Franklin 1995).

The output of DTA is a graphical tree which is "grown" by repeatedly splitting the data into increasingly homogenous subsets. Each split, or node, is defined by a simple rule based on a single independent variable. Rules are selected based on a measure of how well variance within the resulting subsets is reduced. Independent variables can be a combination of continuous and categorical data and the dependent variable can be either continuous (regression trees), or categorical (classification trees).

I used S-Plus v.6 for Windows (Insightful Corp., Seattle, WA) to generate the classification and regression trees. Trees were grown to a minimum size of 10 cases per node. However, this tends to overfit data. The standard approach to obtaining the most parsimonious tree is through a process called "pruning" where the smaller branches explaining the least amount of variation are removed. I used cross-validation to determine the optimum size of the trees (De'ath and Fabricus 2000). Instead of the more common approach of using multiple subsets of the original training data for cross validation, I used the validation data set for this purpose (e.g. Cairns 2001). The node closest to the root node where deviance in the validation data set stopped being reduced was chosen as the pruning point. Cross validation was based on the number of misclassifications for the classification tree and on the amount of deviance explained for the regression tree.

The classification and regression trees were used to generate a map of 'expected' spruce presence/absence and canopy cover. From these, a classification error map was generated for presence/absence and a residual map was generated for canopy cover. These "observed versus expected" maps were then used to assess model accuracy and generality. This was aided by an examination of the spatial distribution of misclassifications and regression tree residuals to identify areas where the model fit particularly well and where it fit poorly.

RESULTS

Mapping

Pixel abundance in the 2.4 m classification indicated that spruce covered 12.5% of the landscape (Figure 4-2). This was inflated to 36.8% in the 16 m presence/absence map. Canopy cover averaged 12.5% (SD=23.8%) across the entire study area, and 34% (SD=28.4%) when null values were omitted (Figure 4-3). Spruce classification accuracy from the QuickBird2 image was high, with overall kappa (κ)=0.866 (Table 4-3). Three areas of the image were identified as slightly problematic and all classification errors identified in the accuracy assessment were located there. These areas were gently sloping, generally north facing areas of low spruce density. Field reconnaissance indicated that they were underlain by permafrost with a ground layer comprised primarily of dwarf birch, feathermosses, and sedges (*Carex* spp.). Spruce, while present, were of small stature and some of these individuals were misclassified.

Presence/Absence Model

The unpruned classification tree contained 76 terminal nodes with a misclassification error rate of 8.6%. Cross-validation indicated pruning the tree to an optimum size of 5 terminal nodes (Figure 4-4a). Misclassification increased to 14.6% after pruning and only two explanatory variables remained. Elevation was clearly the most important of these (Figure 4-4b). Including rock cover as an explanatory variable further reduced misclassification, but its influence was not nearly as significant. In summary, the tree model predicted an 8% probability of spruce occurring at elevations above 1364 m. Lower elevations had a 79% probability of spruce, provided that rock cover was less than 7%. If rock cover was greater than 67% there was a 0% probability of spruce being present.

Comparison of expected and actual distributions (Figure 4-5) indicate that the model was generally robust with an overall accuracy of 85% and κ=0.695 (Table 4-3). False negatives (omissions) were concentrated almost entirely at treeline. False positives (comissions) were three times as prevalent as false negatives due primarily to a large cluster of false positives in the lower left quadrant of the mapped area. This coincides with the area of problematic image classification noted previously.

Abundance Model

The unpruned regression tree contained 62 terminal nodes and explained 71% of the variance in the training data. Cross-validation indicated pruning the tree to an optimum size of 11 terminal nodes (Figure 4-6a). Five of the seven independent variables were used in the pruned tree, which explained 52% of the training data variance. The initial split based on elevation accounted for more than half of this (Figure 4-6b). Elevations greater than 1298 m had little or no spruce (mean=3.2%, median=0%). At lower elevations spruce canopy cover was generally controlled by direct summer solar radiation. A threshold of 497 kWh/m^2 was identified, which generally corresponds to a division between aspects of 135-225° and all other slopes. At elevations less than 1298 m, canopy cover averaged 24.6% when values were below this radiation threshold and doubled to a mean of 49.4% when radiation was above this threshold. Additional variables used in the tree, in order of importance, were rock cover, slope, and geology.

Standard deviations of regression tree residuals are mapped in Figure 4-7. Mean residual value was -4.8 (SD=18.3), indicating that values tended to be over-predicted. This is attributed to the large homogenous areas above treeline which were assigned a prediction of 0.7%, even though spruce was absent in most cases. While regression trees are capable of prediction, only the mean value for a particular class of observations is given. This typically yields high residual values and makes accuracy assessment of predictions rather ineffective. A more telling interpretation of the residual map is to examine the spatial distribution of error. In this case, it is evident that canopy cover in the upper portions of the Quill Creek valley (lower center of map) tended to be underestimated, along with cover in two smaller valleys immediately northeast. There were comparatively fewer areas of substantial overestimation, though an area on a mainly south-facing slope near the junction of Nickel and Quill Creeks in the northeast quadrant of the map is particularly evident.

DISCUSSION

Elevation was clearly the most important variable influencing the distribution of white spruce across this landscape. Although there are other environmental gradients that correlate with elevation, temperature is the most important of these from a biological standpoint and it is not unreasonable to state that temperature, not elevation *per se*, is the gradient of influence. The July 10° C isotherm is often used as a correlate of treeline elevation in mountain regions (Körner 1998). Mean July temperature at the Burwash Landing meteorological station, located at 807 m, is 12.8°. A field-measured lapse rate of 0.65° C per 100m therefore suggests that treeline should be located at approximately 1240 m. The initial splitting rules in the regression and classification trees used elevations of 1299 m and 1365 m and support this general relationship for the Kluane region.

The importance of elevation in spruce presence/absence at this scale of analysis is not surprising. What is interesting is the extent of its importance or, more precisely, the relative unimportance of the other variables. Rock cover, and by extension soil depth, merely served to "fine tune" the classification tree. None of the other variables were significant enough to include in the model. Nevertheless, temperature and soil depth do not account for all variation in spruce presence/absence. The modelled expected distribution was a good general approximation, but there were significant omissions and comissions. These were especially evident at treeline, where the classification rules failed to simulate the transition from forest to tundra, instead predicting an abrupt transition based on the elevation threshold. This suggests that other variables are important at finer scales, but that this influence is effectively cancelled out when the entire landscape is considered.

These finer scale variables could include some or all of the five variables not included in the pruned classification tree. They may be locally important, in which case they would have been omitted in tree pruning. Or, they could be ubiquitously important but not detectable with the data used here. GIS-based modelling approaches are limited by the difficulty of measuring direct gradients and resources across larger areas (Austin 2002). The result is a reliance on correlates of the variable, rather than measures of the variable itself. For instance, landscape curvature was used as a surrogate for snow distribution in the absence of actual measures of snow depth or distribution of spring melt. Yet, in light of the relatively low snow accumulation in the study area, fine-scale distribution and melt-patterns are likely to be equally as influential but, in this case, undetectable (e.g. Beck *et al.* 2005).

Alternatively, the variables acting at finer scales could include factors not even considered here. For instance, Alftine and Malanson (2004) examined the role of positive feedbacks such as wind sheltering and concluded that such processes are important in structuring the pattern of conifer establishment at treeline. Conversely, negative feedbacks including reduced soil temperatures resulting from canopy shading (Körner and Paulsen 2004) may also influence treeline pattern at finer scales. It is impossible to determine the importance of these types of variables from this analysis, although the absence of a "patch forest zone" common in the Rockies and Alps, and lack of extensive flagging or a classic krummholz zone, suggests that wind exposure is not as significant in the Kluane region.

The greater number of variables and terminal nodes in the regression tree indicates that controls on canopy cover are not as simple as those for presence/absence and that the two are not influenced by the same variables to the same extent. Elevation is indeed influential, but this was heavily influenced by the difference between values equal to and greater than zero. More meaningful is an examination of canopy cover only in areas where spruce is present. In these instances, canopy cover is more significantly influenced by the amount of solar radiation a slope receives. Field observations indicated that spruce is actually more abundant on slopes with lower solar radiation (Chapter 2), but that the stature of these individuals is so small that canopy cover is far less than equivalent slopes with greater radiation. Interpretation of the model should therefore be that slopes receiving higher levels of direct radiation tend to support larger trees with greater canopy cover, not necessarily more individuals.

Significant underestimation of canopy cover at lower elevations along Quill Creek is attributed to favourable soil conditions on these sites. Deep alluvial fans exist where smaller tributaries flow into Quill Creek and these support large trees that form forests similar to those found at lower elevations in the Shakwak Trench further east. However, it is unclear why canopy cover was underestimated at higher elevations. Upper portions of the Quill Creek valley, as well as the two adjacent valleys, are defined by relatively high steep walls. It is possible that this topography creates a slightly warmer microclimate, perhaps by way of thermal inversions that reduce cold temperature damage or the channelling of warm air up-valley from their outlets (Beniston 2006).

The large area of canopy cover overestimation in the northeast portion of the study area is known to be occupied by a dense stand of trembling aspen (*Populus tremuloides*). Similar, though smaller, areas of overestimation occupied by aspen or balsam poplar (*Populus balsamifera*) were apparent at or near treeline on other south facing slopes. Such stands can be indicative of disturbances such as fire (Dale *et al.* 2001), though field observations did not offer evidence of this. In the absence of recent disturbance, there are three plausible explanations for why these species might occupy areas near treeline that are otherwise above the temperature minimum for spruce. They may be able to colonize sites with poorer or thinner soils, a factor which DTA indicated was limiting for spruce. In addition, aspen can withstand higher rates of evapotranspiration (Hogg and Hurdle 1995). With limited precipitation, a moisture deficit is not unlikely on south-facing slopes in many years. There is some evidence to indicate that such moisture deficits favour open aspen stands in Yukon and Alaska and that warmer and drier climates could result in a shift in forest composition (Hogg and Wien 2005).

A third explanation is that these deciduous species can prevent colonization of spruce by out-competing them for critical resources in the marginal conditions at treeline. This hypothesis is equally applicable to the willow and birch shrub component and therefore applies to all aspects. There are several locations where there is a remarkably abrupt transition from open spruce forest to large expanses of dense willow and/or shrub cover. This type of abrupt change over relatively smooth environmental gradients is not uncommon at treeline (Wiegand *et al.* 2006). Competitive exclusion, particularly as it relates to seedling establishment and growth, seems a plausible hypothesis in these instances (c.f. Bond 1989). However, I was unable to explore this with DTA at this scale of analysis due to the high correlation between elevation and non-spruce NDVI.

Object-oriented classification may be able to circumvent this issue by providing the capability of accurately mapping the shrub component of the landscape as opposed to relying exclusively on NDVI. In fact, it is likely that such a map would yield several additional possibilities for spatial analysis of vegetation on this landscape. It could also alleviate the pixel-based classification confusion that was associated with image shadows and assist in improving classification of the small statured spruce on north-facing slopes. This is the natural next step for future work using the QuickBird2 image used here, and these techniques are becoming increasingly common as experience with very high resolution imagery increases.

CONCLUSION

A primary characteristic, and advantage, of classification and regression trees is their hierarchical nature. When applied to spatial data, variables that operate at larger scales will be used as splitting criteria at a higher level in the model. Variables that are more local in their influence are used in the decision rules closer to the terminal nodes (Moore *et al.* 1991). In this context, the results of this analysis combine to support four general conclusions regarding the forest-tundra ecotone in southwest Yukon:

i. elevation (and hence temperature) acts at a broader scale than all other variables in influencing the distribution of white spruce and, therefore, treeline location;

ii. direct solar radiation is the primary control over spruce canopy cover, likely by way of its influence on snow melt, soil temperature and permafrost distribution, but it has a negligible role in determining presence/absence at this scale of analysis;

iii. soil availability and depth is the most influential site-specific variable controlling spruce distribution and canopy cover;

iv. the role of environmental factors operating at finer scales is more variable across the landscape and is partially contingent on the elevation (and thus temperature) and aspect (and thus direct solar radiation) of a particular location.

Collectively, these general conclusions suggest significant potential for white spruce to expand its distribution upslope of the current treeline in southwest Yukon with continued climate warming, provided that suitable and adequate substrates are available. However, the variability identified in this analysis indicates that the spatial pattern of advance, as well as changes in canopy cover, will be heavily dependent on local, fine-scale conditions. Forecasting beyond these general, coarse-scale, scenarios requires an understanding of how plant and population-level processes vary in relation to such heterogeneity.

Table 4-1. Categories used to classifiy landscape curvature. Measures of plan and profile curvature were derived from the DEM with values between +0.001 and -0.001 considered plane. Values in brackets indicate the amount of the landscape comprised by each class.

	Plan Curvature		
Profile Curvature	**Concave**	**Plane**	**Convex**
Concave	A (10.0%)	D (13.9%)	G (5.4%)
Plane	B (9.3%)	E (28.4%)	H (12.1%)
Convex	C (3.1%)	F (7.2%)	I (10.4%)

Table 4-2. Environmental variables used as independent variables in the classification and regression trees.

Name	**Description**	**Source**	**Range ($\bar{x}$ ±SD)**	**Rationale**
elev	Elevation (metres)	Original DEM	931 – 2138 (1402.6 ±223.0)	Controls vertical temperature gradient
slp	Slope gradient (degrees)	SAGA GIS	0 – 51.0 (22.6 ±11.2)	Influences drainage and soil development
srad	Direct solar radiation, Jun 1-Aug 31 (kW/m2)	ArcView Solar Analyst	77 – 639 (444.8 ±110.8)	Influences air and soil temperature, snowmelt and evapotranspiration
curv	Slope curvature (categorical)	SAGA GIS	9 classes	Influences snow accumulation and drainage
wet	Topographic wetness (unitless)	SAGA GIS	3.8 – 17.6 (6.7 ±1.8)	Measure of soil moisture potential
geol	Bedrock geology (categorical)	Israel *et al.* 2005	14 classes	Substrate influences soil type which may influence vegetation
rock	Rock & gravel (percent of pixel)	QuickBird MS image	0 – 100 (10.4 ±24.7)	Surrogate for soil depth

Table 4-3. Measures of classification and prediction accuracy. Values for image classification are calculated from 209 random points evaluated with the 0.60 m pan-sharpened image. Values for classification tree predictions are based on the entire study area, excluding areas of topographic shading. Based on formulae presented by Fielding and Bell (1997).

Accuracy Metric	**QuickBird Classification**	**Classification Tree Prediction**
Prevalence	0.517	0.398
Overall diagnostic power	0.483	0.602
Correct classification rate (overall accuracy)	0.933	0.849
Sensitivity (producer's accuracy)	0.917	0.911
Specificity	0.950	0.808
False positive rate (comission error rate)	0.050	0.192
False negative rate (omission error rate)	0.083	0.089
Positive predictive power (user's accuracy)	0.952	0.758
Negative predictive power	0.914	0.935
Misclassification rate	0.067	0.151
Odds-ratio	211.200	43.008
Kappa (κ)	0.866	0.695
Normalized Mutual Information Statistic	0.649	0.414

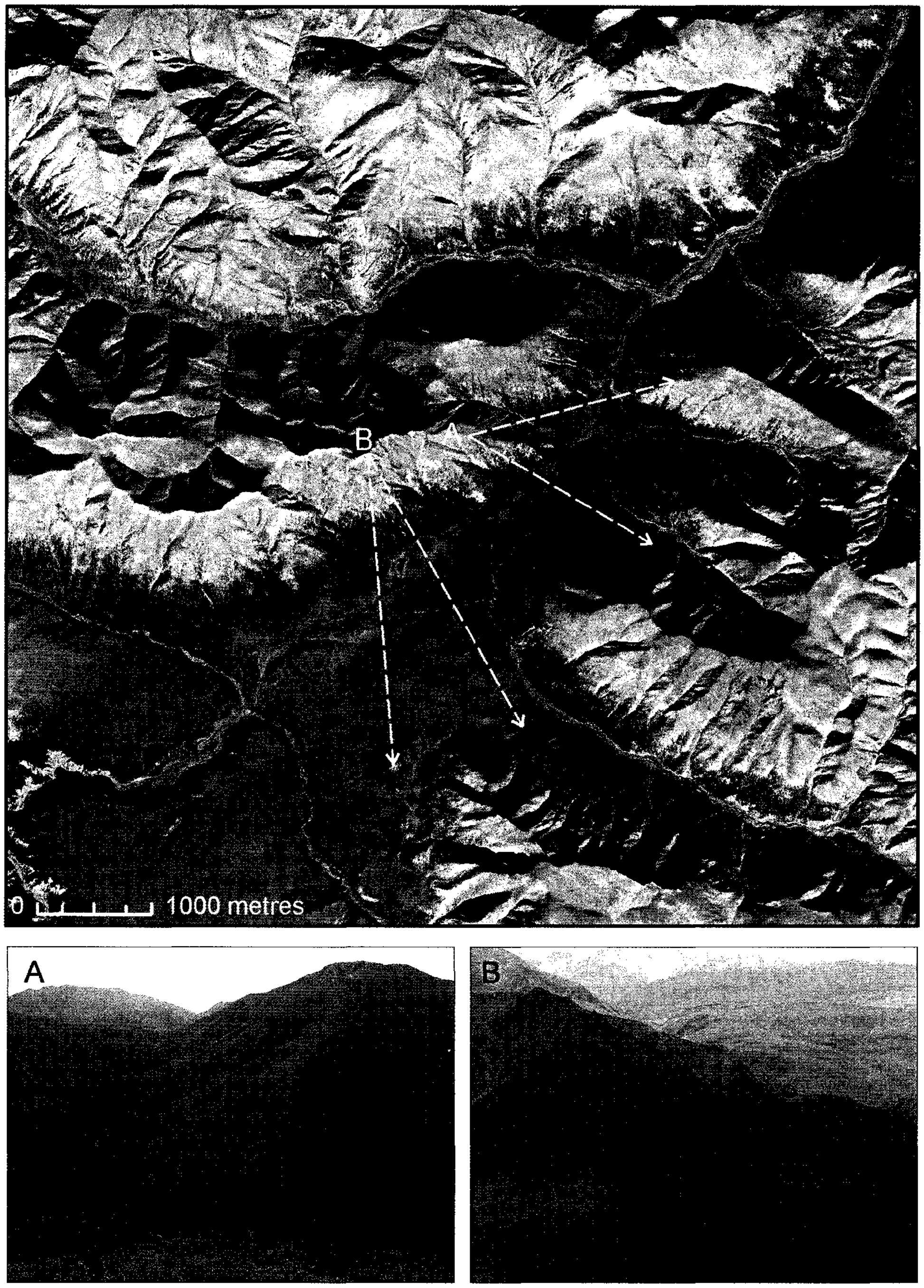

Figure 4-1. The corrected multispectral QuickBird2 image (false colour infrared representation). Vantage point and approximate field of view are shown for the two photographs. (A) illustrates the variation in treeline elevation associated with aspect. (B) illustrates heterogeneity in vegetation pattern.

