CLIMATE CHANGE AND VEGETATION DYNAMICS AT THE
SUBARCTIC ALPINE TREELINE IN NORTHWESTERN CANADA

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ABSTRACT

It is expected that anthropogenic increases in atmospheric levels of CO_2 and other greenhouse gases will have a substantial impact on climate in the next 100 years. Knowledge of the response of high latitude vegetation to past climate variation is useful for understanding the possible response of such vegetation to potential future anthropogenic climate changes. The objectives of this thesis were to investigate climate change, treeline dynamics and vegetation-climate relationships at the subarctic alpine treeline in northwestern Canada on a variety of spatial and temporal scales. In order to address these objectives, three hypotheses were tested: 1) Postglacial treeline change in the Mackenzie Mountains, N.W.T. was driven by changes in the seasonal and latitudinal distribution of solar radiation; 2) Establishment and mortality patterns of trees at treeline are episodic, controlled by climate variations; and 3) The position of the treeline in the Mackenzie Mountains is in equilibrium with current climatic conditions.

The first hypothesis was tested using the palynological analyses of cores from three lakes in the tundra, forest-tundra and open forest of the central Mackenzie Mountains. Although there was no evidence for higher treeline in this region at any time during the Holocene, the data suggest that Picea populations in the forest-tundra were greater than present between about 8000 and 5000 yr BP, and have since declined steadily. These results are consistent with predicted changes in summer insolation based on the Milankovitch theory.

The second two hypotheses were addressed using tree-ring analyses of white spruce at a number of sites in the alpine treeline zone of northwestern Canada. Dendroecological analyses of climate-growth relationships indicated that the response of trees to climate at these sites varied with tree age, which violates a basic assumption of standard dendroclimatic research. Age dependent modelling was therefore used to produce a 350 year record of summer temperatures in northwestern Canada from five sites in the N.W.T. and Yukon. Comparison of this record with white spruce recruitment/survival and mortality patterns indicated that the patterns are episodic, and controlled primarily by climatic variations. A warming trend during the last 150 years has resulted in increases in forest-tundra density, although there is evidence for only minor increases in treeline. The establishment of white spruce seedlings at sites within the upper forest-tundra, including several treeline sites, indicates that the treeline is in equilibrium with current climatic conditions.

These results indicate that 1) climate-growth relationships are complex, and the simplifying assumptions made in order to reconstruct climatic records from radial growth records may in some cases be invalid; 2) in this region the response of white spruce populations to climate change on a variety of timescales has been manifested primarily as an increase in forest-tundra density, with little change in treeline altitude; and 3) seedlings are currently being produced within forest-tundra white spruce populations, and thus a rapid response to further climatic amelioration may be possible.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

ix

x

xi

xii

LIST OF TABLES

CHAPTER ONE

INTRODUCTION

1.1 RATIONALE FOR STUDY

Anthropogenic increases in atmospheric levels of CO_2 and other greenhouse gases are expected to have a substantial impact on global climate over the next 100 years (Houghton et al. 1990; Melillo et al. 1993; Pastor and Post 1993). It has been suggested that considerable changes in the composition, extent and distribution of boreal forests may result from these climate changes (Pastor and Post 1988; Bonan et al. 1990; Prentice et al. 1991; Rizzo and Wilken 1992; Smith et al. 1992). In particular, the potential range of the boreal forest could expand northwards in North America and Eurasia to include portions of the low arctic currently supporting shrub tundra (Rizzo and Wilken 1992; Smith et al. 1992). The relative extents of boreal forest and tundra zones may in turn influence atmospheric CO_2 concentrations through biomass sequestering (D'Arrigo et al. 1987; Callaghan et al. 1992; MacDonald and Szeicz 1994), feedbacks in radiative forcing (Bonan et al. 1992) and the reversion of tundra ecosystems from a net CO_2 sink to a net source (Oechel et al. 1993). Although the potential limits of the boreal forest may extend northwards in the subarctic and/or upslope in montane regions, vegetation response may lag changes in climate (Ritchie 1986; Davis

1989). Knowledge of the response of treeline and forest-tundra communities to climate change is therefore essential for an understanding of the potential response of boreal forest limits to anthropogenic climate changes and hence the possible extent of vegetation induced feedback processes.

The investigation of vegetation responses to past changes in climate using palaeoecological techniques provides a valuable source of information on climate-vegetation interactions which is not possible using modern ecological techniques (Deevey 1969), and can assist in the understanding of potential future changes. The sensitivity of vegetation in high latitude and alpine regions to climate changes on different timescales has been demonstrated by various palaeoecological studies (eg. LaMarche 1973; Ritchie et al. 1983; Payette and Filion 1985; Kullman 1990; MacDonald et al. 1993). The subarctic alpine treeline of northwestern Canada, and the Mackenzie Mountains in particular, could potentially be responsive to past climatic change, but few data are available from this region. The mountains of northwestern Canada are well suited for studies of climate-vegetation dynamics for several reasons. Firstly, past climatic fluctuations in the subarctic have been amplified relative to changes at lower latitudes (Hansen and Lebedeff 1987), and it is expected that potential future anthropogenic changes will also be of greater magnitude at high latitudes (Houghton et al. 1990). Past and potential future vegetation responses to climate variation at the subarctic alpine treeline, therefore, may also be amplified in comparison to the response of vegetation at mid- and low latitudes. Secondly, much of the region was unglaciated in the late Pleistocene

(Figure 1.1), which offers the potential for recovery of long sedimentary records extending well into the Pleistocene. Thirdly, the Mackenzie Mountains are characterized by extensive, rolling plateaus above treeline which, given an altitudinal rise in treeline, have the potential to greatly increase the extent of open forest and/or forest-tundra. Such increases could amplify the signal of treeline variations in fossil pollen and macrofossil records. Finally, disturbance by fire, insect defoliation, or human activity appears to be very infrequent or absent in the treeline zone of the Mackenzie Mountains.

1.2 CLIMATE AND THE TREELINE

In this study the treeline is defined as the uppermost limit of trees with an upright growth form (Rochefort et al. 1994). The location of treeline is governed by a complex and sometimes poorly understood set of interactions between climate and the physiological and reproductive characteristics of trees, but is generally considered to be thermally controlled (Wardle 1974; Tranquillini 1979; Black and Bliss 1980; Crawford 1989; Grace 1989; Stevens and Fox 1991; Sirois 1992). Various bioclimatological explanations have been put forth to account for treeline, primarily the polar treeline, on a continental to global scale. The simplest of these is the often cited fact that treeline generally coincides with the 10° C isotherm in the warmest month (Grace 1989; Sirois 1992). Bryson (1966) noted that in Canada both the northern treeline and the 10° C isotherm correspond with the mean July

18,000 yr BP

14,000 yr BP

12,000 yr BP
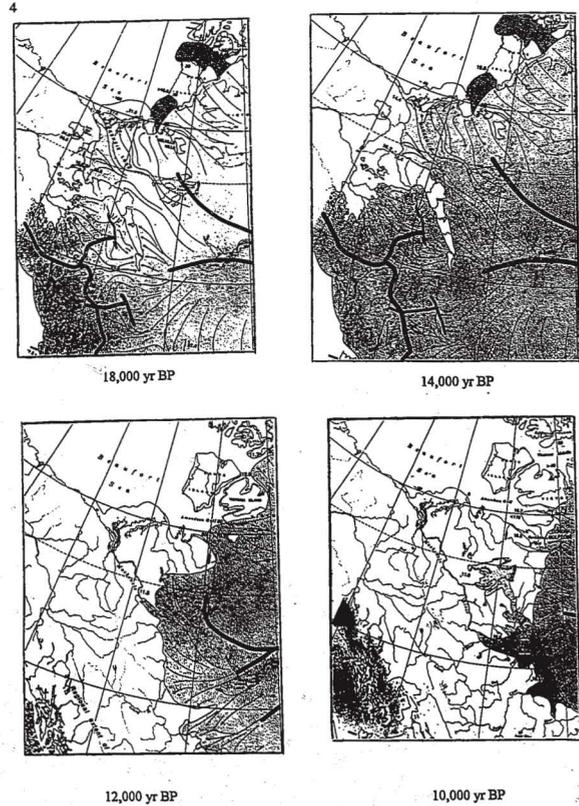
10,000 yr BP

Figure 1.1: Retreat of Laurentide and Cordilleran ice in northwestern Canada, 18,000 yr BP to 10,000 yr BP (from Dyke and Prest 1987).

position of the arctic front, indicating the importance of air mass dominance in determining regional treeline position. The position of the arctic front probably does not directly affect the location of treeline (Sirois 1992), but rather the effects are indirect through its influence on growing season energy budgets (Hare and Ritchie 1972). Vegetation-climate feedbacks appear to be important in establishing the abrupt nature of the forest to tundra transition in many regions (Hare and Ritchie 1972).

At the level of individual organisms, ecophysiological research has emphasized the importance of growing season length and water relations on the survival of trees at treeline (Wardle 1974; Tranquillini 1979; Baig and Tranquillini 1980; Goldstein et al. 1985; Hadley and Smith 1986; Hansen-Bristow 1986; Grace 1989). The shortening of growing season below a certain threshold duration may lead to insufficient development of needle cuticles, which could be further damaged by abrasion from wind-borne snow (Hansen-Bristow 1986; Hadley and Smith 1986). In late winter and spring, water uptake at treeline may be limited by frozen or cold soils while evaporative demand is high due to moderate temperatures, high radiation levels and often strong winds (Tranquillini 1979; Baig and Tranquillini 1980; Richards and Bliss 1986). This may lead to desiccation of needles ('winter desiccation' or 'frost desiccation') and eventually death of the individual, since incompletely developed and/or damaged needles may be unable to control transpirational water losses (Tranquillini 1979; Baig and Tranquillini 1980). Although this explanation for treeline is not universal (Grace 1990) it is clear that

water relations and the length and magnitude of the growing season are important factors controlling treeline through their influence on tree physiology.

Finally, treeline has also been explained in terms of tree reproductive ecology (Sirois 1992). Threshold temperature levels have been determined for the germination of black spruce (Picea mariana; botanical nomenclature in this thesis follows Porsild and Cody (1980)) seedlings, below which germination does not occur (Black and Bliss 1980; Sirois 1988). Thus treeline position may be governed by the ability of trees to successfully regenerate in a certain environment, not simply to survive once established, and treeline may in some cases be defined as the uppermost or northernmost limits of sexual regeneration in tree species.

1.3 RETROSPECTIVE STUDIES OF TREELINE AND FOREST-TUNDRA DYNAMICS AT HIGH LATITUDES

The dynamics of high latitude tree populations at or near their alpine or polar limits has been the subject of numerous studies employing various methodologies. The majority of these studies can be classified as either dendroecological, which here includes the use of radiocarbon and dendrochronologically dated dead tree remains on the ground surface and from sedimentary deposits, and palynological, which involves the analysis of fossil pollen from sedimentary deposits, often supplemented by terrestrial plant macrofossils such as needles and seeds. A summary of Holocene treeline dynamics

at high latitudes is given in Table 1.1.

1.3.1 Dendroecological studies

Intensive dendroecological research programs investigating high latitude forest-tundra and treeline dynamics at timescales ranging from millennial to decadal have been carried out at the upper tree-limit in central and northern Sweden, and at the latitudinal tree-limit in northern Quebec. Five species of trees, Pinus sylvestris, Picea abies, Betula pubescens, Sorbus aucuparia, and Alnus incana reach their altitudinal limits in the forest-tundra ecotone of central and northern Sweden (Kullman 1990). These species have different ecological requirements and therefore respond to climatic fluctuations in different manners, making this region appropriate for retrospective studies of treeline dynamics. Radiocarbon dating of preserved wood from locations above the current treeline has indicated contrasting histories for the Holocene dynamics of Pinus sylvestris and Betula incana, which are consistent with the orbital forcing (Milankovich) model of climate change (Kullman 1990, 1992, 1993). Pinus limits have decreased linearly during the last 8000 years, probably in response to declining seasonality, and in particular lowered summer temperatures. Betula and possibly Alnus tree-limits increased altitudinally until about 4000 yr BP, and although they have since declined have remained above the upper limits of Pinus. This shift is consistent with a reversion towards a moister climate with milder winters. Similar results have been obtained from the alpine treeline in southern Norway (Kvamme 1993). Climatic fluctuations on

TABLE 1.1: Summary of Holocene treeline dynamics at high latitudes (for references see text).

Region		Early Holocene (10-7 ka)	Mid Holocene (7-3 ka)	Late Holocene (3 ka - present)
North America	Quebec	—	maximum forest-tundra density	decreasing density
	Central Canada	—	northward extension of treeline; greater forest-tundra density	treeline retreat; retrogression of forest-tundra
	Northwest Canada	maximum northward extension of treeline; greater forest-tundra density	treeline retreat; retrogression of forest-tundra	vegetation similar to present
	SE Alaska	?	higher treeline, 5250 yr BP, 3600-3000 yr BP	higher treeline 2100-1200 yr BP
Scandinavia	montane	higher Pinus, Betula, Alnus limits	decreasing Pinus limits; maximum Betula, Alnus limits	vegetation similar to present
	northern	maximum northern extension of Pinus, Betula	treeline retreat commencing c. 5000 yr BP	vegetation similar to present
Russia	montane	?	?	higher Larix limits c. 800 yr BP
	northern	maximum northward extension of Larix, Betula (and Picea?)	treeline retreat commencing c. 5000 yr BP	vegetation similar to present

shorter timescales have also impacted on treeline populations in Sweden (Kullman 1986a, 1986b, 1987a, 1987b, 1990). Little Ice Age cooling (c. AD 1550-1880) resulted in lower levels of regeneration in the forest-tundra and drops in the upper limits for all species. Subsequent warming trends have resulted in the increased density of populations within the forest-tundra, and increases in the altitudinal tree-limits of all species on the order of 30-50 m.

The forest-tundra ecotone of northern Quebec is dominated by Picea mariana and Larix laricina, with Picea glauca achieving local dominance in some areas (Payette and Gagnon 1979). Extensive fires within the forest-tundra during the last 3000 years have led to a widespread retrogression of Picea mariana and Larix laricina populations, since a concurrent cooling trend has limited regeneration at many sites (Payette and Gagnon 1985; Gagnon and Payette 1985; Payette and Morneau 1993). The density of forest-tundra has therefore undergone striking reductions in response to climate-fire interactions in the late Holocene, although shifts in the position of the treeline have been less significant. Further studies at shorter timescales have demonstrated the complexity of climate-vegetation interactions in northern Quebec. Altitudinal and latitudinal shifts in response to climatic variation over the past several hundred years have been of low magnitude, and the primary response of Picea mariana, Larix laricina, and Picea glauca treeline populations has been in the form of changing tree densities and shifts in growth forms (Payette and Filion 1985; Payette et al. 1985, 1989; Lavoie and Payette 1992). The most significant change has been one of increasing forest-

tundra density during the last 100 years. The main response of Picea glauca and Picea mariana populations to recent warming at the latitudinal treeline in central Canada (Scott et al. 1987; MacDonald and Szeicz 1994) has also been manifested as an increase in forest-tundra density, with little change in species limits.

Dendroecological studies in Alaska (Denton and Karlen 1977) and the polar Urals of Russia (Gorchakovsky and Shiyatov 1978; Shiyatov 1993) have reconstructed shifts in the altitude of alpine treeline of 50 to 80 m during the Holocene (Table 1.1), although in some areas such shifts may have been enhanced by gradual isostatic uplift (Kullman 1993). Data on the response of treeline population density to climate is unavailable from these sites. Northward extensions of treeline in northernmost Scotland between 4400 and 3800 yr BP (Gear and Huntley 1991) and northern Russia between about 9000 and 5000 yr BP (Khotinsky 1984) have also been reconstructed using radiocarbon-dated wood from beyond the current tree limits.

1.3.2. Palynological studies

The Holocene dynamics of the latitudinal treeline in northern Canada has been the focus of a number of palynological studies. Fossil pollen records from lake sediments, supported by radiocarbon-dated spruce macrofossils, indicate that on the Tuktoyaktuk Peninsula of northwestern Canada Picea mariana and Picea glauca limits were at least 70 km to the north of the current treeline between about 9500 and 5000 yr BP (Ritchie and Hare 1971; Ritchie et al. 1983; Ritchie 1984;

Spear 1983, 1993). Similar evidence from central Yukon (Cwynar and Spear 1991) documents a concurrent, widespread expansion and subsequent retrogression in spruce poulations within the forest tundra. The timing of treeline/forest-tundra expansion in these regions coincides with the period of maximum solar radiation at high latitudes as predicted by the Milankovitch theory of global climatic change. This provides direct support for the Milankovitch hypothesis, although the support is limited by the fact that the Holocene is short with respect to the length of Milankovitch cycles.

The results of early palynological studies on peat deposits north of treeline in central Canada were interpreted as evidence for several advances and retreats of treeline during the mid to late Holocene (Nichols 1967, 1975), but sampling methods were crude, and the interpretation was questionable and unsupported by macrofossil or sedimentary evidence (Ritchie 1985). More recent work on lacustrine deposits (Moser and MacDonald 1990; MacDonald et al. 1993) provides reliable palynological evidence, supported by sediment, geochemical, isotope and diatom analyses, of a northward movement of treeline in central Canada between about 5000 and 3500 yr BP. Pollen evidence from northern Quebec (Richard 1981; Gajewski and Garralla 1992; Gajewski et al. 1993) suggests treeline position has changed little since spruce populations first expanded about 4000 yr BP, though forest-tundra density has decreased over the past 3000 years. These data corroborate the results from dendroecological studies in the same region.

Fewer palynological data are available on Holocene dynamics of the

latitudinal treeline outside of Canada. From about 9000 to 5000 yr BP, when treeline expanded north of its current position in northwestern Canada, both Betula pubescens and Pinus sylvestris tree-limits were located well north of their current positions in northernmost Scandinavia (Hyvarinen 1976). Paynological data from northern Russia (Khotinsky 1984) support the dendroecological evidence for a northward extension of treeline at 9000 to 5000 yr BP. The northern limit of trees in Alaska coincides with the altitudinal treeline on the south slopes of the Brooks Range, and does not appear to have extended northwards or upslope of its current limits at any time in the Holocene (Brubaker et al. 1983; Edwards et al. 1985). Spruce dynamics in this region may have been complicated by the presence of the east-west trending Brooks Range.

Fossil pollen-based investigations of subarctic alpine treeline dynamics are available from a small number of regions in Canada and Scandinavia. Such records are more difficult to interpret than those from the latitudinal treeline, owing to the overrepresentation of pollen from lowland vegetation in spectra from tundra and forest-tundra, and the altitudinal compression of vegetation zones (Markgraf 1980; Fall 1992). Corroborative evidence from plant macrofossils is therefore even more critical in palaeoecological studies of alpine treelines. At a site in the central Mackenzie Mountains of northwestern Canada, MacDonald (1983) provided pollen and macrofossil evidence for a treeline which was higher than at present from 7700 to 5000 yr BP. Declining spruce pollen concentrations at several sites in Labrador during the past 3000 years are suggestive of a late-Holocene drop in

treeline in this region (Lamb 1985), although supporting macrofossil evidence was not available. Palynological studies have also been made on the Holocene treeline history of montane regions in nothern Finland (higher treeline c. 8000 - 4000 yr BP; Hyvarinen 1993) and northern Norway (higher treeline c. 8000 - 4500 yr BP; Vorren et al. 1993). Interpretation of fossil pollen records in these regions is aided by the availability of extensive dendroecological records of treeline dynamics.

1.4 RESEARCH OBJECTIVES

The objectives of this thesis are to investigate climate change, treeline dynamics and vegetation-climate relationships at the subarctic alpine treeline in northwestern Canada, with a focus on the Mackenzie Mountains of the western Northwest Territories. In addressing these objectives, two points became evident. Firstly, treeline dynamics are dependent on processes within the forest-tundra ecotone as a whole, and thus should not be examined on their own, but rather should be examined within the broader context of forest-tundra dynamics. Secondly, ecological patterns and processes operate at different spatial and temporal scales (Delcourt and Delcourt 1991). The resolution of issues such as vegetation-climate equilibrium or the causes of vegetation dynamics depend to a large degree on the scale of investigation (Prentice 1986; Ritchie 1986; Delcourt and Delcourt 1991). An investigation of forest-tundra dynamics should therefore be carried out at several spatial and temporal scales. With these points in mind, three hypotheses

were developed in order to resolve climate change, treeline dynamics, and climate-vegetation relationships at the subarctic alpine treeline of northwestern Canada on a variety of spatial and temporal scales:

1) **Postglacial treeline change in the Mackenzie Mountains was driven by changes in the seasonal and latitudinal distribution of solar radiation.** Substantial northward migration of treeline and/or increase in forest-tundra density has been reconstructed for the period ~9500-5000 yr BP in the Mackenzie Delta region (Ritchie et al. 1983; Ritchie 1984; Spear 1993) and for the period ~5000-3500 yr BP in central Keewatin (Moser and MacDonald 1990; MacDonald et al. 1993). The northward movement of treeline in the Mackenzie Delta region has been attributed to the northward displacement of the arctic front in summer. This displacement may have in turn been a response to a period of maximum summer radiation in the early Holocene, as predicted by the Milankovitch model (Ritchie and Hare 1971; Ritchie et al. 1983). The later timing of treeline advance in central Canada may be due to the influence of residual ice masses, or to shifts in the summer position of the arctic front caused by long-wave frontal characteristics (Moser and MacDonald 1990; MacDonald et al. 1993). An examination of late Pleistocene and Holocene forest-tundra and treeline dynamics in the Mackenzie Mountains allows for study of the influence of orbital forcing on climate and vegetation in an area well removed from the mean summer position of the arctic front, and the location of residual ice masses during the Holocene. Since treeline

position is sensitive to summer insolation (Ritchie et al. 1983), and highest summer insolation in northwestern Canada occurred between 10,000 and 5000 yr BP (Kutzbach 1987), treeline in the Mackenzie Mountains may have reached its maximum elevation at this time. The lack of evidence for treeline advances and/or shift in forest-tundra density between about 10,000 and 5000 yr BP would lead to rejection of this hypothesis.

2) Establishment and mortality patterns of trees at treeline are episodic, controlled by climate variations. The importance of climate and disturbance in driving treeline and forest-tundra dynamics has been demonstrated by numerous studies, although information from the subarctic alpine treeline in northewestern Canada is lacking. There is little evidence for widespread disturbance by non-climatic factors at or near treeline in the Mackenzie Mounains, allowing for evaluation of the role of climate in determining treeline and forest-tundra dynamics in a disturbance-free environment. Evidence for establishment and/or mortality patterns which do not correlate with recorded or reconstructed climate records would lead to rejection of this hypothesis.

3) The position of the treeline in the Mackenzie Mountains is in equilibrium with current climatic conditions. Some researchers have suggested that spruce populations at the treeline in central Canada are currently unable to reproduce and are therefore out of equilibrium with the present climate (Larsen 1965; Elliott-Fisk

1983). These studies, however, were carried out during a climatically unfavourable period in the 1960's and 1970's and may therefore only be valid when climate-vegetation equilibrium is considered on very short timescales (MacDonald and Szeicz 1994). Research in other regions suggest treeline is often in a dynamic equilibrium with climate when considered on all but the shortest timescales (Payette et al. 1985, 1989; Scott et al. 1987; MacDonald and Szeicz 1994). Knowledge of the current state of vegetation-climate equilibrium at treeline in the Mackenzie Mountains will aid in determining its possible responses to any future climate changes. This hypothesis would be rejected if there is no evidence for recent tree regeneration at treeline or in marginal forest-tundra stands in the Mackenzie Mountains.

These hypotheses will be addressed in this thesis using a combination of fossil pollen and dendrochronological techniques. In Chapter Two fossil pollen data from three lakes are used to reconstruct the vegetation history of the central Mackenzie Mountains on a millenial timescale in order to test the first hypothesis. Before the second and third hypotheses could be addressed, it was necessary to develop an annually resolved proxy record of climate variation for the region extending back several centuries. In Chapter Three the suitability of forest-tundra *Picea glauca* for dendroclimatic reconstruction in this area is investigated by examining the relationships between radial growth and climate. Chapter Four outlines the development of a 350-year dendroclimatic record of summer

temperatures for northwestern Canada, and in Chapter Five this record is combined with establishment and mortality data to address the second and third hypotheses outlined above. The final chapter summarizes the major findings and outlines the conclusions of the study.

CHAPTER TWO

LATE QUATERNARY VEGETATION HISTORY OF THE CENTRAL MACKENZIE MOUNTAINS [1]

2.1 INTRODUCTION

Postglacial vegetation development in the Mackenzie River basin of the Northwest Territories (N.W.T.) has been the focus of several studies (Ritchie 1984 and references therein; Slater 1985; MacDonald 1987; Spear 1993). However, published palaeoecological research from the adjacent Mackenzie Mountains is restricted to an 8600 year pollen and macrofossil record from a peat profile (MacDonald 1983; Fig. 1). The Quaternary palaeoecology of the Mackenzie Mountains is of interest for a number of reasons. Firstly, part of the region was unglaciated in the late Pleistocene, and formed the southeastern limit of the ice free area of Beringia (Dyke and Prest 1987). Lake basins within the mountains, west of the maximum Laurentide ice sheet limits, have the potential to provide long sedimentary records extending well into the Pleistocene. Lake basins within the limits of Laurentide ice should provide minimum dates for final retreat of the ice

at its northwestern margin. Secondly, the ice-free area and regions which were deglaciated early may have played a role in the late glacial and postglacial migration of animals, plants and humans (Ritchie 1984; MacDonald 1987). Lastly, there have been substantial but asynchronous fluctuations in the Holocene position of the northern treeline in central and western Canada. In the Mackenzie Delta region, treeline was up to 50 km north of its present position between about 9500 and 5000 yr BP (Ritchie 1984; Spear 1993). In central Canada a northward extension of treeline and/or an increase in density of forest-tundra occurred from 5000 to 3500 yr BP (MacDonald et al. 1993). It has been suggested that the asynchronous nature of these treeline events is due to interactions between long term variations in the seasonal distribution of incoming solar radiation (Milankovitch orbital forcing), the geometry of the arctic front, and the influence of residual ice masses (Ritchie 1984; Moser and MacDonald 1990; MacDonald et al. 1993). Palaeoecological studies at the subarctic alpine treeline of the Mackenzie Mountains offer the potential to examine the influence of orbital forcing on climate in an area well removed from both the mean summer position of the arctic front and the location of residual ice masses during the Holocene. As treeline is sensitive to summer insolation (Ritchie et al. 1983) and highest summer insolation in Northwestern Canada occurred between 10,000 and 5000 yr BP (Kutzbach 1987), it is expected that treeline in the Mackenzies would have reached maximum elevation at that time. Pollen and macrofossil data from Natla bog (MacDonald 1983) suggest treeline may have been locally higher than present

between about 7700 and 5000 yr BP.

In this chapter the fossil pollen records from the sediments of three lakes along an elevational gradient through the open forest, forest-tundra, and tundra zones of the central Mackenzie Mountains are presented. These data are used to provide a minimum deglaciation date for the western edge of Laurentide ice and to document the vegetation history of the central Mackenzie Mountains. Emphasis is placed on (1) early postglacial environmental conditions, as these might have influenced the migration of humans and fauna through the region; and (2) treeline variations, in order to test the hypothesis that treeline changes in the region were controlled by changes in the seasonal distribution of solar radiation.

2.2 STUDY AREA

2.2.1 Geology and Glacial History

The central Mackenzie Mountains (Fig. 2.1) are composed of the inner Backbone Ranges (2000 to 2400 m elevation) and the outer Canyon and Redstone Ranges (1500 to 2000 m elevation), and incised by the Mountain, Carcajou, Keele and Redstone river valleys. The mountains are composed primarily of Silurian and Devonian limestone, dolomite and calcareous shales, with some Precambrian quartzites (Aitken and Cook 1974). Permafrost is discontinuous in the central Mackenzie Mountains. Regional ice retreat dynamics during the late Wisconsin are illustrated in Figure 1.1. Much of the Backbone Ranges were glaciated by
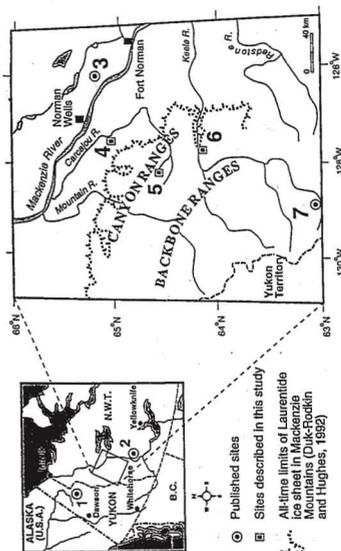
Figure 2.1: Locations of sites discussed in text. 1) Lateral Pond (Ritchie 1984); 2) Eildun Lake (Slater 1985); 3) LacMeleze (MacDonald 1987); 4) Bell's Lake (this study); 5) Andy Lake (this study); 6) Keele Lake (this study); 7) Natla Bog (MacDonald 1983).

Cordilleran ice and/or large montane glaciers in the late Wisconsin and previous advances, though many interfluve areas remained ice-free. The Canyon and Redstone Ranges have been less affected by glaciation (Duk-Rodkin and Hughes 1992). During advances, ice extended along major valleys from sources in the Backbone Ranges to the west, and smaller cirque glaciers expanded from higher peaks within the Canyon Ranges (Duk-Rodkin and Hughes 1991). Although absolute dating of glacial dynamics in this region is poor, a relative chronology has been established (Table 2.1; Hughes et al. 1981; Duk-Rodkin and Hughes 1991, 1992, in press). The earliest event for which evidence is available is a penultimate advance of montane glaciers, locally named the Mountain River Glaciation, whic correlates with the Illinoian phase (Reid in the Yukon) and dates to >80,000 yr BP. The maximum expansion of Laurentide ice in the late Wisconsin occurred at 25-30,000 yr BP. At this time, the ice sheet abutted the eastern and northern front of the Mackenzie Mountains up to elevations of 1100 to 1400 m, and extended up major valleys. Following the maximum Laurentide advance, montane glaciers and/or Cordilleran ice advanced to their maximum late Wisconsin limits. This advance, locally termed the Gayna River Glaciation (correlating with the McConnell phase in the Yukon), occurred <23,000 yr BP. Finally, a re-advance of Laurentide ice, the Katherine Creek Phase, took place after 22,000 yr BP.

2.2.2 Climate and Vegetation

The Mackenzie Mountains are located within the Boreal Climatic Region

TABLE 2.1: Age relationships of Laurentide and Montane glaciations, Mackenzie Mountains, N.W.T. (Hughes et al. 1981; Duk-Rodkin and Hughes 1991, 1992, in press).

Montane	Laurentide
Mountain River Glaciation (Illinoian/Reid) >>80,000 yr BP	?
	maximum Laurentide advance 25-30,000 yr BP
Gayna River Glaciation (Late-Wisconsin/McConnell) <23,000 yr BP ?	retreat
retreat	Katherine Creek Phase re-advance 22,000 yr BP ?

(Hare and Thomas 1979). Norman Wells (Fig. 2.1), on the Mackenzie River, has mean January, July and annual temperatures of -28.7°C, 16.1°C and -6.3°C respectively, and mean annual precipitation of 335 mm (Environment Canada, unpublished station data). In the mountains, temperature seasonality decreases; mean January temperatures range from -20 to -26°C and mean July temperatures from 9 to 14°C (Burns 1973). Annual precipitation is also greater in the mountains, varying from 400 to 750 mm (Burns 1973).

The Mackenzie Valley north to about Norman Wells is occupied by the Upper Mackenzie Section of the boreal forest (Rowe 1977). Well-drained sites are dominated by Picea glauca (white spruce), Betula papyrifera (paper birch) and Populus tremuloides (aspen). Picea mariana (black spruce)-Sphagnum muskeg and Larix laricina (larch) occur on poorly drained surfaces, and Populus balsamifera (balsam popular) is found throughout the region on a variety of substrates. With increasing altitude the forest opens up and grades into alpine forest-tundra. Scattered individuals and groves of Picea glauca and to a lesser degree Picea mariana grow amongst Betula glandulosa (shrub birch)-dominated tundra. Treeline is reached at 800 to 1200 m, depending on aspect, substrate and drainage. Picea glauca is the dominant treeline species, with Picea mariana, Larix laricina and Populus balsamifera occuring sporadically. Upslope of the treeline, shrub tundra dominated by Betula glandulosa and heaths such as Ledum decumbens, Vaccinium vitis-idaea and V. uliginosum predominates, with extensive areas of hummocky Eriophorum (cotton grass) meadows in more poorly drained locations. Salix

(willow) and herbs become prevalent at higher elevations on thin, rocky soils.

2.2.3 Study Sites

To examine the influence of elevation on Late Quaternary vegetation development in the Mackenzie Mountains, and to reconstruct Holocene treeline fluctuations, three small to moderate sized lakes at varying elevations were sampled (Fig. 2.1). Small lake basins (<10 ha) are preferred for palynological studies of treeline, since they collect greater proportions of local pollen than large lakes (Jacobson and Bradshaw 1981). This is particularly true in montane environments, where the pollen from lowland forest communities can dominate samples from tundra and forest-tundra sites (Markgraf 1980; Lamb 1985; Fall 1992).

Bell's Lake (65°01'N, 127°29'W; all lake names are unofficial) is located at an elevation of 580 m at the edge of Katherine Creek Canyon. The lake has a surface area of 1.2 ha and maximum depth of 2.0 m. Bedrock is of the dolomitic Lower Devonian Little Bear Formation (Aitken and Cook 1974). Bell's Lake lies in a depression within a ground moraine, and is within the limits of the Katherine Creek Phase re-advance of Laurentide ice (Duk-Rodkin and Hughes 1991). The surrounding vegetation is an open forest of Picea mariana muskeg in lowlying areas and Picea glauca on uplands. Closed boreal forest grows downslope in the Mackenzie Valley, 5 km to the northeast. Keele Lake (64°10'N, 127°37'W) lies at 1150 m at the headwaters of a small tributary of the Keele River. The surface area of Keele Lake is 9 ha and maximum depth is 1.7 m. This lake lies in bedrock

of the quartzite, dolomite and shale dominated Katherine Group. Laurentide ice extended up the Keele valley to a point a few kilometres northeast of Keele Lake, damming a proglacial lake in the valley west of Keele Lake (Duk-Rodkin and Hughes 1991). The lake is dammed by a moraine deposited during the Mountain River Glaciation. Keele Lake is located in the upper forest tundra a few tens of metres below treeline, and is surrounded by scattered Picea glauca with upright growth forms. More extensive spruce stands grow in the Keele River valley about 3 km to the north. Andy Lake (64°39'N, 128°05'W) is a moderate sized lake (surface area 50 ha; maximum depth 2.9 m) at an altitude of 1360 m at the headwaters of Andy Creek. This lake is larger than optimum, but was the only lake cored above treeline that produced a full Holocene sediment record. Bedrock is dominated by quartzites and dolomites of the Katherine Group, Franklin Mountain Formation, and Little Dal Formation. Andy Lake is located beyond the limits of Laurentide ice, and is dammed by a moraine of the Mountain River Glaciation. The surrounding vegetation is shrub tundra, and Picea occurs within 4-5 km in valleys to the north and northeast.

2.3 METHODS

Cores were raised in April, 1990 from the central, deepest part of each of the lakes using a modified Livingstone piston corer (Wright et al. 1984). The cores were wrapped in plastic and aluminum foil, and stored at 4°C until sampled.

Subsamples of 1 cm³ of sediment were taken at 2.5 to 10 cm intervals for pollen and loss-on-ignition (LOI) analyses (Dean 1974). Calibrated Lycopodium tablets were added to pollen samples to allow calculation of pollen accumulation rates (Maher 1972). Sample preparation followed Faegri and Iverson (1975) and Cwynar et al. (1979). Counts of ≥400 terrestrial pollen grains were made at all levels except the base which had very low pollen concentrations. Morphological characteristics were used to distinguish Picea cf. glauca and Picea cf. mariana pollen (Hansen and Engstrom 1985). Following subsampling, cores were split in half and contiguous 5 to 10 cm long half-core sections were washed through a 0.6 mm screen to recover plant macrofossils.

Chronological control for the cores was provided by ¹⁴C dating. Due to the calcareous nature of much bedrock in the Mackenzie Mountains, AMS dating of terrestrial macrofossils was carried out wherever possible to avoid the potential of old carbon contamination (cf. MacDonald et al. 1991). One basal AMS date was obtained on mollusc shells as no other datable organics were present. Bulk sediments were dated at levels in which macrofossils were not available, and were used only if no reaction occurred with HCl. A total of 9 AMS and 7 bulk sediment dates were obtained.

All ¹⁴C dates were converted to calendar years BP using the calibration program CALIB3 (Stuiver and Reimer 1993). Sedimentation rates were estimated by taking the slope of lines extrapolated through the radiocarbon dates. At each site it was first attempted to fit a linear regression line through the dates, which

would indicate the simplest solution of a constant sedimentation rate. If a linear regression line did not achieve an adequate fit, a curve was hand-fit through the dates, and sedimentation rates were calculated by determining the slope of the line tangent to the curve at each sampling interval. Sedimentation rates were calculated using both calibrated and uncalibrated dates. Pollen accumulation rates were calculated using the calibrated dates owing to the divergence of radiocarbon and calibrated dates in the early Holocene-late Pleistocene. For comparison with published records, however, pollen stratigraphies are described with respect to uncalibrated radiocarbon ages.

The comparative rates and directions of vegetation change over time at the three sites were assesed using Detrended Correspondence Analysis (DCA; Hill and Gauch 1980). Ordination techniques such as DCA reduce the dimensionality of pollen percentage data and thereby aid in their interpretation. DCA was carried out on simplified pollen percentage records for 13 taxa at 500 year intervals. All samples within 150 years of each 500 year interval were averaged for the analysis. Taxa were selected if they occurred in two or more contiguous samples at a minimum of 2% relative frequency, and included Picea cf. glauca, Picea cf. mariana, Populus, Betula, Alnus, Salix, Myrica, Ericaceae, Artemisia, Cruciferae, Gramineae, Cyperaceae, and Sphagnum. Samples from all three sites were ordinated together to allow direct comparisons of sites.

2.4 RESULTS

2.4.1 Sediment Stratigraphy and Radiocarbon Chronology

A 440 cm core was recovered from Bell's Lake, 265 cm core from Keele Lake, and 271 cm core from Andy Lake (Fig. 2.2). The lowermost ¹⁴C date at Bell's Lake was 10,230±150 yr BP (Table 2.2). Sedimentation rates obviously increased from the early to late Holocene, and so were estimated by hand-fitting curves through the five dates (Fig. 2.2). It is possible that the very low early Holocene sedimentation rates are actually the result of a hiatus in deposition, but the pollen stratigraphy (Fig. 2.3a,b) is consistent with continual sedimentation. A date of 11,990±80 yr BP was obtained on shells at the base of the Keele Lake core (Table 2.2). Although aquatic mollusc shells may be prone to 'old carbon' error, comparison of the pollen spectra associated with this date and other similarly dated spectra for the Mackenzie Basin (MacDonal, 1987; Ritchie 1987) suggests the date is reliable. Sedimentation at Keele Lake for both calibrated and uncalibrated dates was modelled by linear regression through the six dates and the sediment-water interface (assumed to be 0 yr BP). Three of the upper dates in the core were obtained on bulk sediment, but a similar AMS date on a terrestrial macrofossil from the same level as one of the bulk dates (Table 2.2) suggests that they are reliable.

Wood near the base of the Andy Lake core was dated at 12,060±80 yr BP (Tab. 2.2). The four upper dates at Andy Lake were all based on the analysis of bulk sediments. We reject the date of 10,460±390 yr BP at 165 cm as

Figure 2.2: Radiocarbon dates and sediment characteristics for the three sites.

TABLE 2.2: Radiocarbon dates (^{13}C corrected) for Mackenzie Mountains sites.

Lab no.[1]	depth (cm.)	^{14}C date (yr. BP) ± 1σ	calibrated date (calendar yr. BP)[2]	material
		Bell's Lake		
TO-2379	108	2340±60	2340	wood frags.
TO-2378	240	4430±70	5020	wood frags.
TO-2377	319	5600±70	6360	wood frags.
TO-2376	395	8740±80	9770	wood frags.
TO-2375	406	10,230±150	12,030	wood frags.
		Keele Lake		
B-65289	50	2610±80	2750	gyttja
B-65290	80	3290±70	3480	gyttja
B-63539	141.5	6460±90	7330	gyttja
TO-3988	142	6120±70	7000	wood frags.
TO-3989	195	9560±70	10,710	wood frags.
TO-2298	260	11,990±80	13,980	shells
		Andy Lake		
B-54929	25	2340±200	2340	gyttja
B-54930	90	4800±70	5530	gyttja
B-54931	125	6290±100	7200	gyttja
B-54932	165	10,460±390[3]	12,370	clayey gyttja
TO-2295	240	12,060±80	14,070	wood frags.

[1] Laboratories: TO, IsoTrace Laboratory (University of Toronto); B, Beta Analytic

[2] Calibrated using Stuiver and Reimer (1993)

[3] rejected date

anomalously old for two reasons. Firstly, the sediments at this level are highly inorganic; LOI is less than 15%, as compared to 25 to 30% for the other bulk dates in this core and 40 to 50% for those in the Keele Lake core (Fig. 2.2). Secondly, including the date in age-depth calculations results in a date for the rise of Picea pollen at 10,000 to 11,000 yr BP, which does not fit with the records of other published sites in northwestern Canada (Ritchie 1984; Ritchie and MacDonald 1986; MacDonald 1987) or the other two sites in this study. Excluding this date from age-depth calculations (Fig. 2.2) gives a nearly linear sedimentation rate and a date for rise of Picea pollen which agrees very closely with that of other sites in the region.

2.4.2 Pollen Stratigraphy

Pollen percentages and accumulation rates are presented in Figs 2.3-2.5. Pollen zones were determined visually using the percentage data for major taxa (Artemisia, Cyperaceae, Salix, Betula, Alnus, Picea). The pollen stratigraphies of the three lakes were very similar, and therefore are described here as regional pollen zones. Temporal boundaries of zones varied to a small degree between sites, so boundaries of regional zones were derived by averaging those at each site. Zone 1, at the base of all cores, is dominated by pollen of herbs (Artemisia, Cyperaceae, Gramineae), and shrubs (Betula, Salix). Zone 2 is characterized by very high proportions of Betula pollen. Zone 3 is characterized by increases in Picea pollen, and in the uppermost zone at all sites, Zone 4, Alnus increases to

Figure 2.3a: Pollen percentage diagram, Bell's Lake, N.W.T.

Figure 2.3b: Pollen accumulation rate diagram, Bell's Lake, N.W.T.

Andy Lake, N.W.T.
pollen percentages

Figure 2.5a: Pollen percentage diagram, Andy Lake, N.W.T.

Keele Lake, N.W.T.
pollen percentages

Figure 2.4a: Pollen percentage diagram, Keele Lake, N.W.T.

Andy Lake, N.W.T.
pollen accumulation rates

Figure 2.5b: Pollen accumulation rate diagram, Andy Lake, N.W.T.

Keele Lake, N.W.T.
pollen accumulation rates

Figure 2.4b: Pollen accumulation rate diagram, Keele Lake, N.W.T.

become a co-dominant pollen type with Betula and Picea. A detailed description of the zones follows.

Zone 1: Artemisia - Graminoid - Betula Zone (c. 11,800 to 10,200 yr BP)

This zone is characterized by high percentages of herbs and graminoids (Artemisia, Gramineae, Cyperaceae and others) and shrubs (Betula, Salix). Artemisia pollen reaches 10-20% at all sites. Gramineae percentages reach 3-12%, and Salix 5-10%. Betula rises from the base of the zone to reach 70-80% at the zone 1/2 boundary. Cyperaceae pollen is much more abundant in zone 1 at Keele Lake than at the other two sites, reaching levels of 30-50%. PAR in zone 1 is consistently low, averaging less than 500 grains.cm^{-2}.yr^{-1} at all of the sites.

Zone 2: Betula Zone (c. 10,200 to 8000 yr BP)

Very high proportions of Betula pollen, 70-85% at all sites, characterize this zone. Cyperaceae occurs at 5-10% at Andy and Bell's Lakes, and 10-25% at Keele Lake. Populus attains its highest values for each site within this zone, averaging 2-3%. Salix and Artemisia decline in zone 2. At Andy and Bell's Lakes Picea cf. glauca and Picea cf. mariana percentages rise near the top of this zone to reach 15-20% total Picea pollen, but subsequently drop to 6-10% before the main Picea rise which delineates the zone 2/3 boundary. No such initial Picea increase is seen at Keele Lake. PAR is in the range of 1000-1500 grains.cm^{-2}.yr^{-1} at Bell's and Andy Lakes, and 500-1500 grains.cm^{-2}.yr^{-1} at Keele Lake. At Andy

Lake trends in PAR correspond closely to pollen percentages. At Keele and Bell's Lakes, the rapid rise in Betula percentages which delineates this zone is greatly diminished in the PAR records.

Zone 3: Picea-Betula Zone (c. 8000 to 6300 yr BP)

A sustained increase in Picea marks the beginning of this zone. Total Picea pollen maintains values of 20-30% at Andy and Keele Lakes and 35-40% at Bell's Lake. Picea cf. glauca is more abundant than P. cf. mariana at the two higher altitude lakes, whereas nearly all Picea pollen in zone 3 at Bell's lake is Picea cf. mariana. Concurrent with increases in Picea are decreases in Betula. Cyperaceae pollen maintains values of 5-10% throughout zone 3 at all sites. Myrica occurs consistently at Bell's Lake and to a lesser degree at Keele Lake. Alnus pollen rises from negligible proportions at the base of the zone to 10-20% at the zone 3/4 boundary. At Bell's Lake and Andy Lake, PAR follows very similar trends to pollen percentages. PAR at Keele lake increase dramatically at the zone 2/3 boundary to reach a postglacial peak at c. 8000 yr BP. These increases are evident for Picea, Betula, Salix, Artemisia, and Cyperaceae and are not reflected in the percentages records.

Zone 4: Picea-Betula-Alnus zone (c. 6300 yr BP to present)

Picea, Betula and Alnus pollen maintain consistent and high proportions throughout zone 4 following the Alnus rise that delineates this zone. Myrica peaks

in the early part of the zone at Bell's Lake, but subsequently disappears. Cyperaceae rises from 5% to 10-15% in the upper 15 cm at Andy Lake. Picea cf. glauca is consistently more abundant than P. cf. mariana at Andy Lake, whereas the reverse is true at Keele Lake. At Bell's Lake Picea cf. mariana is dominant from the base of the zone until about the 80 cm level, where P. cf. glauca increases. Pinus pollen percentages and PAR increase at all sites over the past 6000 years, but this pollen is assumed to be extra-regional, since the northern range limit of Pinus banksiana lies in the Mackenzie Valley to the southeast of Norman Wells. PAR for most taxa decrease throughout this zone at Andy Lake, changes not reflected in pollen percentage records. Total PAR at Keele Lake remains relatively constant throughout the zone. However, Picea cf. glauca and P. cf. mariana PAR declines during this time, despite fairly stable percentage records. PAR at Bell's Lake follows similar trends to percentage data.

2.4.3 Detrended Correspondence Analysis

The results of DCA were plotted in two manners. Taxon ordinations (Fig. 2.6a) indicate groupings of taxa which demonstrate similar trends through time. Distances between taxon ordinations represent ecological similarity (points in close proximity) or ecological dissimilarity (points well separated). On the time-trend ordination of samples (Fig. 2.6b), the locations of samples from each site are plotted in ordination space at 500-year intervals. Samples which plot in close proximity have similar taxonomic composition. The relative importances of

Figure 2.6: Detrended correspondence analysis results. a) taxon ordinations; b) sample ordinations, plotted against age in thousands of radiocarbon years

different taxa within each sample can be determined by comparison with the taxon ordination diagram. The time-trend ordination thus represents the changing composition of vegetation (as inferred from pollen percentages) over time at each site. The trends can be compared between sites to determine periods in which vegetation types were similar and periods in which they were dissimilar.

In the DCA ordination of taxa (Fig. 2.6a), the first axis appears to separate taxa typical of tundra pollen assemblages (Cruciferae, Artemisia, Salix, Cyperaceae; high scores) from taxa typical of forest and forest-tundra (Picea cf. glauca, Picea cf. mariana, Myrica, Sphagnum, Alnus, Ericaceae; low scores). Taxa having intermediate first axis scores are found in both forest and tundra (Gramineae, Betula) or are poorly represented in the late Holocene pollen record (Populus). Taxa indicative of muskeg or bog forest (Myrica, Picea cf. mariana, Sphagnum, and Ericaceae) have relatively high second axis scores.

Sample ordinations plotted over time (Figs. 2.6b) show at all sites a progression from high first axis scores in the basal levels to minimum scores at 4000-5000 yr BP, followed by slight reversions toward tundra taxa up to the present day. The ordination for Bell's Lake is well separated from those of Andy and Keele Lakes along the second axis throughout the length of the records until 1500 yr BP, at which time there is a trend towards lower second axis scores. Andy and Keele Lake are well separated on the second axis before 10,000 yr BP and after 6500 yr BP, but converge during the early to mid-Holocene. Rates of change, approximated by distance in ordination space over time, are most rapid at

all sites between the beginning of the sequence and 5000-6000 yr BP. Rates of change subsequently decreased significantly, although in the last 2000-3000 years there have been minor rate increases towards higher first axis scores at Andy and Keele Lakes, and towards lower second axis scores at Bell's Lake.

2.5 VEGETATION RECONSTRUCTION

2.5.1 Zone 1: Artemisia-Graminoid-Betula zone (c. 11,800 to 10,200 yr BP)

The initial tundra vegetation at all three sites was similar to that found throughout northwestern Canada and adjacent Alaska in the late Pleistocene (Brubaker et al. 1983; Ritchie 1984, 1987; Edwards et al. 1985; MacDonald 1987; Lamb and Edwards 1988). Upland areas supported Artemisia-dominated herb tundra with some low Salix shrubs. Sedge meadows dominated by Carex and Eriophorum, with some ericaceous shrubs, occurred in wetter areas. Betula became increasingly abundant throughout this period. Grain-size measurements and macrofossils at a number of other sites in northwestern North America suggest this early Betula pollen represents shrub birch, B. glandulosa (Brubaker et al. 1983; Ritchie 1984; Edwards et al. 1985; MacDonald 1987; Hu et al. 1993). Low pollen accumulation rates (<500 to 1000 grains.cm^{-2}.yr^{-1}) and low organic content of sediments at all three sites may, in part, reflect inwashed mineral soil and suggests the late Pleistocene vegetation of the central Mackenzie Mountains was quite sparse. In addition, lake productivity may have been low.

Some site specific differentiation of vegetation is apparent in Zone 1, as evidenced by the DCA ordination (Fig. 2.6b). Most significant are the very high percentages of Cyperaceae pollen at Keele Lake, compared to sites in the central and northern Mackenzie basin (Slater 1985; MacDonald 1987). Several sites in both lowland and mountainous regions of Alaska and the Yukon have late Pleistocene spectra with high proportions of Cyperaceae pollen (Brubaker et al. 1983; Edwards et al. 1985; Anderson 1985; Ritchie 1987). Moist sedge meadows were probably more abundant in the region around Keele Lake than at most other previously studied sites in the western Northwest Territories.

2.5.2 Zone 2: Betula Zone (c. 10,200 to 8000 yr BP)

Between about 11,000 and 10,000 yr BP shrub birch became increasingly important in the central Mackenzie Mountains. Decreases in Artemisia and Gramineae PAR suggest Betula glandulosa tundra replaced herb tundra on upland sites, while stable or increasing Cyperaceae PAR indicates sedge meadows still dominated wetter areas.

Poplar woodlands occurred with the shrub tundra near these three sites, and throughout eastern Beringia, at about 10,500 to 10,000 yr BP (Ritchie 1984; Anderson et al. 1988). Pollen morphological and macrofossil data from several other sites in Alaska and the Yukon (Brubaker et al. 1983; Cwynar and Spear 1991; Hu et al. 1993) suggest this Populus pollen probably represents Populus balsamifera. Populus balsamifera occurs in isolated stands as the northernmost tree

species in the Brooks Range of northern Alaska (Edwards and Dunwiddie 1985), and is occasionally present in association with white spruce at treeline in the Mackenzie Mountains.

The first evidence of Picea in the Mackenzie Mountains comes from the continuous appearance of Picea cf. glauca and Picea cf. mariana pollen at Andy and Bell's Lakes at about 8500 yr BP. However, due to the overrepresentation of lowland pollen types in montane terrain (Fall 1992) such changes can only be used to indicate regional presence of Picea. Scattered Picea mariana and Picea glauca were therefore probably present at lower elevations in the regions around Andy, Bell's and Keele Lakes by ~8500-8000 yr BP.

2.5.3 Zone 3: Picea-Betula Zone (c. 8000 to 6300 yr BP)

Widespread expansion of Picea glauca and P. mariana occurred at about 8000 yr BP in the central Mackenzie Mountains. Picea forest and forest-tundra rapidly replaced shrub tundra up to the elevation of at least Keele Lake. At Bell's Lake, high proportions of Picea mariana, Sphagnum and Myrica pollen and spores and the presence of Ericales suggest the establishment of Picea mariana-dominated muskeg around the site, with only minor amounts of Picea glauca. DCA scores reflect the relative predominance of muskeg at Bell's Lake during Zone 3; sample ordinations trend towards lower first axis and higher second axis scores between 8500 yr BP and 6500 yr BP, separating this site from the two higher elevation sites.

Rapid increases in Picea pollen percentages and accumulation rates indicate the increase in Picea, primarily Picea glauca, occurred very rapidly in the vicinity of Keele Lake. This is coincident with increased LOI suggesting increased lake productivity or decreased erosion of mineral soil at this time. Picea glauca forest-tundra or open forest with an understory dominated by Betula glandulosa predominated at this time. Picea mariana-Sphagnum muskeg occurred to a more limited extent on poorly drained sites. Populus populations decreased in Zone 3 relative to the early Holocene. Two lines of evidence suggest the density of Picea populations around Keele Lake may have been higher at this time than at present. Firstly, accumulation rates of Picea pollen were substantially greater in the early to mid Holocene than in the latest Holocene. The initial maximum between 8000 and 7000 yr BP may be an artifact of sediment focusing (Davis et al. 1984). However, steadily declining Picea PAR relative to total PAR throughout the Holocene (Fig. 2.4) is suggestive of gradual declines in Picea abundance. Secondly, very high LOI (70-80%; Fig. 2.2) at the base of Zone 3 could indicate a more productive, densely forested basin with reduced catchment erosion.

The history of Picea in the Andy Lake region is more difficult to reconstruct due to the size of the lake and the resulting high proportion of regional pollen. Picea PAR at Andy Lake is substantially greater in Zone 3 than at present, though Picea pollen percentages do not show any strong, consistent trends after initial increases. This higher PAR may result from sediment focusing, a higher treeline, greater Picea population densities in forest and/or forest-tundra at lower

elevations, increased Picea pollen productivity, or a combination of these factors. Sediment focusing is unlikely to be a major factor due to the shallow bathymetry of Andy Lake. Careful sieving of continuous core segments yielded no macrofossil evidence to support a higher Holocene treeline from this site. Therefore the higher Picea PAR in Zone 3 at Andy Lake likely reflects increased density of Picea glauca forest-tundra near Andy Lake, as suggested by the Keele Lake PAR record.

Decreases in Betula PAR following the arrival of Picea at Andy and Keele Lakes indicate the reduction in open sites as open forest and forest-tundra replaced Betula glandulosa - dominated shrub tundra up to the elevation of treeline. At Bell's Lake, however, Betula PAR increases concurrently with that of Picea, probably owing to the expansion of Betula papyrifera in the Mackenzie Valley and lowlands adjacent to Bell's Lake.

In addition to the changes in abundances of major pollen taxa at the three sites, an elevational gradient is apparent with respect to minor components of the flora throughout Zones 3 and 4. Although it is indicative of muskeg or bog environments, the northern limit of Myrica coincides approximately with that of the boreal forest and is probably climatically determined (Ritchie 1984). The increasing abundance of Myrica pollen with decreasing elevation at these sites in the Mackenzie Mountains may be an indication of the increasing boreal affinities of the lower elevation forests. The relative abundance of forbs such as Artemisia, Thalictrum, Oxyria, Dryas and Gramineae has been greater at higher elevations throughout the Holocene.

2.5.4   Zone 4: Picea-Betula-Alnus Zone (c. 6300 yr BP to present)

Alnus pollen increased throughout Northwestern Canada between 7000 and 6000 yr BP (Ritchie 1984; MacDonald 1987). Alnus expansion in the Mackenzie Mountains appears to have been more rapid at higher elevations, perhaps owing to the more open cover of Betula and Picea and thus reduced competition.

The DCA ordinations suggest retrogression of Picea-dominated vegetation at Andy and Keele Lakes, towards increased importance of tundra taxa over the last 5000 years. These changes may be interpreted as an indication of decreasing regional forest-tundra densities. In particular, the ordinations suggest the mid-Holocene vegetation at Keele Lake was similar to the present-day open forest surrounding Bell's Lake. This interpretation is supported by gradual reductions in Picea PAR during Zone 4 at both Andy and Keele Lakes. Picea glauca has been the dominant spruce throughout the Holocene around Andy Lake (but not locally). At Keele Lake both spruce species occurred during Zone 4, with Picea mariana being slightly more abundant.

A shift from Picea mariana dominance to P. glauca-P. mariana co-dominance took place at about 1700 yr BP at Bell's Lake. This may represent declines in Picea mariana and replacement by Picea glauca, but the absence of concurrent drops in local taxa indicative of peatlands (Sphagnum and Ericaceae; Myrica populations declined in the mid Holocene) suggest the maintenance of boggy areas. The present vegetation around Bell's Lake of Picea mariana muskeg in lowlying areas and open Picea glauca forest on adjacent uplands and ridges has

therefore established only in the past 2000 years.

2.6 DISCUSSION

2.6.1 Glacial History

Both Andy and Keele Lakes are located west of the maximum Laurentide Ice limits (Fig. 2.1; Duk-Rodkin and Hughes 1991), so these ~ 12,000 year records may not represent the full sedimentary records from the sites. Coring terminated in inorganic clays at both sites, but additional organic sediments may have been present below these late Pleistocene clays. A full-glacial or older sedimentary record therefore still remains to be recovered from the ice-free section of the Mackenzie Mountains. The extrapolated date of c. 11,500 yr BP for the onset of sedimentation at Bell's Lake provides the first minimum date for final retreat of Laurentide ice in this region, following the Katherine Creek phase readvance (Table 2.1). A minimum deglaciation date of c. 16,000 yr BP for Laurentide ice at Lateral Pond, in the southern Richardson Mountains (Fig. 2.1; Hughes et al. 1981; Ritchie 1982), suggests the Katherine Creek phase considerably postdates initial ice retreat to the northwest of our region. Nonetheless, it is clear that additional dating control is necessary before an accurate glacial chronology can be developed for this region.

2.6.2 Late Pleistocene to early Holocene transition

The data from this study help clarify the nature of vegetation at the southeastern fringe of Beringia during the Pleistocene-Holocene transition. In the latest Pleistocene, Artemisia dominated herb-shrub tundra occurred at all elevations of the central Mackenzie Mountains and adjacent Mackenzie Valley. This open vegetation at low and high elevations extended from the northern Mackenzie Valley and the Mackenzie Mountains southward to Alberta between c. 12,000 yr BP and 10,000 yr BP and may have provided a biogeographic corridor of similar habitat for the southward and northward migration of fauna and humans at the close of the Pleistocene (MacDonald 1987). A cool, dry climate probably prevailed in the region during this time (Ritchie 1984; COHMAP 1988), though increased precipitation due to local orographic effects may have led to the development of extensive sedge tundra at some montane sites such as Keele Lake and Lateral Pond in the Richardson Mountains of the northern Yukon (Fig. 2.1; Ritchie 1984).

The expansion of Betula glandulosa in northwestern Canada at 11,000-10,000 yr BP is postulated to be a response to rapid, major climatic warming (Ritchie 1984). Expansions of Populus balsamifera populations at the same time have been attributed to the same warming trend (Brubaker et al. 1983; Ritchie 1984; Edwards et al. 1985). In western North America Populus pollen is extremely rare in modern sediment samples from lakes outside the range of the genus (MacDonald and Ritchie 1986). The consistent presence of Populus pollen at >1% frequency in the Andy Lake sediments suggests that a warm late

Pleistocene-early Holocene climate in the central Mackenzie Mountains may have led to the establishment of Populus balsamifera groves up to the elevation of Andy Lake, above the current limit of Populus or Picea. MacDonald (1987), Anderson et al. (1988) and Hu et al. (1993), however, suggest caution be exercised in invoking climate as the sole cause of the Populus rise. The ability of Populus to colonize disturbed or recently deglaciated sites may have contributed to its rapid, early expansion.

2.6.3 Holocene Treeline Change

Picea populations do not appear to have expanded in the Mackenzie Mountains until 1000 or more years after the arrival of spruce in the adjacent Mackenzie Valley. The main increase in Picea pollen occurred at about 8500 yr BP at Andy Lake, 8000 to 8500 yr BP at Keele and Bell's Lakes, and 7700 yr BP at Natla Bog (MacDonald 1983). In contrast, Picea pollen increases occurred at 9000 to 9500 yr BP at Lac Meleze and Eildun Lake in the Mackenzie Valley (Fig. 2.1; Slater 1985; MacDonald 1987). These apparent lags in the expansion of Picea populations may be due to delayed migration owing to the difficulty of dispersing seeds up valley into the mountains (MacDonald 1983) or to errors and inaccuracies in radiocarbon dating. The similarity of dates from the study area and Natla Bog for montane expansion of Picea and from Lac Meleze, Eildun Lake, and other sites for lowland expansion (Slater 1985; MacDonald 1987; Ritchie 1987) argue against the latter possibility being a major factor.

Delayed migration due to slow upvalley seed dispersal may have been important in restricting the arrival of Picea at the Natla Bog site, which is near the Yukon-N.W.T. border, 180 km from the western edge of the Mackenzie Valley (Fig. 2.1). All sites in this study, however, are in close proximity to the Mackenzie Valley. This suggests that slow Picea expansion in the Mackenzie Mountains may be due to less favourable climatic conditions at high elevations until 8500 yr BP. This question remains to be resolved.

Palynological and macrofossil analyses from several sites in northwestern Canada indicate that the northern range of Picea extended a considerable distance beyond current limits between c. 9500 yr BP and 5000 yr BP (Ritchie and Hare 1971; Cwynar and Spear 1991; Spear 1993). These and other ancillary data, such as the early Holocene Populus expansion and northward advances in the range limits of boreal species such as Myrica gale and Typha latifolia, provide strong evidence for a period of greater than present summer warmth from c. 10,500 to 5000 yr BP (Ritchie et al. 1983; Cwynar and Spear 1991). This period coincides with the period of maximum Northern Hemisphere summer insolation as predicted by the Milankovitch Astronomical Theory (Kutzbach 1987).