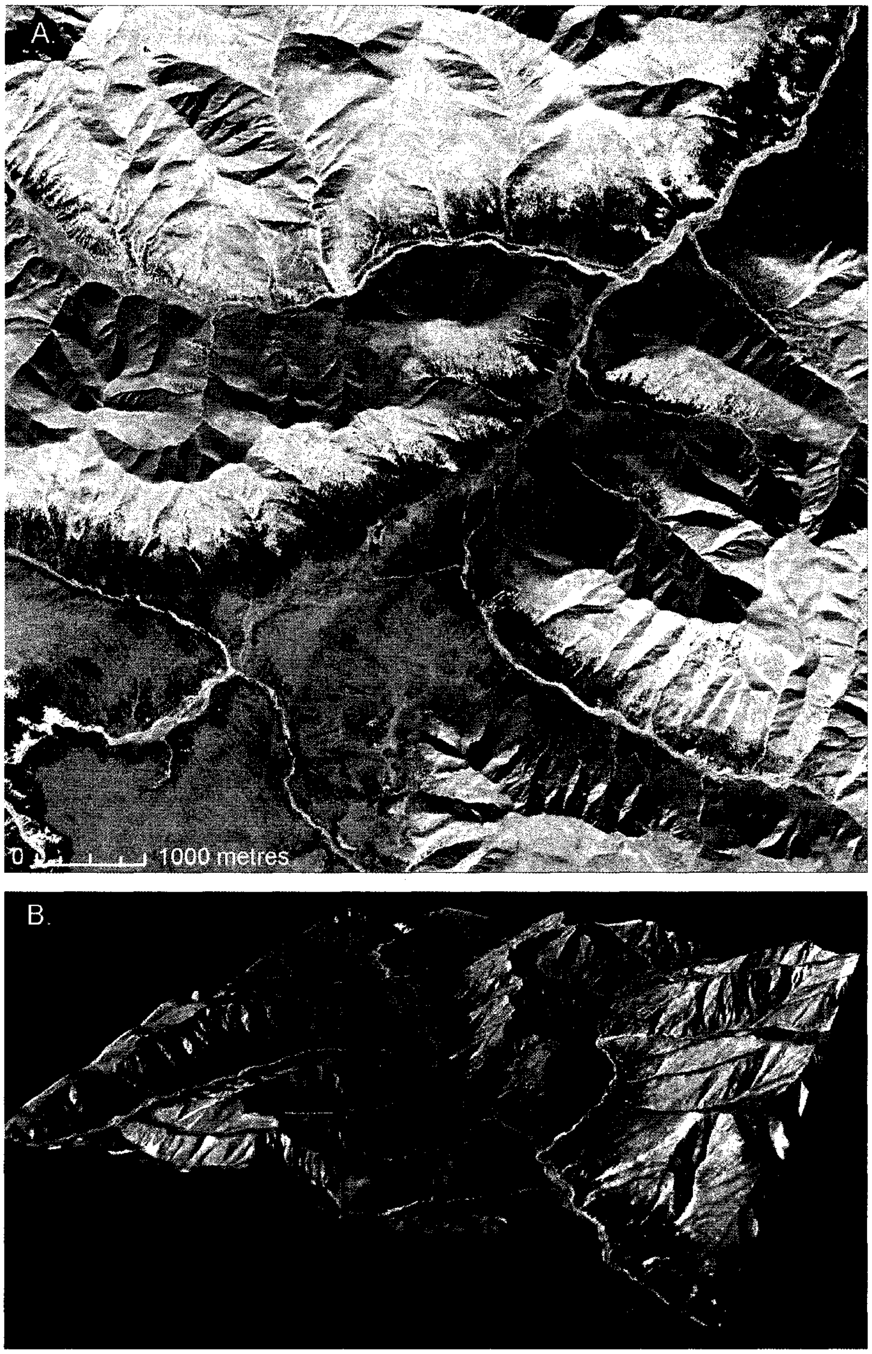

Figure 4-2. (A) Distribution of spruce in the study area at 2.4 m resolution. Pixels classified as spruce are shown in dark green superimposed over a faded true colour representation of the mulitspectral QuickBird2 image. Black indicates areas under topographic shadow or water bodies that were not classified or sampled as part of the decision tree analysis. (B) A 3-dimensional representation of the landscape. Perspective is from the northeast looking southwest.

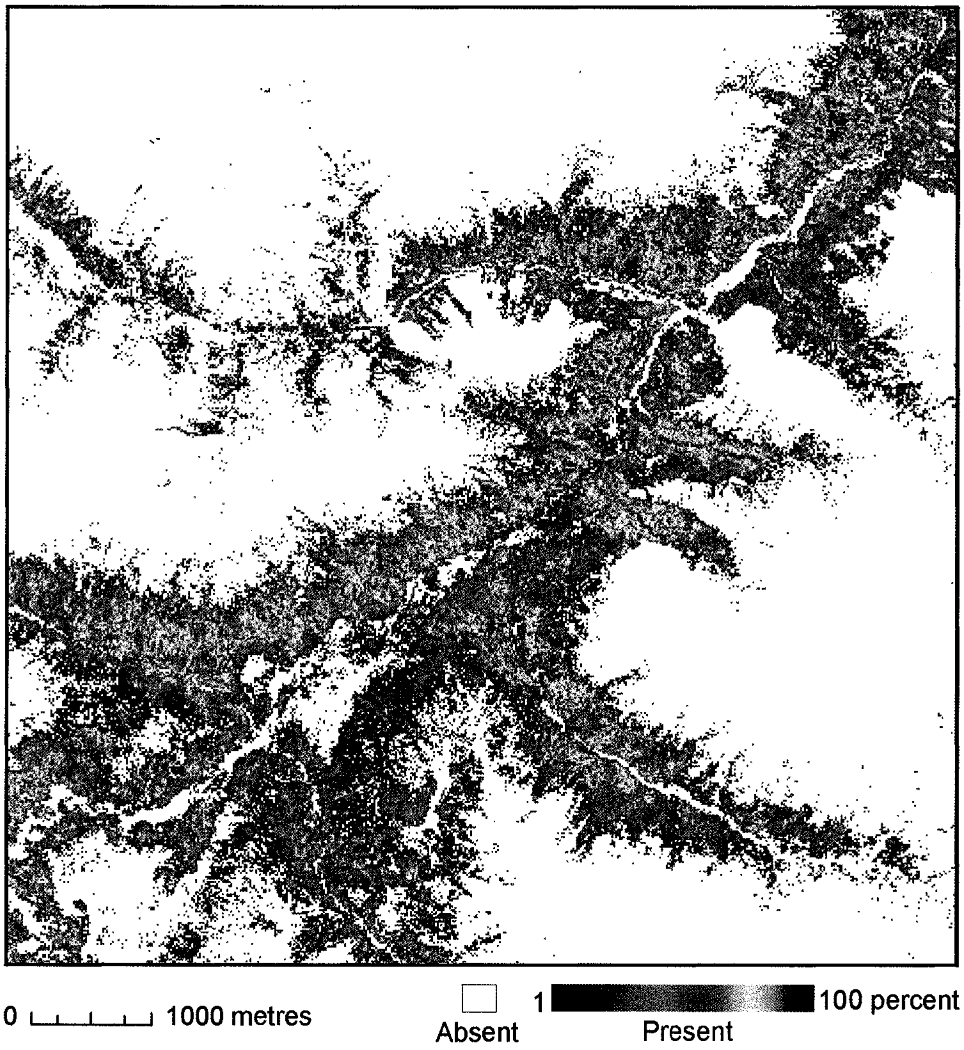

Figure 4-3. Spruce presence/absence and canopy cover (in percent) at 16 m resolution.

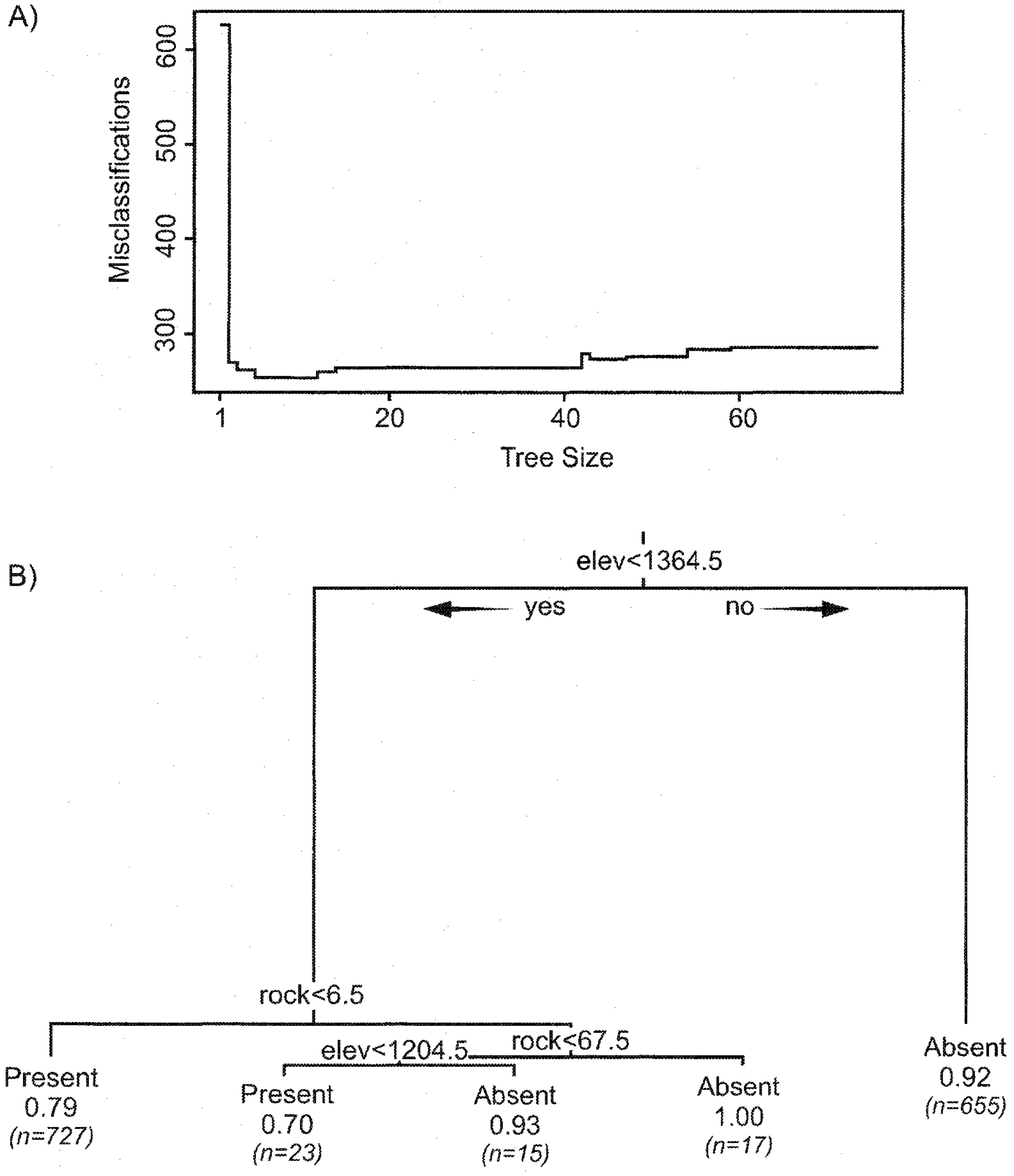

Figure 4-4. Classification tree analysis for spruce presence/absence. (a) Cross validation using the validation data set indicated an optimum tree size of 5 terminal nodes. (b) The pruned classification tree. Starting at the top of the tree each split is represented as an inequality. If the inequality is true, proceed to the left branch of the node; if false, proceed to the right. Presence or absence contingent on these partitions is indicated at each terminal node along with the probability of arriving at that result and the number of data points used in formulating that result. The extent to which misclassification is reduced by each split in the data is represented by the relative lengths of the vertical lines in the tree.

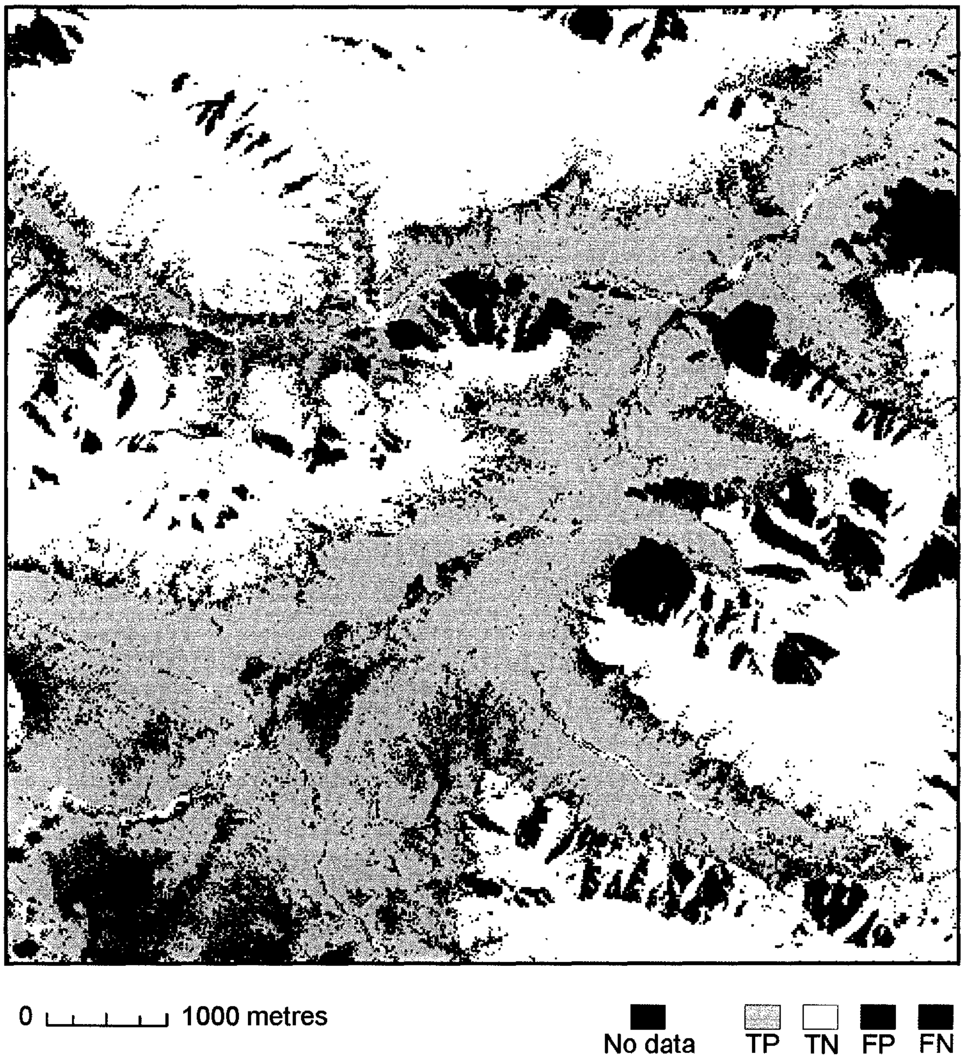

Figure 4-5. Comparison of observed spruce distribution with predictions based on the classification tree model. True positives (TP) and true negatives (TN) indicate areas where the model accurately predicted presence and absence, respectively. False positives (FP) and false negatives (FN) are areas where the model inaccurately predicted presence and absence, respectively. Black areas were not classified due to topographic shading in the QuickBird2 image.

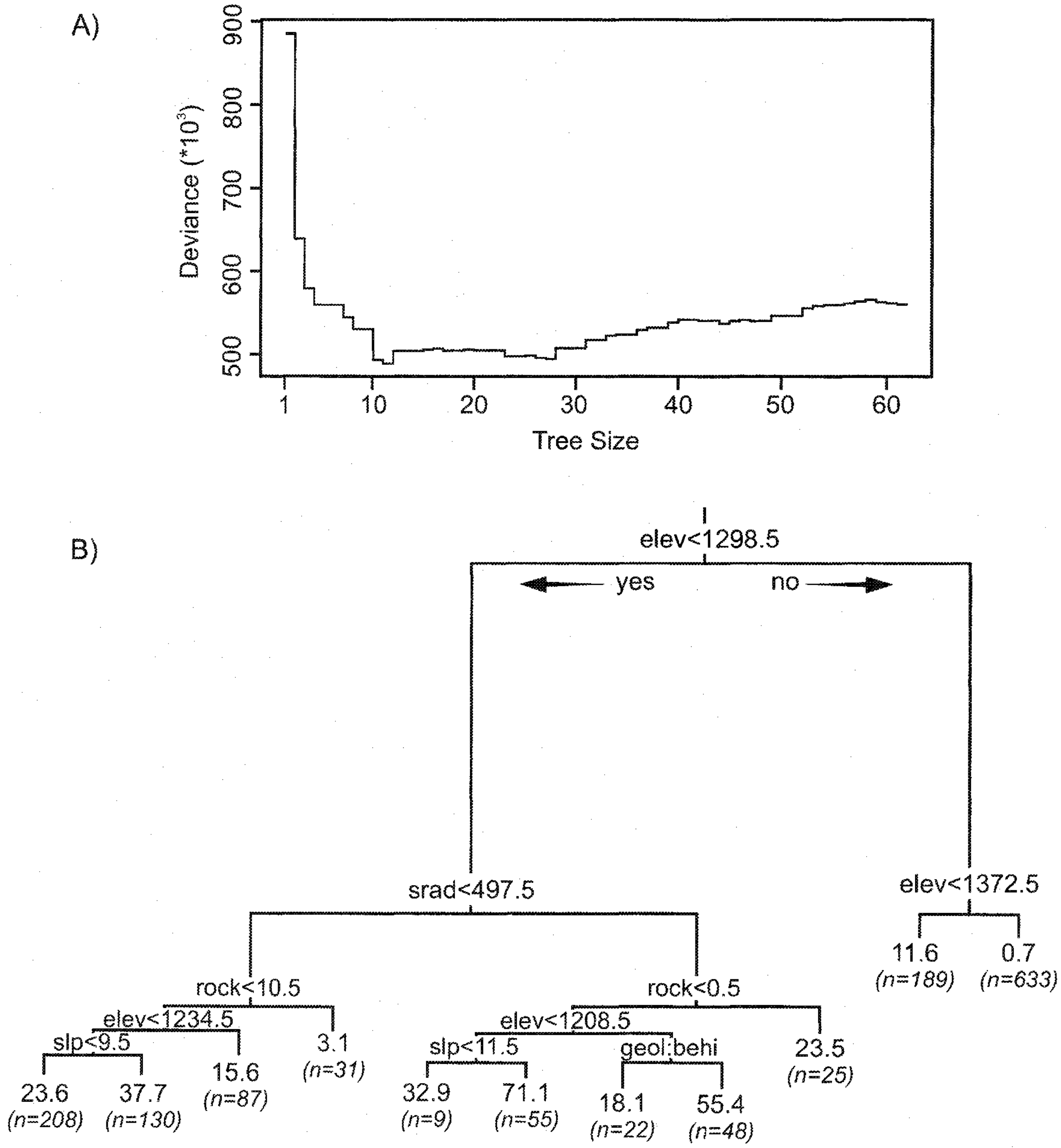

Figure 4-6. Regression tree analysis for spruce canopy cover. (a) Cross validation using the validation data set indicated an optimum tree size of 11 terminal nodes. (b) The pruned regression tree. The value at each terminal node is the mean of all data used in developing the node and, therefore, the predicted response. The proportion of the total sum of squares explained by each split in the data is represented by the relative lengths of the vertical lines in the tree.

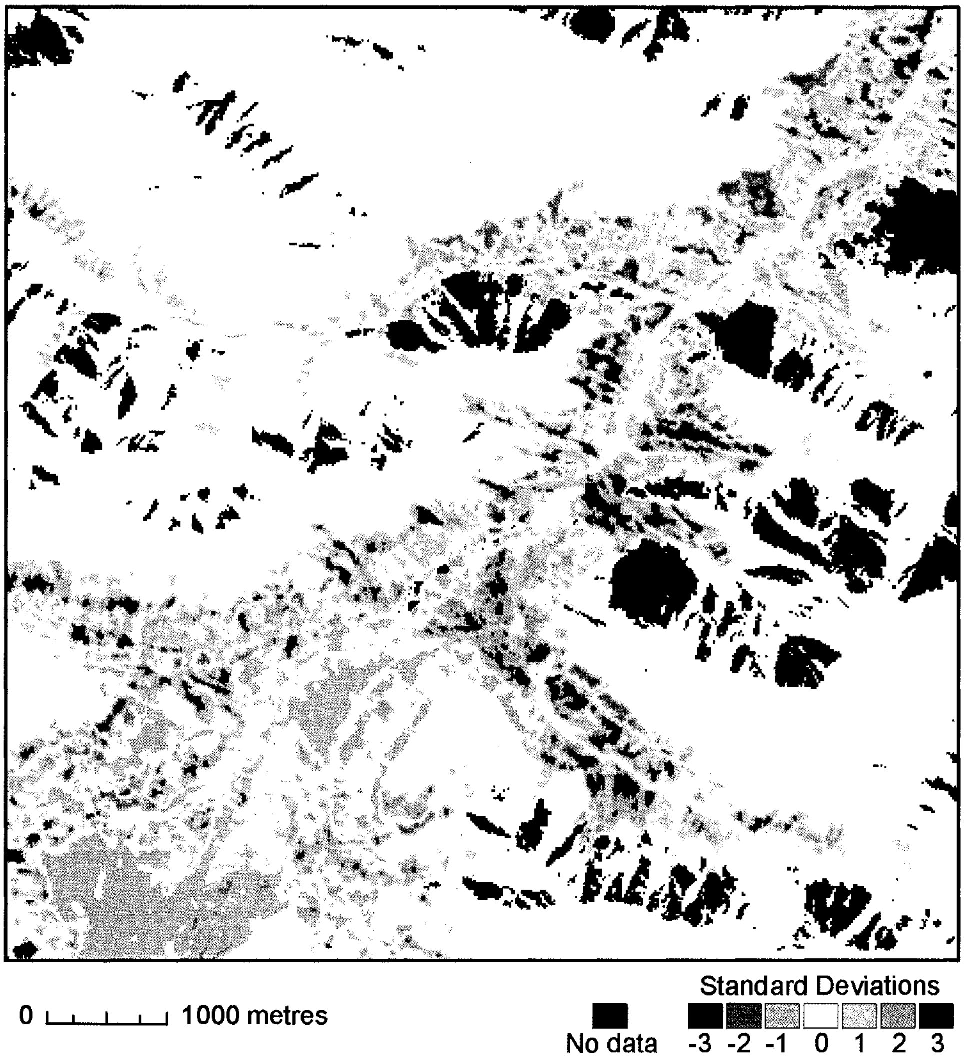

Figure 4-7. Map of regression tree residuals. Input data was canopy cover minus values predicted by the regression tree rules. Standard deviation is equal to 18.3%. Reds indicate underprediction, blues overprediction. Darker values indicate areas of greater error, lighter values indicate less error. Black areas were not classified due to topographic shading in the QuickBird2 image.

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CHAPTER 5

Responses of White Spruce (*Picea glauca*) to Experimental Warming at a Subarctic Alpine Treeline [1]

INTRODUCTION

Temperature is widely considered to be the dominant variable controlling the elevational and latitudinal limits of tree growth, commonly referred to as treeline (Tranquillini 1979, Jobbágy and Jackson 2000, Körner and Paulsen 2004). An extension of this relationship is the hypothesis that future climate warming will cause treeline advance. Empirical support for this hypothesis comes from evidence of higher and more northerly treelines during warmer periods of the mid-Holocene, as well as recent advance of many treelines in response to post-Little Ice Age warming (Rochefort *et al.* 1993, MacDonald *et al.* 2000). Widespread changes to treeline could have important consequences for the Earth's climate system in terms of surface albedo and carbon cycling (Chapin *et al.* 2000). At regional scales, treeline advance could have significant effects on land cover and habitat structure, especially in mountainous areas where an upward advance of treeline could reduce and fragment alpine habitats (Moen *et al.* 2004).

Despite a long history of research, the mechanisms whereby temperature acts to limit the distribution of trees at high altitudes are still not fully understood (Grace *et al.* 2002). Several functional explanations have been offered, including growth-related factors such as limited seed development, germination, and recruitment; a negative

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[1] A version of this chapter has been accepted for publication in *Global Change Biology*.

balance between photosynthesis and respiration; and structure-related factors such as frost damage, winter desiccation, and mechanical damage by wind, snow, and ice (Tranquillini 1979, Sveinbjornsson 2000). Körner (1998) conducted an extensive review of the literature and concluded that while these factors can be important in specific regions or to certain species, they do not offer a universal explanation for the existence of altitudinal treeline worldwide. He proposed a growth limitation hypothesis whereby low temperatures prevent tissue synthesis from matching the minimum requirements for tree growth. In contrast to the carbon balance hypothesis, Körner's hypothesis holds that it is not the supply of photoassimilates *per se* but, rather, their low rate of conversion to plant tissue that prevents individuals from attaining a tree growth-form.

Smith *et al.* (2003) offered a different perspective, stressing the role and mechanisms of seedling growth. Their model of treeline advance depended largely on ecological facilitation in these early stages. This perspective is particularly significant as growth of seedlings and saplings appears to be the most critical period for individuals at alpine treeline (Paulsen *et al.* 2000). Above these canopy heights the plant becomes increasingly coupled to the thermal and radiative conditions of the open atmosphere and decoupled from the shelter and warmth associated with the ground (Paulsen *et al.* 2000, Smith *et al.* 2003). If low temperatures limit the biochemical processes necessary for growth, either by way of a negative carbon balance or insufficient tissue synthesis as the literature suggests, then climate warming is likely to result in an altitudinal advance of treeline by allowing seedlings and saplings to grow faster and extend above the ground-coupled thermal boundary layer with fewer adverse effects.

In situ temperature manipulation is a common technique in assessing the potential effects of climate warming on arctic and alpine plants and plant communities (Arft *et al.* 1999, Walker *et al.* 2006). The most common approach is the use of passive open-top chambers (OTCs), of which several designs have been used (Marion *et al.* 1997). For this study I used passive OTCs to warm 40 young white spruce (*Picea glauca* [Moench] Voss) at two alpine treelines in southwest Yukon, Canada, over four summers. Along with parts of Alaska, the Yukon has seen the most significant climate warming of all subarctic regions over the last half century, and this trend is expected to continue (ACIA, 2004). My objectives were to quantify the effect of increased temperatures on (i) primary and secondary growth and (ii) rates and efficiency of photosynthesis. My goal was to test the hypothesis that a slight increase in temperature in this environment will result in a significant difference in growth, leading to faster recruitment into the tree population and, in turn, treeline advance. The overarching rationale for the study is one related to global change and the prediction of vegetation response to a changing climate. However, the approach also permits an assessment of more fundamental questions related to the existence of alpine treeline and the specific role of temperature on tree growth and distribution at high altitudes.

Given the variety of terms in use (Löve 1970), it is important to clarify my terminology. I refer to the general transition from forest to tundra as the forest-tundra ecotone. Treeline is used with specific reference to the boundary coinciding with the upper altitudinal limit of individuals typical of a tree growth form, which I define as individuals having one clearly dominant stem, generally taller than wide, and tall enough that the crown is coupled with prevailing atmospheric conditions (generally >2 m). The age of small individuals at treeline can vary dramatically. However, in order to avoid confusion I follow conventions based on size and refer to all single-stemmed individuals less than 50 cm as seedlings, despite the fact that germination may have occurred several decades before.

METHODS

I conducted this study from July, 2001 to August, 2004 at an alpine treeline on the west flank of the Ruby Range Mountains of southwest Yukon (61.19° N, 138.36° W). Forests in the region are dominated by white spruce and treeline varies in elevation from 1250 to 1350 m. Aspect plays an important part in this variation, and treeline is 50 to 100 m higher on south-facing slopes than on north-facing slopes (Table 5-1). Structure and community composition of the forest-tundra ecotone also varies. Although the trees are generally smaller in stature, tree density on north-facing slopes is more than three times that of south-facing slopes. Sedges (*Carex* spp.) and feathermosses are the dominant ground flora on north aspects while deciduous ericaceous shrubs are more prominent on south aspects. These differences are due in large part to the occurrence of permafrost on north-facing slopes where there is significantly less direct solar insolation during the snow-free season (Dingman and Koutz 1974).

Experimental Design

Forty open-top chambers (OTCs) were constructed between July 11 and 14, 2001 around naturally established seedlings located just above the current treeline. An additional 40 seedlings were identified to serve as experimental controls. Treatments and controls were divided equally between a largely north aspect and an opposing south aspect. A number of steps were taken to ensure comparability among individuals. Those chosen for the experiment (i) appeared to be in reasonably good health with few dead branches, (ii) were between 20 and 50 cm in height, (iii) were taller than wide, and (iv) had only one prominent vertical leader. The lower density of individuals on the south-facing slope meant that some minor exceptions were required to attain adequate replication. Seedlings that met these criteria were located on each slope prior to OTC construction, and individuals of similar size, condition and microhabitat were identified as pairs. Members of these pairs were then randomly assigned to either the treatment or control group.

Several OTC designs and construction materials were initially considered and prototypes of each were constructed and tested prior to the experiment. The chosen design was a modified cone shape constructed from two transparent Lexan® (GE Plastics, Pittsfield, MA) 1.0 mm polycarbonate panels bolted to two wooden stakes. This design best incorporated the required field elements of durability, low maintenance, and the capacity for *in situ* assembly and disassembly, with the performance requirements of elevated temperatures, minimal interference with precipitation, and no internal shading (see Figure 5-1).

The potential influence of the chambers on snow accumulation and other winter variables was initially unknown and it was deemed prudent to remove half of the chambers at the end of the first growing season, thereby creating a second treatment level (i.e. year-round warming and growing season-only warming). Ten chambers from each slope were randomly chosen to act as the year-round treatments. The remaining 20 chambers were disassembled during mid-August of each year and reassembled during mid-May of the following year. Total length of this growing season-only treatment period was 31 days in 2001, 84 days in 2002, 99 days in 2003, and 80 days in 2004.

Experimental treatment was terminated with the removal of all OTCs on July 28, 2004 and seedlings were harvested two weeks later. The soil surface level was marked on the stem prior to harvest. Seedlings were later cut at this mark and at the root collar. Above- and below-ground fresh biomass was weighed and a sledge microtome was used to obtain a 25 μm section from each stem and root collar. Sections were stained with hematoxylin, mounted on glass slides, and annual growth rings were counted under a stereo microscope at 80x magnification. The larger of the two ring counts was used to age each seedling.

OTC Performance and Environmental Monitoring

OTC performance was assessed *in situ* by simultaneously measuring air temperature and relative humidity inside and outside of randomly selected OTCs. Two Hobo® H08 data loggers with external thermistors (Onset Corporation, Pocasset, MA) were used to measure air temperature 25 cm above the ground and relative humidity 10 cm above the ground. A third thermistor was located near the OTC 100 cm above ground surface to record ambient air temperature and a fourth was installed for the same purpose on the opposite aspect. Data loggers were periodically moved to different OTCs during the first two years of the experiment and data recording intervals varied from five to 60 minutes. A year-round OTC was chosen as the location for instrumentation from September through April when a recording interval of 60 minutes was used. However, damage by animals resulted in only partial data collection from these stations during the second and third winters. Several additional Hobo data loggers and thermistors were acquired in

June, 2003, and two permanent monitoring stations of the same configuration were established on each slope for the remainder of the experiment. A tipping bucket rain gauge with Hobo event data logger was also installed on each slope.

Growing degree-days (GDD) with a threshold of 5°C were used to represent seasonal heat accumulation (Perala 1985). Values were calculated for each treatment type on each aspect for the yearly snow-free period. Values for the growing season-only treatments were assumed to be equivalent to year-round treatments during the treatment period and equivalent to controls for the remainder of the year. Data recorded from July 2003 to July 2004 was used to develop regression equations for estimating GDD in 2001-2003 when simultaneous data were not available for both aspects. Relationships were all highly significant ($r^2 \geq 0.90$, $P \leq 0.001$). GDD prior to the start of the experiment were estimated using regressions with data from the nearest Environment Canada climate station, located 38 km northwest of the study site at Burwash Landing (61.37°N, 139.05°W).

A more extensive temperature monitoring strategy was used from Aug 12, 2003 to July 18, 2004. During this period a single iButton® Thermochron® temperature logger (Dallas Semiconductor Corporation, Dallas, TX) was placed directly under each seedling 2.5 cm above ground surface and bearing 0° from the stem. Data therefore characterized chamber-to-chamber variation in temperature during the monitoring period as well as simultaneous differences between treatments and aspects. Due to their limited memory capacity temperatures were logged every four hours. Battery failure occurred in two iButtons, but data were successfully recovered from the remaining 78.

iButton data from winter 2003-04 were used to identify dates when snow-cover exceeded 2.5 cm. This was accomplished by identifying periods when daily variation in temperature was low, since subnivean temperatures have a suppressed response to diurnal fluctuations (Jones *et al.* 2001). When variance in temperature over each 24-hr period was ≤ 1 it was assumed that the iButton was below snow surface. Two snow-cover indices were derived from the data. The first, snow accumulation period, was defined as the period of the year beginning at the start of the first period when 24h variance was ≤ 1 for three consecutive days ("snow onset") and ending on the day after the last three consecutive day period in the spring ("snow offset") (i.e. first in the dataset and last in the dataset). A second snow index was developed to account for several instances when one or more melt periods were evident during the winter. This second index, "snow days" was calculated simply as the number of days between September 1 and May 31 with a 24h variance ≤ 1. Additionally, a vertical array of iButtons was installed at each weather station for inferring snow depth. iButtons were mounted to wooden stakes at 0, 5, 15, 25, 50 and 75 cm and stakes were installed inside and outside the OTC at each location. An additional iButton was buried 10 cm below soil surface to record soil temperatures.

Seedling Growth

Seedling growth was quantified by measuring total height, stem diameter at ground surface, and annual increment of vertical growth as indicated by the most recent bud scar. In addition, five branches were selected and tagged for measurements of lateral growth. These included the uppermost and lowermost branches with a minimum of two years growth in 2001 and three branches equally spaced between. Total length of each branch, along with the annual increment of apical growth, was measured. All seedlings were measured immediately after construction of the OTCs. Subsequent measurements were taken in August of each year. Measurements were made with vernier callipers to the nearest 0.1 mm, except for total height which was measured with a metre-rule to the nearest 1.0 mm. Qualitative assessments of needle and bud damage were made in May and August of each year. Annual ring widths from 2000-2004 were measured in the lab from the slide-mounted stem sections. Measurements were made to the nearest 0.001 mm using a stereomicroscope at 80x magnification and a Velmex sliding stage micrometer (Velmex Inc., Bloomfield, New York).

In addition to absolute growth, I calculated the relative growth of individuals during the course of the experiment. This was expressed as:

EGI = (Measurement) / (mean of 2000 & 2001 measurements)

where EGI is the experimental growth index, the numerator is the growth increment measured for any given year during the experiment, and the denominator is the average annual growth rate prior to commencement of the experiment (in this case a mean of increments from 2000 and 2001). EGI thereby expressed growth during the experiment as a proportion of pre-experimental rates and helped to correct for the inherent variability in growth among individuals not attributable to experimental factors (Kneeshaw *et al.* 2002).

Physiological response of seedlings was measured at the leaf-level using a Licor LI-6400 portable photosynthesis system with leaf chamber fluorometer and actinic light source (LiCor, Lincoln, Nebraska). Seven seedlings of each treatment level and controls were randomly selected from each slope (42 seedlings total) for simultaneous measurements of gas exchange (expressed as net CO_2 uptake, [A]) and Photosystem II efficiency ([Φ_{PSII}] a function of steady state chlorophyll fluorescence [F_t] and maximal fluorescence [F_m'] in light adapted leaves) (Long *et al.* 1996, Maxwell and Johnson 2000). Measurements were taken between August 3 and 13, 2004, after the OTCs had been removed. Three branches were selected from each seedling for measurement. Each branch was from the upper half of the plant, was unobstructed by other branches, and had a minimum of three years growth. Only current-year growth was inserted into the leaf chamber. For all measurements the chamber temperature was set to 20°C, upstream CO_2 concentration was set at 400 μmol s^{-1}, and relative humidity was kept constant at 60%. Chamber conditions were given a minimum 10 minutes to equilibrate prior to measurement.