There is no evidence for extensive treeline advances at these sites in the central Mackenzie Mountains similar to that for the central Yukon and far northwestern N.W.T. Nonetheless, the apparent Holocene variations in forest-tundra Picea populations, along with other community changes, are consistent with variations in summer radiation as predicted by the Milankovitch model (Kutzbach

1987). Early to mid Holocene warming was probably manifested as an increase in forest-tundra density and perhaps local treeline advances, the development of Populus groves at the elevation of Andy Lake, and the proliferation of Myrica at mid-elevation open forest sites such as Bell's Lake. The Natla Bog pollen and macrofossil record in the Mackenzie Mountains to the southwest of our sites suggests treeline was locally higher than present from c. 7700 yr BP to 5000 yr BP, the timing of which coincides well with maximum Picea PAR at Andy and Keele Lakes. Reversion of the forest-tundra towards a more open association has occurred during the last 5000 years in the Mackenzie Mountains, a change consistent with the predicted gradual reductions in summer radiation (Kutzbach, 1987).

Additional community changes at Andy and Bell's Lake provide evidence for more pronounced cooling in the past 2000 years. Increases in percentages of Cyperaceae pollen and decreases in Alnus at Andy Lake may result from an expansion of sedge meadows around the site, due to a reduction in active layer depth and/or a cooler and moister climate. At Bell's Lake the same cooling trend may have been responsible for a shift in species composition, from extensive Picea mariana-dominated muskeg to a mixed Picea glauca - Picea mariana association similar to the mid Holocene vegetation at the higher elevation Keele Lake. The response of vegetation to late Holocene cooling in the Mackenzie Mountains has therefore varied with altitude. Higher elevation sites have undergone variations in Picea population densities, while at mid elevations there has been a shift in

community composition.

AGE DEPENDENT TREE-RING GROWTH RESPONSES OF SUBARCTIC WHITE SPRUCE TO CLIMATE[1]

3.1 INTRODUCTION

Tree rings are the most widely used proxy data for annually resolved reconstructions of climate extending back several centuries to millennia (Bradley and Jones 1992). Dendrochronological techniques are also commonly used to evaluate current climate-growth relationships of trees (Dang and Lieffers 1989; Tessier 1989; D'Arrigo et al. 1992) and investigate trends such as growth enhancements due to the direct and indirect effects of increased global CO_2 levels (LaMarche et al. 1984; Graumlich 1991; Innes 1991). The physiological mechanisms whereby climatic parameters are translated into radial growth and wood density variations are complex, because radial growth in any one year integrates the effects of both climate and growth over the preceding several years, and is further modified by site-specific environmental factors, disturbance, and stand dynamics (Fritts 1976; Tessier 1989; D'Arrigo et al. 1992). Despite these

complexities, most traditional dendroclimatic and dendroecological analyses have assumed that relationships between climate and radial growth are independent of tree age, once the biological growth function has been removed (Pittock 1982; Smith 1985; Fritts 1989; Van Deusen 1990). If this assumption is invalid, climatic reconstruction based on an even-aged sample may be valid for only the more recent part of the record. Developing a climate record or investigating climate-growth relationships employing indices produced from trees of different ages could lead to further errors, because at any one time different trees within the chronology would be responding in a different manner to climate depending on their age.

Response function analysis (Fritts 1976) and linear regression (Dang and Lieffers 1989; Colenutt and Luckman 1991; D'Arrigo et al. 1992) are the most commonly applied methods of relating climatic data to tree ring parameters and selecting those climatic variables which account for the greatest variance in ring width or density. These methods normally assume the climate-growth function to be both time- and age-invariate. The temporal stability of climate-growth relationships have been examined by dividing the ring width and climate records into two or more sequences, and comparing the response function results (e.g. Smith 1985; Tessier 1989; Serre-Bachet and Tessier 1989). The introduction of the Kalman filter into dendroclimatological analyses (Visser and Molenaar 1988, 1989; Van Deusen 1990) has resulted in the development of continuously variable time dependent relationships between climate and growth. Time dependent analyses have been employed to investigate the effects of stand dynamics (Tessier

1989), changing pollution levels (Innes and Cook 1989; Peterson et al. 1991; Visser and Molenaar 1992), insects (Van Deusen 1988) and climatic change (Cook and Johnson 1989) on radial growth. Without the disaggregation of ring-width data into age classes, however, these methods cannot be used to examine the effects of tree aging. Visser and Molenaar (1988) suggest the Kalman filter may be used for this purpose, but to date this has not been carried out.

The validity of assuming a constant climate-growth response throughout the life of a tree was challenged by Pittock (1982), though the assumption was not tested rigorously. He reasoned that if the root system of a tree increases in extent and spreads into different soil environments with age, then it is questionable to assume its response to climate does not vary with age. Gray (1982) noted that discrepancies between the response functions from tree stands of different ages at a site in France may be due to age dependent physiological processes. On the other hand, Colenutt and Luckman (1991) found no significant differences between the responses of old (average age 303 years) and young (average age 81 years) Larix lyalii chronologies in the Canadian Rocky Mountains, based on linear regression analysis. Fritts (1976) also found no significant differences between chronologies produced from young and old Pinus longaeva trees in California.

In this chapter the fundamental assumption that the climate-growth system is age invariate after removal of the biological growth function is tested. This assumption is tested using response function and linear regression analyses of white spruce (Picea glauca) ring-width data from three sites in northwestern Canada. The

impact of age dependent climate-growth relationships on dendroclimatic reconstruction is then investigated by developing records of June-July temperatures at Norman Wells back to 1909, using both traditional and age dependent models. These models are calibrated over the period 1944-1988 and verified using an extended temperature record stretching from 1909 to 1943.

3.2 STUDY SITES

Much dendrochronological work has been carried out in the circumpolar subarctic (eg. Garfinkel and Brubaker 1980; Jacoby and D'Arrigo 1989; Briffa et al. 1990; Graybill and Shiyatov 1992) because trees at or near their latitudinal limits are likely to demonstrate a strong climatic signal. Sampling for this study was carried out in the Mackenzie and Franklin Mountains near Norman Wells in the western Northwest Territories, Canada (Fig. 3.1). The Mackenzie and Franklin Mountains are underlain by Devonian and Silurian limestones and calcareous shales (Clague 1989), and in the region of the study sites reach altitudes of about 2000 m asl and 1000 m asl respectively. Permafrost is discontinuous in the central Mackenzie Valley and surrounding mountains. The glacial history of this region is complex, as it lies near the confluence of the Laurentide ice sheet with Montane glaciers from the west (Duk-Rodkin and Hughes 1991). The study area lies within the limits of a Late Wisconsinan readvance of the Laurentide ice, dated at about 12,000 yr BP (Duk-Rodkin and Hughes 1991).

Figure 3.1: Locations of the study sites.

The Upper Mackenzie Section of the boreal forest, dominated by Picea glauca, Picea mariana, Betula papyrifera, and Populus balsamifera, extends up the Mackenzie River valley as far as Norman Wells (Rowe 1977). These forests become more open with increasing altitude in the mountains on either side of the river, with treeline being reached at altitudes of 800 to 1200 m, depending on aspect, substrate and drainage. Picea glauca is by far the most important species at treeline, with Picea mariana and Larix laricina occasionally present. Norman Wells is in the Boreal Climatic Region (Hare and Thomas 1979), and from 1951-1980 had a mean annual temperature of -6.3°C and mean annual precipitation of 335 mm (Environment Canada, unpublished station data).

Within the study area, three Picea glauca-dominated sites on flat to moderately inclined south facing slopes with well drained, relatively thin soils were selected (Fig. 3.1). None of the selected stands showed any evidence of disturbance, and the maximum age of spruce varied from about 360 to 500 years. Stands supporting open-grown spruce with an upright form were selected to minimize the effects of stand dynamics and tree form on radial growth records. The Skipping Bullet site (64°59'N, 127°34'W) is located in Picea glauca forest-tundra at an elevation of 950 m, about 20 to 30 m below the upper tree limit. Mature trees reach a maximum height of 3-4 m, and the density of stems greater than 5 cm diameter is about 11 per 100 m². The site is on a well but not excessively drained south facing slope of 24°. Soils are 10-15 cm thick over stony till or bedrock. The Katherine Creek site (64°58'N, 127°29'W) is on a level

terrace above Katherine Creek, at 680 m elevation. Much of the terrace is poorly drained and dominated by Picea mariana and Larix laricina. Well-drained areas, like the sampled stand, support open Picea glauca forest on soils about 20 cm thick overlying stony fluvial deposits. Mature trees reach a maximum of 10-12 m height, and the density of stems >5 cm diameter is 19 per 100 m². Both of these sites are in the front range of the Mackenzie Mountains, 50 km southwest of Norman Wells. A stand was also sampled on Discovery Ridge (65°21'N, 126°42'W), in the Franklin Mountains 10 km northeast of Norman Wells. This site is in forest-tundra on a south-facing slope at and elevation of 820 m, about 20 to 30 m below the upper tree limit. Picea glauca, growing in open stands, is the dominant tree and the only species sampled, but Larix laricina was also fairly common at Discovery Ridge. Mature trees reach about 6-7 m in height, but stem density data are not available. Soils are thin and stony, with many areas of exposed bedrock.

3.3 METHODS

3.3.1 Chronology construction

At each of the stands, between 30 and 33 trees of all ages were double cored (at approximately 90°) or disked. To obtain an accurate age estimate, coring or disking was carried out as close to the ground level as possible. Suppressed trees or trees of obviously vegetative origin were avoided. Basal flaring, which

may distort radial growth trends on radii very near the ground, was generally not apparent. Once sanded with progressively finer grades of sandpaper, cores and disks were cross-dated using the technique of Yamaguchi (1991). Cross-dating was simplified by the presence of very few missing rings, and a number of distinctive light rings (Filion et al. 1986) which were present on the majority of trees. Two radii were measured for most but not all trees. Fifty-one radii were included from Katherine Creek, 54 from Skipping Bullet, and 52 from Discovery Ridge. Measurement was carried out on a Velmex UniSlide traversing table connected to an AcuRite III digital counter with a precision of ±0.001 mm.

At each site, trees were grouped into 100-year age classes based on their age in 1989. 100-year age classes were chosen as a compromise between sufficient sample size and sufficient disaggregation of the data. Individual chronologies were standardized using modified negative exponential detrending or a straight line of negative or horizontal slope (Fritts 1976; Jacoby and Cook 1981). At open subarctic or arid sites, negative exponential detrending removes the growth trends from raw ring-width series while retaining most low frequency variations which are potentially climate-driven (Jacoby and Cook 1981; Cook 1985; Graumlich 1991). Mean chronologies for each age class at each site were calculated from the individual indices by autoregressive modelling using the program ARSTAN to maximize the climatic signal (Holmes 1992).

If the assumption of age-invariate response to climate is violated at these sites, the unmodified age class indices should not be used in the analyses. As tree

ages decrease back in time, their response to climate would diverge from that of the calibration period, even when the data are disaggregated into age classes. For this reason it was necessary to modify the chronologies for each age class so that the ages of component trees remain approximately equal to the age at calibration throughout the record. To do this the ages of all individual trees at each site in 1939 were recalculated, fifty years before the most recent year of analysis (1989). The trees were then reassigned into the 100-year age classes based on those ages. ARSTAN was used to standardize indices and calculate chronologies for these rearranged age classes. The final age-corrected chronologies for each age class used indices from the 1989 age classes during the period 1940 to 1989, and indices from the 1939 age classes during the period 1890 to 1939. The mean age of trees used to calculate the index chronology for each age class is thus approximately the same in 1890 as it is in recent years.

3.3.2 Analysis of climate-growth relationships

Relationships between climate and radial growth were investigated using response function analysis and linear regression, both performed by the program RESPO (Holmes 1992). The response function technique involves multiple regression analysis using the principal components of monthly climate data as the predictors and the detrended indices of ring widths as predictands (Fritts 1976; Briffa and Cook 1989; Warren 1989). The climate data generally used include monthly mean temperatures and monthly precipitation for the growth year as well

as the previous year. The use of response functions reduces the effects of interdependancies between climate variables, but results can vary drastically depending on the number of months of climate data used in the analysis, whether or not prior growth variables are included, and the choice of confidence level at which variables are admitted to the regression equation (Blasing et al. 1984). For these reasons, correlation coefficients between ring-width indices and untransformed climatic variables were calculated along with the response function coefficients. Both of these analyses assume that linear relationships occur between climate and radial growth (Warren 1989). Linear relationships were tested for by plotting ring width indices against climatic variables.

Mean monthly temperatures and monthly precipitation data from Norman Wells (65°17'N, 126°46'W; elevation 64 m) were used in the response function analyses and calculations of correlation coefficients. These data are available from 1944 to 1989. Climate data extending from August of the growth year back to May of the previous year were included in the analyses, which therefore covered the period 1945 to 1989. These analyses were carried out for each age class at each site. The 400-500 year classes at Katherine Creek and Discovery Ridge were developed from only four and three radii respectively, but response function analyses indicated climate accounted for a large proportion of variance in rings width in both cases. It was nevertheless decided to eliminate these age classes from the subsequent multiple regression modelling due to the small sample sizes.

To determine if any age-related trends in the results were a consequence of

the conservative detrending techniques employed, response function analysis was carried out and correlation coefficients calculated using indices detrended with a more flexible cubic spline (Cook and Peters 1981) having a 50% frequency cutoff of 128 years. This detrending removes most variance in the ring-width records with a frequency of more than 128 years. The effects of stand dynamics and other non-climatic factors may be reduced, at the expense of long-term climatic information.

3.3.3 Dendroclimatic modelling

Tree-ring records from the subarctic are commonly used to develop reconstructions of summer temperatures or growing season degree-days (Garfinkel and Brubaker 1980; Jacoby et al. 1985; Briffa et al. 1988, 1990, 1992). To examine the potential impact of age dependence on climatic reconstruction, tree-ring data from the three sites were used to develop two estimates of summer temperatures at Norman Wells extending back to 1909 using stepwise multiple regression. An extended Norman Wells temperature record (1909-1989) has been developed by correlation and combination with the record from Fort Norman, about 60 km SE of Norman Wells, as a part of recent work by the Canadian Climate Centre to produce a database of long-term temperature records in Canada (Gullett et al. 1992). In its different forms, multiple regression is the technique most commonly applied in dendroclimatic reconstruction (Hughes et al. 1984; Jacoby et al. 1985, 1989; Briffa et al. 1988, 1990). June-July temperature was

selected as the parameter to be estimated based on response function results and preliminary multiple regression analyses which indicated it provided the strongest calibration statistics (see Results).

The first analysis took age dependent climate relationships into account by using each modified age class from each of the sites as a separate predictor of temperature (Tab. 3.1). Ring width indices in year t+1 from each age class were also included as predictors, as other studies at or near treeline (Jacoby et al. 1985; Briffa et al. 1988) have indicated previous summer temperatures often correlate well with ring width in the current year. Standard reconstructions of climate were developed using all trees over 200 years old at each of the three sites (Table 3.1). Again, ring width indices for the current year and year t+1 were used as predictor variables. These indices were produced using the same standardization and autoregressive modelling techniques as were used to calculate the age class indices, but did not take into account tree aging. Many dendrochronological studies in northern North America use only trees greater than about 200 years old (Cropper and Fritts 1981; Jacoby and Cook 1981; Arquilliere et al. 1990; Colenutt and Luckman 1991).

Stepwise multiple regression was carried out using the program SYSTAT. The level of significance at which variables enter and are removed from the regression can greatly affect the reliability of results (Arbaugh and Peterson 1989). The alpha for entry and removal were therefore set at $\alpha = 0.05$. These rigorous criteria minimize the selection of incorrect or insignificant variables while

TABLE 3.1. Variables available for dendroclimatic modelling. (n = number of radii comprising index record).

AgeDep	Models	n	Standard	Models	n
KC 0-100	KC 0-100 t+1	14	KC >200	KC >200 t+1	28
KC 100-200	KC 100-200 t+1	9	SB >200	SB >200 t+1	30
KC 200-300	KC 200-300 t+1	13	DR >200	DR >200 t+1	31
KC 300-400	KC 300-400 t+1	11			
SB 0-100	SB 0-100 t+1	13			
SB 100-200	SB 100-200 t+1	11			
SB 200-300	SB 200-300 t+1	16			
SB 300-400	SB 300-400 t+1	14			
DR 0-100	DR 0-100 t+1	10			
DR 100-200	DR 100-200 t+1	11			
DR 200-300	DR 200-300 t+1	12			
DR 300-400	DR 300-400 t+1	16			

maximizing the percent variance explained by the model (Arbaugh and Peterson 1989). In order to maintain consistency with the response function analyses, multiple regression modelling used the 1944-1988 temperature record from Norman Wells for calibration. The calibration period was cut off at 1988, because ring widths in year t+1 were included as predictor variables and our ring width data end in 1989.

Verification of the modelling results was carried out using the extended temperature records from 1909 to 1943. The verification statistics included the correlation coefficient (r), reduction of error statistic (RE), and coefficient of efficiency (CE). The level of significance cannot be tested for RE and CE, but positive values indicate a significant reconstruction (Jacoby and D'Arrigo 1989; Briffa et al. 1990). An RE or CE of 1 indicates a perfect reconstruction. The CE provides a better measure of verification when the actual mean temperatures are significantly different between calibration and verification periods (Briffa et al. 1988).

3.4 RESULTS

3.4.1 Radial growth records

The age-adjusted ring-width index records extending back to 1890 are given in Fig. 3.2. At any given site, different age classes display differing trends during most of the last 100 years. However, convergence is seen in some instances, for

Figure 3.2: Detrended ring-width indices during the period 1890-1989, by age class. The records have been adjusted for tree age by reassigning individual trees into age classes in 1939 and recalculating indices.

example during the 1920's and 1930's at Discovery Ridge. During the 20th century, younger trees at Katherine Creek and Skipping Bullet generally show increasing radial growth, while older trees maintain constant growth or show a decline. These trends are for the most part reversed at Discovery Ridge, with older trees demonstrating significant increases in growth in the last 100 years. The decline in growth of trees in 1940, most pronounced at the Skipping Bullet site, is evident in the raw data and not an artifact of age class recalculation in 1939.

3.4.2 Climate-growth relationships

Preliminary analyses suggested that linear relationships exist between the climate and ring-width data. Response function and linear regression analyses (Figs. 3.3-3.5) indicate that climate accounts for a high amount of the variance in tree-ring width. At Katherine Creek (Fig. 3.3), the percent variance explained ranges from 32% to 79% depending on age class. Trees <200 years old show a significant positive response to June and August temperatures of the growth year, and little response to previous summer temperatures. Older trees display increasingly negative response to current spring and previous summer temperatures, and positive response to previous fall temperatures. Responses to precipitation show few trends, and have far fewer significant correlation and response function coefficients than temperature responses. Unlike other studies at the subarctic treeline (Garfinkel and Brubaker 1980; Jacoby and Cook 1981), summer precipitation does not appear to be an important factor at Katherine Creek, except
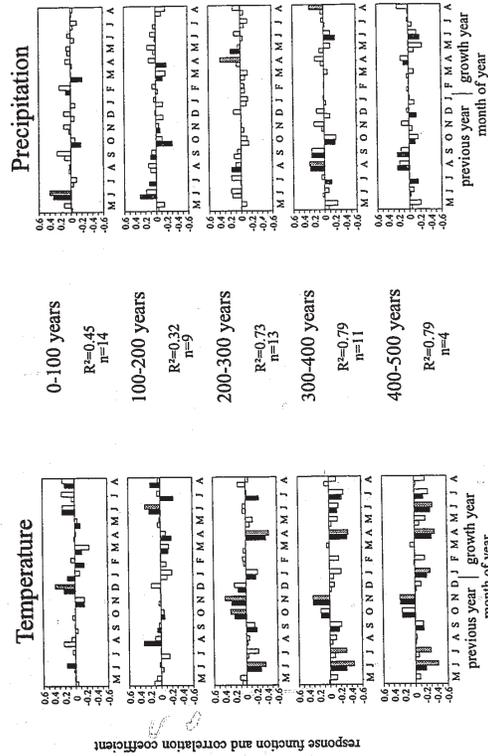
Figure 3.3: Response function results and correlation coefficients for Katherine Creek. Each pair of bars represents the response function coefficient (left) and correlation coefficient (right) for a given month. Response function coefficients significant at p<0.05 are shaded black, and correlation coefficients significant at p<0.05 are shaded grey. R indicates the proportion of variance in ring width accounted for by the response function model. The number of radii in each age clas is given by n.
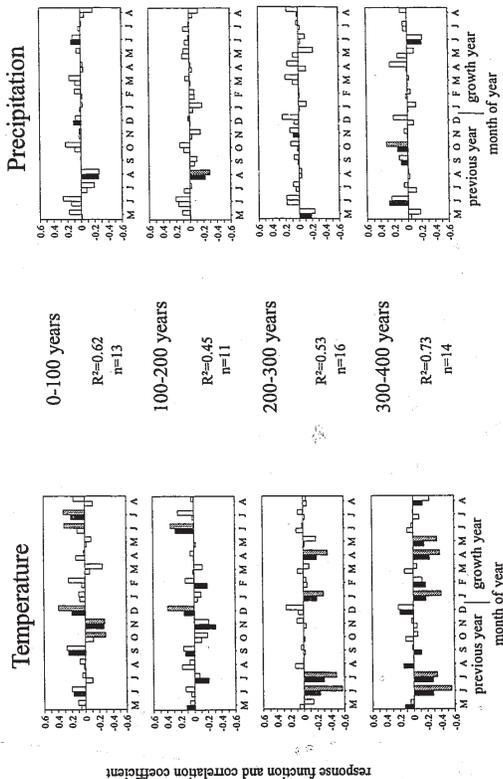
Figure 3.4: Response function results and correlation coefficients for Skipping Bullet. Legend as in Fig. 3.3.
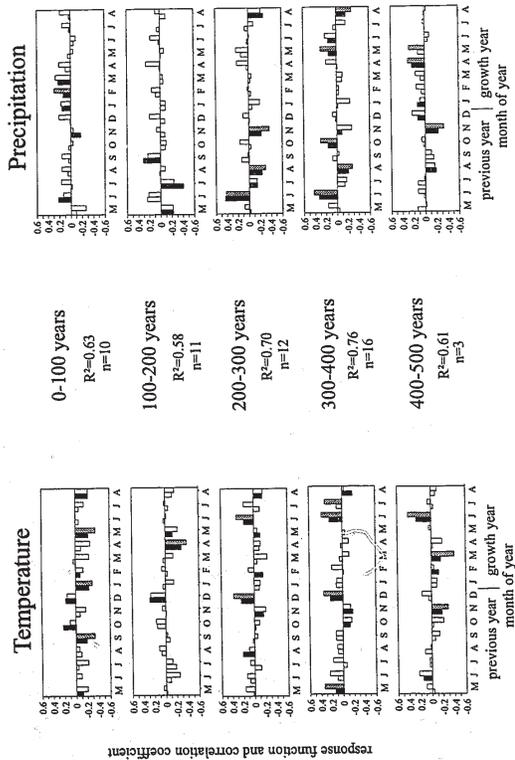
Figure 3.5: Response function results and correlation coefficients for Discovery Ridge. Legend as in Fig. 3.3.

perhaps for a negative correlation with June precipitation in older trees.

The percent variance in ring-width explained by climate at Skipping Bullet (Fig. 3.4) ranges from 45% to 73%. Like Katherine Creek, young trees at Skipping Bullet respond positively to summer warmth in the growing season but show no strong response in the previous year. Trees greater than 200 years old show no significant response to summer temperatures in the growing season, but strong negative response to spring and previous summer temperatures. Results of the precipitation analyses demonstrate no trends and very few significant variables.

At Discovery Ridge (Fig. 3.5), the variance explained ranges from 58% to 76%. The trends in response function and linear regression results by age class are generally reversed in comparison to the Mackenzie Mountains sites, although temperatures in the previous year are less important. Young trees display significant negative correlations with current spring temperatures but little response to current or previous summer temperatures. Radial growth of trees greater than 200 years old correlates significantly with June and sometimes July temperatures. In comparison to the two Mackenzie Mountains sites, precipitation appears to be a more important factor at Discovery Ridge. Precipitation in the previous summer is often correlated significantly with growth, and older trees display significant correlations with current spring precipitation.

3.4.3 Dendroclimatic modelling

Although growing season temperature trends are often developed from

subarctic ring width records, the exact parameters reconstructed tend to vary. Preliminary multiple regression analyses was used to determine the climatic parameters to be reconstructed. Results (Table 3.2) indicated that for both standard and age dependent models, June-July temperatures provided by far the highest percentages of variance explained. The models produced by multiple regression analyses to reconstruct June-July temperatures are also given in Table 3.2, and their calibration and verification statistics are given in Table 3.3. The stepwise procedure reduced the number of predictor variables from 24 to 4 for the age dependent model (AgeDep1) and from 6 to 3 for the standard model (Standard1). AgeDep1 uses Skipping Bullet 200-300 year old trees for years t and t+1, Skipping Bullet 300-400 year old trees for year t, and Discovery Ridge 200-300 year old trees for year t+1. The Standard1 reconstruction uses trees >200 years old from Skipping Bullet for years t and t+1, and trees >200 years old from Discovery Ridge for year t+1.

The validity of multiple regression assumptions regarding independence of regression residuals, homogeneity of variance and normality was examined using plots of residuals against time, residuals against estimated values, and expected normal values of the residuals against observed normal values of residuals. These plots suggest these assumptions were not violated.

The results of these analyses indicate that AgeDep1 provides a better estimation of June-July temperatures than Standard1 (Table 3.3; Fig. 3.6). During the period of calibration, AgeDep1 explains 61% of the variance (adjusted for loss

TABLE 3.2. Comparison of variables selected and calibration R^2_{adj} for different multiple regression models (SB is Skipping Bullet, DR is Discovery Ridge).

Season	Model	R^2_{adj}
June (Age Dependent)	JunTemp=13.663+1.797(SB 200-300)-4.378(SB 200-300 t+1)+3.231(DR 200-300 t+1)	0.37
June (Standard)	JunTemp=17.046-4.408(SB >200 t+1)+2.025(DR >200 t+1)	0.35
July (Age Dependent)	JulTemp=17.758+1.437(SB 200-300)-2.436(SB 200-300 t+1)	0.24
July (Standard)	JulTemp=19.430-2.338(SB >200 t+1)	0.16
June-July (Age Dependent)	JJTemp=15.662+3.673(SB 200-300)-4.067(SB 200-300 t+1)-2.424(SB 300-400)+2.676(DR 200-300 t+1)-400)+2.676(DR 200-300 t+1)	0.61
June-July (Standard)	JJTemp=16.188+1.190(SB >200)+1.602(DR >200 t+1)-3.536(SB >200 t+1)	0.47
June-August (Age Dependent)	JJATemp=16.516-1.467(SB 200-300 t+1)	0.11
June-August (Standard)	JJATemp=16.845-1.697(SB t+1)	0.12

TABLE 3.3. Calibration and verification statistics, June-July temperature estimations, Norman Wells

MODEL	CALIB.	N	n	R	R^2_{adj}	VERIF.	r^2	RE	CE
AgeDep1	1944-1988	24	4	0.80	0.61	1909-1943	0.36	0.62	0.25
Standard1	1944-1988	6	3	0.72	0.47	1909-1943	0.54	0.55	0.10

NOTE: N is the initial number of candidate predictor variables in the stepwise multiple regression, and n is the final number of predictor variables after elimination of insignificant variables by stepwise procedure. R is the multiple correlation coefficient and r is the correlation coefficient (all significant at p<0.01). R^2_{adj} is the variance in climate explained by the model, adjusted for degrees of freedom. RE is the reduction of error statistic and CE is the coefficient of efficiency.
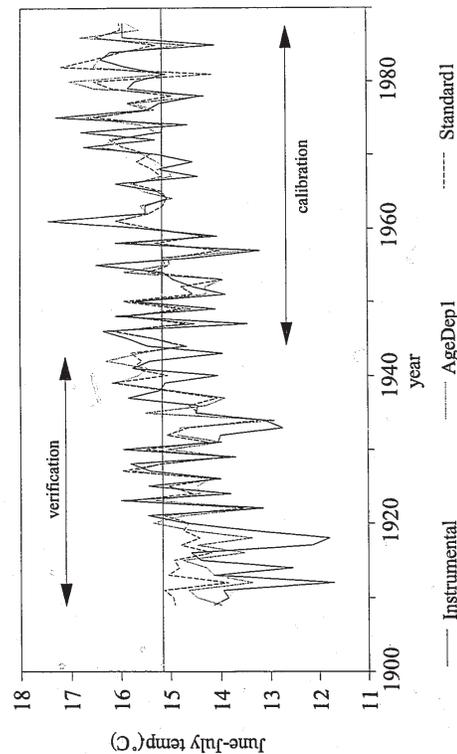
Figure 3.6: Norman Wells June-July temperature estimations (1909-1989) for AgeDep1 and Standard1 models, compared to the instrumental temperature record. The horizontal line indicates the 1951-1980 mean June-July temperature.

of degrees of freedom) in the temperature record, while Standard1 explains 47%. Verification of these models during the period 1909 to 1943 shows both reconstructions are significant, with AgeDep1 in all cases providing the better verification statistics. The correlation coefficients are nearly identical at $r=0.56$ for AgeDep1 and $r=0.54$ for Standard1, both significant at $p<0.01$. Values of RE are also similar, but again higher for AgeDep1. Age dependent modelling results in a more substantial improvement in the CE. June-July temperatures at Norman Wells during the verification period (mean$=14.2$°C) are substantially cooler than during the calibration period (mean$=15.4$°C). Because the CE is more sensitive than the RE to changes in measured temperatures between calibration and verification periods (Briffa et al. 1988), its higher value for AgeDep1 indicates that model's improved ability to reconstruct the cooler temperatures during the period of verification. Both models tend to overestimate temperatures before about 1920, but this tendency is much more pronounced with the Standard1 model.

3.5 DISCUSSION

3.5.1 Causes of age dependent climate-growth response

The results of the dendroecological analyses indicate that at these sites the radial growth response of trees to climate varies significantly with tree age. Trees less than 200 years old respond differently to climate, and summer temperatures in particular, than trees greater than 200 years old. The assumption of an age

invariate climate-growth response may be invalid at these sites. Differences between the Mackenzie Mountains and Franklin Mountains sites indicate there is also a site-specific component to these responses. There are several potential explanations for the age dependent results. First, the age dependent responses may reflect genotypic differences between the cohorts that comprise each age class. White spruce is known to display a high degree of site specific selection (Nienstaedt and Zasada 1990). For example, seedlings that were established during the mid-19th century may face selective pressure imposed by cool climatic conditions during that period (Grove 1988) and could respond to climate in a different manner than trees which established during a warmer period. If this were true, the growth response of an individual to climate would depend on the time of its establishment and the prevailing climate at that time. In the absence of any genetic data, this possibility is addressed by calculating the correlations between the radial growth of individual trees at each site, standardized using modified negative exponential detrending or a horizontal line, and the Norman Wells June-July temperature for the period 1944-1989. The correlation coefficients were plotted against tree age, and for illustrative purposes only (recognizing that many of the data points have a correlation coefficient with $p>0.05$), linear regression ($p<0.05$ in all cases) was performed on these scatter plots. The plots (Fig. 3.7) suggest generally linear trends between tree age and the response of the trees to climate, with the transition in response occurring at ~200 years of age. There are no apparent age specific groupings that would suggest relationships between this
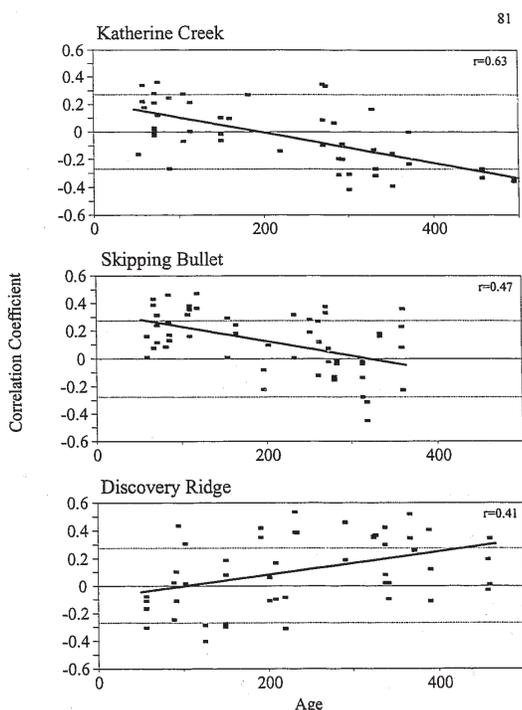
Figure 3.7: Correlations between radial growth of individual trees and Norman Wells June-July temperature, by age. Dotted lines indicate the 95% confidence limits.

response and variations in genotypes due to the climate at time of establishment, such as the ending of cool Little Ice Age conditions in the late 19th century (Grove 1988). At these sites it therefore appears unlikely that climate-driven genotypic differentiation led to age dependent radial growth responses to climate.