Maximum quantum yield ([F_v/F_m] a function of minimal [F_o] and maximal [F_m] fluorescence) (Maxwell and Johnson 2000) was measured from dark adapted needles on the remaining three seedlings of each treatment type not subjected to gas exchange measurements, as well as four additional controls from each slope. Three branches on each of these seedlings were dark adapted for a minimum 20 minutes using aluminum foil. The leaf chamber was then clamped onto the branch and conditions allowed to restabilize before measurements were taken.

All measurements were recalculated in the lab to incorporate actual leaf area. Following each field measurement, the point on the branch which aligned with the centre of the chamber was marked. The branch was then removed and a circular punch was used to cut away needle material not contained in the chamber. Projected leaf area of this sample was then measured in the lab using the digital technique described by Bond-Lamberty *et al.* (2003).

Statistical Analysis

Statistical analysis was carried out using SPSS 12.02 (SPSS Inc., Chicago, Illinois). All data were tested for normality and homogeneity of variance prior to analysis. Data were transformed when these assumptions were violated, except in the case of bivariate comparisons where a nonparametric alternative was possible. A Bonferroni adjustment was used for multiple comparisons.

The efficacy of the OTCs was tested by comparing data collected with the Hobo loggers simultaneously inside and outside an OTC. Daily averages, maximums and minimums were calculated for each temperature monitoring event and analyzed using a paired *t*-test or a Wilcoxon signed ranks test for data not normally distributed. Continuous datasets were divided into spring (April 1 –May 31), summer (June 1 – August 31), fall (September 1 – October 31), and winter (November 1 – March 31). Relative humidity data were analyzed in the same manner with values arcsine square-root transformed prior to analysis.

iButton temperature data were analyzed using a two-way repeated measures analysis of variance (rm-ANOVA) with treatment level (control [C], growing season warming [GS], and year-round warming [YR]) and aspect (north [N] and south [S]) as between-subject factors. Daily mean, maximum and minimum temperatures were compared for the periods August 14 to October 15, 2003, and May 15 to July 18, 2004. Data from October 15, 2003 to May 15, 2004 were excluded to avoid the influence of snow. Day of year for "snow onset" and "snow offset", as well as the total number of "snow days" determined from iButton data were compared using a 2-way ANOVA.

Finally, soil temperature data collected with the iButtons was analyzed using a mixed-model rm-ANOVA to assess differences between aspect and treatment during the two periods. Weekly average temperatures were calculated from the data to reduce the number of time-steps within the model. Location of the paired iButtons, nested within aspect, was included as a random variable in the model.

Absolute measurements and relative indices of seedling growth were distilled into three categories for analysis: (i) vertical growth, including incremental measurements of the terminal leader and the EGI calculated from them; (ii) lateral growth, including incremental measurements of the five lateral leaders and the EGI calculated from them; and (iii) radial growth, including measurements of the annual rings and the EGI calculated from them. Absolute growth (calculated as the sum of annual increments in 2002, 2003 and 2004) was analyzed using a two-way ANOVA with treatment (T) and aspect (A) as fixed factors. Measurements were square-root transformed to achieve normality or homoscedasticity. The same ANOVA model was used to analyze net carbon uptake (A), PSII efficiency (Φ_{PSII}), and maximum quantum yield (F_v/F_m). For these analyses, the three measurements from each seedling were averaged to yield a single data point for each individual. Relative growth was analyzed using a two-way repeated measures ANOVA with year (2001-2004) as the within-subjects factor and treatment (T) and aspect (A) the between-subjects factors. In all cases data did not meet the assumption of sphericity and a multivariate approach using the Wilks' lambda test statistic was used (von Ende 2001). The health of two seedlings – a control and growing season-only warming – declined rapidly between the first and second year of the experiment. These were known to be in poor health at the onset of the experiment and I am confident that the decline was not a result of treatment. A third seedling died following destruction of an OTC by a bear during 2004. Data collected from all three seedlings were removed from analyses.

RESULTS

Temperature

Average daily temperatures measured with Hobo thermisters were significantly greater inside the OTCs than those measured outside OTCs during all snow-free monitoring periods (21 paired *t*-tests, $P<0.001$ for all but one comparison). The average difference over the course of the experiment was 1.77° (SE ±0.06). The magnitude of this difference varied seasonally (Figure 5-2), averaging 2.65° in April and May, 1.83° in June, July and August, and 0.81° in September and October. Temperature differences also varied at a diurnal scale. Warmer temperatures prevailed inside OTCs during daylight hours while slightly cooler temperatures prevailed inside OTCs at night (Figure 5-3). Year-round warming treatments had the highest GDD sum, followed by growing season-only warming and controls, respectively (Figure 5-4). Year-to-year variation was dependent on prevailing conditions in each year, as well as the duration of experimental treatment.

Data collected with the iButtons yielded similar results (Table 5-2). Daily mean temperatures inside OTCs averaged 1.7° higher during the period from August to October, 2003 (rm-ANOVA $F_{2,72} = 62.2$, $P<0.001$) and 1.9° higher from May-July, 2004 ($F_{2,72} = 24.6$, $P<0.001$). Daily maximums and minimums were also significantly greater in 2003 (T_{max}: $F_{2,72} = 16.2$, $P<0.001$; T_{min}: $F_{2,72} = 53.6$, $P<0.001$) and 2004 (T_{max}: $F_{2,72} = 3.9$, $P=0.004$; T_{min}: $F_{2,72} = 59.9$, $P<0.001$). Differences detected between aspects were seasonal, with the south-facing slope experiencing warmer temperatures in the latter part of the growing season. Daily mean temperatures were approximately 0.4° higher on the south aspect ($F_{1,72} = 4.4$, P=0.040) and daily maximums 1.4° higher ($F_{1,72} = 6.9$, P=0.011) during the August-October period, but daily minimums were not significantly different ($F_{1,72} = 0.52$, P=0.473). In contrast, there were no significant differences in mean and maximum temperatures in the May to July period (T_{mean}: $F_{1,72} = 0.8$, P=0.357; T_{max}: $F_{1,72} = 1.07$, P=0.304) but minimum temperatures were consistently lower on the south aspect (T_{min}: $F_{1,72} = 3.8$, P=0.056). There were no significant interactions between aspect and treatment.

Statistical analysis of weekly means indicated that soil temperatures were significantly warmer inside OTCs during both periods (2003: $F_{1,24.2} = 40.57$, P<0.001; 2004: $F_{1,18.2} = 56.97$, P<0.001) (Table 5-3). Overall, soil temperatures measured on the south aspect were warmer than those on the north aspect. However, an interaction between aspect and week in the 2003 data ($F_{8,6.6} = 4.44$, P=0.036) indicated this difference was not significant after temperatures dropped below 0° C. An interaction between aspect and treatment in the 2004 data ($F_{1,18.2} = 7.51$, P=0.013) indicated that significant aspect-related differences were limited to soil temperature outside of OTCs.

Precipitation

Precipitation at Burwash Landing totaled 263 mm in 2001, 222 mm in 2002, 321 mm in 2003 and 276 mm in 2004. Respectively, 197 mm, 170 mm, 246 mm and 153 mm fell as rain. There was no significant difference between daily rainfall at Burwash Landing and at the treeline study site during the period for which concomitant data are available (July

1 to October 31, 2003) (Wilcoxon signed ranks test, Z=-0.180, P=0.857). There was no significant difference in daily rainfall on the north and south aspect during the same period (Z= -0.759, P=0.448). There were also no significant differences between average daily relative humidity inside and outside the OTC during any of the snow-free monitoring periods (5 paired t-tests, $\bar{x}$ P=0.415).

Length of the 2003-2004 snow season varied significantly with aspect (ANOVA $F_{1,72}$ = 35.07, P<0.001) and treatment ($F_{2,72}$ = 9.60, P<0.001). Snow season averaged 28 days shorter on the south aspect and 23 days shorter inside OTCs. The difference in aspect resulted largely from a delayed spring snow melt on the north aspect. Differences in treatment were due largely to delayed snow accumulation inside OTCs (Table 5-2). Snow depths inferred from the vertical arrays of iButtons varied among the four weather stations and there was no consistent trend related to maximum snow depth inside or outside of OTCs (Table 5-3). Maximum depths at north aspect stations were between 25 and 50 cm while those at south aspect stations were between 15 and 25 cm. Maximum snow depth at Burwash Landing during this period was 38 cm. Temperature data from winter 2001/02 and 2002/03 indicates that the 25 cm Hobo thermisters were not covered by snow at any time. Maximum snow depth at Burwash Landing during these winters was 15 cm and 23 cm, respectively.

Growth Response

The average age of all seedlings at the start of the experiment was 27 years (SD=4.7) with no significant difference between aspects (t-test: t_{75}=-1.543, P=0.127). Total fresh biomass of seedlings in 2004 averaged 97 g (SD=68.9), with seedlings on the south aspect weighing 50 g more than on the north aspect (Mann-Whitney U test: Z=-2.934, P=0.003). Plants on the south aspect averaged 85% of total fresh weight above-ground while north aspect plants averaged 80% above-ground (t-test: t_{75}=6.186, P<0.001).

ANOVA results based on absolute growth data are presented in Table 5-4, and results of the repeated measure ANOVAs for relative growth are presented in Table 5-5. Data from both analyses generally concur, indicating that initial differences in size had little influence on the growth rate of individuals during the course of the experiment. This is supported by weak relationships between experimental growth and initial size (Figure 5-5).

On average, vertical leaders of seedlings inside OTCs grew 4.0 cm (back-transformed value) more than control seedlings, but there was no significant difference between year-round and growing season-only treatments (Figure 5-6). Mean relative growth rate of vertical leaders on treated seedlings increased over the course of the experiment but remained constant in control seedlings (Figure 5-7). There was no difference in the absolute growth of vertical leaders with respect to aspect. Relative growth tended to be greater in treatment seedlings on the south aspect, but the difference was not significant and there were no significant within-factor interactions related to aspect (Table 5-5).

Absolute growth of lateral leaders on the five measured branches averaged 7.9 cm (back-transformed value) greater for south aspect seedlings (Figure 5-6) and relative growth was also greater (Figure 5-7). There were no significant differences in absolute lateral growth related to treatment, though seedlings inside year-round OTCs tended to be lower compared to all other treatments. Seedlings inside year-round OTCs did have significantly lower relative lateral growth in 2002 and 2003, but there were no differences in 2004. All mean values of relative growth for lateral leaders decreased significantly over the four year period.

Absolute radial growth during the experiment was influenced significantly by aspect, with rings growing 10% more on the south aspect compared with the north-facing slope (Figure 5-6). Treatment did not have an effect on absolute radial growth over the four years, but annual variations in relative growth were significantly affected by treatment (Table 5-5). This was mainly a result of high variability in the average radial growth of year-round treatments (Figure 5-7).

Needle mortality or dieback, ranging in extent from slight to severe, was observed in the spring of each year on 35% to 45% of all seedlings. Dieback was usually limited to the upper half of plants and typically affected new needles on leaders and branches. In some instances, damage was severe enough to result in the eventual death of entire branches or meristems, and initiation of new apical meristems in the subsequent year. A greater proportion of plants on the south aspect experienced dieback, and this damage also tended to be more severe than on the north aspect (Figure 5-8). Plants with dieback in any given year were more likely to have experienced damage in other years. This indicates that certain plants were more susceptible than others, likely a result of less favorable microenvironmental conditions. The exception to this pattern appears to be plants which were inside OTCs for the entire year. The condition of these plants tended to improve over the experiment (Figure 5-8).

Leaf-level Responses

Net photosynthesis was 41% greater in new growth of warmed seedlings compared with control seedlings (ANOVA $F_{2,36} = 5.85$, $P=0.006$), although there was no significant difference between OTC types. No differences between aspects were detected (Figure 5-9). In contrast, significant differences in Φ_{PSII} were detected between seedlings on north and south aspects, ($F_{1,36} = 14.97$, $P<0.001$), but not between treatment types (Figure 5-9). F_v/F_m averaged 0.770 (±0.018 SD) across all treatment-aspect combinations, with no notable trends related to treatment or aspect.

DISCUSSION

Microenvironment and OTC Performance

A significant effort was placed on evaluating the efficacy of the OTCs and results confirm that the design was successful in increasing temperature. This was achieved primarily by increasing air temperatures during daylight hours in the May to September period. The higher air temperatures inside OTCs resulted in significantly warmer soil temperatures, shorter snow periods, and larger annual heat sums. It is probable that other environmental variables, most notably wind and moisture, were also altered by the OTCs (see discussion in Marion *et al.* 1997). However, the extent of these changes and their specific effect on seedling growth is unknown in my experiment.

Passive OTCs rely on solar radiation to achieve the desired warming effect. The declining temperature differential in late summer and fall is attributable to declining daylight hours. The slightly lower nighttime air temperatures inside OTCs have been observed at other arctic and alpine sites as well (see Marion *et al.* 1997). Wada *et al.*

(1998) suggested the phenomenon was related to strong daytime temperature differences that cause a convective air flow inside the OTC that acts to cool air temperatures. However, I am uncertain about the exact mechanism at this site.

Monitoring confirmed the hypothesized natural environmental differences between aspects. Despite greater elevation, air and soil temperatures on the south-facing slope were higher than those on the north-facing slope, though the difference in air temperature was not significant during late spring and summer when both slopes receive ample direct solar insolation. Lower total insolation on north aspects results in cooler air temperatures, lower soil temperatures, longer snow period and, in turn, the presence of permafrost across the treeline ecotone (cf. Dingman and Koutz 1974).

Spruce Growth Response

Experimental warming had an effect on the growth and physiology of seedlings, though it varied across metrics (Table 5-6). Most significantly, growth of vertical leaders on individuals inside OTCs was significantly greater than control seedlings, but there was no difference between OTC treatment levels. White spruce exhibits determinate growth, and much of its primary growth in any year is determined largely during bud formation in the previous year (Grossnickle 2000), so the delayed response to warming was not unexpected. However, analysis of annual relative growth indicated that seedlings on the south aspect did not respond as quickly to growing season warming as they did to year-round warming in subsequent years, and seedlings on the north aspect did not respond particularly quickly to either treatment. The overall pattern of different responses between treatment levels matches with total growing degree days for each treatment and is consistent with observations that significant differences in air temperature influence vertical growth (James *et al.* 1994).

The variance in vertical growth increased in treated seedlings over the course of the experiment. Inspection of the data indicates that different plants responded to the same treatment at very different rates, and some were no different than controls. This divergent response was particularly evident in growing season treatment seedlings on the south aspect and is related to patterns in needle mortality. This dieback is a common phenomenon at treeline and is generally attributed to desiccation which occurs when frozen soil or stems prevent water losses from being replaced (Havranek and Tranquillini 1995, Körner 1998). Cuticle abrasion by wind and blowing snow is an important factor (Hadley and Smith 1986) and insufficient maturation of new tissues during the short treeline growing season increases susceptibility (Tranquillini 1979, Baig and Tranquillini 1980). Mid-winter thaws that trigger an increase in photosynthetic activity and are followed by a return to sub-freezing temperatures can also result in needle mortality (Schaberg 2000). Dieback was most prevalent at the top of individuals, presumably the portions extending above snow, and snow depth was lower on the south aspect where most damage was observed.

Two possibilities could account for the reduction of needle mortality in the year-round treatment seedlings on the south aspect, though they are not necessarily mutually exclusive. First, extended warming during the fall period may have allowed tissue to mature more completely which may reduce susceptibility (Tranquillini 1979). Second, it is possible that OTCs sheltered these seedlings and reduced wind abrasion near the snow surface (Hadley and Smith 1987). In either case, it is evident that while annual heat sum is a good indicator of potential vertical growth, winter damage on some individuals tempered the benefit of increased growth resulting from warmer temperatures (cf. Lloyd 1998).

Owens *et al.* (1977) report cumulative heat sum as being an important variable controlling lateral shoot growth in white spruce and this could account for the aspect-related difference in branch growth. However, an OTC effect should also have been observed if air temperature was the primary variable at work. I attribute the difference to reduced soil temperatures on the north aspect, perhaps in combination with a delayed onset of growth caused by extended snow cover. Low soil temperatures have been associated with reduced growth in many *Picea* species (Grossnickle 2000) and differences in soil temperature between aspects were consistently greater than differences in air temperature.

A lack of shelter has been cited as a factor promoting the elongation of branches on treeline conifers at the expense of vertical growth (Smith *et al.* 2003) and this may have augmented the longer branch growth on the south aspect where fewer trees and less snow results in greater exposure. Although a significant interaction was not detected by the ANOVA, reduced lateral growth was evident in year-round treated seedlings on the south aspect. All branches exhibited an age-dependent decline in growth, likely due to competition and differential allocation of resources between successive branch whorls (Fraser 1962). However, year-round treatment seedlings on the south aspect had a more rapid decline than the other groups, providing further evidence of a shift towards a more tree-like growth stature during the course of the experiment.

Ring widths of mature white spruce at Yukon treelines are generally most sensitive to annual variation in temperature (Jacoby and Cook 1981). However, as with lateral shoot growth, there was a significant difference in ring growth between the north and south aspect, but no consistent difference between OTC treatments and controls. Unlike shoot growth, radial growth in white spruce can extend into the fall period depending on prevailing conditions (Fraser 1962, Grossnickle 2000). Cooler temperatures and reduced insolation in late summer and early fall likely shorten the period of cambial activity in north aspect seedlings and annual differences seem to be related to temperatures during this period. For example, ring widths were highest in 2002 and the August to October mean temperature at Burwash Landing that year was 2.2° C above the 30-year normal. In the four other years, the difference ranged from -0.3° to +0.8° C. Year-round treatment seedlings on the south aspect experienced the highest late summer-early fall temperatures, yet they diverged from this growth pattern. Drought stress as a result of high temperatures has been identified as a factor limiting ring growth in some treeline white spruce in Yukon and Alaska and provides one possible explanation (D'Arrigo *et al.* 2004, Wilmking *et al.* 2004).