Second, the age dependent responses may simply be artifacts of the conservative detrending techniques employed. Radial growth of trees in temperate regions is often influenced to a large extent by stand dynamics or other nonclimatic factors (Conkey 1986), necessitating the use of cubic splines (Cook and Peters 1981) or other flexible detrending techniques. Open growth trees at their altitudinal or latitudinal limits, however, are unlikely to be influenced by stand dynamics. Spline detrending of indices from these trees can lead to a suppression of long-term climatic trends (Briffa et al. 1992). Response function and linear regression analyses of spline detrended indices at Katherine Creek (Fig. 3.8) and the other two sites either show similar trends to those in Figs. 3.3-3.5, or had a lower percentage of ring width variance explained by climate. This suggests the detrending techniques employed, which are standard for trees at or near treeline (Jacoby and Cook 1981; Jacoby and D'Arrigo 1989; Graumlich 1991), are sufficient for these analyses and do not contribute to the age dependent climate-growth responses.

Finally, the responses may reflect physiological changes related to aging. Changes in hormone relations, root, shoot and cambial growth patterns, the ratio of photosynthetic to nonphotosynthetic tissues, and the availability and translocation
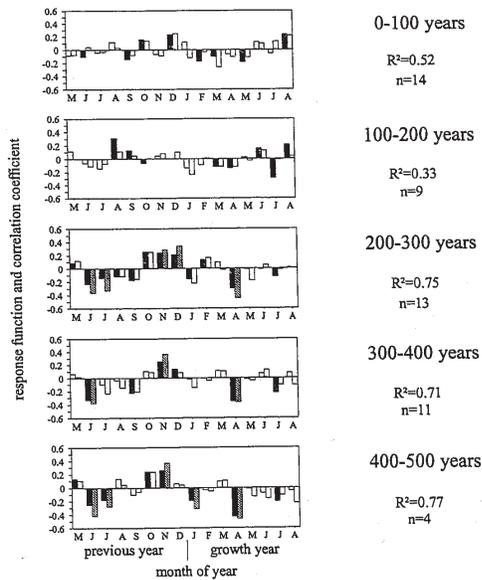
Figure 3.8: Response function results and correlation coefficients for temperature at Katherine Creek, detrended using a cubic spline. Legend as in Fig. 3.3.

of water and metabolites that occur during aging (Duff and Nolan 1953; Kozlowski 1971; Kramer and Kozlowski 1979; Harcombe 1987) could affect the relationship between tree growth and climate and be sensitive to intersite variability. Because genotypic differences and stand dynamics appear unlikely to be causal factors, it is concluded that the age dependent response of radial growth to climate at these three sites is likely due to physiological changes that accompany aging and can be site-specific. Identifying the precise physiological factors causing age dependent responses of the trees to climate is difficult for two reasons.

First, tree growth at treeline depends on a complex system of physiological and environmental controls (Fritts 1976; Tranquillini 1979; Hansen-Bristow 1986; D'Arrigo et al. 1992). Summer temperatures are important to tree growth at treeline as cool conditions and a short growing season can restrict dry matter production and lead to incomplete tissue maturation (Tranquillini 1979; Goldstein et al. 1985). In spring, water uptake at treeline may be limited by frozen or cold soils while evaporative demand is high due to moderate temperatures, high radiation levels and often strong winds (Tranquillini 1979; Baig and Tranquillini 1980; Richards and Bliss 1986). When combined with incompletely developed needle cuticles, warm spring temperatures can lead to desiccation damage of needles and eventually death of the individual (Baig and Tranquillini 1980). The importance of spring and summer temperatures during the growth year are commonly reflected in dendroecological analyses of trees at the arctic and northern alpine treelines. Response function and linear regression analyses generally exhibit

significant positive correlations between summer temperatures and radial growth (Garfinkel and Brubaker 1980; Jacoby and Cook 1981; Jacoby et al. 1988; Briffa et al. 1990; D'Arrigo et al. 1992; Graybill and Shiyatov 1992). Significant negative correlations with spring temperatures are found at many sites (Garfinkel and Brubaker 1980; Jacoby and Cook 1981; D'Arrigo et al. 1992), indicative of winter desiccation. Cool summer temperatures and a warm autumn can lead to increased storage of carbohydrates and improved growth in the following year, resulting in negative correlations with previous summer temperatures and positive correlations with previous fall temperatures (Garfinkel and Brubaker 1980; Jacoby and Cook 1981).

Second, the age dependent response of trees in this study appears to be different at Discovery Ridge compared to the Mackenzie Mountains sites. Notably, only younger trees at Skipping Bullet and Katherine Creek and older trees at Discovery Ridge display the positive response to summer temperatures normally noted at treeline or subarctic sites. Older trees at Katherine Creek show decreased growth in response to warm summer temperatures, while at Skipping Bullet older trees show no significant response to warm summer temperatures. In contrast, it is the young trees at Discovery Ridge which do not respond in a significant manner to warm summers.

Water relations are one potential cause for age and site dependent differences in the relationships between tree growth and climate in our study area. Many workers (e.g. Wardle 1974; Tranquillini 1979; Baig and Tranquillini 1980;

Goldstein et al. 1985; Hadley and Smith 1986; Richards and Bliss 1986) have stressed the importance of water relations in controlling tree growth and survival at treeline. Goldstein et al. (1985) report that resistance to the translocation of water in Picea glauca at treeline in the Brooks Range of northern Alaska increases when soil temperatures drop below 9°C. To avoid desiccation, stomata close in response to cool soil temperatures. The efficiency of water translocation through a tree also decreases with increasing age, due in part to increasing root to shoot distances, the development of non-conductive heartwood, and a progressively thinning sheath of new xylem (Kozlowski 1971; Kramer and Kozlowski 1979). As a result, water deficits may become more pronounced with age. It is possible that the strong negative response to spring temperatures in older trees at Skipping Bullet and Katherine Creek could result from the increasing effects of winter and spring desiccation with age as water translocation becomes less efficient. Though warm summers are generally important at treeline in order to maintain a positive carbon balance and allow for tissue maturation (Tranquillini 1979; Crawford 1989), they can also have a negative impact because CO_2 uptake may be reduced by stomatal closure in response to high evaporative demand (Goldstein et al. 1985). Water translocation deficiencies of older trees may accentuate the negative impacts of high summer temperatures, and this could account for the insignificant or negative responses to summer temperatures at the two Mackenzie Mountains sites. The precipitation response function and linear regression results at Skipping Bullet and Katherine Creek indicate no consistent trends in terms of moisture stress affecting

growth. However, moisture stress due to reduction in translocation efficiency would not necessarily depend on meteoric water supply, but instead on the ability to transport that moisture from roots to photosynthetic tissue. In addition, northern precipitation data are subject to both greater measurement errors and greater site-to-site variability than temperature data (Hare and Thomas 1979).

The possibility that water relations cause the age-dependent behaviour of trees at the Skipping Bullet and Katherine Creek sites cannot be tested without ecophysiological analyses. It also does not explain why responses were reversed at Discovery Ridge. Younger trees there appear to be more stressed by warm summer temperatures, perhaps as a result of poor root development in the shallow, rocky soils. Older trees display climate-growth responses more characteristic of traditional subarctic dendroecological analyses. If spring and summer stress of older individuals does result from reductions in efficiency of water translocation, the mechanism is highly site-specific and does not appear to be operating at Discovery Ridge.

3.5.2 Implications for dendroclimatic reconstruction

The improved performance of the age dependent model of climatic estimation over the standard model indicates the age of component trees making up a chronology should be taken into account when reconstructing climate at a site where age dependence has been demonstrated. As tree ages decrease back in time in the standard model, their response to climate diverges from that of the

calibration period. This divergence results in an overestimation of temperatures early in the record.

This study has demonstrated that at these three sites, there is a shift in correlations between climate and tree growth at about 200 years of age. Age-corrected radial growth records extending back 100 years (Fig. 3.2) suggest that this has not occurred solely during the period of response function calibration (1944-1988). The development of a dendroclimatic record using 'traditional' techniques from a site at which age dependent relationships are present could lead to errors in reconstruction for two reasons. The mixing of signals from trees of substantially different ages could confound climatic reconstructions produced from mixed-age samples. The mean age of trees used to develop a reconstruction may vary markedly with time, particularly when dead trees are included in the analysis (see Fig. 2 in Briffa et al. 1992). In addition, a climate-growth model based upon a calibration data set of trees >200 years in age may provide spurious estimates of past climate for the early part of the dendroclimatic record when the trees are <200 years old. This problem may be more significant, since much dendrochronological research in northern North America has used only trees greater than about 200 years old (Cropper and Fritts 1981; Jacoby and Cook 1981; Arquilliere et al. 1990; Colenutt and Luckman 1991). This potential source of early error can occur even with samples of homogenous age, and cannot be removed through time dependent analyses (Van Deusen 1990).

3.6 CONCLUSIONS

This study has demonstrated that, at certain sites, the assumption of age invariate climate-growth responses may be invalid. This conclusion is subject to some limitations imposed by the data and analytic methods, however. Firstly, the study is limited to a relatively small sample of one species at three sites in the same region. Secondly, site differences are important in determining the nature of tree responses to climate, and these three sites are somewhat diverse. The age dependent responses, though, are evident between groups of trees within each site, where the environment is more homogeneous than between sites. Site differences appear to modify the manner of age dependent responses but do not affect the conclusions. It is true that when constructing zonal or hemispheric dendroclimatic records from a network of sites, chronologies displaying strong common trends at high and low frequencies are favoured (Jacoby and D'Arrigo 1989). Sites at which age dependence occurs are likely to be eliminated from such analyses, since they would be less likely to demonstrate common trends due to site-specific responses. Thirdly, in using response function and linear regression analyses it is assumed that linear relationships exist between climate and growth. Preliminary analyses indicated that this was generally true for these data. The use of response surfaces (Graumlich 1991) circumvents this assumption by examining the nonlinear interactions of two separate climate variables with radial growth. Fourthly, the method of reclassifying trees into age classes in 1939 in this study is admittedly crude, and the conclusions are dependent on the assumption that climate-growth

relationships for a given age class of trees remains constant in time. Ideally, a continuous function describing tree response to climate in relation to age would provide a much more elegant solution, and the Kalman Filter (Visser and Molenaar 1988; Van Deusen 1990) is promising in this respect. Finally, determining the physiological causes of age dependent responses is difficult, due in part to a limited literature on the ecophysiology of the subarctic alpine treeline. There is little direct evidence with which to support the tentative hypothesis that at some sites increasing moisture stress with age can lead to negative growth responses of older trees to summer temperatures. It is clear that further research into the physiological processes of tree aging as they relate to climate-growth relationships is needed.

The results of this analysis are highly suggetive of the potential importance of age dependent response of tree growth to climate, but are by no means definitive. However, these results do suggest that data for other species and other sites should be collected to determine the extent of age dependent responses and their influence on dendroclimatic reconstruction. Testing for age dependent relationships is straightforward and should therefore be an essential part of dendroclimatic analyses. Once identified, age-dependent relationships can be used to recover a detailed climatic signal by taking into account the ages of component trees in a reconstruction. The disaggregation of trees into age classes may allow a greater number of predictor variables to be incorporated into dendroclimatic analyses.

DENDROCLIMATIC RECONSTRUCTION OF SUMMER TEMPERATURES IN NORTHWESTERN CANADA SINCE AD 1638[1]

4.1 INTRODUCTION

The subarctic is an important zone in which to examine past climatic change, since past and potential future climatic fluctuations have been and will be magnified there relative to lower latitudes (Hansen and Lebedeff 1987; Houghton et al. 1990; Lonergan et al. 1993). The usefulness of dendrochronological techniques for reconstructing subarctic climate change has been demonstrated by a number of studies (eg. Jacoby and Cook 1981; Briffa et al. 1988; Graybill and Shiyatov 1992; D'Arrigo et al. 1992). While regional reconstructions of summer temperatures or heat sums based on tree-rings have been made for parts of northwestern North America (Garfinkel and Brubaker 1980; Jacoby et al. 1985), no such reconstructions have yet been published from the subarctic alpine treeline along the boundary of the N.W.T. and the Yukon. A record of recent climate variation in the subarctic-alpine region of northwestern Canada will be useful to

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91

92

compare with previously published studies from across the northern treeline, which indicate significant variations over the past 400 years (Jacoby and D'Arrigo 1989; D'Arrigo and Jacoby 1992), and more central sites in the boreal forest, which are more complacent (Schweingruber et al. 1993). Such a record will thus contribute to understanding of zonal and regional climate variability during the past few centuries.

A fundamental assumption of most dendroclimatic and dendroecological research is that the radial growth response of trees to climate does not vary with age once the biological growth trend has been removed (Pittock 1982; Fritts and Guiot 1989; Van Deusen 1990). However, it has been demonstrated that at some sites at the subarctic-alpine treeline of the N.W.T. this assumption may be invalid (Chapter 3). At three sites in the Mackenzie and Franklin Mountains of the western N.W.T., the response of white spruce (Picea glauca) radial growth to climate changed with tree age. At two of the sites, only trees less than 200 years old demonstrated significant positive correlations with summer temperatures, while at the third site only trees greater than 200 years old displayed such responses. Physiological changes related to aging have been suggested as the probable causal mechanism resulting in age dependence. These age-dependent responses could potentially result in erroneous reconstructions of past climate if tree age is not taken into account during modelling. The study of age dependent growth response to climate in the Mackenzie and Franklin Mountains was subject to a number of limitations, however, including small sample sizes, a limited spatial extent, and a

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93

simplistic method of chronology calculation.

The objective of this study is to develop a long proxy record of summer temperatures for interior northwestern Canada using age-dependent modelling techniques. The limitations of the preceeding study are addressed by extending spatial coverage, increasing sample sizes, and incorporating more rigorous techniques of chronology computation and dendroclimatic modelling. Response function, linear regression and principal component analyses are used to test for age dependent behaviour of Picea glauca at two subarctic alpine treeline sites in central and northern Yukon. These data are then combined with new and previously presented (Chapter 3) data from three sites in the N.W.T. to produce both age dependent and standard (age independent) reconstructions of June-July temperatures in northwestern Canada extending back to AD 1638. These results are used to examine where standard modelling techniques may lead to erroneous reconstructions of climate at sites where age dependence has been demonstrated.

4.2 STUDY AREA

The study area includes the northern Yukon Territory and northwestern Northwest Territories (Fig. 4.1), and contains a diverse array of landscapes and vegetation types (Ritchie 1984). Very steep climatic gradients, relating to the relative dominance of Pacific and Arctic air masses, occur at the boreal forest-tundra transition (Hare and Ritchie 1972). Sampling for this study was restricted
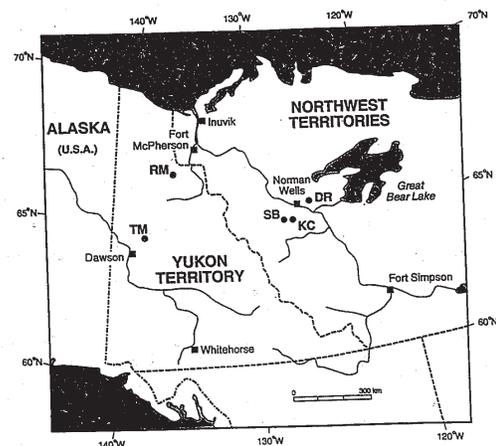

94

Figure 4.1: Locations of the study sites.

to montane regions in the interior of northwestern Canada in order to maintain a relatively homogenous climate regime. Details of the three sites in the Franklin and Mackenzie Mountains of the Northwest Territories (Discovery Ridge (DR), Katherine Creek (KC), and Skipping Bullet (SB)) are given in the preceeding chapter. Two additional sites were sampled for this study, in the Richardson Mountains of northern Yukon Territory and the southern Ogilvie Mountains of central Yukon.

The Richardson Mountains are composed of shales, limestones and dolomites (Ritchie 1984) and reach elevations of 1000 to 1500 m. Picea glauca forest and woodlands dominate lower elevation sites in the Richardson Mountains, with Larix laricina and Picea mariana occurring less frequently. Picea glauca is the species predominant at treeline, which occurs at 750 to 850 m elevation on south-facing slopes but may be several hundred metres lower in elevation on adjacent north-facing slopes (Ritchie 1984). Mean annual temperature at the nearest climate station at Fort McPherson (Fig. 4.1) is -9.0°C, and mean annual precipitation is 405 mm (Environment Canada, unpublished station data).

The southern Ogilvie Mountains are a granitic batholith reaching elevations of 2000 to 2200 m. Lower elevation sites in the southern Ogilvies, within the Eastern Yukon section of the boreal forest (Rowe 1977), are dominated by Picea glauca forest, with Picea mariana, Larix laricina, Betula papyrifera, Betula neoalaskana, Populus tremuloides and Populus balsamifera also occurring. Treeline occurrs at 1100 to 1200 m elevation as very scattered, open-grown stands

of Picea glauca. Slope aspect is not as critical in determining treeline elevation in this region as compared to the Richardson Mountains. The nearest climate station is Dawson, 70 km to the southwest. Mean annual temperature at Dawson is -4.7°C and mean annual precipitation is 326 mm (Hare and Thomas 1979).

Within each of the two regions, an open Picea glauca dominated site within 50 m of upper treeline was selected for dendrochronological sampling. There was no evidence for recent disturbance at either site. The Richardson Mountains (RM) site (66°43'N, 136°17'W) is located at 780-800 m elevation in open Picea glauca woodland on a gentle south-facing slope. Mature trees reach diameters of 40 cm, heights of 12-14 m, densities of 2-3 stems per 100 m², and a maximum age of ~490 years. The ground cover and dominated by graminoids and heaths. Soils are 25-30 cm deep and moderately drained. The Tombstone Mountain (TM) site (64°31'N, 138°19'W) in the southern Ogilvies is also in open Picea glauca woodland, on a gradual northeast-facing slope at 1120-1140 m elevation. Mature trees are up to 45 cm in diameter and 15 m in height, with stem densities of ~2 per 100 m². The maximum age of Picea glauca at this site is ~550 years. Soils are 30 cm deep and moderately drained. The ground cover is dominated by 100 to 150 cm tall Betula glandulosa shrubs.

4.3 SAMPLING AND CHRONOLOGY CONSTRUCTION

4.3.1 Methods

At each site, open grown non-krummholz Picea glauca trees of all ages were double cored or disked as close to the ground as possible, but above any basal flare. Trees having obvious vegetative origins were not sampled. At the Discovery Ridge, Tombstone Mountain and Richardson Mountains sites, standing or prostrate dead trees were sampled if the approximate location of the root collar could be determined. Cores and disks were cross-dated using the techniques of Yamaguchi (1991). Cross-dating of living and dead trees was simplified by the presence of very few missing rings, and a number of distinctive light rings (Filion et al. 1986) present on many trees. Two radii were measured for most trees. The Katherine Creek sample was the same as used in the previous study. The Skipping Bullet and Discovery Ridge sample sizes were increased by the addition of mature and dead trees not analyzed previously. Sample sizes ranged from 30 trees (51 radii) at Katherine Creek to 73 trees (130 radii) at Tombstone Mountain, for a total of 260 trees and 448 radii. Measurement was carried out using a Velmex UniSlide traversing table and an AcuRite III digital counter with a precision of ±0.001 mm. For age dependent modelling, it was necessary to estimate the age of every tree sampled. The number of years for trees to reach coring or disking height was estimated using age-height regressions developed from trees disked at ground level. If coring missed the pith, the number of rings to the pith was also estimated geometrically.

In traditional dendrochronological analyses, site chronologies are developed using trees of various ages, generally greater than about 200 years old for longer chronologies. No adjustment is made for changing tree ages throughout the chronology. If age dependent climate-growth relationships are present, transfer functions estimating climate from tree rings developed during the recent part of a chronology will not be valid when applied to early portions of the chronology, when tree ages differ significantly from the calibration period. It has already been demonstrated that age dependent relationships occur at the three N.W.T. sites (Chapter 3). It is therefore necessary to produce chronologies in which the ages of component trees remain similar to the ages at calibration for the length of the chronology.

Figure 4.2 outlines the method of chronology construction for 100-year age classes. Previous work (Chapter 3) has shown that a 100-year age class differential is sufficient to capture the variation added to chronologies due to age dependence. At a given site, all radii are first standardized using modified negative exponential detrending or a straight line of negative or horzontal slope (Fig. 4.2a; Fritts 1976). This method is standard for trees at or near treeline (Jacoby and Cook 1981; Graumlich 1991; D'Arrigo et al. 1992; D'Arrigo and Jacoby 1993). Each detrended and standardized radius is disaggregated into 100 year sections based on the estimated pith date of the tree (Fig. 4.2b). All of the radius sections for each 100 year age class (Fig. 4.2c) are then combined to produce a chronology for each of the age classes at each site (Fig. 4.2d). Chronologies were developed by bi-
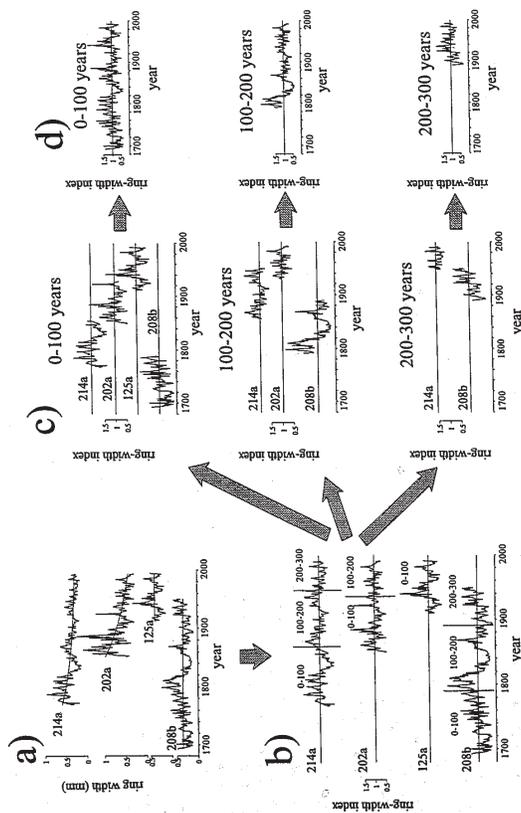
Figure 4.2: Outline of methodology for the development of age corrected chronologies from raw ring-width measurements. For description see Section 4.3.1.

weight robust averaging (Grissino-Mayer et al. 1993) of the detrended radius sections. Autoregressive modeling ('prewhitening') of chronologies was not carried out as it may remove some variance in tree-ring records which is potentially climate driven (Jacoby and D'Arrigo 1989; D'Arrigo and Jacoby 1992). Graybill and Shiyatov (1992) demonstrate that, although interannual variations are more pronounced in a climatic reconstruction produced using prewhitening than in a reconstruction without autoregressive modelling, longer-term variations are essentially identical. Given a large number of radii and a continuum of tree ages ranging from ~50 years to >400 years, these methods produce chronologies with sufficient sample depth (>5 radii) extending back several hundred years.

The differences between radial growth records for all age classes at all sites were investigated qualitatively using principal components analysis (PCA). PCA was carried out on all 20 chronologies (four age classes at each of the five sites) for the period 1890-1989, using the program SYSTAT. This PCA results in a loading on each of 20 axes for each of the 20 chronologies, although the first two axes explain the majority of the variance in the data. Chronologies with similar trends will tend to have similar component loadings on these first two axes.

4.3.2 Results

The age-corrected ring width chronologies for 100 year age classes at the five sites during the period 1890 to 1988 are illustrated in Fig. 4.3. Differences in radial growth are evident between all age classes at each site, but are most
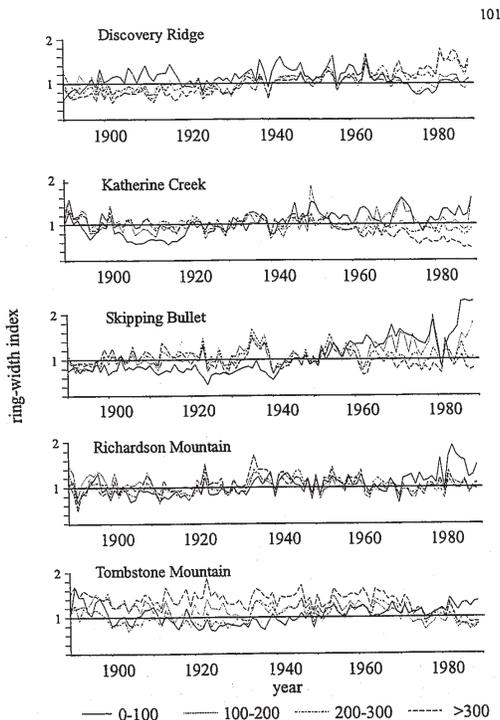
Figure 4.3: Age-corrected ring width indices, by age class, for the period 1890-1989. These indices were used in the response function and linear regression analyses and the first set of Principal Components Analyses (Fig. 4.4).

pronounced between youngest and oldest trees. The growth trends of age classes at most sites tend to diverge in the early and late 20th century, and converge in the mid 20th century.

A principal components biplot of 1st and 2nd axis loadings for each chronology was constructed to illustrate the differences between radial growth records of older and younger trees at all five sites (Fig. 4.4). No strong trends are discernable along the first axis, which explains 31% of the variance in the chronologies. The second axis, explaining an additional 26% of the variance, tends to separate groups of age classes within individual sites. The youngest age class at each of the Richardson Mountains and Tombstone Mountain sites have negative second axis scores, while trees greater than 100 years old at both of the sites have positive second axis scores. A similar divergence, at about 200 years old, is seen in the results for Discovery Ridge, Katherine Creek, and Skipping Bullet. Trees less than 200 years old at Skipping Bullet and Katherine Creek and greater than 200 years old at Discovery Ridge have negative second axis scores, while the remaining ages classes have positive second axis scores. An exception is Discovery Ridge 100-200 years, which has a slightly negative second axis score.

4.4 ANALYSIS OF CLIMATE-GROWTH RELATIONSHIPS

4.4.1 Methods

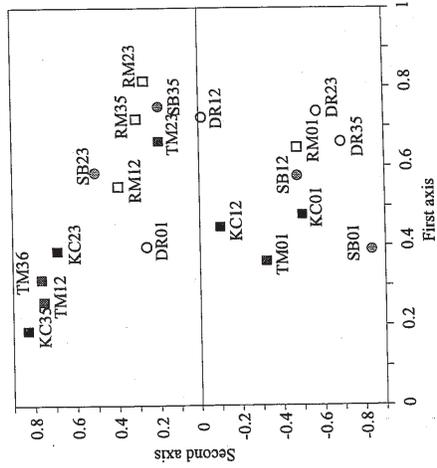Relationships between climate and the age-corrected radial growth records

Figure 4.4: Principal components biplot of first and second axis loadings for age class chronologies at Discovery Ridge (DR), Katherine Creek (KC), Skipping Bullet (SB), Richardson Mountains (RM), and Tombstone Mountain (TM) sites. Lower and upper limits of age classes, in hundreds of years, follow site designations (i.e. SB01 = Skipping Bullet 0-100 years). Period of analysis was 1890-1989.

for each of the 100-year age classes at the five sites were analyzed using response function analysis (Fritts 1976) and linear regression, performed by the PRECON program (Fritts 1993). Mean monthly temperatures and monthly precipitation data from Dawson, Yukon Territory (64° 04'N, 139°26'W, elevation 324 m) were used for the analyses of the Richardson Mountains and Tombstone Mountains sites. These data are available from 1903-1992. Several missing values were filled in by comparison with data from Eagle, Alaska and Mayo, Yukon. Although Fort McPherson is closer to the Richardson Mountains site than is Dawson, its climate record has numerous missing values for the early 20th century and was therefore not used. Data from Norman Wells, N.W.T. (65°17'N, 126°46'W; elevation 64 m) were used for analyses of the three N.W.T. sites. By comparison and correlation with records from Fort Good Hope and Fort Norman in the Mackenzie Valley, the Norman Wells monthly temperature and precipitation record has been lengthened to cover the period 1911-1989. Climate data extending from September of the growth year back to May of the previous year were included in the analyses.

4.4.2 Results

Climate accounts for a large amount of variance in radial growth at all five sites (Fig. 4.5). Only results for temperature are presented here, as precipitation results demonstrated fewer significant variables and no consistent trends. Differences in response between trees of different ages are apparent at all sites. Despite the revised method of chronology construction and the extended period of
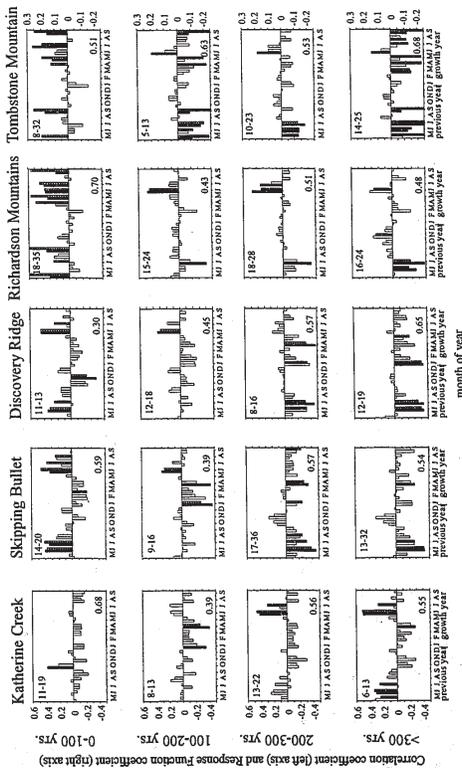
Figure 4.5: Response function results and correlation coefficients for monthly temperature. Each pair of bars represents the response function coefficient (left) and correlation coefficient (right) for a given month. Response function coefficients significant at p<0.05 are shaded black, and correlation coefficients significant at p<0.05 are shaded grey. R values (lower right) indicate the proportion of variance in ring width accounted for by the response function model, including both temperature and precipitation. Sample size range (minimum and maximum number of radii during 1911-1989 analysis period) is given in the top right corner for each plot.

analysis, results for the Discovery Ridge, Skipping Bullet and Katherine Creek sites were very similar to those of the initial analyses (Chapter 3). At Skipping Bullet and Katherine Creek, only trees less than 200 years old show a significant positive response to summer temperatures. Older trees at these sites demonstrate a significant negative response to previous summer and current spring temperatures, but do not respond significantly to summer temperatures in the growth year. At Discovery Ridge these trends are reversed, with only trees greater than about 200 years old responding in a significant positive manner to summer temperatures.

The radial growth response of trees greater than 100 years old at the two Yukon sites is different from that of younger trees. Trees less than 100 years old at the Richardson Mountains display significant postitive correlations with spring and summer temperatures in both the growth year and previous year (Fig. 4.5). The radial growth of older trees shows consistent negative responses to previous June and July temperatures and postitive response to June temperatures in the growth year. Trees less than 100 years old at Tombstone Mountain respond to climate in a similar manner to those at the Richardson Mountains (Fig. 4.5). Older trees show strong negative responses to temperature in the previous summer, and spring and late summer of the growth year. Significant positive responses to temperatures occur only in June of the growth year.

4.5 DENDROCLIMATIC MODELLING

4.5.1 Methods

Age-corrected and standard chronologies from all five sites were used to produce reconstructions of June-July temperatures for northwestern Canada extending back to 1638. A regional climate record for the period 1909-1989 was produced by averaging temperature records from Dawson and Norman Wells. Preliminary multiple regression analyses using a variety of summer temperature variables (Table 4.1) indicated that estimations of June and June-July temperature consistently provided the best calibration results for both age dependent and standard models. June-July temperature was therefore selected as the variable to be reconstructed, as it provides more information on summer conditions than simply June temperature.

Age-corrected chronologies were used to develop the age dependent (AgeDep) climate reconstruction. Rather than using all of the original 100-year age classes, age classes demonstrating similar climate-growth responses (Fig. 4.5) were grouped together into broader classes at each of the five sites, and new chronologies prepared following the method outlined in Fig. 4.2. This procedure maximized sample sizes for each chronology used in the reconstruction. Results of response function, linear regression and principal component analyses (Figs. 4.4, 4.5) were used to select the revised age classes, with an emphasis on homogenous response to summer temperatures. A second climatic reconstruction (Standard) was carried out using more traditional techniques of chronology construction.

TABLE 4.1: Results of preliminary multiple regression analyses.

summer climate variables	adjusted R^2, AgeDep model	adjusted R^2, Standard model
Early calibration (1909-1958)		
June	0.48	0.36
July	0.16	0.23
August	n.s.	0.1
June-July	0.46	0.48
July-August	0.05	0.12
June-August	0.23	0.41
Late calibration (1939-1988)		
June	0.41	0.41
July	0.18	0.07
August	0.12	n.s.
June-July	0.41	0.41
July-August	0.17	n.s.
June-August	0.17	0.12
Full calibration (1909-1988)		
June	0.41	0.41
July	0.15	0.26
August	0.02	0.04
June-July	0.47	0.54
July-August	0.08	0.15
June-August	0.26	0.41

n.s. denotes no candidate predictor variables were significant at alpha=0.1

Chronologies for the Standard reconstruction were developed using the same detrending and averaging techniques as for age dependent indices, but included all trees greater than 200 years at each site, and were not age-corrected. Dendrochronological studies in northern North America often use only trees greater than about 200 years old (Cropper and Fritts 1981; Jacoby and Cook 1981; Arquillière et al. 1990; Colenutt and Luckman 1991).

Stepwise multiple regression was used to reconstruct temperatures from the tree-ring data. Multiple regression can be sensitive to multicollinearities between predictor variables, so PCA was carried out on the tree-ring chronologies to provide a set of orthogonal (uncorrelated) eigenvectors (note that this PCA is a separate procedure from the PCA used to compare trends between age classes, outlined in Section 4.3.1). These eigenvectors were then used as candidate predictor variables in the multiple regression procedure. PC eigenvectors lagged forward by one year (t+1) were also entered as candidate predictors, as previous summer temperatures have been shown to correlate significantly with ring width in the current year in this and other treeline studies (Fig. 4.5; Jacoby et al. 1985; Briffa et al. 1988). Incorrect or insignificant candidate predictors were eliminated by the stepwise procedure to maximize the percent variance explained by the model. The α-values for entry and removal of variables were set at 0.1 (Arbaugh and Peterson 1989).

Before climatic reconstructions were carried out, preliminary models were calibrated using 50 year portions of the instrumental climate data and verified using

the remaining 30 years of data witheld from calibration. Early calibration was carried out during the period 1909-1958 with verification in 1959-1988, and late calibration used the period 1939-1988 with a verification period of 1909-1938. Verification statistics included the Pearson product-moment correlation coefficient (r), reduction of error statistic (RE), coefficient of efficiency (CE), and the first-difference sign test (Fritts 1976). The RE and CE are commonly used in dendroclimatology, though their level of significance cannot be tested (Briffa et al. 1988). A postive value generally indicates a significant reconstruction. Following initial calibration-verification procedures, both AgeDep and Standard models were recalibrated using the entire 80 year climate record and the resultant transfer functions applied to the tree-ring based eigenvectors back to 1638 to produce a 350 year record of June-July temperatures.

4.5.2 Results

At the two Yukon sites, age-corrected chronologies were constructed for trees less than 100 years old and trees greater than 100 years old (Fig. 4.6; Table 4.2). At the three N.W.T. sites, age-corrected chronologies were constructed for trees less than 200 years old and trees greater than 200 years old. Variability of growth trends is evident both between sites and between age groups within a site (Fig. 4.6). Most chronologies show increased growth in the mid to late 18th century and decreased growth in the early to mid 19th century. Differences between age groups are most evident in the 20th century, but also occur at other

TABLE 4.2: Statistics of chronologies.

Chronology	total no. series	interval (≥ 4 series)	interval (≥ 5 series)	mean sensitivity	first order autocorrelation
AgeDep Chronologies					
KC 02	51	1540-1989	1619-1989	.14	.73
KC 25	27	1730-1989	1820-1989	.13	.73
SB 02	77	1619-1989	1625-1989	.16	.64
SB 25	54	1790-1989	1790-1989	.17	.58
DR 02	73	1431-1991	1532-1991	.15	.74
DR 25	39	1700-1991	1730-1991	.17	.65
RM 01	94	1638-1992	1638-1992	.18	.70
RM 15	82	1660-1992	1687-1992	.18	.65
TM 01	93	1490-1992	1591-1992	.14	.66
TM 16	81	1550-1992	1600-1992	.13	.72
Standard Chronologies					
KC Std.	28	1540-1989	1611-1989	.13	.75
SB Std.	55	1619-1989	1625-1989	.18	.63
DR Std.	55	1431-1991	1532-1991	.15	.76
RM Std.	55	1638-1992	1638-1992	.17	.67
TM Std.	70	1490-1992	1526-1992	.13	.77
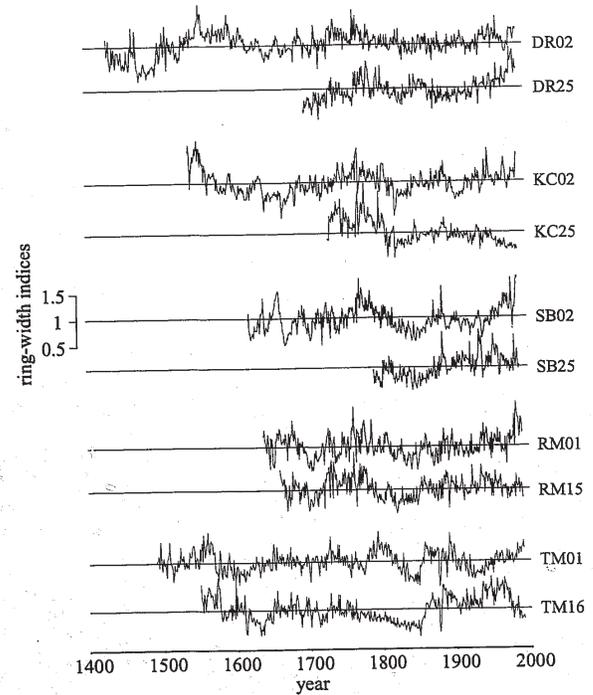
Figure 4.6: Age-corrected ring width indices for age groups used in AgeDep reconstruction. DR25, KC25, SB25 and RM15 were eliminated prior to modelling to increse length of reconstruction. Site and age class designations follow legend for Fig. 4.4.

times such as the period 1780-1820 at Tombstone Mountain. The four shortest age-corrected chronologies (DR 25, KC 25, SB 25 and RM 15) were eliminated during subsequent analyses, leaving six chronologies, each having five or more radii extending back to 1638. The Standard chronologies (Fig. 4.7; Table 4.2) have periods of common variance, but tend to diverge strongly in the 20th century. All five of these chronologies have five or more radii extending back to 1638.

The plot of first eigenvector scores for the AgeDep chronologies (Fig. 4.8), which explains 46% of the variance in the data, shows strong low-frequency trends are present in the chronologies. First eigenvector scores for the Standard chronologies (Fig. 4.9), explaining 54% of the variance, show similar but less pronounced low-frequency trends. The results of stepwise multiple regression modelling using all PC eigenvectors and their lags (t+1) are given in Table 4.3 and Fig. 4.10. For all three AgeDep models, the stepwise procedure reduced the 12 candidate predictors (six eigenvectors plus lags) to the same five significant variables, an indication of the stability of the models. The significant variables selected from the 10 candidate predictors (five eigenvectors plus lags) in Standard models varied depending on the calibration period. Early and late calibration of AgeDep models accounted for 46% and 41% of the variance (adjusted for loss of degrees of freedom) in the temperature record, respectively (Table 4.3; Fig. 4.10). All verification statistics for the AgeDep models were significant, except for the slightly negative value of CE for early calibration. The initial Standard calibration models account for comparable amounts of variance in the temperature record

Figure 4.7: Ring width indices used in Standard climate reconstruction.

Figure 4.8: Scores for all eigenvectors (E.V.) produced in PCA of age-corrected ring width indices. The percent variance of data accounted for by each eigenvector is given in parentheses.

Figure 4.9: Eigenvector scores from PCA of Standard indices. The percent variance of data accounted for by each eigenvector is given in parentheses.

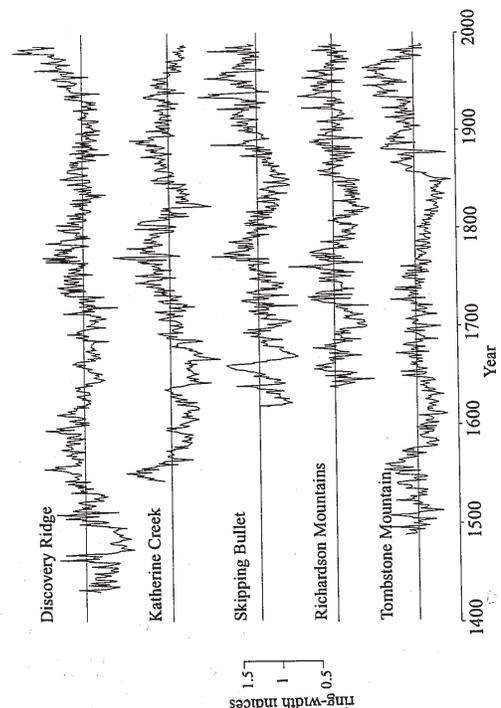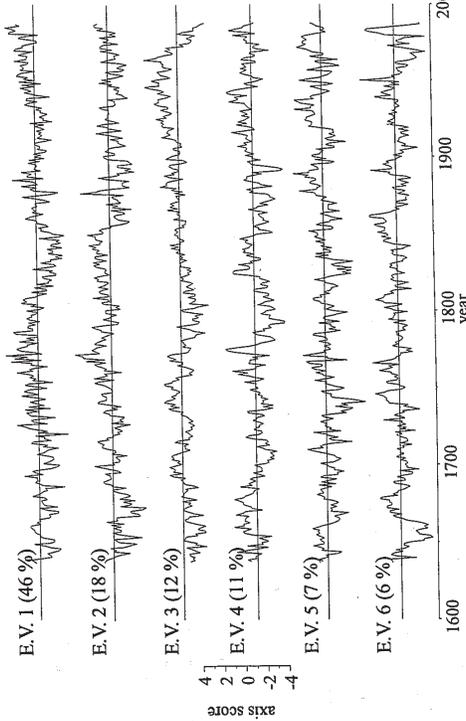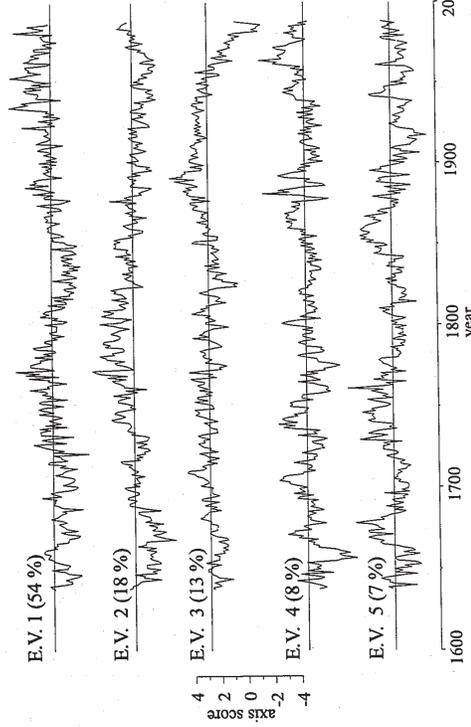(48% for early calibration, 41% for late calibration). Verification statistics, however, were significant for only three of eight tests. In particular, the strongly negative CE values suggest an inability of these models to accurately reconstruct temperatures when the mean changes significantly between calibration and verification periods. This shortcoming is confirmed by plots of estimated vs. measured temperatures for the early and late calibration Standard models (Fig. 4.10).

The AgeDep full calibration model explains 47% of variance in the climate record, adjusted for loss of degrees of freedom, while the Standard model explains 54% (Table 4.3). Examination of the residuals for both models suggest multiple regression assumptions regarding independence of regression residuals and homogeneity of variance were not violated, although AgeDep tended to overestimate temperatures in the early 1930's. The reconstructed June-July temperatures for northwestern Canada (Fig. 4.11) show divergence between AgeDep and Standard reconstructions, particularly during cool periods in the 17th, 18th and 19th centuries. The AgeDep reconstruction suggests temperatures were below the 1951-1980 mean throughout most of the last 350 years, with the exception of the mid to late 18th century. Particularly cool temperatures, ~1.5 °C below the current mean, are reconstructed for 1700-1710 and 1810-1860. Since the mid 19th century the AgeDep reconstruction indicates a long-term warming trend has occurred. The Standard reconstruction suggests temperatures were at or near the current mean for most of the period of reconstruction, except for cooler

TABLE 4.3: Calibration and verification statistics for models reconstructing June-July temperatures in northwestern Canada.

calibration period	verification period	model[a]	calibration[b]			verification[c]			
			R	R²	adjusted R²	r	RE	CE	sign test
		AgeDep models							
1909-1958	1959-1988	JJTEMP = 14.3+0.63(X1)-0.32(X2)+0.41(X4)+0.20(X5)+0.54(X2L)	.71	.51	.46	.58**	.44	-.03	20/7*
1939-1988	1909-1938	JJTEMP = 14.6+0.36(X1)-0.35(X2)+0.20(X4)+0.29(X5)+0.32(X2L)	.69	.47	.41	.59**	.52	.22	21/7*
1909-1988	-	JJTEMP = 14.4+0.54(X1)-0.31(X2)+0.26(X4)+0.25(X5)+0.36(X2L)	.71	.50	.47	-	-	-	-
		Standard models							
1909-1958	1959-1988	JJTEMP = 15.0+0.56(X1)+0.38(X5)-0.47(X1L)+0.47(X3L)	.73	.53	.48	.57**	-.01	-.87	19/9 ns
1939-1988	1909-1938	JJTEMP = 15.4+0.34(X1)-0.40(X1L)+0.25(X5L)+0.26(X2L)	.67	.46	.41	.66**	.34	-.14	19/8 ns
1909-1988	-	JJTEMP = 14.9+0.55(X1)-0.52(X1L)+0.38(X5L)-0.31(X3)-0.49(X3L)	.75	.57	.54	-	-	-	-

[a] X denotes the PCA eigenvector; L denotes PCA chronology lagged forward one year
[b] R is the multiple correlation coefficient; R² is the variance explained; adjusted R² is the variance explained, adjusted for degrees of freedom
[c] r is the correlation coefficient; RE is the reduction of error statistic; CE is the coefficient of efficiency
** p≤0.001; * p≤0.05; ns denotes p>0.05; significance levels cannot be calculated for RE and CE, but a positive value denotes a significant reconstruction
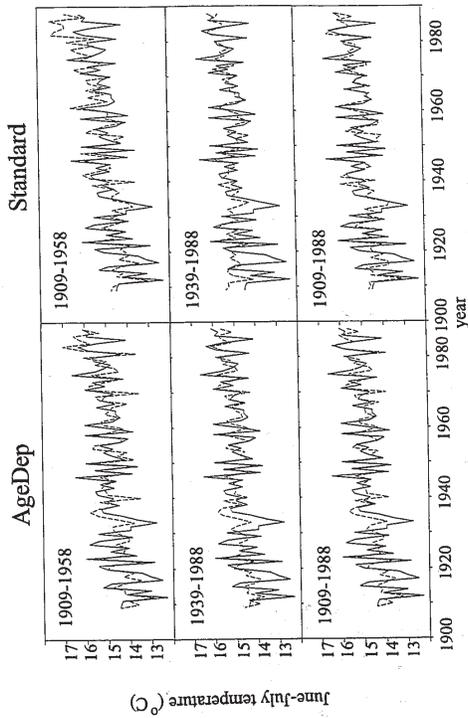
Figure 4.10: Actual (solid line) and estimated (dashed line) June-July temperatures for northwestern Canada developed using early, late and full calibration periods for AgeDep and Standard models.
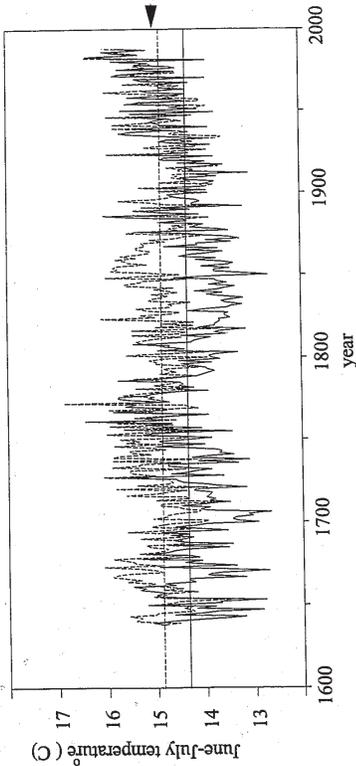
Standard

AgeDep

June-July temperature (°C)

1909-1958   1939-1988   1909-1988

year

Figure 4.11: Reconstructed June-July temperatures for northwestern Canada developed using AgeDep (solid line) and Standard (dashed line) models. Horizontal lines indicate the mean temperature for 1638-1988 for each reconstruction. Arrow at right indicates the mean 1951-1980 June-July temperature from instrumental data.

June-July temperature (°C)

year

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periods from 1700 to 1720 and 1900 to 1940. There is no evidence in this reconstruction for a sustained warming trend since the mid 19th century.

4.6 DISCUSSION

4.6.1 Age dependent climate-growth response

The dendroecological analyses of ring width records from Discovery Ridge, Skipping Bullet, Katherine Creek, the Richardson Mountains and Tombstone Mountain confirm that the radial growth response of Picea glauca to climate varies with tree age at these sites. Although the age-dependent differences at the two new Yukon sites are not as dramatic as at the N.W.T. sites, there is a clear shift in temperature response at about 100 years of age. Genotypic differences between cohorts of different ages were rejected as a potential cause for age dependence in the previous study. Stand dynamics are also unlikely to have caused these responses, owing to the very open nature of the sampled stands. It follows that the responses are likely to be physiologically based.

All trees at both the Richardson Mountains and Tombstone Mountain sites show positive response to warm temperatures at some time in the summer of the growth year. In a dendroecological study of several sites along the North American treeline, D'Arrigo et al. (1992) note that ring widths correlate with local temperatures for a relatively short interval in the summer. At the Yukon sites, trees greater than 100 years old tend to respond positively to temperature only

during June, while there are negative or no significant responses to previous summer, and current spring and late summer temperatures. These responses are fairly typical for sites in northern North America (Garfinkel and Brubaker 1980; Jacoby and Cook 1981; D'Arrigo et al. 1992). However, young trees at both sites show a much more prolonged period of positive response to growing season temperatures, which extends from late spring to late summer. The physiological cause for age dependent behaviour cannot be rigorously tested without ecophysiological analyses. Nonetheless, these results are compatible with the hypothesis developed in the previous study, based on analyses of the N.W.T. sites, that the age dependent responses result from increasing moisture stress with age. Water translocation deficiencies in older trees may lead to temperature-induced moisture stress at critical times of the year, such as late spring and late summer. In spring, water demand is high due to moderate temperatures, high radiation levels, and often strong winds, but uptake is restricted owing to cold or frozen soils (Tranquillini 1979). In early summer, water supply is adequate and warm temperatures should lead to increased photosynthesis and growth. By late summer, temperatures are still warm but soil moisture may have declined to the point of restricting growth. Younger trees generally have more efficient water translocation mechanisms (Kozlowski 1971; Kramer and Kozlowski 1979), possibly making them less susceptible to moisture stress in spring and late summer and resulting in a longer period of positive temperature responses. Thus, evidence from four of five sites suggest that increasing water stress with age leads to a reduction in, or even

loss of, the season of positive temperature response. The response of old vs. young trees to climate at the Discovery Ridge site, however, was reversed from the other two N.W.T. sites (Fig. 4.5). The differences between age dependent responses at the five sites, particularly the reversal at Discovery Ridge, indicate that mechanisms leading to age dependent climate-growth responses are highly site-specific.

4.6.2 Comparison of AgeDep and Standard models

In the previous chapter it was suggested that the development of a dendroclimatic record using traditional techniques from a site at which age-dependent relationships are present could lead to errors in reconstruction. These errors would result from the mixing of signals from trees of different ages, and the divergence of tree ages back in time from age at time of calibration. Age dependent climate-growth responses have been clearly demonstrated for the five sites in this study, and the AgeDep temperature reconstruction differs substantially from the Standard reconstruction. The violation of a basic assumption renders the traditional dendroclimatic approach to temperature reconstruction invalid at these sites. Although the Standard models produce calibration statistics comparable to other studies in northern North America (Jacoby et al. 1985; D'Arrigo and Jacoby 1992), the verification of these models indicate the reconstructions are poor. AgeDep calibration statistics show no improvement over those for the Standard calibrations, but verification suggests considerably greater reliability of
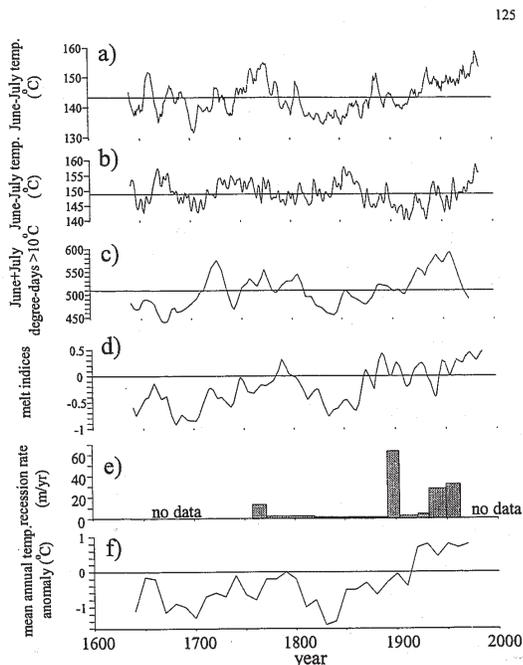
reconstructions.

Several tree-ring based temperature or degree-day reconstructions are available for northern North America for comparison with the AgeDep reconstruction (Garfinkel and Brubaker 1980; Jacoby et al. 1985; Jacoby et al. 1988; D'Arrigo and Jacoby 1992). Of these, the Alaska-Yukon record of Jacoby et al. (1985) is most appropriate for comparison, as it reconstructs June-July degree-days on a regional scale, and extends to the western edge of our northwestern Canada reconstructions. Comparison of the records (Fig. 4.12a,c) indicates good correspondence with the AgeDep reconstruction. Both records suggest summer temperatures were cooler than present during the 17th century and warmer than present in the latter part of the 18th century. Minima occurred in the early to mid 19th century, the end of the 'Little Ice Age' (Grove 1988). Long-term warming since the end of the Little Ice Age has been interrupted by several shorter term fluctuations. There are several differences between the two reconstructions, however. Very low temperatures in AgeDep around 1700 do not appear in the Alaska-Yukon record, whereas a maximum at around 1730 in that record is much less pronounced in the AgeDep record. AgeDep also compares favourably with D'Arrigo and Jacoby's (1992) more general reconstruction of northern North America mean annual temperatures, particularly in the cool period at ~1700 and prolonged cooling in the mid 19th century.

It has been demonstrated that ice core melt records from high latitude ice caps correspond well with regional and zonal summer temperatures (Koerner 1977;

Figure 4.12: Comparison of proxy summer temperature records for North America, 1638-1988. a) AgeDep and b) Standard tree ring reconstructions of northwestern Canada June-July temperatures, smoothed with a 5-year binomial filter; c) tree-ring based reconstruction of Alask-Yukon degree-days over 10 C in June+July, smoothed with a 20-year filter (Jacoby et al 1985); d) percent melt layers in core from southern Greenland Ice Cap (Bradley and Jones 1993); e) recession rate of Lemon Creek glacier, southeastern Alaska (Heusser and Marcus 1964); and f) composite summer temperature anomalies for North America, developed from tree ring and ice core records (Bradley and Jones 1993).

Herron et al. 1981; Bradley and Jones 1992, 1993). One such record, from the southern Greenland ice cap (Bradley and Jones 1993), shows good correspondence with the AgeDep reconstruction (Fig. 4.12d). Both the melt record and AgeDep indicate summer temperatures cooler than the late 20th century for most of the period 1638 to 1880, with maxima occurring in the late 1700's, late 1800's and mid to late 1900's. A long-term warming trend over the past 150 years is evident in both the melt record and the AgeDep reconstruction. Bradley and Jones (1993) have also developed a 600 year composite temperature record for North America, based on a combination of three ice core and three tree-ring studies (Fig. 4.12f). This record compares very favourably with the AgeDep reconstruction. Finally, periods of increased recession rate of the Lemon Creek glacier in the Glacier Bay region of Southeastern Alaska (Fig. 4.12e; Heusser and Marcus 1964) correspond well with periods of increased summer temperatures in the AgeDep reconstruction. Such records should be interpreted cautiously, though, owing to dating uncertainties and lags in glacial response to climatic changes (Bradley and Jones 1993).

The Standard reconstruction for Yukon-N.W.T. summer temperatures from these subarctic alpine sites (Fig. 4.12b) compares much less favourably with the tree-ring, ice core melt and glacial recession records. Temperatures warmer than or equal to present throughout most of the 17th to 19th centuries, as reconstructed with the Standard model, are not apparent in any of the other proxy records. The greatest decoupling between Standard and AgeDep results occurred during the 17th, 18th and 19th century cool phases.

The similarities between AgeDep and the reconstruction of Jacoby et al. (1985) indicates that age dependent climate-growth responses were probably not of critical importance at the sites making up that reconstruction. Nonetheless, it is possible that age dependent factors at the Alaska-Yukon sites have led to differences in detail between the reconstructions, particularly in their early portions. For example, the relative amplitudes of early and late 18th century maxima apparent in the Greenland ice core melt record (Fig. 4.12d), and the late 19th century peak in temperatures indicated by both glacial recession and ice cap melt layer records (Fig 4.12d,e) all appear to be recorded more accurately in the AgeDep reconstruction than in that of Jacoby et al. (1985).

Since sites not demonstrating common long-term variance are often excluded from regional and large scale climate reconstructions (Chapter 3; Jacoby and D'Arrigo 1989), sites with age dependent behaviour may be eliminated from such analyses. For example, the poor performance of the Standard models during verification in this study should lead to their rejection. The distinct decoupling of AgeDep and Standard model reconstructions during cool periods of the past 350 years clearly illustrates the errors which may occur in reconstruction using sites where the climate-growth response varies with tree age. Minor age dependent relationships may lead to subtle errors in reconstructions, particularly during their early portions. This may be reflected in the sensitivity of the AgeDep record to minor temperature variations which are poorly recorded in some earlier studies. Testing for age dependent relationships, either directly or by employing rigorous

verification criteria to identify the possible presence of such relationships, should be a standard procedure in dendroclimatic studies.

4.6.3 Implications of the reconstruction

The development of a 350 year summer temperature record for northwestern Canada is important for a number of reasons. Firstly, it provides historical context for recent changes evident in the instrumental climate record. During the past 350 years, June-July temperatures in this region have varied over a range of about 3 °C. Potential causes of decadal to century scale climate changes include volcanic activity, variations in the solar radiative constant, oscillations in oceanic thermohaline circulation, and changes in atmospheric CO_2 concentrations (Grove 1988; Jacoby and D'Arrigo 1989; Stocker and Mysak 1992). The steady rise in temperatures since 1850 evident in this and most other climatic reconstructions from North America (Innes 1991; Bradley and Jones 1993) may simply be a natural recovery from cool conditions during the Little Ice Age, or may be the first stages of a response to anthropogenic increases in greenhouse gases (Jacoby and D'Arrigo 1989; Cohen 1990; Bradley and Jones 1993; D'Arrigo and Jacoby 1993). The AgeDep reconstruction of summer temperatures allows this warming to be placed in a long-term historical context for northwestern Canada. Summer temperatures in this region during the late 20th century have been greater than at any time in the past 350 years except the 1770's, although the magnitude of post Little Ice Age warming (~ 1.5 °C) is not unprecedented during this period. Between 1700 and 1770

there was an apparent increase in June-July temperatures of similar magnitude. Our data therefore suggest the recent warming trend does not exceed the natural climatic variability of the past 350 years in northwestern Canada. This conclusion is subject to the limitations of reconstructing long-term climate trends from tree ring data, however, and does not eliminate the possibility of recent anthropogenic impacts. Jacoby and D'Arrigo (1989) conclude that the post-Little Ice Age warming trend apparent in their reconstruction of mean annual Northern Hemisphere temperatures does exceed the levels of natural climate variability of the past 300 years. With an extended Northern Hemisphere temperature record of the past 600 years, Bradley and Jones (1993) suggest the recent warming trend may be interpreted in the same way, but may also be interpreted as the conclusion of a gradual rise in temperatures since the early 1500's.

Long proxy climate records are also valuable tools in the interpretation of long term vegetation and faunal dynamics. Dendroecological studies in northern Quebec (Payette and Filion 1985; Payette et al. 1985, 1989) and Churchill (Scott et al. 1987; Scott and Craine, in press) indicate climatic changes have had a substantial impact on subarctic plant and animal populations during the past several centuries. Few dendroecological studies are available from the subarctic alpine treeline of northwestern Canada, though palaeoecological research indicates it has been sensitive to climatic change during the Holocene (Chapter 2; Ritchie 1984; Cwynar and Spear 1991). The 350 year record of summer temperatures developed here can be used to help evaluate the importance of climate in determining recent

plant population dynamics in northwestern Canada.

Finally, the proxy climate record allows evaluation of the magnitude of potential future climate warming. Although the cause of the post-Little Ice Age warming trend is not yet clear, global circulation models suggest substantial warming of northern climate is very probable in the next few decades in response to increasing concentrations of greenhouse gases (Cohen 1990). Given a doubling of CO_2, summer (June-August) temperatures in the Mackenzie Valley could rise by 3 to 7°C (Lonergan et al. 1993). This represents an increase with a magnitude two to four times greater than that reconstructed for the past 150 years. An increase of such magnitude will likely have significant impacts on the environment of northwestern Canada, particularly in the transition between boreal forest and tundra (Bonan et al. 1990; Rizzo and Wiken 1992). The economy of the western N.W.T. is also potentially sensitive to the projected climate change, due in part to the importance of seasonally dependent transportation networks such as river barges and ice roads (Lonergan et al. 1993).