The specific physiological mechanisms that limit tree growth at treeline continue to be debated in the literature. The results from the leaf-level measurements do not resolve the debate, but do provide information useful for further evaluation. Air temperature is known to have a significant, though varied, effect on photosynthetic rates in treeline conifers (Häsler 1982, James *et al.* 1994). However, measurements in this experiment were obtained more than one week after OTC removal and leaf temperature was standardized across all measurements. It is possible that there were lasting effects on soil temperature from the OTCs and that these affected photosynthesis at the time of measurement. Delucia (1986) and Landhäusser *et al.* (2001) concluded that a threshold soil temperature exists between 5° and 8° C for *Picea*, above which little additional photosynthetic capacity is gained. This matches the mean subarctic alpine treeline soil temperatures of 6-7° C measured by Körner and Paulsen (2004), as well as those at this site. Slight differences in soil temperature near this threshold would therefore account for the significant differences I observed. A second explanation is that continuous exposure to higher air temperatures during needle flush and maturation resulted in physiological adaptations such as differences in needle thickness, stomatal density, or chloroplast density, structure and function, or differences in the ability to utilize nutrients (Lichtenthaler 1996).

The significant aspect-related difference in Φ_{PSII} is an indication that environmental conditions between the two slopes were significant enough to affect photochemical reactions and, potentially, influence the efficiency of carbon fixation. Slot *et al.* (2005) observed the same pattern in *Pinus sylvestris* seedlings in northern Russia and attributed it to different seasonal and diurnal light regimes, specifically high light levels on the south exposure. They found evidence that this invoked the photoprotective properties of the xanthophyll pigment cycle to protect against cold temperature-induced photoinhibition, a factor thought to inhibit distribution and growth of conifers at treeline in the central Rocky Mountains (Germino and Smith 2000, Germino *et al.* 2002, Johnson *et al.* 2004). Slot *et al.* (2005) conclude that cold temperature-induced photoinhibition is the cause of significantly lower densities of conifer seedlings on south exposures at their Russian study site, a pattern also observed at this Yukon study site.

CONCLUSION: IMPLICATIONS FOR TREELINE DYNAMICS

The abundance of small individuals above treeline from a wide range of age classes indicates that establishment is not a factor limiting treeline elevation. According to Körner (1998), a key question is why such populations do not develop into forests but remain nested in graminoid or shrubby ground cover, or form krummholz mats. These results indicate that warmer temperatures lead to increased vertical growth of these individuals, possibly because of higher photosynthetic rates. This supports the hypothesis that future climate warming will allow seedlings and dwarf individuals to more rapidly achieve a canopy height sufficient enough to withstand the negative effects associated with extending above the more favourable microclimate at ground surface, possibly resulting in an advance of treeline (Paulsen *et al.* 2000, Grace *et al.* 2002, Smith *et al.* 2003). However, my results also indicate that the reality is far more complex, and future changes are likely to vary in ways that are disproportionate to the amount of warming due to initial differences in exposure.

In subarctic areas, the advance of alpine treeline appears to be limited by slow growth on north-facing slopes where reduced solar insolation results in lower soil temperatures and a shorter snow-free period. My results indicate that future climate warming will cause seedlings to grow taller and faster on these slopes. However, this change in growth rate is not likely to be rapid enough to result in an advance of treeline unless air temperature increases are sufficient to cause a concomitant increase in soil temperatures and active layer depth.

In contrast, subarctic alpine treelines are limited by winter desiccation and possibly cold-induced photoinhibition on more exposed south aspects, where temperatures are higher, solar irradiance greater, and snow depth lower. An increase in the length of the growing season, greater snow depth, higher night-time temperatures, or combinations thereof, could facilitate a change in treeline structure or elevation on these slopes. However, equally important is the need for these conditions to be met in several successive years. Indeed, Camarero and Gutiérrez (2004) provide evidence that climatic stability, not just favourable conditions, were required for treeline advance in the Spanish Pyrenees. In combination with favourable conditions, such stability would allow young individuals to accumulate the benefits of small increments of annual growth without the disproportionate effects of damage prior to attaining tree status, after which time they are increasingly able to withstand the negative consequences of such intermittent events.

Kennedy (1995) cautioned against asserting that OTCs simulate future global climate change. Indeed, the pattern of warming created in this experiment differs from that expected to occur in western subarctic North America in the future and, in fact, from that currently being experienced. In particular, minimum daily temperatures are increasing more rapidly than daily maximums, and data indicate that winter temperatures are increasing more than summer temperatures (Stafford *et al.* 2000). However, my conclusions regarding potentially different responses to climate warming between aspects are supported by the stand reconstructions in Chapter 2 which indicate that an extended period of warming in the early-mid 20th century resulted in an advance of treeline on south-facing slopes paired with an increase of spruce density, but not with a significant advance on north-facing slopes. Based on my experimental results it seems that future climate warming in subarctic regions will lead to an advance of treeline or a significant increase in tree density at treeline as existing seedlings or dwarf conifers become more capable of attaining a tree stature. However, the extent of change will be highly contingent on the year-to-year, seasonal, and diurnal patterns of warming, and associated changes in precipitation.

Table 5-1. Mean characteristics of alpine treeline on the two slopes under study. Seedling density obtained via three 2m x 100m belt transects on each slope. Other values obtained via random point centered quarter method (n=6 points & 24 trees per slope). Seedlings defined as individuals <0.50 m; trees defined as individuals ≥1.50 m. SE=standard error, SD=standard deviation. Student's *t*-test was used to test the null hypothesis that values between the two slopes did not differ. Bolded text indicates P values <0.05.

	Aspect			
Variable	**South**	**North**	***t′* (DF)**	***P***
Elevation range (m)	1300-1360	1250-1290	—	—
Seedling density (ha^{-1}) (±SE)	100 (±28.9)	375 (±57.7)	4.26 (2.94)	**0.025**
Tree density (genet ha^{-1}) (±SE)	65.8 (±13.1)	259.7 (±51.7)	3.64 (5.64)	**0.012**
Tree height (m) (SD)	2.40 (1.1)	2.45 (0.9)	0.16 (43.09)	0.873
Root crown diameter of primary stem (cm) (SD)	11.0 (6.8)	8.6 (3.2)	-1.58 (32.53)	0.124
Number of stems per individual (SD)	8.2 (7.2)	3.2 (3.6)	-3.02 (33.67)	**0.005**
Canopy cover per genet (m^2) (SD)	12.9 (9.7)	4.1 (4.1)	-4.08 (31.18)	**<0.001**

Table 5-2. Mean iButton Thermochron data (08/14/03-10/15/03 and 05/15/04-07/18/04) collected from seedlings on north (N) and south (S) aspects. iButtons were placed directly under each seedling, 2.5 cm above ground surface, and facing north from the stem. Logging interval was 4.0 hr.

	Control		**Growing Season Warming**		**Year-Round Warming**	
	N (n=20)	**S (n=19)**	**N (n=10)**	**S (n=10)**	**N (n=9)**	**S (n=10)**
Average Temperatures (C°) (Aug 13-Oct 15)						
Daily mean	4.4	4.9	4.8	4.8	6.3	6.6
Daily maximum	12.6	14.2	14.0	14.5	15.8	17.6
Daily minimum	-0.7	-0.5	-0.7	-0.7	1.0	0.6
Average Temperatures (C°) (May 15-Jul 18)						
Daily mean	13.6	13.4	16.3	15.0	14.7	15.3
Daily maximum	27.5	27.0	31.3	28.8	29.1	29.7
Daily minimum	3.8	3.7	5.2	4.9	5.3	4.9
Snow Period						
Mean snow-on date	11/5/03	11/9/03	11/13/03	11/11/03	11/22/03	11/23/03
Mean snow-off date	5/9/04	4/11/04	5/7/04	4/22/04	5/6/04	4/2/04
Mean number of days >2.5 cm snow	184.0	141.6	173.0	149.3	163.2	115.6

Table 5-3. Mean soil temperatures (08/14/03-10/15/03 and 05/15/04-07/18/04) at 10 cm depth, and peak winter mean snow depth (average of inferred depths from 02/01/04-02/29/04) inside (In) and outside (Out) OTCs at each of the four permanent weather stations. N = North, S = South. Two replicates each. *Resolution of snow depth is limited by spacing of iButtons.

Aspect and Location		**Mean Soil Temperature (C°)**		**Inferred Snow Depth* (cm)**
		08/14-10/15	**05/15-07/18**	
N_1	In	1.9	4.6	25-50
	Out	1.5	2.8	25-50
N_2	In	2.5	6.6	25-50
	Out	1.9	5.0	15-25
North Mean (±SE)		1.9 (±0.1)	4.8 (±0.2)	25-50
S_1	In	3.8	5.9	10-15
	Out	3.1	5.4	3-5
S_2	In	2.8	5.9	3-5
	Out	2.2	4.7	10-15
South Mean (±SE)		3.0 (±0.1)	5.5 (±0.2)	5-15

Table 5-4. ANOVA results of absolute growth differences for primary and secondary growth. T=Treatment; A=Aspect.

	Vertical Leader				**Lateral Leaders**				**Annual Rings**			
	df	**MS**	**F**	**P**	**df**	**MS**	**F**	**P**	**df**	**MS**	**F**	**P**
A	1	0.572	0.959	0.331	1	11.003	14.202	**<0.001**	1	172.226	4.256	**0.043**
T	2	5.054	8.476	**0.001**	2	1.610	2.079	0.133	2	4.731	0.117	0.890
A*T	2	0.082	0.137	0.872	2	0.692	0.893	0.414	2	50.481	1.247	0.293
Error	71	0.596			71	0.775			71	40.467		

Table 5-5. Repeated measures ANOVA of relative growth differences for primary and secondary growth. T=Treatment; A=Aspect; Y=Year (repeated). [1]Values based on Wilks' lambda are reported.

	Vertical Leader				Lateral Leaders				Annual Rings			
Between Subjects	**df**	**MS**	**F**	**P**	**df**	**MS**	**F**	**P**	**df**	**MS**	**F**	**P**
A	1	0.009	0.045	0.833	1	0.971	6.692	**0.012**	1	0.104	1.171	0.283
T	2	1.049	5.099	**0.009**	2	0.364	2.510	0.088	2	0.059	0.658	0.521
A*T	2	0.378	1.835	0.167	2	0.037	0.254	0.777	2	0.000	0.004	0.996
Error	70	0.206			71	0.145			71	0.089		

	Vertical Leader				Lateral Leaders				Annual Rings			
Within Subjects[1]	**F**	**Ndf**	**Ddf**	**P**	**F**	**Ndf**	**Ddf**	**P**	**F**	**Ndf**	**Ddf**	**P**
Y	4.941	3	68	**0.004**	40.300	3	69	**<0.001**	38.730	3	69	**<0.001**
Y*A	2.211	3	68	0.095	5.356	3	69	**0.002**	2.373	3	69	0.078
Y*T	2.236	6	136	**0.043**	2.834	6	138	**0.012**	4.543	6	138	**<0.001**
Y*A*T	1.083	6	136	0.376	0.638	6	138	0.700	0.565	6	138	0.758

Table 5-6. Summary of main results for each growth metric, including factors with significant differences and the specific trend detected. Treatments: C = control, GS = growing season warming, YR = year-round warming. Aspects: N = north, S = south.

Metric	**Factor**	**Trend**
Vertical Growth	Treatment	C<GS=YR
Lateral Growth	Aspect	N<S
Radial Growth	Aspect	N<S
A	Treatment	C<GS=YR
Φ_{PSII}	Aspect	N>S
Fv/Fm	None	–

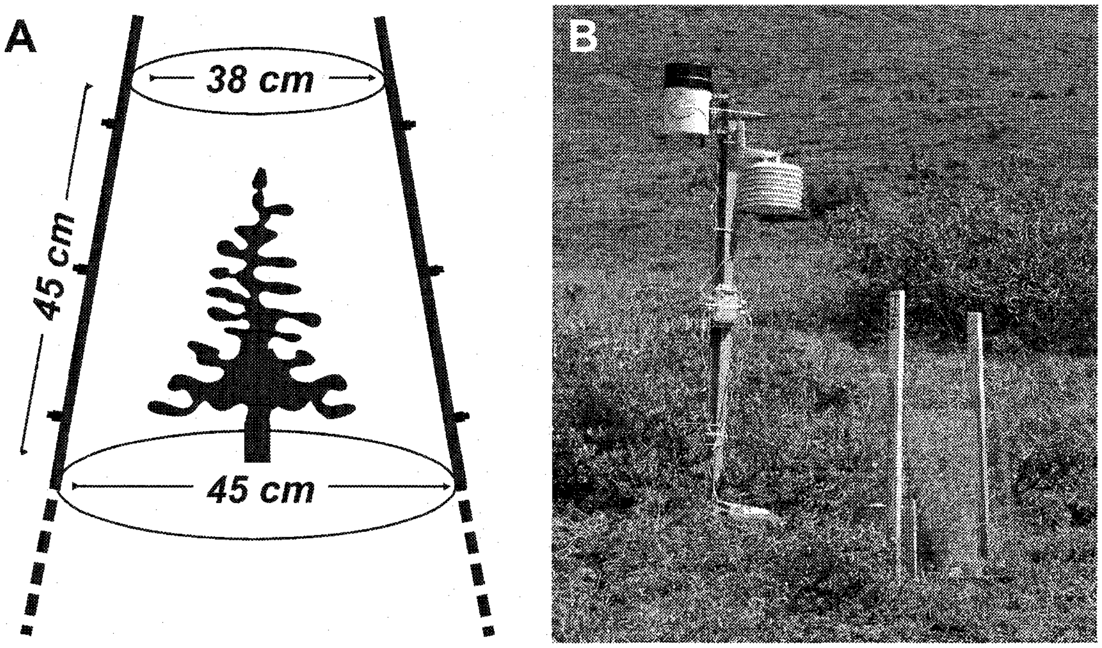

Figure 5-1. (a) Design of the Lexan®-constructed open-top chamber (OTC) used in this study. (b) Photograph of an OTC and mini-meteorological station at treeline.

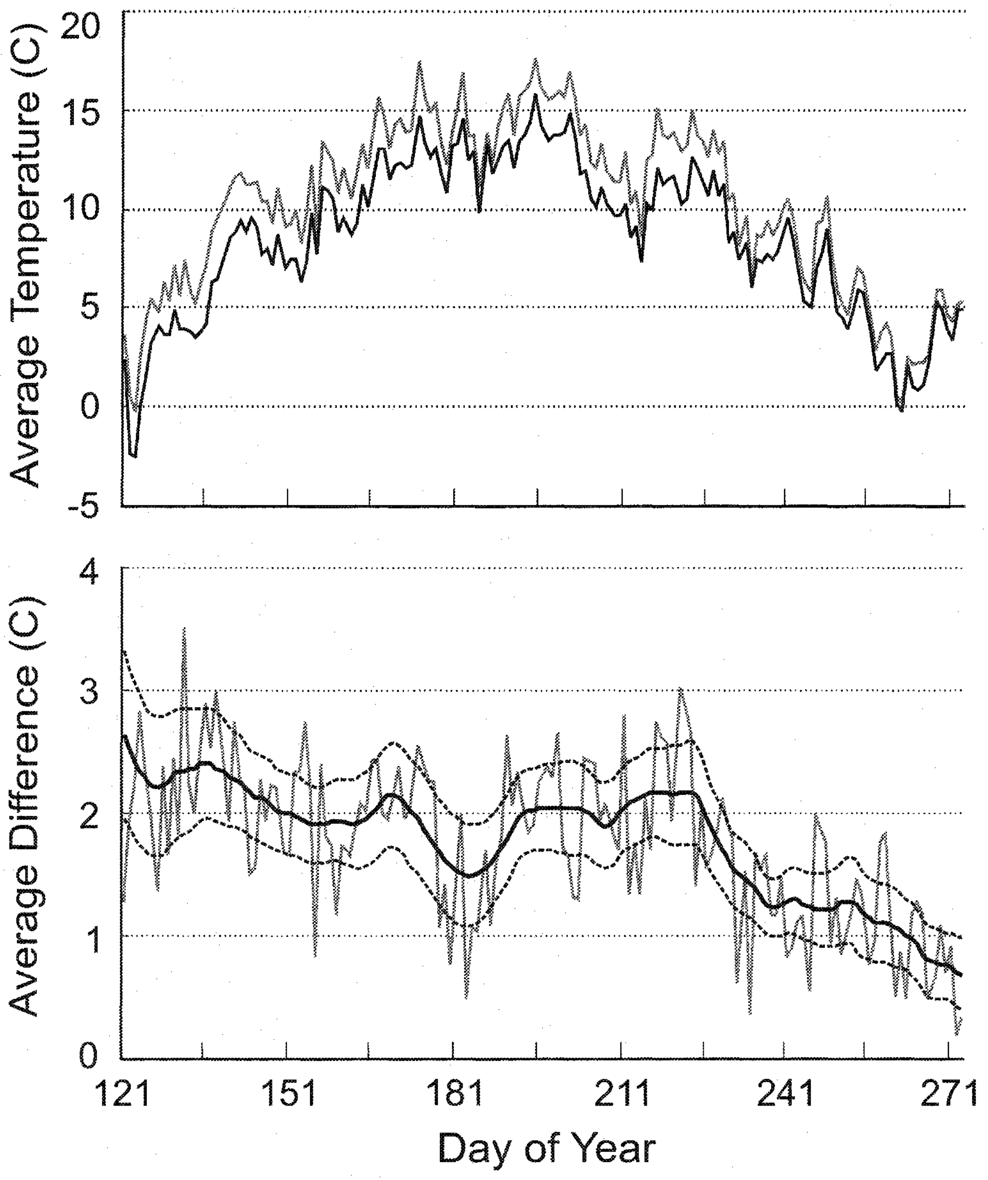

Figure 5-2. Top: Mean daily temperatures measured at 25 cm inside (gray line) and outside (black line) OTCs averaged across aspects over the duration of the experiment. Bottom: Difference between mean daily temperatures inside and outside OTCs. The thin solid line represents values for each day of year averaged over the duration of the experiment. The thick solid line is a smoothed 15-day running mean of the data. Dashed lines show ± 1 standard error of the smoothed running mean.