CHAPTER FIVE

RECENT WHITE SPRUCE DYNAMICS AT THE SUBARCTIC ALPINE TREELINE OF NORTHWESTERN CANADA

5.1 INTRODUCTION

Relationships between climate and the physiological and reproductive characteristics of trees are important in governing the location of polar and alpine treelines (Tranquillini 1979; Black and Bliss 1980; Kullman 1990). In particular, the dynamics of tree populations at their latitudinal and altitudinal limits have been closely linked to the limiting influence of low summer temperatures on the production of viable pollen and seeds and on the germination and subsequent survival of seedlings (Kearney 1982; Beaudoin 1989; Grace 1989). Substantial variations in temperature during the past several centuries (Grove 1988; Bradley and Jones 1992), particularly at mid- to high latitudes (Hansen and Lebedeff 1987; Briffa et al. 1992; D'Arrigo and Jacoby 1992), have influenced the position of polar and altitudinal treelines (LaMarche 1973; Luckman and Kearney 1986; Scuderi 1987; Clague and Mathewes 1989; Kullman 1990; Carrara et al. 1991; Shiyatov 1993; Spear 1993) and the density of marginal forest-tundra stands (Payette and Filion 1985; Scott et al. 1987; MacDonald and Szeicz 1994).

Although the Holocene dynamics of the northern treeline in northwestern Canada have been the focus of several fossil pollen studies (Ritchie and Hare 1971; Ritchie et al. 1983; Cwynar and Spear 1991; Spear 1993), little is known of recent alpine treeline dynamics in this region due to a lack of dendrochronological studies. In the only published record to date, Ritchie (1982) documented a 20 m increase in treeline elevation during the period 1900-1940 in the Richardson Mountains of the Yukon. Sampling for this study, however, was limited to ~50 Picea glauca and Larix laricina individuals at a single site. The mountains of northwestern Canada are well suited for dendrochronological studies of climate-vegetation dynamics at treeline for several reasons. Firstly, the relative longevity of the dominant treeline species (Picea glauca; maximum age 500-600 years) allows for long-term dendroecological analyses. Secondly, non-climatic disturbances such as fire, insect defoliation, or anthropogenic impact appear to be very rare or non-existant in isolated forest-tundra stands within this region (J.M. Szeicz, pers. obs.; H.F. Cerezke, pers. comm.), which permits analysis of climate-vegetation dynamics in a system that is relatively undisturbed by other factors, and increases the potential for preservation of dead spruce remains both above and below current treeline. Finally, past variations in climate at high latitudes have been of greater magnitude than at lower latitudes (Hansen and Lebedeff 1987), which may have amplified vegetation changes at high latitude treelines.

In this chapter, dendroecological techniques are used to reconstruct the recent population dynamics of Picea glauca at the alpine treeline of northwestern

Canada in order to test two hypotheses: 1) the recruitment/survival and mortality patterns of Picea glauca at treeline are episodic, controlled by climate variations; and 2) the position of treeline in this region is in equilibrium with current climatic conditions. The first hypothesis was tested by developing age structures for populations of living Picea glauca, and cross-dating dead Picea remains, in stands at or near treeline, and comparing these results to proxy climate records. The second hypothesis was tested through examination of treeline stands for evidence of recent seed regeneration. Intensive sampling for this study was focused on the mountains of the western N.W.T. The recruitment/survival patterns and current reproductive status of Picea glauca at its upper limits were analyzed at ten stands in the Mackenzie Mountains. Preservation of dead conifer remains was poor at these sites, so mortality patterns of Picea glauca were studied at a site in the adjacent Franklin Mountains. Further sampling was carried out at several sites in the Yukon to corroborate the results from the N.W.T. on a regional scale. Age structures and current reproductive capacity were assesed at two stands in northern and central Yukon. Conifer remains at these sites were again poorly preserved, and mortality patterns were therefore studied at a third site in the central Yukon. For the purposes of this study, treeline is defined as the uppermost limits of individuals having an upright growth form.

5.2 STUDY SITES

The majority of the sampling for this study was carried out in the Franklin and Mackenzie Mountains of the western N.W.T., while corroborative sampling took place in the Richardson and Ogilvie Mountains and Klondike Plateau of central and northern Yukon (Fig. 5.1). General descriptions of the vegetation, climate and geology of the four mountain regions have been given in chapters 3 and 4. The Klondike Plateau comprises an upland region extending west of Dawson in the west-central Yukon. The plateau, unglaciated in the late Wisconsin (Dyke and Prest 1987), is intersected by numerous deep river valleys, and reaches elevations of 1000-1300 m. Vegetation is similar to that of the Ogilvie Mountains (Chapter 4), with treeline occurring at 1200 to 1250 m elevation. Mean annual temperature at Dawson is -5.1 °C and mean annual precipitation is 303 mm (Environment Canada, unpublished station data).

The primary study area for this research is a 30 km² region in the Carcajou Range of the Mackenzie Mountains, within which ten of the stands sampled for age structure are located (Fig. 5.1). The deeply incised Katherine Creek canyon along the northern and eastern limits of this region appears to be an effective fire break separating forest-tundra stands from the relatively frequently burned lowland boreal forest in the Mackenzie Valley to the north (Rowe et al. 1974; Wein 1975). Lowlands and north-facing slopes adjacent to the Skipping Bullet Creek watershed (informal name) are poorly drained and dominated by hummocky Eriophorum tundra with scattered Picea mariana and Larix laricina individuals. South- and
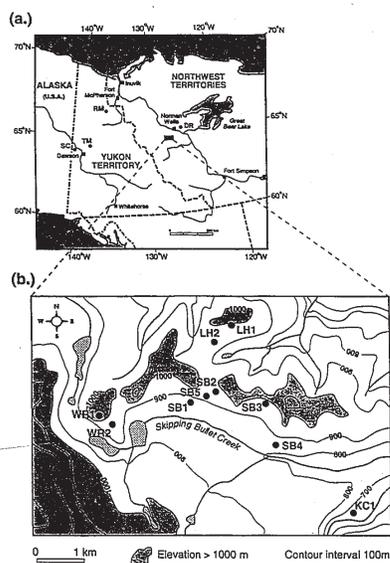
Figure 5.1: Locations of the study sites. a) Yukon and Franklin Mtns., N.W.T. sites.
b) Carcajou Range study region, Mackenzie Mountains, N.W.T.

southwest-facing slopes to the north of the watershed are steeper and generally well drained. Soils are thin, from 10 to 30 cm deep, and permafrost was not observed at any sites. Picea glauca grows in scattered, open stands along these slopes, separated by Betula glandulosa and heath dominated shrub tundra in moderate to well-drained areas and Eriophorum tundra where drainage is poor. Picea mariana and Larix laricina occur infrequently in these stands. Picea glauca is the sole tree species present at treeline. In this region treeline on south-facing slopes occurs at 970 to 1010 m elevation, and is characterized by well separated, open-grown individuals of upright tree-form and up to 300 to 500 cm height, small discrete islands dominated by one or several large upright individuals of similar height, or extensive, dense islands of krummholz individuals with contorted growth forms and a dense, continuous canopy 200 to 300 cm high. At and above the upper limit of tree growth, low tundra dominated by herbs and dwarf shrubs such as Dryas integrifolia, Arctostaphylos alpina, Vaccinium vitis-idaea, V. uliginosum, Andromeda polifolia, Potentilla fruticosa, grasses, lichens and bryophytes, is interspersed with extensive areas of frost-shattered calcareous bedrock. Prostrate, matted Picea glauca individuals, 10-20 cm tall, are occasionally found in the tundra beyond treeline, but the upper limit of species growth generally coincides fairly closely with the treeline as defined above.

Nine stands (Fig. 5.1; SB1-5, WR1-2, LH1-2) were sampled within the forest-tundra along the north side of the Skipping Bullet drainage. The stands selected are representative of the various growth forms of white spruce at or near

treeline. Two stands (SB1, SB4) are in the lower forest-tundra, characterized by a fairly continuous, but open, cover of white spruce with occasional tundra openings. Four stands (SB2, SB3, SB5, WR2) are in the upper forest-tundra, but below the upper limit of white spruce growth. These stands are characterized by scattered, open grown white spruce islands separated by extensive tundra openings. Three stands (LH1, LH2, WR1) were sampled at treeline, each representing one of the treeline forms described above. A tenth stand (KC1) was sampled in the open forest of a terrace located within Katherine Creek canyon. White spruce predominates in this stand, though black spruce and larch were also fairly common in more poorly drained surrounding areas.

For comparison with the data from the Mackenzie Mountains, two stands at the upper limit of tree growth in the Yukon were also sampled (Fig. 5.1). One of these (RM) is located at 850 m altitude on a south-facing slope in the Richardson Mountains, 50 m above the dendroclimate site described in Chapter 4. At its upper limits white spruce grows both as discrete, erect individuals and in small islands dominated by several erect stems. Low tundra, dominated by graminoids, Dryas integrifolia and heaths, dominates above treeline and in openings in the upper forest-tundra. A second stand, Swede Creek (SC), was sampled at 1250 m elevation on a gentle S-facing slope in the Klondike Plateau. The growth forms of treeline white spruce are similar at this site to those at RM, though black spruce also occurs at treeline as clonal islands with numerous erect stems. Tundra openings are dominated by Arctostaphylos alpina, Dryas integriflia, Salix spp., low

Betula glandulosa, and bryophytes, with many areas of exposed shattered rock.

Mortality patterns of white spruce were studied at the Discovery Ridge site in the Franklin Mountains of the N.W.T., described in Chapter 3, and the Tombstone Mountain site in central Yukon, described in Chapter 4.

5.3 METHODS

5.3.1 Age structure analysis

At each stand sampled for age structure a rectangular quadrat was laid out with the objective of censuring 50 to 100 white spruce individuals. The size of quadrats varied from 45 m^2 to 450 m^2 owing to variations in the density of spruce populations at different sites. All quadrats were divided into 5 m x 5 m or 3 m x 3 m subquadrats in order to resolve small-scale spatial trends in spruce recruitment. All living and dead trees of all species within each quadrat were recorded and sampled. Stems were either disked or cored as close to ground level as possible to obtain an accurate age determination. Growth form, height, diameter at base, origin (layer or seed), and presence of male or female strobili were noted for each individual. An individual was considered to have originated by layering if root development was observed, but a vegetative connection existed with another stem. The root systems of individuals of questionable origin were excavated to locate any possible connections. Since very young seedlings may be overlooked in the sampling of large quadrats with dense ground cover, four randomly located 4 m^2

quadrats were examined closely for the presence of seedlings at each site.

Age determinations of all stems were made following fine sanding of disks and cores. The number of years for trees to reach coring height was estimated using age-height regressions developed from young trees disked at ground level. Although age-height relationships are sometimes weak in forest-tundra stands (Payette and Filion 1985), such estimations should introduce little error into subsequent analyses because a) coring was carried out within 20-30 cm of ground level, and the resultant corrections were seldom greater than 20 years; and b) the establishment histograms were constructed using 10-year age classes. If coring missed the pith, the number of rings to the pith was estimated geometrically following the technique of Baker (1992). The radius of the circle containing the innermost ring was estimated, and the number of rings occurring within that radius was then estimated using the average ring width for the entire core. Accurate age determinations were not possible for several trees due to severely rotten piths; these individuals were assigned a minimum age based the number of well preserved rings. The estimated year of establishment was determined for each stem based on its age at time of sampling (1990 for Mackenzie Mountains. sites, 1993 for Yukon sites). Fine-scale spatial trends in _Picea glauca_ age structures were investigated within three of the treeline stands. Quadrats at these stands (LH1, LH2, and SC) extended 15 to 30 m downslope from the upper limits of spruce growth, which allowed for the resolution of elevational shifts in spruce establishment on the scale of metres.

Age structures are records of both establishment and subsequent survival to the time of sampling. A lack of trees dating to a certain period may be the result of a lack of establishment at that time, high mortality rates of trees which established at that time, or a combination of these factors (Johnson and Fryer 1989). Age structure data from the 12 sites were analyzed using mathematical age models to determine if temporal trends have occurred in the recruitment/survival of white spruce at or near treeline in this region. To maximize sample sizes for these analyses the ten Mackenzie Mountains sites were grouped into upper forest-tundra (LH1, LH2, SB2, SB3, SB5, WR1, WR2), lower forest-tundra (SB1, SB4) and open forest (KC1), and RM and SC were merged together. Two models were used to examine the age structure of these populations, the negative exponential function (ln(frequency) vs. age) and the power function (ln(frequency) vs. ln(age); Hett and Loucks 1976; Legere and Payette 1981; Agren and Zackrisson 1990). Both of these models assume a constant recruitment rate in the population, but while the negative exponential function also assumes a constant mortality rate, the power function allows for a changing mortality rate with age (Hett and Loucks 1976). Recruitment/survival residuals were calculated by subtracting predicted age class frequencies, based on the selected mathematical model, from observed age class frequencies, for each decade of the analysis. These deviations of the actual age structure from the predicted age structure may reflect changing patterns of recruitment/survival over time (Legere and Payette 1981; Agren and Zackrisson 1990; Payette et al. 1990). The oldest 1% of individuals in each of the three

populations were eliminated to avoid the influence of outliers on age models, and a value of 1 was added to each age class frequency before log transformation to permit inclusion of empty age classes (Agren and Zackrisson 1990). Individuals of seed and layer origin were combined for these analyses. After about 100 years vegetative connections appear to decompose, complicating the determination of stem origin in older individuals.

Statistical relationships between recruitment and summer temperatures were tested for by calculating Pearson correlation coefficients between recruitment/survival residuals and reconstructed June-July temperatures in northwestern Canada (Chapter 4). Temperatures were averaged over ten year periods corresponding to the years included in each age class (1980-1989, 1970-1979, and so on). Since patterns of successful recruitment are determinded in part by post-establishment mortality, and mortality rates of trees are influenced by climatic factors, particularly when young (Brubaker 1986; Kullman 1987a; Kozlowski et al. 1991), recruitment/survival residuals may demonstrate significant statistical relationships with temperatures for a period following establishment. To test for this possibility, four new June-July temperature records were produced, in which decadal temperatures were averaged forward in time to integrate 20, 30, 40, and 50 year long periods. Thus the 50 year forward mean temperature for the 1800-1809 decade represents the average temperature for the period 1800-1849, for the 1810-1819 decade represents the average temperature for the period 1810-1859, and so on. Pearson correlation coefficients were then calculated between

recruitment/survival residuals and each of these forward mean temperature records. These regression analyses were carried out over an interval extending from the first decade of recruitment/survival data, which varied depending on the dataset being analyzed, to the decade 1940-1949.

5.3.2 Analysis of mortality patterns

Although abundant, well preserved dead conifer remains were not present at any of the twelve stands at which detailed age structure analyses were carried out, they were found at two sites sampled for dendroclimatological analyses. At Discovery Ridge numerous prostrate and erect snags were present both above and below the current treeline. At Tombstone Mountain snags were fairly abundant within the upper forest-tundra, though none were found in the tundra above treeline. To examine the mortality patterns of white spruce at these two sites, sections were collected from dead snags for dendrochronological dating. Complete or partially complete remains were sectioned at the base to allow determination of the approximate time of establishment. For most remains, including all of the samples from above treeline at Discovery Ridge, the location of the root collar could not be determined, precluding accurate determination of time of establishment. Sections were sanded with progressively finer grades of sandpaper, and cross-dated using the ring-width and light ring chronologies developed from living forest-tundra individuals at the same site (Filion et al. 1986; Yamaguchi 1991; Chapter 3). Weathering of older dead tree remains removes the bark and

an unknown number of outer rings. Payette et al. (1989) have estimated this loss to be on the order of 10-20 years. Some of the partially buried prostrate remains at Tombstone Mountain had bark preserved on the protected side while the exposed side was weathered. The differences in ring counts on weathered vs. protected radii amounted to 13 years in a sample which died in 1818, 18 years in a sample which died in 1838, and 6 years in a sample which died in 1955. Based on these results and those of Payette et al. (1989), a weathering loss correction of 20 years was added to samples dating to the 19th century and 10 years to those from the 20th century. This correction provides a first approximation of stem death dates, but it is crude and thus for mortality analyses both establishment and death dates were plotted in 20 year classes.

5.3.3 Radial growth trends

The development of tree-ring chronologies from forest-tundra white spruce allows for the examination of growth responses to changing local environmental conditions and may assist in the interpretation of recruitment/survival and mortality patterns. Tree-ring chronology development for the Skipping Bullet, Discovery Ridge, Richardson Mountains and Tombstone Mountain sites was outlined in Chapter 4. Although it has been demonstrated that the radial growth response of trees at these sites varies with tree age, the chronologies are here being used simply for comparitive purposes and are therefore the Standard chronologies uncorrected for tree age.

5.4 RESULTS

5.4.1 Stand characteristics and age structure analyses

A summary of the structural and reproductive characteristics of the twelve stands sampled for age structure data is given in Table 5.1. Both maximum age and maximum size of white spruce generally decrease with increasing altitude, although there is much variation around these trends. Stem densities do not appear to be dependent on stand altitude, although the extent of tundra patches between tree stands within the forest-tundra does tend to increase with increasing altitude. Seedling abundance varied a great deal both between and within sites. Seedlings were absent at two of the treeline stands, rare at two others, and relatively abundant at the fifth (LH1). Layering occurred frequently in upper forest-tundra stands, but was far less common in lower forest-tundra and open forest stands. The production of both male and female strobili occurred at all sites up to and including those at the upper limit of tree growth, except at LH2 at which only a few female cones and no male cones were present. The youngest cone-bearing tree at any of the twelve sites was 41 years old, and thus the proportion of cone-bearing trees was calculated using the subset of the population with age greater than 40 years to avoid undue influence of young trees not yet able to produce cones.

Height vs. age histograms for white spruce at the ten Mackenzie Mountains sites are presented in Fig. 5.2. The relationship is weakest for the three treeline stands (WR1, LH1, LH2) and strongest for KC1, in the open forest. At all stands but KC1 tree height increases little after 120-150 years of age. Relationships

Table 5.1: Stand characteristics

Stand	vegetation type[a]	altitude (m)	distance from local treeline (m)	quadrat size (m²)	species[b]	n	max. age (yrs.)	max. height (cm)	max. diam. (cm)	seedling density[c]	seed origin ≤1cm diam.	seed origin >1cm diam.	horiz. layers	vertical layers	dead	δ	$\female$
												density of stems / 100 m²				% trees ≥ 40 yrs. with cones	
Mackenzie Mountains sites, N.W.T.																	
WR1	U F-T	1010	0	54	WS	173	205	230	21	0	0	117	161	43	4	11	10
LH1	U F-T	980	0	450	WS	99	201	590	30	4	5	10	1	5	1	33	67
WR2	U F-T	970	20	45	WS	97	206	400	14.5	3	0	67	127	22	18	33	28
SB3	U F-T	960	20	300	WS	93	190	350	20	2	13	11	2	5	3	10	12
SB2	U F-T	955	20	300	WS	96	335	375	22	1	5	18	7	5	8	19	16
LH2	U F-T	950	0	225	WS	100	234	500	18	0	1	17	20	7	3	0	3
SB5	U F-T	910	60	150	WS	107	275	450	31	6	21	25	13	13	3	21	20
SB1	L F-T	880	100	225	WS	62	423	800	31	3	4	20	2	2	0	36	44
					L	5	130	405	8.5		3	28	0.3	0	3	19	43
SB4	L F-T	825	155	300	WS	100	348	1000	31	0	111	89	4	7	5	12	21
KC1	OF	680	~300	75	WS	158	265	1150	29	0	0	7	0	0	0	60	60
					BS	5	218	710	12	0	0	0	0	0	0	0	0
					L	1	19	61	1.5	0	0	1	0	0	0	0	0
Yukon Sites																	
RM	U F-T	850	0	75	WS	66	275	460	20	0	0	58	7	24	15	27	25
SC	U F-T	1250	0	450	WS	50	~290	700	30	0	1	9	1	2	0	3	17
					BS	24	115	220	7	0	0	4	1	1	0	0	100

[a] U F-T, upper forest-tundra; L F-T, lower forest-tundra; OF, open forest
[b] WS, white spruce; BS, black spruce; L, larch
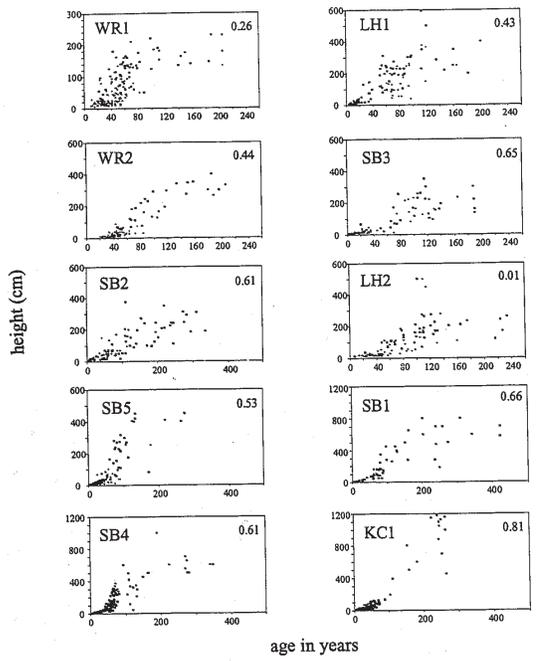[c] seedlings ≤10 yrs. old in 4 2mx2m seedling plots

Figure 5.2: Height vs. age scattergrams for the ten Mackenzie Mountains sites. Squares indicate individuals of probable seed origin, pluses indicate individuals of layer origin. The variance explained by linear regression of all points is given in the upper right of each graph (p<0.001 for all sites except LH2 where p>0.05).

between age and diameter are stronger than with height at all sites except SB1 and

SB3 (Fig. 5.3). In general, diameter increases linearly with age.

Age-class histograms for white spruce at the ten Mackenzie Mountains sites,

plotted against year of establishment (Fig. 5.4) show differing age structures, but

several trends are apparent. At all sites small numbers of individuals which

established before 1850 were present. Between 1850 and 1900 successful

establishment increased, and the great majority of trees surviving at all sites today

became established between the mid to late 19th century and the present. Trees

which established in recent decades were uncommon at several sites (WR1, WR2,

LH2, SB4) and common or abundant at others (LH1, SB1, SB2, SB3, SB5, KC1).

Recruitment/survival patterns were studied in detail at two treeline stands in the

Mackenzie Mountains. At one of these (LH1), the maximum age of Picea glauca

in each section of the quadrat increased downslope from the upper limits of spruce

growth (Fig. 5.5). In the uppermost 5 m of LH1 all individuals dated to the 20th

century. At LH2, in which Picea glauca was growing in seven discrete islands,

there is no evidence for upslope movement of spruce over time (Fig. 5.6). The

oldest trees in several of these islands became established in the mid 18th to early

19th century (islands a,c,e,g), with the majority of stems establishing by seed or

layering following 1850. The remaining islands have developed almost entirely

from seed regeneration between the late 19th and early 20th centuries.

Interpretation of age structures was aided by grouping of sites into

vegetation types (Fig. 5.7). Most trees currently growing in the upper forest-
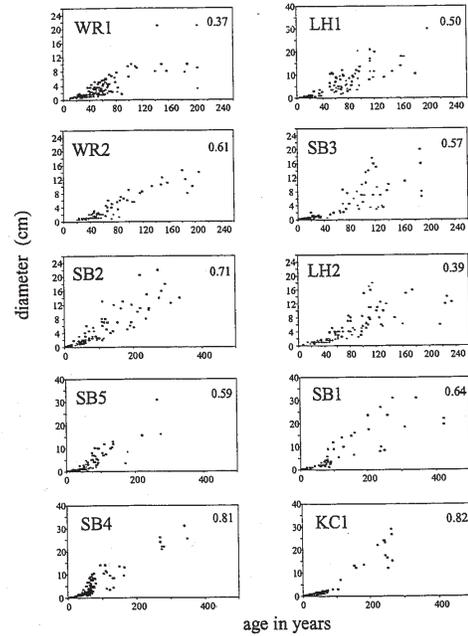
Figure 5.3: Diameter vs. age scattergrams for the ten Mackenzie Mountains sites. Legend as for Fig. 5.2 (p<0.001 for all sites).
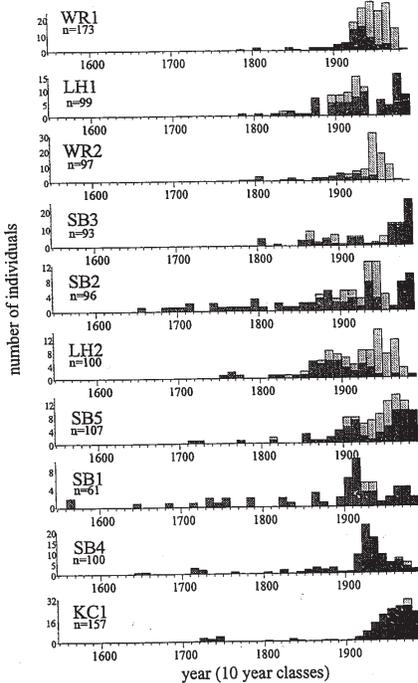
Figure 5.4: Age structure histograms for the ten Mackenzie Mountains sites, plotted against year of establishment. The sites are arranged in order of decreasing altitude, from the top down. Light grey bars indicate individuals of layer origin, dark grey bars indicate individuals of probable seed origin.

Figure 5.5: White spruce age structures for subsections within LH1 stand, Mackenzie Mountains. The distances from the upper limit of the quadrat are indicated in the upper left corner of the last three histograms. Legend as in Fig. 5.4.
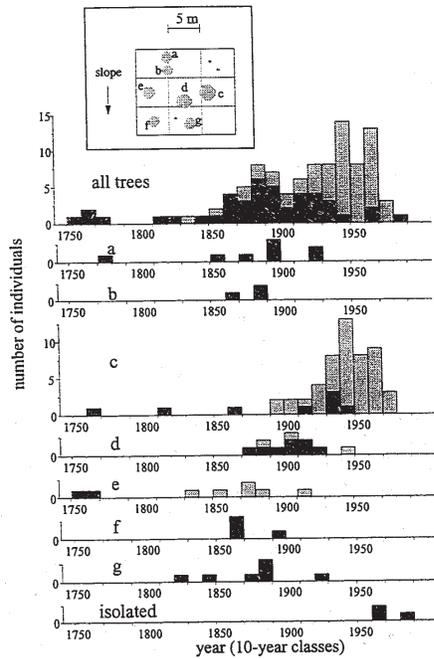
Figure 5.6: White spruce age structures for islands and isolated individuals within LH2 stand, Mackenzie Mountains. A plan of the stand, indicating location of the seven tree islands (each assigned a letter) and three isolated white spruce (plus symbols) is given at the top left. Legend as in Fig. 5.4.

tundra have become established since the late 19th century, although small numbers date to the mid 19th century or earlier. Establishment of layers occurred primarily during the mid 20th century. Trees dating to the mid 18th century or earlier were more common in the lower forest-tundra. A large proportion of trees in this zone date to the early 20th century, while establishment has dropped off during the past 50 years. In the open forest, most trees currently growing established either in the mid 18th century or in the last 60 years.

Analyses of the grouped age structures using both negative exponential and power function models indicated that negative exponential modelling provided the best fit in the upper and lower forest-tundra populations, and the power function a better fit in the open forest (Table 5.2). Rather than use two different models depending on the population, it was decided for consistency to use the negative exponential model for all populations. Although this model provided a very close fit for the upper forest-tundra population, the temporal distribution of residuals is not random but instead demonstrates long-term trends (Fig. 5.8a). These trends compare relatively well with trends in both the radial growth of open-grown _Picea glauca_ at the Skipping Bullet site (Fig. 5.8d) and 10-year means of reconstructed June-July temperatures in northwestern Canada (r=0.53, p≤0.05; Table 5.3; Fig. 5.8e). All records show high values in the mid to late 18th century, followed by a rapid drop in the early to mid 19th century, and subsequent increases to the mid 20th century. At this point the records diverge, as a dramatic drop occurs in the upper forest-tundra establishment residuals. The correlations between
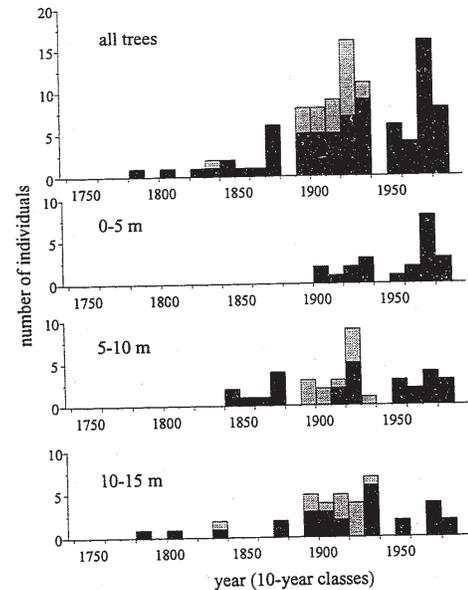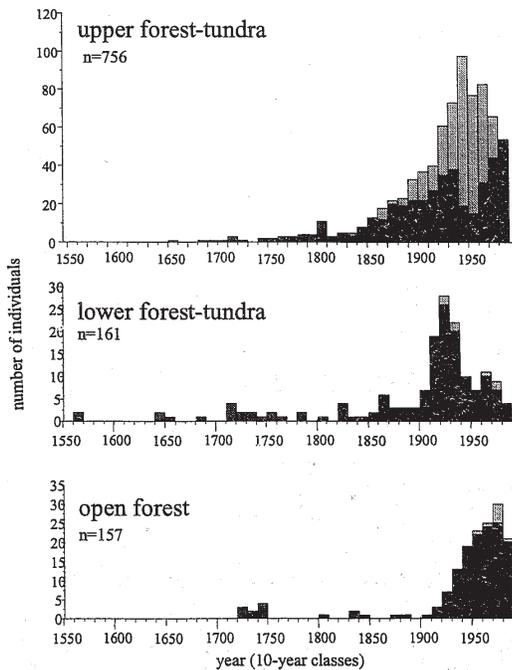
Figure 5.7: Age structure histograms for the Mackenzie Mountains sites, merged into vegetatin types. Legend as for Fig. 5.4.

TABLE 5.2: Pearson correlations between recruitment/survival records and mathematical age models.