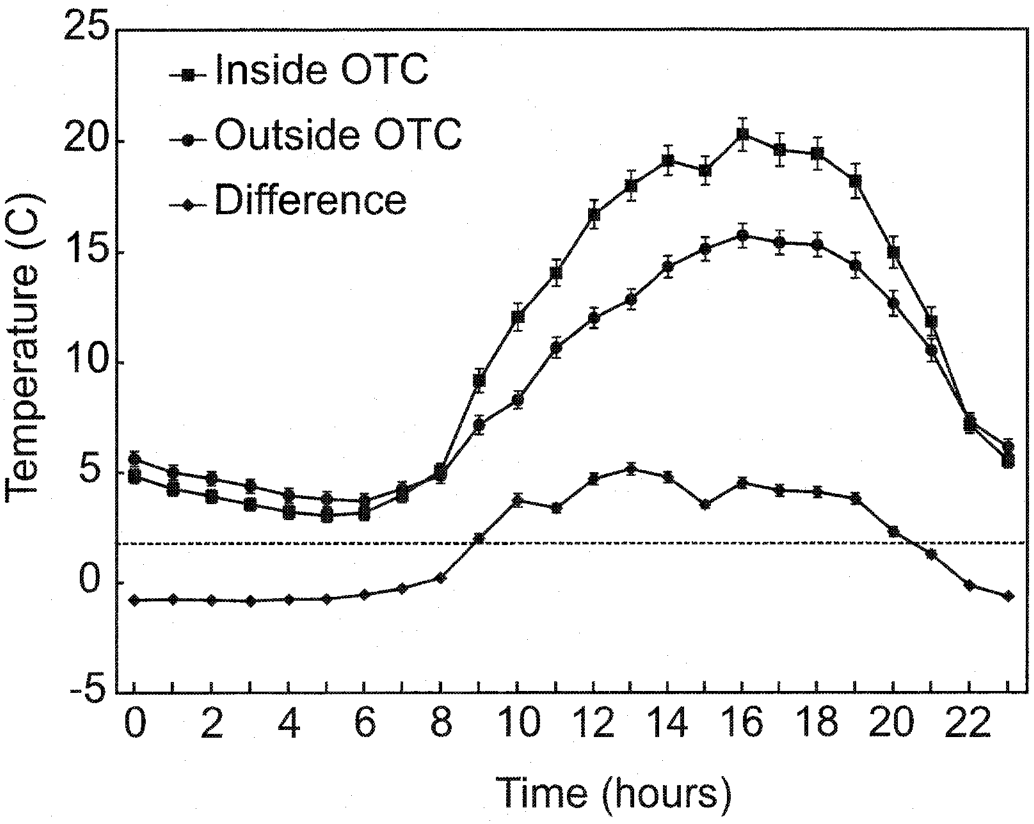

Figure 5-3. Hourly values of air temperature measured at 25 cm (mean ± SE) inside and outside an OTC on the north-facing slope during 2003. Values are averaged from 05/15 to 09/15. The lower line represents the mean hourly difference between the two measurements. Dashed line indicates mean daily difference (1.8° C).

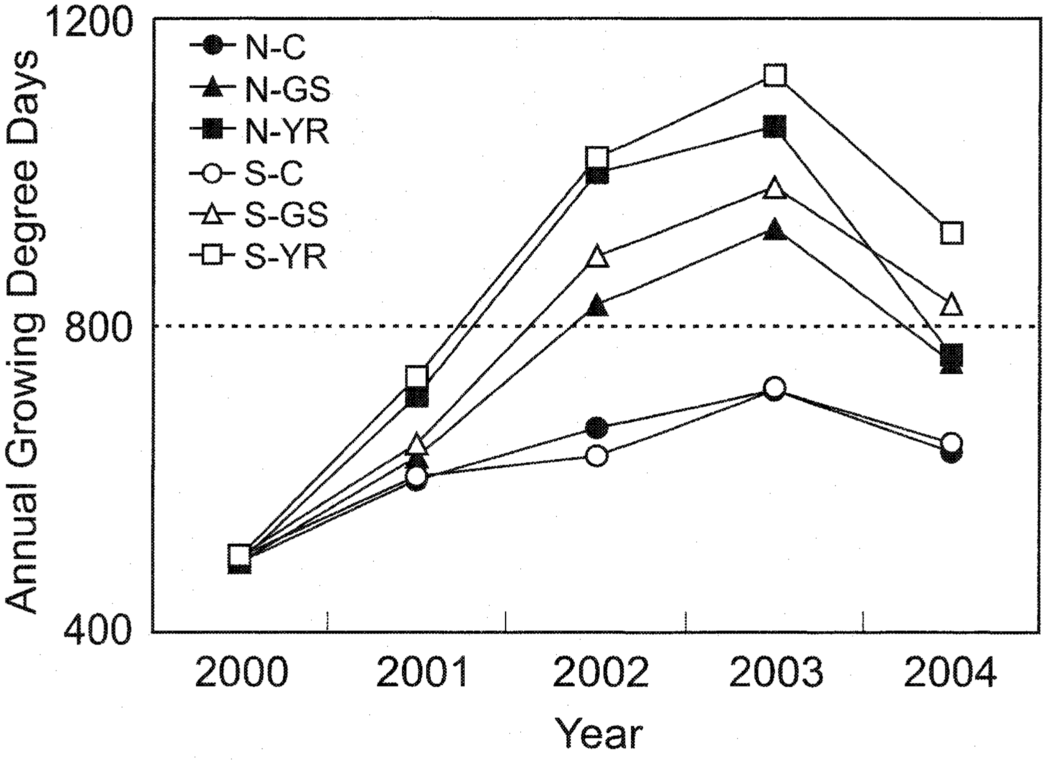

Figure 5-4. Average annual growing degree days (April 15 to October 15) calculated for control seedlings (circles), growing season-only treatments (triangles), and year-round treatments (squares) on north (solid symbols) and south (open symbols) aspects. Period for 2004 ended July 28. Values are calculated from measurements obtained 25 cm above ground surface. Experimental warming began in July 2001, accounting for the similar values in 2000 and smaller differences in 2001.

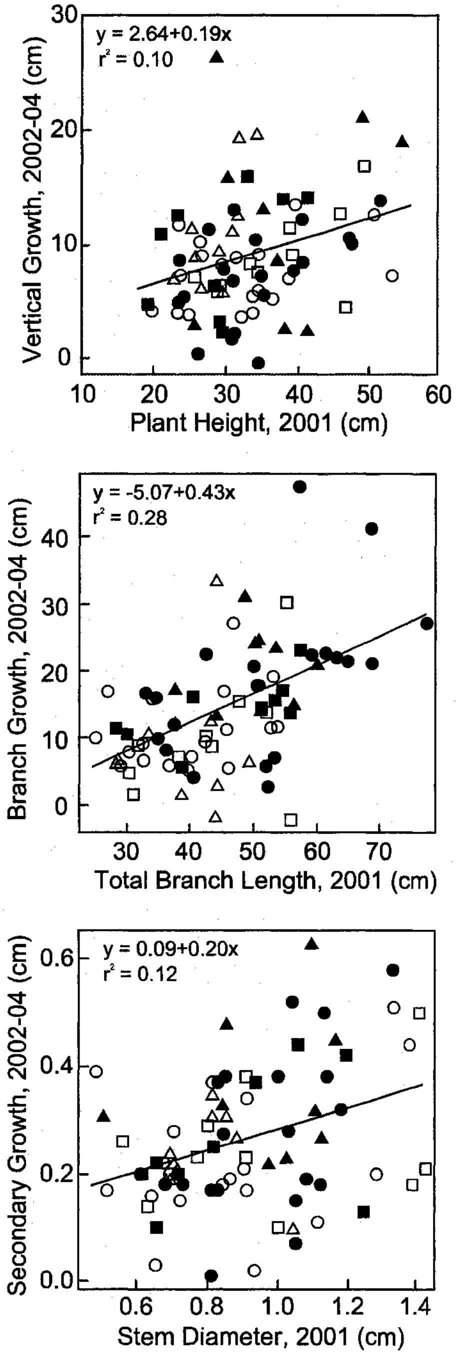

Figure 5-5. Relationships between initial size (measured prior to OTC construction in 2001) and net growth during the experiment (2002-2004) for control seedlings (circles), growing season-only treatments (triangles), and year-round treatments (squares) on north (solid symbols) and south (open symbols) aspects. Regression lines are fit though all data points. Non-transformed data are presented.

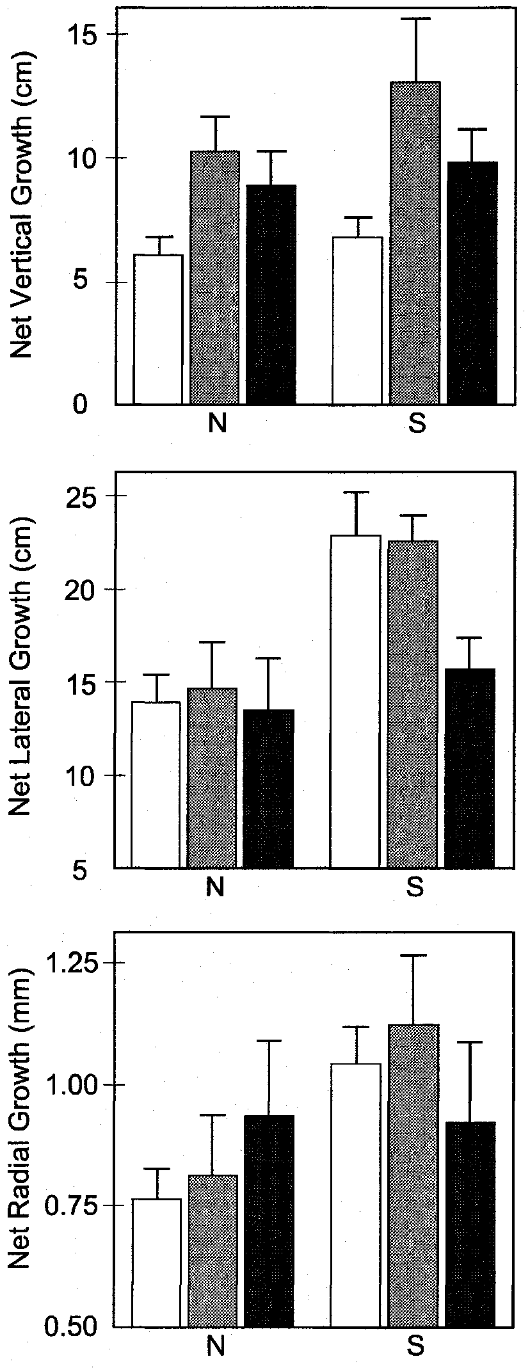

Figure 5-6. Absolute vertical leader, lateral leader (sum across five branches), and radial growth during the course of the experiment (2002-2004) (mean ± SE). Control = white bars, growing season warming = grey bars, year-round warming = black bars. True data means are presented, while transformed values ($\sqrt{[x+0.5]}$) were used in the statistical analysis. See Table 5-4 for ANOVA results.

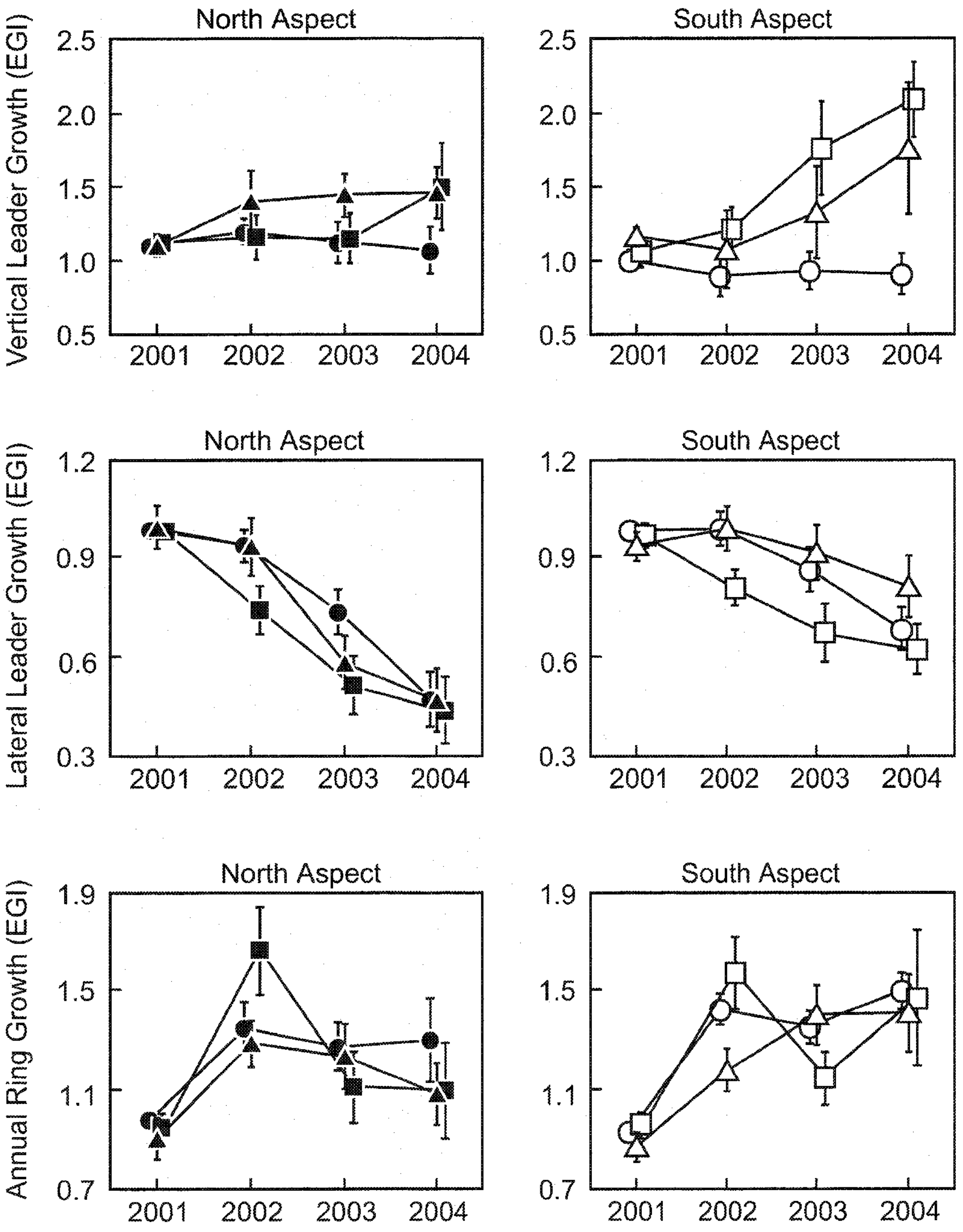

Figure 5-7. Mean (± SE) experimental growth index (EGI) of vertical leaders, lateral leaders (sum across five branches) and annual rings in each year. See Table 5 for repeated measures ANOVA results. Symbology: control seedlings (circles), growing season-only treatments (triangles), and year-round treatments (squares) on north (solid symbols) and south (open symbols) aspects.

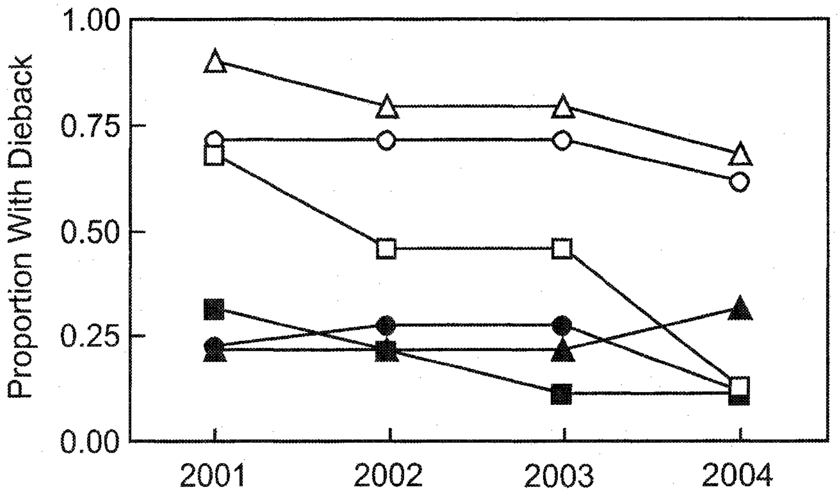

Figure 5-8. Proportion of individuals with needle dieback, based on annual spring observations. Symbology: control seedlings (circles), growing season-only treatments (triangles), and year-round treatments (squares) on north (solid symbols) and south (open symbols) aspects.

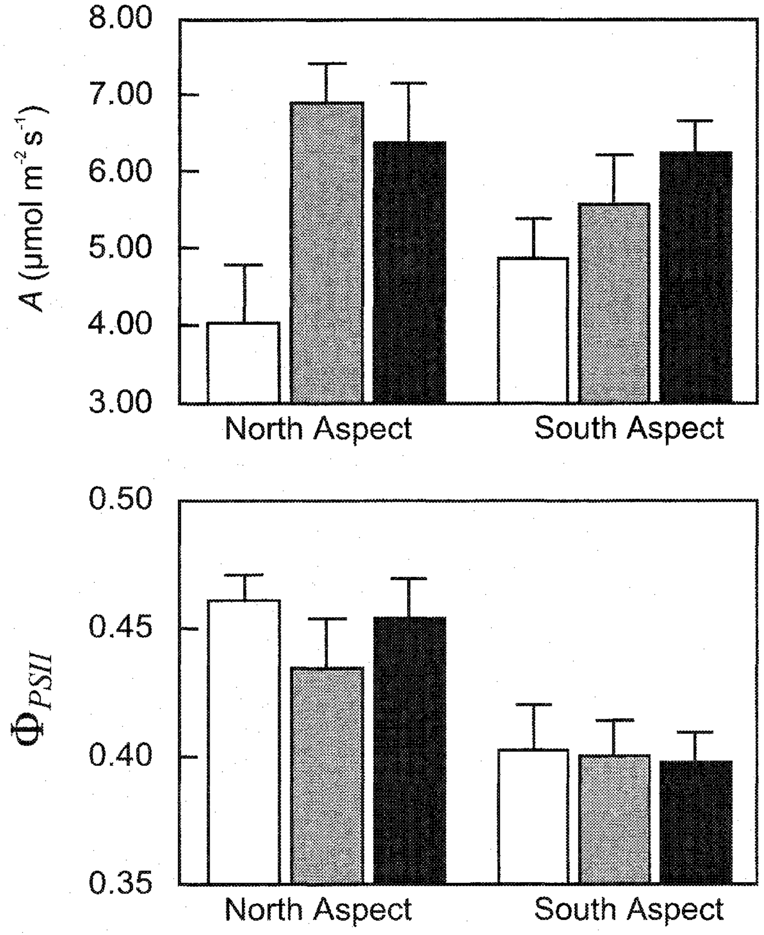

Figure 5-9. Net photosynthesis (top) and Photosystem II efficiency (bottom) (mean ± SE). Control = white bars, growing season warming = grey bars, year-round warming = black bars.