Stand	Period	Negative exponential model	Power function model
upper forest-tundra (Mackenzie Mtns.)	1740-1989	0.96**	0.87**
lower forest-tundra (Mackenzie Mtns.)	1640-1989	0.73**	0.68**
open forest (Mackenzie Mtns.)	1720-1989	0.68**	0.80**
upper forest-tundra (Yukon)	1760-1989	0.56*	0.40

* p≤0.01; ** p≤0.001

TABLE 5.3: Pearson correlations between reconstructed temperatures for northwestern Canada and upper forest-tundra establishment residuals, Mackenzie Mountains.

extent of averaging for climate record	Mackenzie Mountains			Yukon upper F-T
	upper F-T	lower F-T	open forest	
10-yr mean	0.53*	0.14	0.20	0.37
20-yr forward mean	0.58**	0.28	0.28	0.35
30-year forward mean	0.62**	0.42*	0.35	0.40
40-year forward mean	0.63**	0.48**	0.42*	0.40
50-year forward mean	0.66**	0.57***	0.48*	0.40

* p≤0.05; ** p≤0.01; *** p≤0.001

Figure 5.8: Age structure analysis results and radial growth records for the merged Mackenzie Mountains data. a-c), recruitment/survival residuals from negative exponential models, plotted against year, for a) upper forest-tundra sites, b) lower forest-tundra sites, and c) open forest site. d) ring-width chronology from Skipping Bullet dendroclimate site. e) tree-ring based reconstruction of June-July temperatures in northwestern Canada.
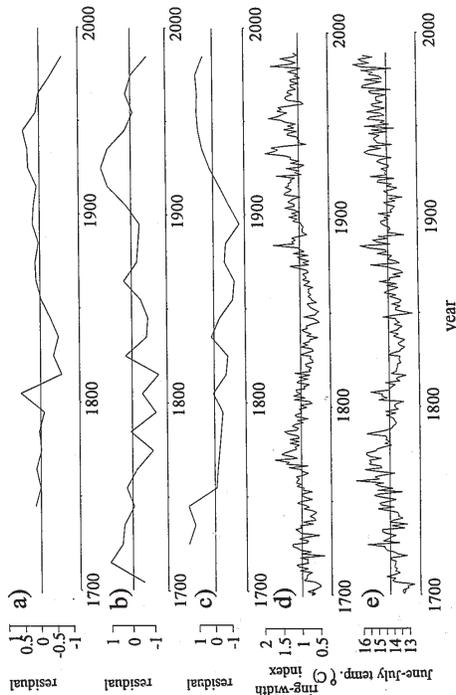
establishment residuals and summer temperatures increase with the extent of forward averaging of temperatures, to a maximum with the 50-year forward mean ($r=0.66$, $p \leq 0.01$; Table 5.3). Temporal trends are also apparent in residual plots for the lower forest-tundra (Fig. 5.8b) and open forest (Fig. 5.8c), although concurrence with ring-width and proxy climate records is not as strong. Correlations between residuals and 10-year mean temperatures are not significant (lower forest-tundra: $r=0.14$, $p>0.05$; open forest: $r=0.20$, $p>0.05$; Table 5.3), but increase to significant values with forward averaging of temperatures, to a maximum with temperatures integrated forward in time over 50 years (lower forest-tundra: $r=0.57$, $p \leq 0.001$; open forest: $r=0.48$, $p \leq 0.05$; Table 5.3).

Results of age-class analyses for the two Yukon sites, located at the extreme upper limits of Picea glauca growth, are presented in Figs. 5.9 and 5.10. Most Picea at both sites established either in the late 18th to very early 19th century, or between 1890 and 1960 (Fig. 5.9a, c). One dense Picea mariana clone, which developed primarily between 1900 and 1940, was present just below treeline at SC (Figs. 5.9d, 5.10). The maximum age of Picea glauca in each section of SC increased downslope from the upper limits of spruce growth (Fig. 5.10). All spruce in the upper 15 m of this quadrat have established in the 20th century.

Sample sizes were too small to model white spruce age structures at the SC and RM separately, so data were combined for the two sites. The negative exponential model again provided a better fit for the age structure than the power function model (Table 5.2). The low degrees of variance explained by either
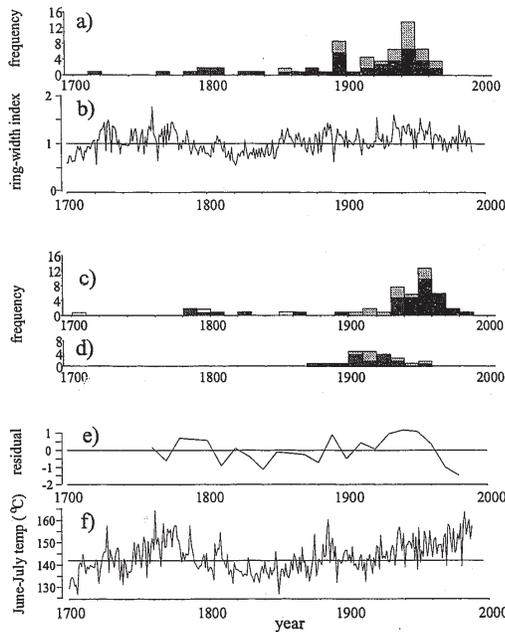
Figure 5.9: Age structure and radial growth records for the Yukon sites. a) white spruce age structure and b) ring-width chronology for the Richardson Mountains site. c) white spruce and d) black spruce age structure for the Swede Creek site. e) recruitment/survival residuals from negative exponential model of data from the two sites merged, plotted against year. f) tree-ring based reconstruction of June-July temperatures in northwestern Canada. Legends as in Fig. 5.4.
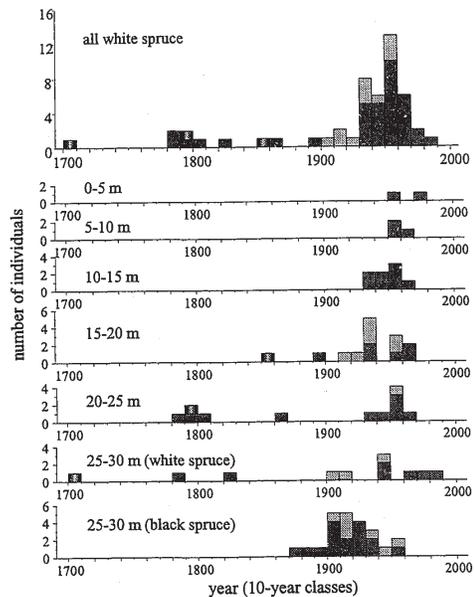
Figure 5.10: White and black spruce age structures for subsections within Swede Creek stand, Yukon. The distances from the upper limit of the quadrat (treeline) are indicated in the upper left corner of the histograms. Legend as in Fig. 5.4, with patterned bars representing minimum establishment dates from incomplete cores.

model may in part reflect the small sample size. The plot of residuals from the negative exponential model demonstrates long-term temporal trends (Fig. 5.9f) which visually compare favourably with the Tombstone Mountain ring-width chronology (Fig. 5.9e) and the regional temperature reconstruction (Fig. 5.9f), although no significant correlations were found with temperatures at the time of establishment, or integrated forward in time (Table 5.3). Negative residuals in the early to mid 19th century coincide with a period of low growth indices and cool reconstructed summer temperatures. Declining establishment during recent decades coincides with a period of reduced radial growth at TM, though reconstructed summer temperatures have continued to increase in the late 20th century.

5.4.2 White spruce mortality patterns

At the Discovery Ridge site, a total of 30 dead conifer remains were sampled on a hilltop between 5 and 20 m above the current upper limits of spruce growth, and an additional 24 samples were collected from within the upper forest-tundra. Twelve of the above treeline samples and 13 of the forest-tundra samples were identified as _Larix laricina_ after fine sanding and examination of cell structure, and were therefore excluded from subsequent analyses. Since no living black spruce are present at this site, all samples identified as spruce were assumed to be white spruce. Ten of the white spruce samples from above treeline and eleven from the forest-tundra were successfully cross-dated. In addition, a radiocarbon date of 980 ± 80 yr BP (Beta-54926) was obtained on a spruce sample

from above treeline. This date was made using wood from years 280 to 300 of the sample, which had a total of 403 rings. Using the calibration program of Stuiver and Reimer (1993), the dates of the inner and outer rings on this sample correspond to approximately 730 and 1130 AD respectively.

The lifespans and approximate establishment and mortality dates of the Discovery Ridge samples are plotted in Fig. 5.11, along with the 560 year radial growth record produced from living and dead trees within the forest-tundra (Chapter 4). The oldest sample from above treeline became established in about 1400, while the remaining samples had pith dates in the 16th and early 17th centuries. These dates are minima, since the root collar of many partial, prostrate remains could not be located. All of the cross-dated individuals from above treeline died in the 19th century, and 9 out of the 10 died between 1800 and 1860. These spruce had a wide range of estimated ages at the time of death, and do not appear to be from a single cohort. The estimated establishment dates of dead trees in the forest-tundra are roughly similar to those above treeline, with two trees also establishing in the mid 18th century. However, mortality of forest-tundra spruce has occurred fairly consistently over the past 170 years. Fifteen samples were collected in the upper forest-tundra at the Tombstone Mountain site. Twelve of these were successfully cross-dated, and are plotted in Fig. 5.11. Establishment patterns are generally similar to those at Discovery Ridge, and mortality has occurred throughout the past 190 years.
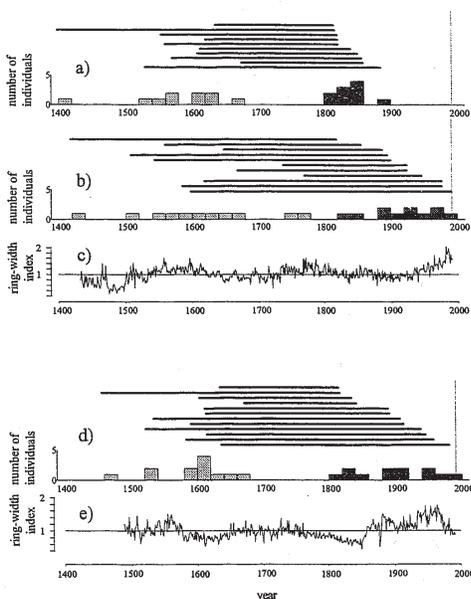
Figure 5.11: Results of dendrochronological dating of dead stems. a-b) approximate lifespans and establishment and death dates for a) dead stems from above current treeline and b) dead stems from within the current forest-tundra, at Discovery Ridge. c) ring-width chronology for Discovery Ridge. d) approximate lifespans and establishment and death dates for dead stems currently within the forest-tundra at Tombstone Mountain. e) ring-width chronology from Tombstone Mountain. Dark grey bars on histograms indicate approximate date of death, corrected for decomposition of outer rings. Light grey bars indicate minimum dates of establishment based on pith ages.

5.5 DISCUSSION

5.5.1 Climate and the periodicity of treeline population dynamics in the Mackenzie Mtns.

The results of this study suggest that successful regeneration of _Picea glauca_ at the alpine treeline of the Mackenzie Mountains has been episodic, and controlled to a large degree by climate. Late 16th to early 17th century minimum pith dates for currently dead spruce at Tombstone Mountain and Discovery Ridge indicate a possible establishment peak during the 16th century, which coincides with a period of above average radial growth of open-grown _Picea glauca_ at these sites and also of _Picea mariana_ at treeline in northern Quebec (Payette et al. 1989). Lowered rates of successful regeneration in the upper forest-tundra during the early 19th century correspond with the culmination of Little Ice Age cooling in the early 19th century (Jacoby et al. 1985; Grove 1988; D'Arrigo and Jacoby 1992). Increases in spruce recruitment/survival during the past 150 years parallel a hemispheric-wide increase in annual and seasonal temperatures, which peaked in the mid-20th century (Hansen and Lebedeff 1987; D'Arrigo and Jacoby 1993). This association of successful establishment with large-scale climatic variation is exhibited in the significant correlation between 10-year means of reconstructed summer temperatures and recruitment/survival residuals in the upper forest-tundra during the period 1740-1949.

Two factors, however, tend to confound the relationship between climate variation and regeneration in the upper forest-tundra. Firstly, extensive layering

by Picea glauca in these marginal stands may maintain populations during periods unfavourable for seedling regeneration. This may explain the close fit of the negative exponential model with the upper forest-tundra age structure data, although the merging of seven heterogenous sites for the analysis may also be a factor. Similar dampening of Picea mariana age structures in northern Quebec have been attributed to the occurrence of extensive layering (Payette and Gagnon 1979; Legere and Payette 1981; Payette et al. 1985). This hypothesis is difficult to test at our sites without genetic analyses, owing to the apparent decomposition of vegetative connections after about 100 years which masks the origin of individuals that successfully established during the culmination of the Little Ice Age in the early 19th century.

Secondly, successful establishment is not simply related to temperature at the time of germination. Summer temperatures for up to 50 years following establishment are important in determining recruitment success, probably through their influence on seedling mortality rates (Black and Bliss 1980; Kozlowski et al. 1991). This indirect evidence for climatic control of seedling mortality patterns cannot be corroborated directly, as past trends in the mortality of young individuals are extremely difficult to document owing to the rapid decomposition of remains. The remains of mature trees, however, are much more likely to be preserved. Although there is no strong evidence for periodicity in the mortality of older trees at Tombstone Mountain or Discovery Ridge below current treeline, the mass mortality of spruce at their extreme upper limits at Discovery Ridge during the

culmination of the Little Ice Age indicates the mortality of mature individuals may be driven by extreme climatic events.

Modification of microenvironments by tree establishment and growth may also lead to non-linear responses of establishment and mortality to climate variations (Pastor 1993; MacDonald and Szeicz 1994). Such modification may initiate a positive feedback which promotes further establishment and survival of seedlings and layers. Tree islands or even individual stems tend to trap snow and modify local wind regimes, supplying moisture essential for seedling survival and protecting shoots from abrasion and desiccation (Black and Bliss 1980; Lavoie and Payette 1992; Scott et al. 1993; Rochefort et al. 1994). Such stems or islands, for example the older stems within tree islands at LH2, may thus serve as foci for expansion by seed and layering during periods of climatic amelioration (Pastor 1993; MacDonald and Szeicz 1994). It is suggested, therefore, that age structures at treeline and in the upper forest-tundra result from non-linear climatic forcing of establishment and mortality patterns.

The successful recruitment of Picea glauca in lower forest-tundra and open forest stands appears to have increased in response to post-Little Ice Age climatic amelioration, but the climatic signal in recruitment/survival residuals may be confounded by other factors. Root competition (Agren and Zackrisson 1990) and a dense shrub layer, for example, may limit successful seedling establishment and lead to suppression of seedling and sapling growth in dense open-canopy stands.

5.5.2 Treeline equilibrium

The recent establishment of seedlings at many upper forest-tundra stands, including some at treeline, indicates that Picea glauca populations at their uppermost limits in this area are in many cases self-perpetuating. Both male and female strobili are being produced in nearly all forest-tundra stands, and although they were not tested for viability, recent seedling establishment suggests at least some are viable. These results support the hypothesis that the position of treeline in the Mackenzie Mountains is in equilibrium with current climatic conditions on a regional scale. Recent regeneration both at treeline and in the upper forest-tundra, however, has been spatially variable. Low levels of recent regeneration at some sites may be the result of locally unfavourable environmental conditions, as indicated by the concurrence of recent drops in recruitment/survival residuals with late 20th century declines in growth trends of open-grown Picea glauca at the Skipping Bullet, Richardson Mountains, and Tombstone Mountain dendroclimate sites. Drops in recent establishment levels at sites with widespread layering, though, are possibly an artefact of the inability to document young layers. Lower branches may be 20-30 years old before they are buried and develop roots, so young layers are seldom found.

5.5.3 Recent treeline dynamics

Studies in Scandinavia (Kullman 1986, 1990), northern Quebec (Payette and Filion 1985), the Richardson Mountains (Ritchie 1982) and northern Alaska

(Cooper 1986) have suggested that in many regions the altitudinal limits of spruce establishment have increased by 20-50 m in the last 100 years, in response to post-Little Ice Age warming. While radial growth and recruitment/survival records provide much evidence for a warming trend at the sites in this study during the past 100 to 150 years, the presence of trees dating back to the late 18th century or earlier at all treeline stands sampled precludes any altitudinal increases in treeline or tree establishment on the scale of tens of metres. Evidence from two of the treeline stands nonetheless indicates that upslope movement of Picea glauca has occurred since ~1850 on a small scale, corresponding to ~2-5 m of altitude. Most trees established since 1850 in the upper sections of both quadrats have upright growth form and some are greater than 200 cm tall, indicating a minor altitudinal increase in treeline has resulted from the upslope spread of spruce.

The mass mortality of spruce on a hilltop at its upper limits at Discovery Ridge led to a drop in treeline elevation of ~20 m during the culmination of the Little Ice Age. Reestablishment of spruce above its 19th century limits has not occurred at this site, despite ameliorating climatic conditions during the past 150 years. With the inclusion of the radiocarbon-dated spruce snag from above treeline at this site and the presence of many undated spruce remains, it is evident that treeline was higher than present between at least 700 and 1100 AD, which coincides with a period of higher treeline in the southern Canadian Rockies (Luckman 1986), and ~1400 and the mid 1800's. Two possible explanations may account for the inability of treeline to recover to pre-19th century levels. Firstly,

the hilltop site may be able to support spruce, but the slow response of treeline position to climate change has delayed recovery. Secondly, and more likely, the hilltop environment may currently be unsuitable for spruce establishment and survival. In this case, the survival of spruce throughout a long period of fluctuating climatic conditions at such a site would be an indication of vegetation resilience to climatic change, in part through local alteration of microclimates (Payette et al. 1989; Scott et al. 1993). The loss of spruce from the hilltop, and the resulting loss of microclimatic modification, may preclude future establishment until some climatic threshhold is passed.

5.5.4 Regional corroboration of results

The general similarity of recruitment/survival and mortality patterns at the two Yukon sites with results from the Mackenzie Mountains corroborates the conclusions that these patterns are primarily climate driven, and that treeline is currently in equilibrium with climate. Insignificant correlations between reconstructed temperature trends and recruitment/survival residuals at SC and RM may result from small sample sizes and local environmental conditions which have diverged from regional climate patterns. During the past 100 to 150 years the general trend within these forest-tundra stands in northwestern Canada has therefore been one of consolidation and increasing population density, with only minor changes in the upper limits of trees. These results are analagous to post-Little Ice Age responses in the forest-tundra of central Sweden (Kullman 1987b),

northern Quebec (Payette and Filion 1985), Churchill (Scott et al. 1987), and central Keewatin (MacDonald and Szeicz 1994).

CHAPTER SIX

SUMMARY AND CONCLUSIONS

6.1 SUMMARY OF RESULTS AND TESTING OF HYPOTHESES

The objectives of this study were to investigate climate change, treeline dynamics and vegetation-climate relationships at the subarctic alpine treeline in northwestern Canada on a variety of spatial and temporal scales, with a focus on the Mackenzie Mountains of the western N.W.T. Three hypotheses were developed in order to address these objectives, and were tested using a combination of fossil pollen and dendrochronological approaches. These hypotheses will each be examined below.

1. Postglacial treeline change in the Mackenzie Mountains was driven by changes in the seasonal and latitudinal distribution of solar radiation.

To test this hypothesis sediment cores were obtained from three lakes in the tundra, forest-tundra and open forest of the central Mackenzie Mountains and analyzed for fossil pollen. Basal dates on all three cores were between c. 11,500 and 12,000 yr BP. Herb tundra occurred at all elevations until about 10,200 yr BP, when it was replaced by Betula glandulosa dominated tundra. Populus

balsamifera probably grew up to and beyond the current treeline in the early Holocene. Picea arrived in the central Mackenzie Mountains by 8500 yr BP, and expanded to the elevation of the current treeline by 8000 yr BP. Although there is no evidence for a higher Picea treeline at any time during the Holocene, pollen accumulation rates suggest Picea population densities in the forest-tundra were greater than present between at least 8000 yr BP and 5000 yr BP and have since declined steadily. These results are supported by detrended correspondence analysis of pollen records from the forest-tundra and tundra sites, which indicate an increasing tundra affinity to the vegetation since 5000 yr BP. At the open forest site, Picea population density has not declined in the late Holocene, but the forest composition has shifted towards a greater affinity with higher elevation sites since 5000 yr BP. Both higher limits of Populus balsamifera in the early Holocene and increased forest-tundra density in the early to mid Holocene are suggestive of warmer temperatures at that time. These changes in the treeline vegetation of the central Mackenzie Mountains during the postglacial are consistent with predicted changes in summer insolation based on the Milankovitch theory.

2) Establishment and mortality patterns of trees at treeline are episodic, controlled by climate variations.

This hypothesis was tested by developing a 350-year dendroclimatic record of summer temperatures for northwestern Canada, and comparing this record to establishment and mortality patterns of Picea glauca at or near the alpine treeline

in the N.W.T. and Yukon. First, the suitability of forest-tundra Picea glauca for dendroclimatic reconstruction was assesed using dendroecological analyses of radial growth records from trees at three sites in the Mackenzie and Franklin Mountains of the N.W.T. Response function and regression analyses suggested that the response of Picea glauca radial growth to climate at these sites varies with tree age once the biological growth trend has been removed, which violates a fundamental assumption of most dendroclimatological research. These apparent age dependent responses are site-specific and probably reflect physiological changes related to aging. It is possible that trees are becoming increasingly moisture stressed with age due to a reduction in the efficiency of water and nutrient translocation mechanisms. Preliminary dendroclimatic modelling indicated that such age-dependent relationships may result in less accurate reconstructions of past climate if the ages of component trees are not taken into account.

Picea glauca ring-width records from an expanded network of five sites in the N.W.T. and Yukon were next used to confirm the presence of age dependent climate-growth relationships at sites outside of the initial study area, and develop a long reconstruction of summer temperatures for northwestern Canada. Response function and linear regression analyses indicated that the radial growth response of trees to climate varied with age at all sites. Age dependent and standard (age independent) models were used to develop two reconstructions of June-July temperatures for northwestern Canada extending back to AD 1638. The standard reconstruction suggested temperatures were similar to or warmer than present

during most of the past 350 years, and bore little resemblance to any independent proxy climate records. The age dependent reconstruction, however, suggested temperatures were cooler than present throughout most of the past 350 years, particularly at c. 1700 and in the mid 18th century, and compared favourably with published tree-ring, ice core melt and glacial recession records for northern North America.

To investigate temporal trends in Picea glauca establishment patterns, age structure data were collected from ten stands at or near treeline in the Mackenzie Mountians, and two stands at treeline in the central and northern Yukon. Data on mortality patterns were obtained by cross-dating dead spruce remains from one site in the Franklin Mountains, N.W.T., and one site in the Ogilvie Mountains, Yukon. Analyses of age structures using mathematical models indicated there were temporal trends in the establishment/survival of Picea glauca in the upper forest-tundra, and these trends correlated significantly with the proxy record of summer temperatures produced using age dependent dendroclimatic modelling techniques. The mortality patterns of spruce have also been influenced by climatic variations, as suggested by the importance of summer temperatures in determining recruitment success for at least 50 years following establishment, and the mass mortality of Picea glauca during the culmination of the Little Ice Age at a site currently above treeline. These data thus support the hypothesis that establishment and mortality patterns of trees at treeline in northwestern Canada are episodic, and controlled primarily by climatic varitions. Although there have been very minor increases in

the altitude of treeline at two sites, the main impact of recent climatic changes at these sites, in particular during the past 100 to 150 years, has been one of increased tree density within the forest-tundra.

3) The position of the treeline in the Mackenzie Mountains is in equilibrium with current climatic conditions.

To test this hypothesis, the reproductive characteristics of all trees in stands sampled for age structure were recorded. Seedlings were present at all but one forest-tundra stand, including two of three treeline stands. Similarly, seedlings were found at one treeline stand in the Yukon, although they were absent at the second. In combination with the discussion of hypothesis 2 above, these results support the hypothesis that treeline in the Mackenzie Mountains, and northwestern Canada in general, is in equilibrium with climate on a regional scale. Successful seedling establishment is occurring at many sites, although the patterns are not spatially uniform owing to site-specific differences.

6.2 CONCLUSIONS

The results of this study, in combination with previously published research, enable several conclusions to be reached with regards to climate change, treeline dynamics and vegetation-climate relationships at the subarctic alpine treeline in northwestern Canada:

1) Both fossil pollen and dendrochronological data indicate that the forest-tundra ecotone in the mountains of northwestern Canada has undergone significant responses to past climate changes on a variety of timescales. The responses have been manifested primarily as variations in tree population densities within the forest-tundra on both long and short timescales, and perhaps compostional shifts in dominant vegetation types at lower elevations. Local altitudinal shifts in treeline have been recorded in the fossil pollen record (MacDonald 1983) and the dendrochronological record (Chapter 5), but appear to be less important than population fluctuations within the forest-tundra itself. These results lead to a reiteration of the conclusions of Payette and Filion (1985) that changes in the influx or relative abundances of tree pollen at sites at or beyond treeline, in the absence of macrofossil, sedimentological or other supportive evidence, do not necessarily indicate a considerable displacement of treeline.

2) Substantial and well documented fluctuations (i.e. those based entirely on, or supplemented by, macrofossil, sedimentological, or palaeolimnological data) in the location of alpine and latitudinal treelines at mid and high latitudes have been used to infer past climatic changes on the scale of centuries to millenia (eg. LaMarche 1973; Luckman and Kearney 1986; Scuderi 1987; Clague and Mathewes 1989; Carrara et al. 1991). It follows that shifts in the altitudinal limits of trees may be useful for monitoring the impact of potential future anthropogenic climate changes (Rochefort et al. 1994). Theoretical (Slayter and Noble 1992; Noble 1993) and empirical (Scott et al. 1987; Payette et al. 1989; MacDonald and Szeicz

1994) work, however, suggests that the resilience of treeline postion to climatic change and the complexity of climate-treeline dynamics complicates its use in monitoring short-term anthropogenic climate changes. It is possible that temperatures may have to pass a threshold level before significant treeline response occurs (MacDonald and Szeicz 1994). The results of this study concur with those conclusions. The study also demonstrates, however, that the dynamics and radial growth of Picea glauca populations within the forest-tundra have been influenced to a large degree by climate in the past and therefore may be sensitive to potential future anthropogenic climate changes. Seedlings are currently being produced in most of these populations and thus a rapid response to further climatic amelioration may be possible. Increases in density of the forest-tundra, even without an advance of treeline, may influence vegetation-climate feedback processes such as biomass sequestering, radiative feedback, and carbon release from tundra soils. The findings of earlier studies in central Canada suggesting treeline was out of equilibrium with the present climate (Larsen 1965; Elliott-Fisk 1983), which could dampen any significant response to future climate changes, may have resulted from a consideration of equilibrium on only the shortest temporal timescale. Sites in those studies were sampled during a 20-30 year period of cool temperatures in northern North America (MacDonald and Szeicz 1994) which may have restricted recruitment success.

3) The age dependent radial growth response of Picea glauca to climate at all sites in this study demonstrate that climate-growth relationships are complex and

the simplifying assumptions made in order to reconstruct climatic records from radial growth records may in some cases be invalid. The impact of such responses can be avoided if they are recognized and taken into account during climatic modelling. Further ecophysiological research is clearly needed to better understand climate-growth relationships, particularly the processes associated with tree aging.

APPENDIX

RAW DATA STORAGE AND AVAILABILITY

Raw tree-ring and palynological data from this research will be submitted to two international data banks, which allow free access to data for all contributors and other interested researchers.

Pollen data will be submitted to:

North American Pollen Database
Illinois State Museum
1011 East Ash,
Springfield, Illinois 62703
U.S.A.

Tree-ring data will be submitted to:

International Tree-Ring Data Bank
Laboratory of Tree-Ring Research
University of Arizona,
Tucson, Arizona 85721
U.S.A.

REFERENCES

Agren, J. and Zackrisson, O. (1990). Age and size structure of Pinus sylvestris populations on mires in central and northern Sweden. Journal of Ecology 78: 1049-1062.

Aitken, J.D. and Cook, D.G. (1974). "Carcajou Canyon map-area (96D), District of Mackenzie, Northwest Territories." Geological Survey of Canada Paper 74-13, Energy, Mines and Resources Canada, Ottawa, Canada.

Anderson, P.M. (1985). Late Quaternary vegetational change in the Kotzebue Sound area, northwestern Alaska. Quaternary Research 24: 307-321.

Anderson, P.M., Reanier, R.E., and Brubaker, L.B. (1988). Late Quaternary vegetational history of the Black River region in northeastern Alaska. Canadian Journal of Earth Sciences 25: 84-94.

Arbaugh, M.J. and Peterson, D.L. (1989). Variable selection in dendroclimatology: an example using simulated tree-ring series. Forest Science 35: 294-302.

Arquilliere, S., Filion, L., Gajewski, K. and Cloutier, C. (1990). A dendroecological analysis of eastern larch (Larix laricina) in subarctic Quebec. Canadian Journal of Forest Research 20: 1312-1319.

Baker, W.L. (1992). Structure, disturbance, and change in the Bristlecone pine

forests of Colorado, U.S.A. Arctic and Alpine Reserach 24:17-26.

Beaudoin, A.B. (1989). The response of the treeline zone to climatic change in the Canadian Rocky Mountains. The Canadian Geographer. 33: 83-86.

Baig, M.N. and Tranquillini, W. (1980). The effects of wind and temperature on cuticular transpiration of Picea abies and Pinus cembra and their significance in desiccation damage at the alpine treeline. Oecologia 47: 252-256.

Black, R.A. and Bliss, L.C. (1980). Reproductive ecology of Picea mariana (Mill.) BSP., at treeline near Inuvik, Northwest Territories, Canada. Ecological Monographs 50: 331-354.

Blasing, T.J., Solomon, A.M. and Duvick, D.N. (1984). Response functions revisited. Tree-Ring Bulletin. 44: 1-15.

Bonan, G.B., Shugart, H.H. and Urban, D.L. (1990). The sensitivity of some high-latitude boreal forests to climatic parameters. Climatic Change 16: 9-29.

Bonan, G.B., Pollard, D. and Thompson, S.L. (1992). Effects of boreal forest vegetation on global climate. Nature 359: 716-718.

Bradley, R.S. and Jones, P.D. (1992). "Climate Since A.D. 1500." Routledge, London.

Bradley, R.S. and Jones, P.D. (1993). 'Little Ice Age' summer temperature variations: their nature and relevance to recent global warming trends. The Holocene 3: 367-376.

Briffa, K.R., Jones, P.D., Pilcher, J.R., and Hughes, M.K. (1988). Reconstructing summer temperatures in northern Fennoscandinavia back to A.D. 1700 using tree-ring data from Scots pine. Arctic and Alpine Research 20: 385-394.

Briffa, K.R., Jones, P.D., Wigley, T.M.L., Pilcher, J.R. and Baillie, M.G.L. (1983). Climate reconstruction from tree rings: Part I, basic methodology and preliminary results for England. Journal of Climatology 3: 233-242.

Briffa, K.R. and Cook, E.R. (1989). Methods of response function analysis. In "Methods of dendrochronology." (Cook, E.R. and Kairiukstis, L.A., eds.) Kluwer, Dordrecht. pp. 240-247.

Briffa, K.R., Bartholin, T.S., Eckstein, D., Jones, P.D., Karlen, W., Schweingruber, F.H., and Zetterberg, P. (1990). A 1,400 year tree-ring record of summer temperatures in Fennoscandia. Nature 346: 434-439.

Briffa, K.R., Jones, P.D., Bartholin, T.S., Eckstein, D., Schweingruber, F.H., Karlen, W., Zetterberg, P., and Eronen, M. (1992). Fennoscandian summers from AD 500: temperature changes on short and long timescales. Climate Dynamics 7: 111-119.

Brubaker, L.B. (1986). Responses of tree populations to climatic change. Vegetatio. 67: 119-130.

Brubaker, L.B., Garfinkel, H.L., and Edwards, M.E. (1983). A Late Wisconsin and Holocene vegetation history from the central Brooks Range: implications for Alaskan paleoecology. Quaternary Research 19: 194-214.

Bryson, R.A. (1966). Air masses, streamlines and the boreal forest. Geographical Bulletin 8: 228-269.

Burns, B.M. (1974). "The climate of the Mackenzie Valley-Beaufort Sea, Vols. I and II." Climatological Studies No. 24, Environment Canada, Toronto, Canada.

Callaghan, T.V., Sonesson, M. and Somme, L. (1992). Responses of terrestrial plants and invertebrates to environmental change at high latitudes. Philosophical Transactions of the Royal Society of London B,338: 279-288.

Carrara, P.E., Trimble, D.A., and Rubin, M. (1991). Holocene fluctuations in the northern San Juan Mountains, Colorado, U.S.A., as indicated by radio-carbon dated conifer wood. Arctic and Alpine Research. 23: 233-246.

Clague, J.J. (1989). Quaternary geology of the Canadian Cordillera. In "Quaternary Geology of Canada and Greenland." (Fulton, R.J., ed.) Ottawa: Geological Survey of Canada. pp 15-95.

Clague, J.J. and Mathewes, R.W. (1989). Early Holocene thermal maximum in western North America: new evidence from Castle Peak, British Columbia. Geology 17: 277-280.

Cohen, S.J. (1990). Bringing the global warming issue closer to home: the challenge of regional impact studies. Bulletin of the American Meteorological Society 71: 520-526.

COHMAP members (1988). Climatic changes of the last 18,000 years: observations and model simulations. Science 241: 1043-1052.

Colenutt, M.E. and Luckman, B.H. (1991). Dendrochronological investigation of Larix lyallii at Larch Valley, Alberta. Canadian Journal of Forest Research 21: 1222-1233.

Conkey, L.E. (1986). Red spruce tree-ring widths and densities in eastern North America as indicators of past climate. Quaternary Research 26: 232-243.

Cook, E.R. (1985). "A time series anaiysis approach to tree-ring standardization." Unpublished Ph.D. dissertation, University of Arizona, Tucson, Az.

Cook, E.R. and Peters, K. (1980). The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. Tree-Ring Bulletin 41: 45-53.

Cook, E.R. and Johnson, A.H. (1989). Climate change and forest decline: a review of the red spruce case. Water, Air and Soil Pollution 48: 127-140.

Cooper, D.J. (1986). White spruce above and beyond treeline in the Arrigetch Peaks region, Alaska. Arctic. 39: 247-252.

Crawford, R.M.M. (1989). "Studies in Plant Survival." Blackwell Scientific Publications, Oxford.

Cropper, J.P. (1984). Relationships among tree-ring width chronologies from Alaska and the Yukon. Arctic and Alpine Research 16: 245-254.

Cropper, J.P. and Fritts, H.C. (1981). Tree-ring chronologies from the North American arctic. Arctic and Alpine Research 13: 245-260.

Cwynar, L.C. and Spear, R.W. (1991). Reversion of forest to tundra in the central Yukon. Ecology 72: 202-212.

Cwynar, L.C., Burden, E. and McAndrews, J.H. (1979). An inexpensive sieving method for concentrating pollen and spores from fine-grained sediments. Canadian Journal of Earth Science 16: 1115-1120.

Dang, Q.L. and Lieffers, V.J. (1989). Climate and annual ring growth of black spruce in some Alberta peatlands. Canadian Journal of Botany 67: 1885-1889.

D'Arrigo, R.D., Jacoby, G.C. Jr. and Free, R.M. (1992). Tree-ring width and maximum latewood density at the North American tree line: parameters of climatic change. Canadian Journal of Forest Research. 22: 1290-1296.

D'Arrigo, R.D. and Jacoby, G.C. Jr. (1992). Dendroclimatic evidence from northern NorthAmerica. In "Climate since A.D. 1500." (Bradley, R.S. and Jones, P.D., Eds.) pp. 29-311. Routledge, London.

D'Arrigo, R.D. and Jacoby, G.C. Jr. (1993). Secular trends in high northern latitude temperature reconstructions based on tree rings. Climatic Change 25: 163-177.

Davis, M.B. (1989). Lags in vegetation response to greenhouse warming. Climatic Change 15: 75-82.

Deevey, E.S. (1969). Coaxing history to conduct experiments. BioScience 19: 40-43.

Delcourt, H.R. and Delcourt, P.A. (1991). "Quaternary Ecology: A paleoecological perspective." Chapman and Hall, London.

Denton, G.H. and Karlen, W. (1977). Holocene glaical and tree-line variations in

the White River Valley and Skolai Pass, Alaska and Yukon Territory. Quaternary Research 7: 63-111.

Duff, G.H. and Nolan, N.J. (1953). Growth and morphogenesis in the Canadian forest species. I. The controls of cambial and apical activity in Pinus resinosa Ait. Canadian Journal of Botany 31: 471-513.

Duk-Rodkin, A. and Hughes, O.L. (1991). Age relationships of Laurentide and montane glaciations, Mackenzie Mountains, Northwest Territories. Geographie physique et Quaternaire 45: 79-90.

Duk-Rodkin, A. and Hughes, O.L. (1992). Pleistocene montane glaciations in the Mackenzie Mountains, Northwest Territories. Geographie physique et Quaternaire 46: 69-83.

Duk-Rodkin, A. and Hughes, O.L., in press. Quaternary geology of the northeastern part of the central Mackenzie Valley Corridor. Geological Survey of Canada Bulletin 458.

Dyke, A.S. and Prest, V.K. (1987). Late Wisconsin and Holocene history of the Laurentide ice sheet. Geographie physique et Quaternaire. 41: 237-263.

Edwards, M.E., Anderson, P.M., and Brubaker, L.B. (1985). Late Wisconsin and Holocene vegetational history of the upper Koyukuk region, Brooks Range, AK. Canadian Journal of Botany 63: 616-646.

Edwards, M.E., and Dunwiddie, P.W. (1985). Dendrochronological and palynological observations on Populus balsamifera in northern Alaska. Arctic and Alpine Research 17:271-278.

Elliott-Fisk, D.L. (1983). The stability of the northern Canadian tree limit. Annals of the Association of American Geographers 73: 560-576.

Faegri, K. and Iversen, J. (1975). "Textbook of Pollen Analysis, 3rd. Ed." Blackwell, Oxford.

Fall, P.L. (1992). Pollen accumulation in a montane region of Colorado, U.S.A.: a comparison of moss polsters, atmospheric traps, and natural basins. Review of Palaeobotany and Palynology 72: 169-197.

Filion, L., Payette, S., Gauthier, L. and Boutin, Y. (1986). Light rings in subarctic conifers as a dendrochronological tool. Quaternary Research 26: 272-279.

Fritts, H.C. (1976). "Tree rings and climate." Academic Press, London.

Fritts, H.C. and Guiot, J. (1989). Methods of calibration, verification and reconstruction. In "Methods of dendrochronology." (Cook, E.R. and Kairiukstis, L.A., Eds.) pp. 163-218. Kluwer, Dordrecht.

Fritts, H.C. (1993). PRECON 3.0 User's Manual. Dendrochronological Modeling, Tucson, Az.

Gagnon, R. and Payette, S. (1985). Regression holocene du couvert coniferien a la limite des forets (Quebec nordique). Canadian Journal of Botany 63: 1213-1225.

Gajewski, K. and Garralla, S. (1992). Holocene vegetation histories from three sites in the tundra of northwestern Quebec, Canada. Arctic and Alpine Research 24: 329-336.

Gajewski, K., Payette, S., and Ritchie, J.C. (1993). Holocene vegetation history at the boreal forest-shrub tundra transition in northwestern Quebec. Journal of Ecology 81: 433-443.

Garfinkel, H.L. and Brubaker, L.B. (1980). Modern climate-tree growth relationships and climatic reconstruction in sub-Arctic Alaska. Nature 286: 872-874.

Gear, A.J. and Huntley, B. (1991). Rapid changes in the range limits of Scots pine 4000 years ago. Science 251: 544-547.

Goldstein, G.H., Brubaker, L.B. and Hinckley, T.M. (1985). Water relations of white spruce (Picea glauca (Moench) Voss) at treeline in north-central Alaska. Canadian Journal of Forest Research 15: 1080-1087.

Gorcharovsky, P.L. and Shiyatov, S.G. (1978). The upper forest limit in the mountains of the boreal zone of the USSR. Arctic and Alpine Research 10: 349-363.

Grace, J. (1989). Tree lines. Philosophical Transactions of the Royal Society of London B 324:

Grace, J. (1990). Cuticular water loss unlikely to explain tree-line in Scotland. Oecologia 84: 64-68.

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

Gray, B.M. (1982). Comment on transfer functions. In "Climate from tree rings." (Hughes, M.K., Kelly, P.M., Pilcher, J.R. and LaMarche, V.C., eds.)

Cambridge University Press, Cambridge. pp. 56-58.

Graybill, D.A. and Shiyatov, S.G. (1992). Dendroclimatic evidence from the northern Soviet Union. In "Climate since A.D. 1500." (Bradley, R.S. and Jones, P.D., Eds.) pp 393-414. Routledge, London.

Grissino-Mayer, H., Holmes, R. and Fritts, H.C. (1992). International Tree-Ring Data Bank Program Library User's Manual. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Az.

Grove, J.M. (1988). "The Little Ice Age." Methuen, London.

Gullett, D., Skinner, W. and Vincent, L. (1992). Development of an historical Canadian climate database for temperature and other elements. Climate Bulletin 26: 125-131.

Hadley, J.L. and Smith, W.K. (1986). Wind effects on needles of timberline conifers: seasonal influence on mortality. Ecology 67: 12-19.

Hansen-Bristow, K. (1986). Influence of increasing elevation on growth characteristics at timberline. Canadian Journal of Botany 64: 2517-2523.

Hansen, A.J. and di Castri, F. (eds.)(1992). "Landscape Boundaries: consequences for biotic diversity and ecological flows" Ecological Studies, Vol. 92. Springer-Verlag, New York, New York.

Hansen, B.C.S. and Engstrom, D.R. (1985). A comparison of numerical and qualitative methods of separating pollen of black and white spruce. Canadian Journal of Botany 63: 2159-2163.

Hansen, J. and Lebedeff, S. (1987). Global trends of measured surface air

temperature. Journal of Geophysical Research 92: 13345-13372.

Harcombe, P.A. (1987). Tree life tables. BioScience 37: 557-568.

Hare, F.K. and Ritchie, J.C. (1972). The boreal bioclimates. The Geographical Review 62: 333-365.

Hare, F.K. and Thomas, M.K. (1979). "Climate Canada, 2nd edition." John Wiley & Sons Canada Ltd., Toronto, Canada.

Herron, M.M., Herron, S.L. and Langway, C.C. Jr. (1981). Climatic signal of ice melt features in southern Greenland. Nature 293: 389-391.

Hett, J.M. and Loucks, O.R. (1976). Age structure models of balsam fir and eastern hemlock. Journal of Ecology 64: 1029-1044.

Heusser, C.J. and Marcus, M.G. (1964). Historical variations of Lemon Creek Glacier, Alaska, and their relationship to the climatic record. Journal of Glaciology 5: 77-86.

Hill, M.O. and Gauch, H.G., Jr. (1980). Detrended correspondence analysis: an improved ordination technique. Vegetatio 42, 47-58.

Holmes, R.L. (1992). Dendrochronology program library user's manual. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Az.

Houghton, J.T., Jenkins, G.J., and Ephraums, J.J. (Eds.) (1990). "Climate change: the IPCC scientific assessment." Cambridge University Press, Cambridge, U.K.

Hu, F.S., Brubaker, L.B. and Anderson, P.M. (1993). A 12,000 year record of vegetation change and soil development from Wien Lake, central Alaska.

Canadian Journal of Botany 71: 1133-1142.

Hughes, M.K., Schweingruber, F.H., Cartwright, D. and Kelly, P.M. (1984). July-August temperature at Edinburgh between 1721 and 1975 from tree-ring density and width data. Nature 308: 341-344.

Hughes, O.L., Harington, C.R., Janssens, J.A., Matthews, J.V., Morlan, R.E. Jr., Rutter, N.W. and Schweger, C.E. (1981). Upper Pleistocene stratigraphy, palaeoecology and archaeology of the northern Yukon interior, Eastern Beringia. 1. Bonnet Plume Basin. Arctic 34: 329-365.

Hyvarinen, H. (1976). Flandrian pollen deposition rates and tree-line history in northern Fennoscandia. Boreas 5: 163-175.

Hyvarinen, H. (1993). Holocene pine and birch limits near Kilpisjarvi, western Finnish Lapland: pollen stratigraphical evidence. In "Oscillations of the Alpine and Polar Tree Limits in the Holocene", (Frenzel, B., ed.). Gustav Fischer Verlag, Stuttgart. pp. 19-27.

Innes, J.L. (1991). High-altitude and high-latitude tree growth in relation to past, present and future global climate change. The Holocene. 1: 168-173.

Innes, J.L. and Cook, E.R. (1989). Tree-ring analysis as an aid to evaluating the effects of pollution on tree growth. Canadian Journal of Forest Research 19: 1174-1189.

Jacobson, G.L. and Bradshaw, R.H.W. (1981). The selection of sites for paleovegetational studies. Quaternary Research 16: 80-96.

Jacoby, G.C. Jr. and Cook, E.R. (1981). Past temperature variations inferred from

a 400-year tree-ring chronology from Yukon Territory, Canada. Arctic and Alpine Research 13: 409-418.

Jacoby, G.C. Jr., Cook, E.R. and Ulan, L.D. (1985). Reconstructed summer degree days in central Alaska and northwestern Canada since 1524. Quaternary Research 23: 18-26.

Jacoby, G.C. Jr., Ivanciu, I.S., and Ulan, L.D. (1988). A 263-year record of summer temperatures for northern Quebec reconstructed from tree-ring data and evidence of a major climatic shift in the early 1800's. Palaeogeography, Palaeoclimatology, Palaeoecology 64: 69-78.

Jacoby, G.C. Jr. and D'Arrigo, R. (1989). Reconstructed northern hemisphere annual temperature since 1671 based on high-latitude tree-ring data from North America Climatic Change 14: 39-59.

Johnson, E.A. and Fryer, G.I. (1989). Population dynamics in lodgepole pine-Engelmann spruce forests. Ecology 69: 1335-1345.

Kearney, M.S. (1982). Recent seedling establishment at timberline in Jasper National Park, Alberta. Candian Journal of Botany. 60: 2283-2287.

Khotinskiy, N.A. (1984). Holocene vegetation history. In "Late Quaternary Envrionments of the Soviet Union." (Velichko, A.A., ed.). University of Minnesota Press, Minneapolis, Mn. pp. 179-200.

King, G.A. (1993). Vegetation and pollen relationships in eastern Canada. Canadian Journal of Botany 71: 193-210.

Koerner, R.M. (1977). Devon Island ice cap: core stratigraphy and paleoclimate.

Science 196: 15-18.

Kozlowski, T.T. (1971). "Growth and Development of Trees, Vol. 1." Academic Press, New York.

Kozlowski, T.T., Kramer, P.J., and Pallardy, S.G. (1991). "The Physiological Ecology of Woody Plants." Academic Press, San Diego, Ca.

Kramer, P.J. and Kozlowski, T.T. (1979). "Physiology of woody plants." Academic Press, London.

Kullman, L. (1986a). Recent tree-limit history of Picea abies in the southern Swedish Scandes. Canadian Journal of Forest Research. 16: 761-771.

Kullman, L. (1986b). Late Holocene reproductional patterns of Pinus sylvestris and Picea abies at the forest limit in central Sweden. Canadian Journal of Botany 64: 1682-1690.

Kullman, L. (1987a). Little Ice Age decline of a cold marginal Pinus sylvestris forest in the Swedish Scandes. New Phytologist 106: 567-584.

Kullman, L. (1987b). Long-term dynamics of high-altitude populaions of Pinus sylvestris in the Swedish Scandes. Journal of Biogeography 14: 1-8.

Kullman, L. (1990). Dynamics of altitudinal tree-lines in Sweden: a review. Norsk geografisk Tidsskrift. 44: 103-116.

Kullman, L. (1992). Orbital forcing and tree-limit history: hypothesis and preliminary interpretation of evidence from Swedish Lappland. The Holocene 2: 131-137.

Kullman, L. (1993). Holocene thermal trend inferred from tree-limit history in the

Scandes Mountains. Global Ecology and Biogeography Letters 2: 181-188.

Kutzbach, J.E. (1987). Model simulations of the climatic patterns during the deglaciation of North America. In "North America and adjacent oceans during the last deglaciation. The Geology of North America, v. K-3" (W.F. Ruddiman and H.E. Wright, Jr., eds.). Geological Society of America, Boulder, Colorado. pp. 425-447.

Kvamme, M. (1993). Holocene forest limit fluctuations and glacier development in the mountains of southern Norway,and their relevance to climate history. In "Oscillations of the Alpine and Polar Tree Limits in the Holocene", (Frenzel, B., ed.). Gustav Fischer Verlag, Stuttgart. pp. 99-113.

LaMarche, V.C. Jr. (1973). Holocene climatic variations inferred from tree-line fluctuations in the White Mountains, California. Quaternary Research 3: 632-660.

LaMarche, V.C. Jr., Graybill, D.A., Fritts, H.C. and Rose, M.R. (1984). Increasing atmospheric carbon dioxide: Tree-ring evidence for growth enhancement in natural vegetation. Science 225: 1019-1021.

Lamb, H.F. (1985). Palynological evidence for postglacial change in the position of tree limit in Labrador. Ecological Monographs 55: 241-258.

Lamb, H.F. and Edwards, M.E. (1988). The Arctic. In "Vegetation History." (B. Huntley and T. Webb, III, eds.). Kluwer Academic Publishers. pp. 519-555.

Landhausser, S.M. and Wein, R.W. (1993). Postfire vegetation recovery and tree

establishment at the Arctic treeline: climate change-vegetation response hypotheses. Journal of Ecology 81: 665-671.

Larsen, J.A. (1965). The vegetation of Ennadai Lake area, N.W.T.: Studies in subarctic and arctic bioclimatology. Ecological Monographs 35: 37-59.

Larsen, J.A. (1989). "The Northern Forest Border in Canada and Alaska." Springer-Verlag,

Lavoie, C. and Payette, S. (1992). Black spruce growth forms as a record of changing winter environment at treeline, Quebec, Canada. Arctic and Alpine Research 24: 40-49.

Legere, A. and Payette, S. (1981). Ecology of a black spruce (Picea mariana) clonal population in the hemiarctic zone, northern Quebec: population dynamics and spatial development. Arctic and Alpine Research 13: 261-276.

Lonergan, S., DiFrancesco, R. and Woo, M-K. (1993). Climate change and transportation in northern Canada: An integrated impact assessment. Climatic Change 24: 331-351.

Luckman, B.H. (1986). Reconstruction of Little Ice Age events in the Canadian Rocky Mountains. Geographie physique et Quaternaire. 40: 17-28.

Luckman, B.H. and Kearney, M.S. (1986). Reconstruction of Holocene changes in alpine vegetation and climate in the Maligne range, Jasper National Park, Alberta. Quaternary Research 26: 244-261.

MacDonald, G.M. (1983). Holocene vegetation history of the upper Natla River

area, Northwest Territories, Canada. Arctic and Alpine Research 15: 169-180.

MacDonald, G.M. (1987). Postglacial vegetation history of the Mackenzie River Basin. Quaternary Research 28: 245-262.

MacDonald, G.M., Beukens, R.P., and Kieser, W.E. (1991). Radiocarbon dating of limnic sediments: a comparative analysis and discussion. Ecology 72: 1150-1155.

MacDonald, G.M., Edwards, T.W.D., Moser, K.A., Pienitz, R., and Smol, J.P. (1993). Rapid response of treeline vegetation and lakes to past climate warming. Nature 361: 243-246.

MacDonald, G.M. and Ritchie, J.C. (1986). Modern pollen spectra from the western interior of Canada and the interpretation of late Quaternary vegetation development. New Phytologist 103: 245-268.

MacDonald, G.M. and Szeicz, J.M. (1994). Climatic change and the central Canadian treeline. Proceedings of the Association of American Geographers annual meeting, San Francisco, Ca.

Maher, L.J. Jr. (1972). Absolute pollen diagram of Redrock Lake, Boulder County, Colorado. Quaternary Research 2: 531-553.

Markgraf, V. (1980). Pollen dispersal in a mountain area. Grana 19: 127-146.

Melillo, J.M, McGuire, A.D., Kicklighter, D.W., Moore, B., Vorosmarty, C.J., and Schloss, A.L. (1993). Global climate change and terrestrial net primary production. Nature 363: 234-240.

195

Moser, K.A. and MacDonald, G.M. (1990). Holocene vegetation change at treeline north of Yellowknife, Northwest Territories, Canada. Quaternary Research 34: 227-239.

Nichols, H. (1967). Pollen diagrams from sub-Arctic central Canada. Science 155: 1665-1668.

Nichols, H. (1975). "Palynological and paleoclimatic Study of the Quaternary displacement of the Boreal Forest-tundra Ecotone in Keewatin and Mackenzie, Northwest Territories, Canada." Occasional Paper 15, Institute of Arctic and Alpine Research, University of Colorado, Boulder.

Nienstaedt, H. and Zasada, J.C. (1990). White spruce. In "Silvics of North America, Vol. 1. Conifers." (Burns, R.H. and Honkala, B.H., eds.) USDA Forest Service, Washington, D.C. pp. 204-226.

Noble, I.R. (1993). A model of the responses of ecotones to climate change. Ecological Applications. 3: 396-403.

Oechel, W.C., Hastings, S.J., Vourlitis, G., Jenkins, M., Riechers, G. and Grulke, N. (1993). Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. Nature 361: 520-523.

Pastor, J. (1993). News and Views. Nature 361: 208-209.

Pastor, J. and Post, W.M. (1988). Response of northern forests to CO_2-induced climate change. Nature 334: 55-58.

Pastor, J. and Post, W.M. (1993). Linear regressions do not predict the transient responses of eastern North American forests to CO_2-induced climate

196

change. Climatic Change 23: 111-119.

Payette, S. (1983). The forest-tundra and present tree line of the northern Quebec-Labrador Peninsula. Nordicana 47: 3-24.

Payette, S. and Gagnon, R. (1979). Tree-line dynamics in Ungava peninsula, northern Quebec. Holarctic Ecology. 3: 239-248.

Payette, S. and Gagnon, R. (1985). Late Holocene deforestation and tree regeneration in the forest-tundra of Quebec. Nature 313; 570-572.

Payette, S. and Filion, L. (1985). White spruce expansion at the tree line and recent climatic change. Canadian Journal of Forest Research 15: 241-251.

Payette, S., Filion, L., Gauthier, L. and Boutin, Y. (1985). Secular climate change in old-growth tree-line vegetation of northern Quebec. Nature 315: 135-138.

Payette, S., Filion, L., Delwaide, A. and Begin, C. (1989). Reconstruction of tree-line vegetation response to long-term climate change. Nature 341: 429-432.

Payette, S., Filion, L. and Delwaide, A. (1990). Disturbance regime of a cold temperate forest as deduced from tree-ring patterns: the Tantaré Ecological Reserve, Quebec. Canadian Journal of Forest Research 20: 1228-1241.

Payette, S. and Morneau, C. (1993). Holocene relict woodlands at the eastern Canadian treeline. Quaternary Research 39: 84-89.

Peterson, D.L., Arbaugh, M.J. and Robinson, L.J. (1991). Regional growth changes in ozone-stressed ponderosa pine (Pinus ponderosa) in the Sierra

197

Nevada, California, U.S.A. The Holocene 1: 50-61.

Pittock, A.B. (1982). Climatic reconstruction from tree-rings. In "Climate from tree rings." (Hughes, M.K., Kelly, P.M., Pilcher, J.R. and LaMarche, V.C., Eds.) pp. 62-65. Cambridge University Press, Cambridge.

Porsild, A.E. and Cody, W.J. (1980). "Vascular Plants of Continental Northwest Territories, Canada." National Museums of Canada, Ottawa.

Prentice, I.C., Sykes, M.T., and Cramer, W. (1991). The possible dynamic response of northern forests to global warming. Global Ecology and Biogeography Letters 1: 129-135.

Richard, P. (1981). "Paleogeographie postglaciare en Ungava par l'analyse pollinique. Collection Paleo-Quebec." Les Presses de l'Universite du Quebec, Montreal.

Richards, J.H. and Bliss, L.C. (1986). Winter water relations of a deciduous timberline conifer, Larix lyallii Parl. Oecologia,69: 16-24.

Ritchie, J.C. (1982). The modern and late-Quaternary vegetation of the Doll Creek area, north Yukon, Canada. New Phytologist 90: 563-603.

Ritchie, J.C. (1984). "Past and Present Vegetation of the Far Northwest of Canada." University of Toronto Press, Toronto.

Ritchie, J.C. (1985). Quaternary pollen records from the western interior and arctic of Canada. In "Pollen Records of Late-Quaternary North American Sediments." (Bryant, V.M., Jr. and Holloway, R.G., eds.) American Association of Stratigraphic Palynologists Foundation, Dallas, Tx. pp. 327-

198

352.

Ritchie, J.C. (1986). Climate change and vegetation response. Vegetatio 67: 65-74.

Ritchie, J.C. (1987). "Postglaical Vegetation of Canada." Cambridge Univ. Press, Cambridge,

Ritchie, J.C., Cwynar, L.C. and Spear, R.W. (1983). Evidence from northwest Canada of an early Holocene Milankovitch thermal maximum. Nature 305: 126-128.

Ritchie, J.C., Hadden, K.A. and Gajewski, K. (1987). Modern pollen spectra from lakes in arctic western Canada. Canadian Journal of Botany 65: 1605-1613.

Ritchie, J.C., and Hare, F.K. (1971). Late Quaternary vegetation and climate near the arctic tree line of northwestern Canada. Quaternary Research 1: 331-341.

Ritchie, J.C. and MacDonald, G.M. (1986). The postglaical spread of white spruce. Journal of Biogeography 13: 527-540.

Rizzo, B. and Wiken, E. (1992). Assessing the sensitivity of Canada's ecosystems to climatic change. Climatic Change 21: 37-55.

Rochefort, R.M., Little, R.L., Woodward, A., and Peterson, D.L. (1994). Changes in sub-alpine tree distribution in western North America: a review of climatic and other causal factors. The Holocene 4: 89-100.

Rowe, J.S., Bergsteinsson, J.L., Podbury, G.A. and Hermesh, R. (1974). "Fire Studies in the Machenzie Valley." ALUR 73-74-61, Arctic Land Use

Research Program, Dept. Indian and Northern Affairs, Information Canada.

Rowe, J.S. (1977). "Forest Regions of Canada." Department of the Environment, Canadian Forest Service, Publ. 1300.

Scott, P.A., Hansell, R.I.C. and Fayle, D.C.F. (1987). Establishment of white spruce populations and responses to climatic change at the treeline, Churchill, Manitoba, Canada. Arctic and Alpine Research 19: 45-51.

Scott, P.A., Hansell, R.I.C., and Erickson, W.R. (1993). Influences of wind and snow on treeline environments at Churchill, Manitoba, Canada. Arctic 46: 316-323.

Scott, P.A. and Craine, I.T.M. (in press). The lynx cycle: a climatic perspective. Climate Research.

Scuderi, L.A. (1987). Late-Holocene upper timberline variations in the southern Sierra Nevada. Nature 325: 242-244.

Serre-Bachet, F. and Tessier, L. (1989). Response function analysis for ecological study. In "Methods of dendrochronology." (Cook, E.R. and Kairiukstis, L.A., eds.) Kluwer, Dordrecht. pp. 247-258.

Shiyatov, S.G. (1993). The upper timberline dynamics during the last 1100 years in the polar Ural Mountains. In "Oscillations of the Alpine and Polar Tree Limits in the Holocene", (Frenzel, B., ed.). Gustav Fischer Verlag, Stuttgart. pp. 195-204.

Sirois, L. (1992). The transition between boreal forest and tundra. In "A Systems Analysis of the Global Boreal Forest." (Shugart, H.H., Lemans, R., and

Bonan, G.B., eds.) Cambridge University Press, Cambridge, U.K.

Slater, D.S. (1985). Pollen analysis of postglacial sediments from Eildum Lake, District of Mackenzie, N.W.T., Canada. Canadian Journal of Earth Sciences 22: 663-674.

Slayter, R.O. and Nobel, I.R. (1992). Dynamics of montane treelines. In "Landscape boundaries: consequences for biotic diversity and ecological flows" (Hansen, A.J. and di Castri, F., eds.). Ecological Studies, Vol. 92. Springer-Verlag, New York, New York.

Smith, M.W. (1985). Obtaining climatic information from tree rings. In "Our geographic mosaic: research essays in honour of G.C. Merrill." Ottawa: Carleton University Press. pp. 158-170.

Smith, T.M., Shugart, H.H., Bonan, G.B., and Smith, J.B. (1992). Modeling the potential response of vegetation to global climate change. Advances in Ecologcial Research 22: 93-116.

Spear, R.W. (1983). Paleoecological approaches to a study of tree-line fluctuation in the Mackenzie Delta region, N.W.T.: preliminary results. Nordicana 47: 61-72.

Spear, R.W. (1993). The palynological record of late Quaternary arctic treeline in northwestern Canada. Review of Palaeobotany and Palynology 79: 99-112.

Stevens, G.C. and Fox, J.F. (1991). The causes of treeline. Annual Review of Ecology and Systematics. 22: 177-191.

Stocker, T.F. and Mysak, L.A. (1992). Climatic fluctuations on the century time scale: a review of high-resolution proxy data and possible mechanisms. Climatic Change 20: 227-250.

Stuiver, M. and Reimer, P.J. (1993). CALIB3 program. Quaternary Isotope Laboratory, University of Washington.

Tessier, L. (1989). Spatio-temporal analysis of climate-tree ring relationships. New Phytologist 111: 517-529.

Tranquillini, W. (1979). "Physiological ecology of the alpine timberline." Springer, Berlin.

Van Deusen, P.C. (1988). Red spruce tree ring analysis using a Kalman filter. In "Analyses of Great Smoky Mountain red spruce tree ring data." (Van Deusen, P.C., ed.). USDA Forest Service, Southern Forest Experimental Station, General Technical Report SO-69, pp. 57-67.

Van Deusen, P.C. (1990). Evaluating time-dependent tree ring and climate relationships. Journal of Environmental Quality. 19: 481-488.

Visser, H. and Molenaar, J. (1988). Kalman filter analysis in dendroclimatology. Biometrics, 44: 929-940.

Visser, H. and Molenaar, J. (1989). Detecting time-dependent climatic responses in tree rings using the Kalman filter. In "Methods of dendrochronology." (Cook, E.R. and Kairiukstis, L.A., eds.) Kluwer, Dordrecht. pp. 270-277.

Visser, H. and Molenaar, J. (1992). Estimating trends and stochastic response functions in dendroecology with an application to fir decline. Forest

Science. 38: 221-234.

Vorren, K.D., Jensen, C., Mook, R., Morkved, B. and Thun, T. (1993). Holocene timberlines and climate in north Norway. In "Oscillations of the Alpine and Polar Tree Limits in the Holocene", (Frenzel, B., ed.). Gustav Fischer Verlag, Stuttgart. pp. 115-126.

Wardle, P. (1974). Alpine timberlines. In "Arctic and Alpine Environments." (Ives, J.D., ed.) Methuen, London. pp. 371-402.

Warren, W.G. (1989). Tree rings and pollution: trend removal or trend estimation? In "Forest Statistics." (Pelz, D.R., ed.) Abtteilung Fur Forstliche Biometrie, Universitat Freiburg. pp. 304-317.

Wein, R.W. (1975). "Vegetation Recovery in Arctic Tundra and Forest-Tundra After Fire." ALUR 74-75-62. Arctic Land Use Research Program, Dept. Indian and Northern Affairs, Information Canada.

Woodward, F.I. (1987). "Climate and Plant Distribution." Cambridge University Press, Cambridge, U.K.

Wright, H.E. Jr., Mann, D.H. and Glasser, P.H. (1984). Piston corers for peat and lake sediments. Ecology 65: 657-659.

Yamaguchi, D.K. (1991). A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research. 21: 414-416.