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CHAPTER 6

Synthesis and Conclusion

INTRODUCTION

Extensive research has been conducted to determine how various environmental factors influence tree-forming species to result in alpine treeline. Körner (1998) examined the relationship between latitude and elevation of alpine treelines worldwide and concluded that "a direct thermal rather then [*sic*] any other explanation of treeline altitude is most plausible" (pg. 450). He conducted a thorough review of the literature in an attempt to identify a functional cause for this relationship. Four mechanisms were identified: (i) cold-related stress, (ii) tissue loss due to disturbance, (iii) reduced reproduction and seedling survival, and (iv) a negative carbon balance. However, Körner concluded that while they may be locally important, they can not offer "a unifying theory for alpine treeline" (pg. 453) that is applicable worldwide. In response, he proposed a fifth, "growth limitation", hypothesis whereby the synthesis of functional tissues is prevented by a low temperature threshold.

There is a certain elegance associated with a universal explanation for treeline. However, it cannot be expected to match the actual treeline position in any location better than ±100 m elevation (Körner 1998). In short, a purely ecophysiological explanation emphasizes biotic potential, rather than environmental reality. It is extremely useful at coarse scales of examination, but becomes more problematic at increasingly finer scales. At these scales, other factors including snow cover, soil type, drainage, disturbance, nutrient status, facilitation, herbivory, and competition become influential. If treeline is to be useful as an indicator of climate change, and if accurate predictions of habitat change are to be made at a scale meaningful for resources management, then these other variables must also be considered.

However, it is too confusing to assert that *everything* matters, even though it may be true. A way of organizing this complexity in an understandable and relevant way is required. This is useful not just for predictive forecasts, but also to examine and understand the relationship between pattern and process at the ecotone (i.e. how treeline position and structure influence ecological processes, and *vice versa*) which can further influence responses to climate change. To this end, Holtmeier and Broll (2005) developed a scale-based perspective of the variables influencing pattern and process at treeline. The perspective offered in Figure 6-1 builds on this by incorporating a temporal perspective based on the work of Delcourt and Delcourt (1992) who illustrated the fundamental linkage between spatial and temporal scales in ecotone dynamics.

Recognition of scale and its influence is an important step in ecological investigations; but explicitly incorporating scale into such investigations is a more difficult step (e.g. see examples in Peterson and Parker 1998). The use of hierarchy theory facilitates this by allowing simplification of complex, multiscale, systems. The observer is able to focus on a particular subset of ecological processes and patterns while simultaneously considering the influence of the adjacent higher and lower levels in the ecological hierarchy (Parker and Pickett 1998). By using the hierarchical framework described earlier (recall Figure 1-6, Chapter 1), this research attempted to go beyond simply acknowledging the importance of scale and actually incorporate it into the design and implementation of ecological research.

The following sections provide a synthesis of the four main investigations that comprised this research. Results from each chapter are briefly summarized and avenues for potential future research are identified. These results, along with experience gained in carrying out the research, are then used to distill several lessons and conceptual tools for considering potential responses of subarctic alpine forest-tundra ecotones to future climate change. Finally, the experience using hierarchical theory as a framework for scientific study is evaluated.

SUMMARY OF RESULTS

The Landscape-Scale: Is Temperature Omnipotent?

The results of the species distribution modeling contribute to a wealth of studies that have demonstrated the importance of temperature as the primary control over treeline elevation. Both the classification (presence/absence) and regression (abundance-canopy cover) trees illustrated its influence. However, residual analysis indicated that there is a significant amount of variation not accounted for by temperature alone, and that other variables play important roles at finer scales. In this regard, the results clearly support the scale-based model presented in Figure 6-1.

Decision tree analysis was useful in demonstrating the hierarchical nature of variables. However, with the exception of solar radiation and rock cover, just what these other variables are was not especially evident. This is partially, or perhaps largely, a function of the spatial extent of the analysis. If the analysis had been confined exclusively to treeline, rather than the landscape as a whole, then the classification and regression trees may have been able to identify these variables, presuming they were included in the analysis. Colinearity between variables may also be reduced at this scale, permitting use of the NDVI attribute discussed in Chapter 4.

To this end, an avenue for future work appears to be a boundary analysis (see Jacquez *et al.* 2000) to systematically define the forest-tundra ecotone so that data sampling can be focused there. Several approaches using the 2.4 m spruce classification, or an object-based classification of the pan-sharpened QuickBird2 image, could be used. A multiscale image segmentation of the pan-sharpened image could also be used to accomplish this (Hay *et al.* 2001). Indeed, a comparison of the two methods in delimiting the subzones of the forest-tundra ecotone could prove useful.

The Stand-Scale: Examining Pattern and Process

Results of the dendroecological investigation indicated that treeline elevation and stand density increased significantly during the early-mid 20th century, but that this change was not uniform across sites. Spruce advanced rapidly on south-facing slopes and treeline rose 65 to 85 m in elevation. Treeline did not advance on north-facing slopes, but stand density across the ecotone increased 40 to 65 percent. Aspect differences were likely due primarily to the differential presence of permafrost and additional variability was related to slope and vegetation type. Repeat photography supports these results, but the time span is shorter. The most common changes observable between 1947 and 1989 were (i) increases in the canopy size of individual trees and (ii) increases in stand density resulting from the establishment of new individuals. Several instances of treeline advance were also observed.

The increases in spruce density were strongly correlated with reconstructed summer temperatures. The period of rapid change in the second quarter of the 20th century coincided with a 30-year period of above average temperatures, beginning in 1920. The highest correlations were obtained using a 30-50 year window of forward averaging. This supports one of the postulates of the experimental warming: that treeline dynamics are controlled to a greater extent by conditions influencing recruitment than by establishment alone.

Despite the significantly positive correlations, reliance on climate reconstructions derived from areas outside of southwest Yukon is not ideal. Luckman *et al.* (2002) carried out a dendroclimatological study of the Kluane region and found a tremendous amount of intra-regional heterogeneity. Analysis of the extensive ring-width database derived from this study could be used to refine this work and would improve understanding of the relationships between climate and spruce population dynamics. Furthermore, a growing body of literature based on examples from treelines in Alaska and Yukon suggests that tree growth can be limited by one climatic factor at one time, and another in a subsequent period (e.g. Wilmking *et al.* 2004) and that moisture availability is a critical factor in this change (D'Arrigo *et al.* 2004). An analysis of ring-widths could be used to examine potential links between this individual-level variation with the population-level dynamics already analyzed.

Evidence for an advance of shrubs was found at two sites where there was an absence of older individuals in plots at higher elevations and a disproportionately large number of individuals in the oldest age class, indicative of a sudden population establishment. However, interpretation of shrub advance was limited by the relatively short lifespan of willow stems when compared to the possible, but largely undeterminable, age of the parent genet.

In general, the importance of shrubs has been overlooked at treeline ecotones worldwide. While the experience gained in applying dendroecological techniques to the shrub component should prove useful in future studies, there are limitations to its use. Complementary methods, such as repeat photography, also need to be used. My assessment of the small scale aerial photographs used in this research is that it would be very difficult to ascertain shrub change from them in all but the most obvious instances. However, there are photographs with better resolution (e.g. 1:10,000) for specific locations in the Kluane region that extend back to *ca.* 1970. The changes which were detected in shrub populations *via* dendroecology were more recent than for spruce. Therefore, there is potential for using this more recent, larger scale, aerial photography to document changes in shrub distribution and abundance in southwest Yukon.

The Tree-Scale: Identifying the Mechanisms of Change

Open-top chambers increased air temperatures during the growing season by 1.8°C and annual growing degree-days by one-third. Warmed seedlings grew significantly taller and had higher photosynthetic rates compared with control seedlings. The OTCs tended to reduce winter dieback over the course of the experiment. Soil temperatures averaged 1.0°C warmer and the snow-free period was nearly one month longer on the south aspect. These seedlings grew longer branches and wider annual rings than seedlings on the north aspect, but had reduced Photosystem II efficiency and experienced higher winter needle mortality.

These results indicate that climate warming will enhance vertical growth rates of young conifers, with implications for future changes to the structure and elevation of treeline. However, responses to climate warming are likely to be contingent upon exposure-related differences. Growth of seedlings on north-facing slopes seems to be limited by low soil temperature in the presence of permafrost, while growth on south-facing slopes appears limited by winter desiccation and cold-induced photoinhibition.

Hobbie and Chapin (1998) concluded that treeline is in part a consequence of an inability of trees to establish in tundra. However, my observations of abundant dwarf individuals above treeline suggest this may be more applicable to areas well beyond the distributional limit of spruce, rather than within or near the forest-tundra ecotone. Still, the probability of establishment and survival of white spruce, or "upslope invasibility", is unlikely to be universal. Resler *et al.* (2005) conducted an examination of microhabitat features facilitating the establishment of conifer seedlings in Glacier National Park, Montana. A similar study would be useful for subarctic alpine treeline and would identify the micro-scale variables that facilitate seed germination and seedling survival and, in turn, result in the coarse-scale heterogeneity expressed in the woodland and shrubland zones.

LESSONS FOR CONSIDERING TREELINE DYNAMICS

Scale-based Responses to Climate Warming

Although this thesis has emphasized spatial scale of observation, temporal scale is also critical, and the two are directly linked (Delcourt and Delcourt 1992; recall Figure 6-1). Based on the results of this research, treeline response to climate variation and change can be characterized using three domains of scale. I refer to these as "pathways of change". As should now be evident, these are simplifications of reality. Moreover, they are inextricably linked to each other, but the division provides a useful approach for simplifying their interconnections. It is important to note that all three pathways occur simultaneously. They are not independent of another but are, instead, dependent on the scale of observation.

1. ***Macropath: climate warms and treeline advances.*** I refer to this as a macropath since this is the response evident when the scale of observation is enlarged to encompass timeframes of several centuries. When we consider change at this time scale, variables such as soil moisture, patterns of snow melt, preexisting vegetation types, etc., play a much smaller role. Infrequent fine-scale processes (e.g. soil frost heave) are insignificant in determining the outcome. Fine-scale processes that happen frequently (e.g. cold-reduced photosynthesis) remain important unless they are swamped by processes occurring at larger scales (e.g. permafrost thaw). In macropaths it is the large scale variables that tend to have the greatest influence on how treeline responds to climate change.

2. ***Mesopath: climate warms and the structure of the ecotone changes.*** This pathway is likely to be evident when the scale of observation is on the order of decades to centuries. The terrain variables such as aspect, slope, and soil cover and depth explored in Chapter 4 are critical influences at this scale. How change proceeds is highly contingent on the conditions at the mesoscale and various

factors can cause multiple positive and negative feedbacks. For example, the preexisting configuration of the vegetation (e.g. abrupt vs. gradual treeline, patchiness, etc.) can encourage establishment *via* sheltering of trees, or hinder it *via* shading and cooling of soil temperatures. Because of these multiple variables and the uncertainties associated with them at the temporal scale of concern (the "dilemma of middle number systems", O'Neill and King 1998, pg. 13), the mesopath is the most difficult scale at which to predict change. Unfortunately, it is also the scale at which predictions are most required.

3. ***Micropath: climate warms and tree growth increases.*** This pathway centers on the response of individual trees to temperature warming. In terms of treeline dynamics it is relevant in that it determines the probability of survival. It is the response evident when the scale of observation is limited to timeframes on the order of up to a decade. When we consider change at this small scale, site specific variables such as soil moisture, snow depth and patterns of melt, and adjacent species become critical and can enhance, moderate, or negate the effects of warmer temperatures regardless of their frequency. However, the extent of response is also size-dependent, with smaller individuals being more influenced by the fine-scale variations.

MacDonald *et al.* (1998) identified three possible responses of treeline to a warming climate: (1) increased growth of individual trees, (2) increased population density of trees at treeline, and (3) expansion of the geographic distribution of trees (i.e. invasion into tundra). In many ways the pathways outlined above align themselves with these three response types. Although McDonald *et al.* did not tie them to particular scales, the results of this research (particularly Chapter 3) suggest that they tend to be hierarchical, meaning that response type 1 can occur in the absence of type 2 and 3, but that type 3 does not generally occur without type 2 or 1 first occurring.

Solar Radiation and Subarctic Treelines

Large topographic relief defines mountains, but the heterogeneity this produces is not limited to the vertical dimension. Topographic relief also results in solar gradients, and solar energy drives ecosystems. The effects of these solar gradients grow particularly strong at higher latitudes where the sun's angle is low. One of the common threads linking the results of the four investigations is that the properties and dynamics of subarctic alpine treelines are heavily influenced by the amount of solar radiation they receive. North-facing slopes receive substantially less direct solar radiation than south-facing slopes. As a result, they retain snow longer and have lower soil temperatures. Permafrost is common at treeline on these slopes and this impermeability results in high rates of runoff and increased soil moisture. In contrast, south-facing slopes lose snow quicker and experience high rates of evapotranspiration. Permafrost is generally absent at treeline and excess moisture tends to infiltrate soils rather than generating lateral flow (Carey and Woo 1998). The differences in vegetation that these conditions set up are substantial.

The fact that vegetation on opposing slopes vary in response to solar radiation is a longstanding theme in biogeography and ecology (e.g. Weaver and Clements 1929). That these differences are accentuated at higher latitudes because of lower solar angles is not new either (cf. Dingman and Koutz 1972). However, comparison of ecological processes between opposing slopes has been far less common than comparison of pattern such as vegetation structure or species composition. This research has illustrated that there are fundamental process-related differences between slopes that receive low and high amounts of direct radiation and, importantly, that these differences exist across multiple scales of observation and biological levels. It is critical that this is taken into consideration when planning research, designing sampling and analysis, interpreting results, and modelling future change.

Taxonomic Dependence

Alpine treelines worldwide are often referred to in aggregate, as are arctic treelines. Many of the same physiological phenomena limiting tree growth have been observed at multiple sites. However, by considering them collectively, we also tend to forget that different species comprise different treelines worldwide, and different species have different life histories and climatic tolerances. Although there are clearly generalities that can be made, there are also species-related differences that must be considered. These are as important as the scale-dependent considerations emphasized in this thesis.

A comparison of white spruce with black spruce provides a useful example of this. Both can occur at treeline in subarctic North America. However, conclusions drawn from studies of treeline dynamics for one species are not necessarily applicable to the other (Lloyd *et al.* 2005). Black spruce is phenotypically more plastic than white spruce and has a much higher capacity for vegetative regeneration (Vallée and Payette 2004). It is thought that this permits it to maintain populations in areas for an extended period of time, hundreds and perhaps thousands of years, if climate drops to suboptimal conditions (Laberge *et al.* 2000). White spruce undergoes masting which, as indicated here, can be an important factor in its dynamics at treeline. The rapid advance of treeline observed in the Kluane region might not have been possible for black spruce.

Conditions for Treeline Advance

In combination, the process related investigations (Chapters 2 and 5) shed light on the conditions required for an advance of treeline in the Kluane region. Four general life history stages can be identified. However, the climatic conditions favouring survival in each stage are not identical across the four stages and the notion of a separate regeneration niche (Grubb 1977) is particularly relevant here. These conditions are frequently met in southwest Yukon, but they must occur in sequence and must be sustained over multiple years if an advance is to occur.

1. Seeds must be produced: Vegetative regeneration may lead to significant increases in stand density. However, propagation by seed is necessary for a significant advance of the altitudinal limit of white spruce beyond the pace of a slow creep. Moreover, as Zasada and Gregory (1969) note, "only a heavy seed crop will satisfy the demands made by forest fauna and still leave enough seed for regeneration" (pg. 22). Given lower viability of seeds produced at treeline, it seems that mast events would be essential in this regard. However, mast events are contingent on a specific set of climatic conditions which must be met in an

exacting order if adequate amounts of seed are to be dispersed (Figure 6-2).

2. Seeds must germinate: Germination of white spruce seeds depends on a variety of conditions including adequate substrate, moisture, and high enough temperatures (Fraser 1971). Short viability of spruce seeds (i.e. 1-2 years) means that these conditions have to be met in the year or two immediately following a mast event (Nienstaedt and Zasada 1990).

3. Seedlings must emerge above the ground coupled atmospheric layer: This seems to be a critical factor limiting the advance of treeline. The presence of seedlings and dwarf individuals above treeline suggests that establishment is not limiting. Instead, these individuals appear unable to extend above the favourable thermal conditions and sheltering provided at ground level. Based on my results, a warmer climate could provide conditions for this to occur. However, these conditions must be persistent. One winter of low snow cover, or a mid-winter thaw followed by a return to sub-freezing conditions (Figure 6-3), could effectively negate the gains made from multiple years of advantageous conditions.

4. Individuals must mature into a tree growth form: Emergence above the ground-coupled thermal layer does not necessarily ensure recruitment into tree form. Individuals at treeline continue to experience unfavourable growth conditions which determine the extent to which they take on characteristics of a krummholz-type growth form versus an upright tree-type growth form (Holtmeier 2003).

> These conditions, including all the classic climatic variables such as temperature, growing season, snow cover and wind, would likely require some amelioration for tree growth forms to predominate.

In addition to this succession of age-climate requisites, large-scale disturbances including fire, insect outbreaks, slope failure and avalanches must be absent. The latter two conditions do not seem to be important at the relatively low treeline elevation of southwest Yukon, unless precipitation significantly increases in the future. However, at a regional scale, the former two conditions are important in forest dynamics at lower elevations and may become increasingly so as climate warming continues (Ogden 2006).

More Shrubs: A Concurrent, or even Alternate Response

Denton and Karlen (1977) found evidence of more advanced treelines in the form of subfossil trees 75 m above present treeline in the Kluane region ca. 5000 years BP, indicating that there is potential for future advance. However, in light of the aforementioned prerequisites for treeline advance, and the order in which they must proceed, it is difficult to foresee an advance of spruce beyond an additional 100 metres elevation in the next century. Indeed, there is the possibility that the advance of the early to mid 20th century documented in Chapters 2 and 3 was exceptional; perhaps just a return to "normal" after centuries of suppression during the Little Ice Age.

In terms of potential extent, increased deciduous shrub biomass and abundance may be a more significant vegetation response to climate warming. This change has been observed at many locations beyond arctic treeline in Alaska since the mid 20th century

(Sturm *et al.* 2001a, Tape *et al.* 2006). Sturm *et al.* (2001b) concluded that there is significant potential for landscape transformation, particularly as a result of extensive positive feedbacks resulting from altered snow cover and surface albedo, and associated changes in runoff, shading, and CO_2 exchange. Dwarf birch and many species of shrub-forming willow already grow well above treeline and the limitations imposed on spruce as a consequence of permafrost distribution may be less consequential for these species. Additionally, Bond's Hypothesis (Bond 1989) would suggest that, all else being equal, these deciduous species have a competitive advantage over spruce seedlings in the high light environment beyond treeline (Becker 2000).

The potential for concurrent treeline and shrubline advance leads to additional questions regarding interactions between spruce and shrubs that also need to be addressed. For example, how important is competition or facilitation between the two? Is a shrubline advance required before an advance of treeline, or does it hinder treeline advance? These are not simply academic questions. The second generation coupled global climate model (CGCM2; Flato *et al.* 2000) projects a mean annual temperature increase of 3.4 degrees for southwest Yukon by 2080 using a moderate CO_2 increase (Scenario B). Based on a 0.65° C lapse rate, the current thermal elevation of treeline would rise 525 m (Table 6-1). Thus, the potential for change in this region is substantial (Figure 6-4), and the implications of such change must be considered.

HIERARCHY THEORY: WAS IT USEFUL?

Hierarchy theory has been advanced as a way of unifying ecology through the fundamental concept of scale, and even as a tool for integrating aspects of complexity theory (see Manson 2001), such as chaos, catastrophe, and self-organization, into scientific investigation (Allen and Hoekstra 1992). Explicit consideration of scale is its hallmark, but its holistic approach is also a critical trait. Still, despite this potential, it is not a panacea. It is intuitively strong as a metatheory but, like complexity theory, it relies heavily on metaphors rather than empirical examples (cf. Proctor and Larson 2005).

One of the greatest problems with hierarchy theory is that it does not offer validation of the chosen hierarchy *a priori* (O'Neill and King 1998). Systems can be defined in multiple ways and hierarchies established by different researchers investigating the same questions may be very different. Divisions may seem arbitrary and the broader cross-scale conclusions are contingent on the scale-levels defined at the outset. Thus, it is important to offer a *post hoc* evaluation of the hierarchy used.

An important gauge for use in evaluating the hierarchical framework used here is to examine the extent to which the results of the different investigations support or oppose each other. From this perspective, it seems that the framework was relatively successful. For instance, the landscape-scale analysis illustrated the importance of temperature in determining spruce distribution, and the dendroecological analysis indicated that recent spruce dynamics were heavily influenced by a period of above-average temperatures. The experimental warming provided data to support the hypothesis that treeline elevation is not limited by establishment but, rather, by recruitment. The more significant forward lag indicated by climate-recruitment correlations obtained from stand level data also support this.

It was originally hoped that this dissertation could provide some of the empirical examples required to advance the consideration of scale and the use of hierarchy theory in addressing its challenges. To some extent this has been achieved. However, the extent to which cross scale interactions at treeline can be identified using only the results of these four investigations is limited. This could be related to the breadth of the research questions which were posed. Cross-scale conclusions were more successful within each investigation (e.g. the leaf level – plant level – population level hierarchy of the experimental warming) where the research questions were more focused, compared to between investigations where the questions were broad and less defined.

CONCLUSION

The research presented here is the first in-depth study of forest-tundra ecotone dynamics in southwest Yukon and the first to examine the ecotone in subarctic North America from an explicitly multiscale perspective. The basic methods used in each component of the investigation have been used elsewhere, some quite extensively. However, by integrating them within a single study I have been able to shed some light on how patterns and processes that occur at multiple scales influence the expression and dynamics of the entire forest-tundra ecotone. This includes variation in individual-level processes such as photosynthesis and meristem growth, population-level processes such as reproduction and recruitment, and the influence of landscape-scale variations on distribution and abundance.

By definition, one of the primary characteristics differentiating alpine from arctic treeline is steep topographic gradients. Although this is convenient, it is difficult to separate the two phenomena in areas of high relief at high latitudes. For instance, in Alaska's Brooks Range, treeline is heavily influenced by both altitude and latitude

(Griggs 1934). Separation becomes clearer with decreasing latitude, but even in subarctic mountains there remain many similarities (Viereck 1979). For this reason, many of the results of this research are as applicable to arctic treeline as they are to alpine treeline, even though alpine treeline has been emphasized. Indeed, given the similarities in species composition and environmental conditions, it may be that there are more lessons here for arctic treeline than for alpine treelines at lower latitudes.

Table 6-1. Potential changes to alpine habitat in a *ca.* 16,000 km^2 area of the Kluane region, southwest Yukon, if treeline advances. Figures are based on a binary landscape configuration; areas were classified as being either below or above treeline. "Current" refers to the areas currently above treeline based on an approximate location of treeline derived from Yukon Forest Resource Inventory (FRI) maps. "100m Rise" refers to the areas above treeline after a 100m altitudinal advance. "525m Rise" refers to the areas above treeline after a 525m altitudinal advance. This latter scenario is based on a 3.4° C climate warming and an altitudinal lapse rate of 0.65° C. See Figure 6-4 for maps of each scenario.

	Current	**100m Rise**	**525m Rise**
Total Area (ha)	811014	575797	175481
Number Patches	86	471	316
Mean Area/Patch (ha)	61.1	246.8	162.0
Summary		Large contiguous tundra areas divided into small patches;	Most of Ruby Range tundra gone; Kluane Ranges fragmented
Scenario		Alpine Habitat Fragmentation	Alpine Habitat Loss

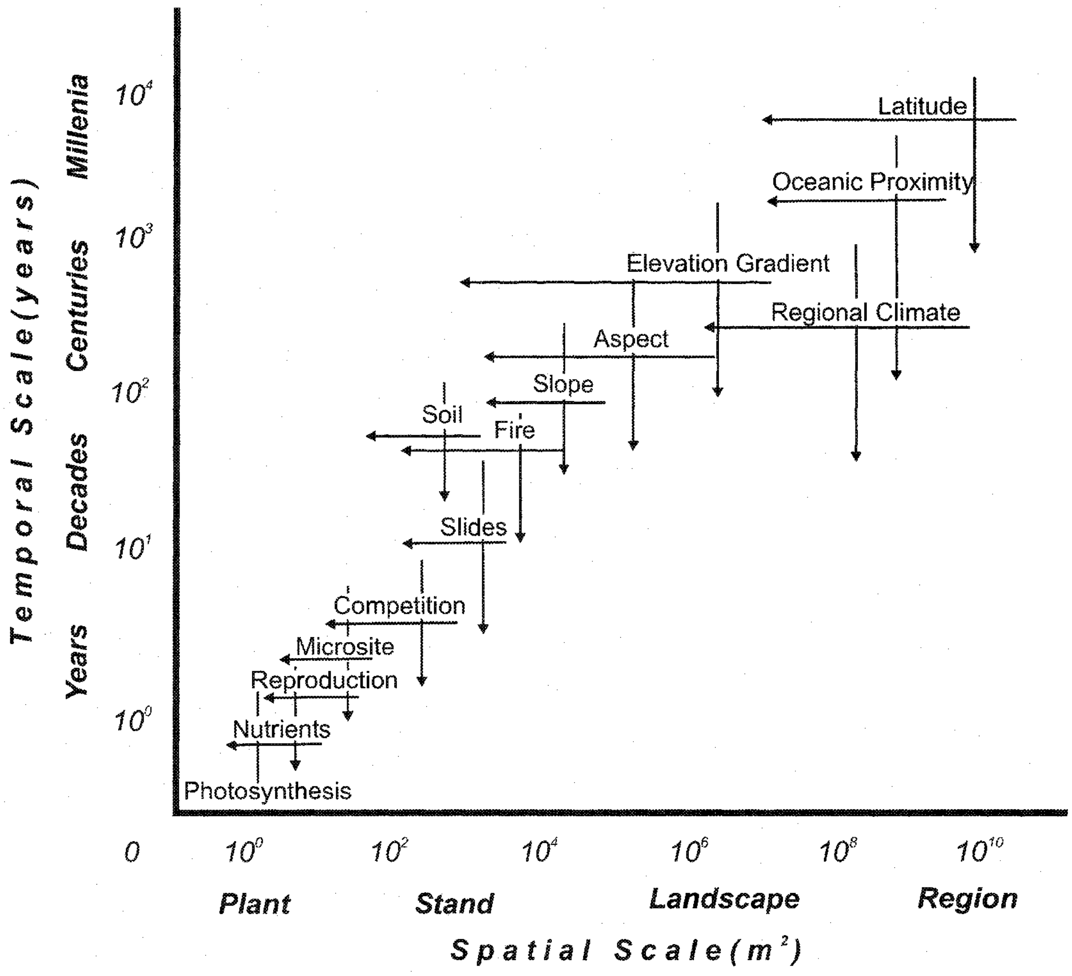

Figure 6-1. Hierarchy of scale illustrating selected limits to and constraints on alpine treeline and its dynamics using the "Ecotone Scale Paradigm" proposed by Delcourt & Delcourt (1992).

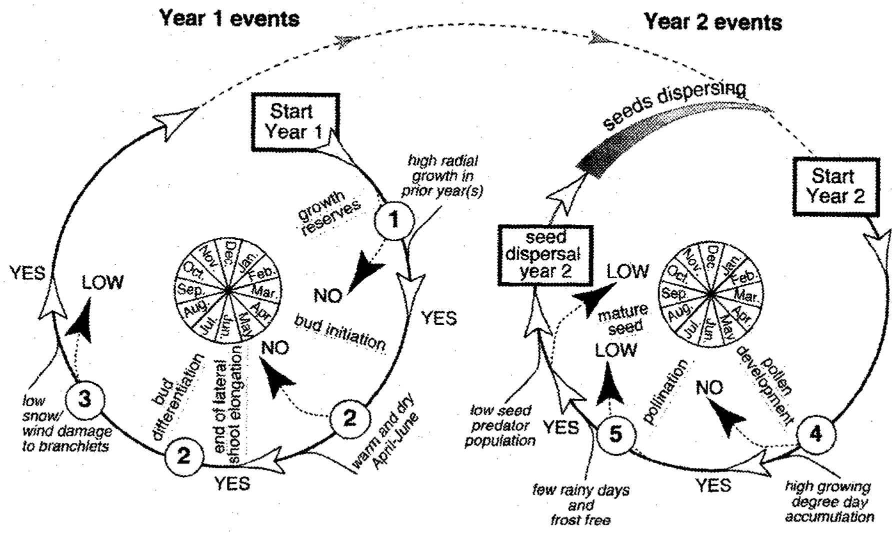

Figure 6-2. Critical gateways (numbered circles) leading to the production of white spruce seed crops. Events begin at the top of the left-hand circle (start year 1) and continue clockwise, then proceed to the top of the right-hand circle and proceed clockwise to seed dispersal at the end of year 2. timing of gateways during the year is indicated by position on yearly circle with months indicated. Open arrows indicate critical thresholds being met by conditions identified on the outer perimeter of circle and seed-crop production proceeds through the gateway; filled arrows (pointed inward on circle) indicate either condition not met or marginal conditions likely to result in a low seed crop. Figure and caption taken from Juday *et al.* (2003).

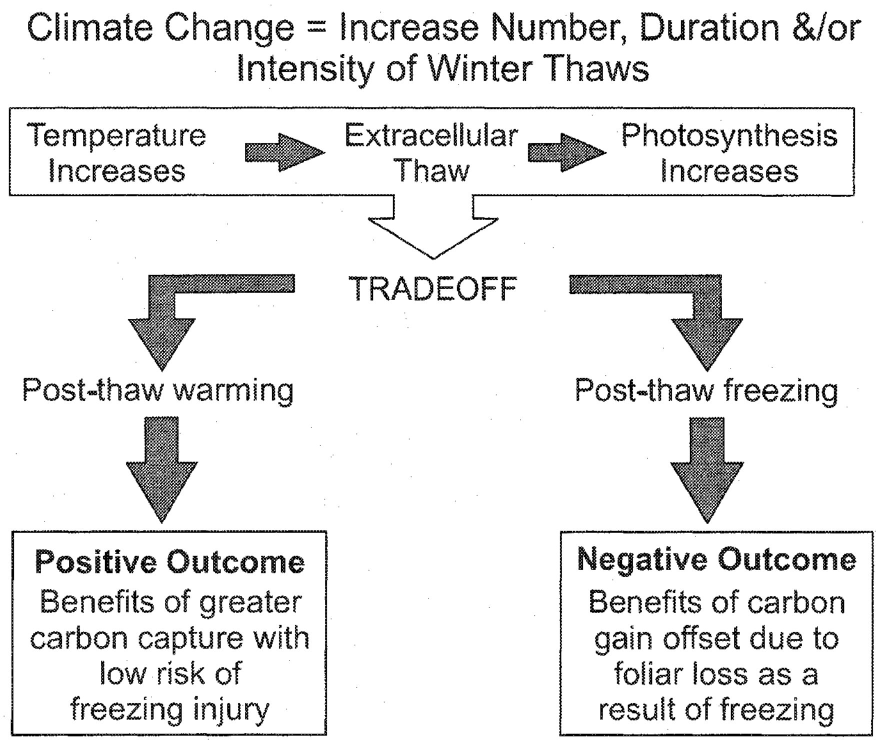

Figure 6-3. Potential responses of spruce to warmer winter climate. Consequences of thaws on physiology could depend on trends in temperatures following thaws. After Schaberg (2000).

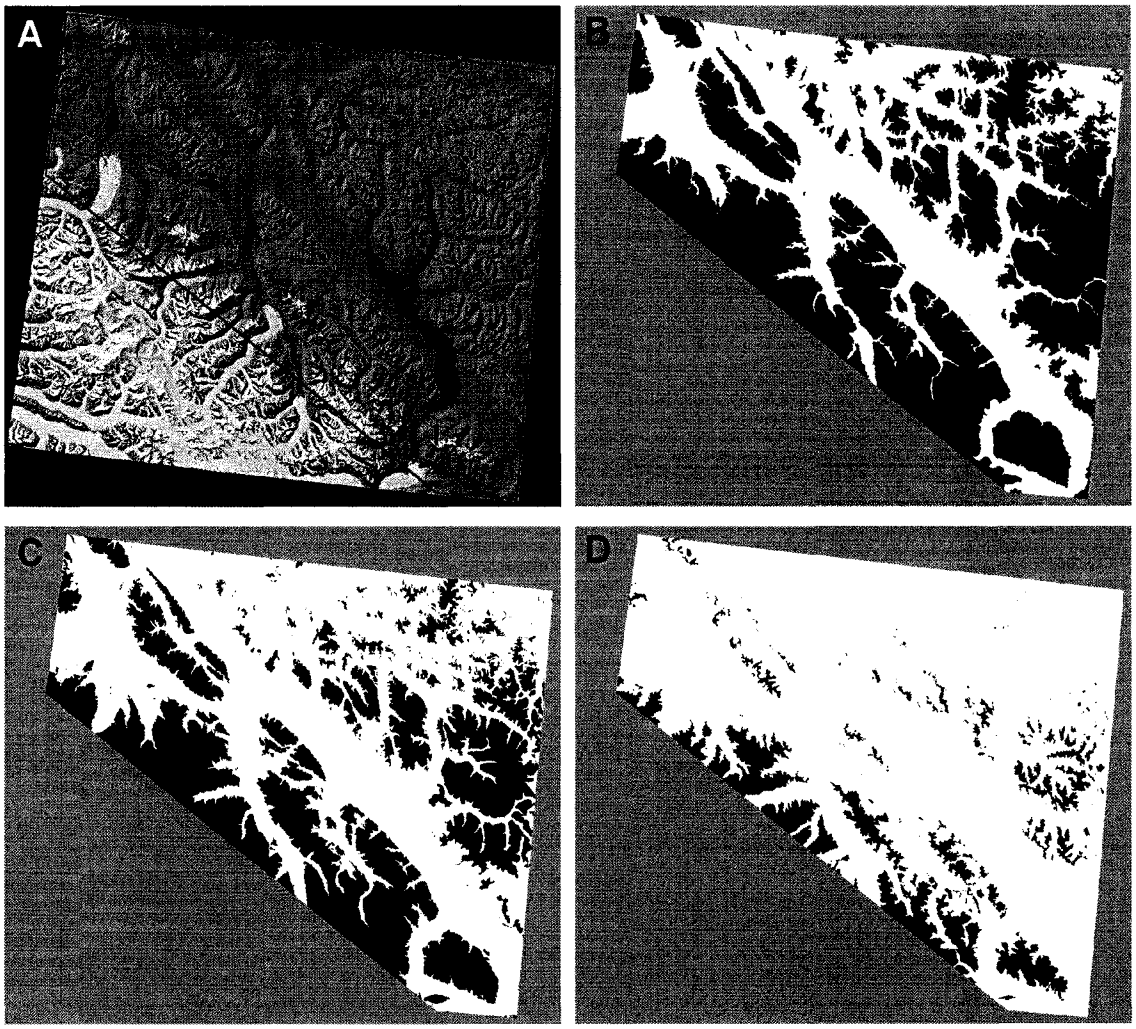

Figure 6-4. A simple binary model of treeline changes in response to climate warming in the Kluane region, southwest Yukon. Scenarios are based on a GIS-based elevation buffer of current treeline. (A) Shaded relief map of the region. Approximate position of treeline (in yellow) was derived primarily from the Yukon Forest Resources Inventory. Glaciers in white, waterbodies in blue. The red polygon indicates the area of analysis. (B) Binary map of the existing landscape; white represents areas below treeline, black areas above treeline. (C) Landscape configuration if treeline advanced 100 m. This advance is consistent with the changes observed in response to warming during the early to mid 20th century. (D) Landscape configuration if treeline advanced 525 m. Based on a thermal lapse rate of 0.65° C per 100 m, this change in the potential elevation of treeline could be expected if average annual temperatures increase by 3.4° C, which the Canadian Global Circulation Model (Flato *et al.* 2000) predicts will occur by 2080. Statistics associated with each landscape configuration are listed in Table 6-1.

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