THE UNIVERSITY OF CALGARY

PERMAFROST, FIRE, AND THE REGENERATION OF WHITE SPRUCE AT ARCTIC TREELINE NEAR INUVIK, NORTHWEST TERRITORIES, CANADA

by

DAVID F. GREENE

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE

DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF GEOGRAPHY

CALGARY, ALBERTA

JUNE 1983

THE UNIVERSITY OF CALGARY

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled, "Permafrost, Fire, and the Regeneration of White Spruce at Arctic Treeline Near Inuvik, Northwest Territories, Canada", submitted by David F. Greene in partial fulfillment of the requirements for the degree of Master of Science.

Stuart A. Harris

Dr. Stuart A. Harris (Supervisor)
Department of Geography

Arthur Limbird

Dr. Arthur G. Limbird
Department of Geography

Dennis Parkinson

Dr. Dennis Parkinson
Department of Biology

Date: 13 June, 1983

ABSTRACT

Adjacent burned and unburned upland stands at the southwest corner of the 1968 Inuvik burn were examined. A secondary site (unburned) was studied in the nearby Caribou Hills escarpment. Shallow active layers are poorer habitats than are deep active layers for white spruce because of a slower rate of thaw (effective growing season length), lower seed dispersal capacity, lower cone production, and poor seedbed creation (because of the depth of the Of) by fire. Fire delimits the range of white spruce by restricting it to areas where the probability of surviving fire is high, e.g., the steeper valley sides and the most deeply incised or sinuous perennial creeks. However, nutrient availability may be a problem at sites with relatively low fire frequency. Areas where survival through fire is likely, also tend to possess deep active layers. Although such sites are not uncommon, many remain uncolonized because of the poor seed dispersal capacity of these white spruce stems.

ACKNOWLEDGEMENTS

Funding for this thesis was provided by the Arctic Institute of North America, the Faculty of Graduate Studies, the Department of Geography, and Dr. S. A. Harris (NSERC grant A7483). The Department of Forestry at Inuvik provided me with some free helicopter time. The Inuvik Scientific Resource Centre gave me a great deal of logistical support.

Dr. Dale Vitt of the University of Alberta identified the bryophytes. Dr. James Case of the University of Calgary identified the lichens. Valuable discussions of method and interpretation were freely suffered by C. Tarnocai, S. C. Zoltai, S. A. Harris, A. Limbird, E. A. Johnson, D. Jelinski, H. D. Allen, and Craig Pinto.

Some of the tables and figures were fashioned by H. D. Allen and M. Koetsier. M. Styx and R. Wheate were always willing to advise on the design of the figures. C. Pilger was an invaluable source of information in the soils lab. Field assistance was provided by M. Bosch and D. Privette. I should especially thank Privette who worked for almost nothing.

Dr. A. Limbird must be acknowledged for his help with the interpretation of the soils data, the permafrost conference manuscript, and for the wine party. I drank at least $35 of his wine in a single night.

E. A. Johnson deserves particular thanks for the unbelievable amount of time he spent with someone who wasn't even in his own department. If there is anything of value in the plant ecology in this thesis, the credit is his.

Dr. S. A. Harris, my supervisor, was always ready with support and criticism. The cheerful manner in which he waded through the fetid sewage I call prose deserves a purple heart of some sort. And trying to get a figure or table out of me is like pulling teeth. Most supervisors are a constant source of sorrow for their graduate students, but the only demand mine ever made was that I work hard. As a final testament: whenever I needed a letter written on my behalf, I never had to wait more than a few days. How many graduate students can say that?

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

CHAPTER I

INTRODUCTION

Objectives

The objective of this study is to broadly delineate the factors which control the distribution of white spruce (*Picea glauca*) in the northern forest-tundra near Inuvik, N.W.T., with particular emphasis on the constraints on regeneration. The results can then be used in interpreting the regional white spruce treeline. Although white spruce forms the conifer treeline species over almost 50 percent of arctic North America, most of the previous work on arctic treeline has dealt with black spruce (*Picea mariana*).

Terminology

Clarity is best served by defining at the outset some terms which are traditionally vague, frequently used by different authors in different ways, or which are given a special definition for the purposes of this thesis. In most cases, the special definitions are used to simplify the discussions in Chapters 4 and 5.

1. South, west, and southwest aspects are referred to as south-facing slopes. All other aspects are called north-facing slopes. This will facilitate generalizations about the local distribution of white spruce. The transects actually used for data collection were laid out on an almost exact north-south compass bearing.

2. For the purposes of this thesis, a "deep active layer" is one which was more than 50 cm deep as of August 6, 1982. "Shallow active layers" were less than 50 cm in thickness.

3. Seed dispersal capacity is defined as that distance from a seed-source within which the great majority of the seed rain falls. Magnitude of the seed rain is not implied.

4. Fire intensity and severity have been defined in many ways by fire ecologists (Viereck and Schandelmeier, 1980). In this thesis, fire intensity or severity are used synonomously to indicate the depth of the organic layer remaining immediately after a burn. The heat given off or the amount of material burned is not implied in this definition.

5. Seedling establishment is defined ad hoc as the survival of a seedling beyond four years of age.

6. All soil terms used in this thesis are those of the Canadian System of Soil Classification (1978).

7. The growth habit distinction between tree and non-tree seems to me unimportant (but see Hustich, 1979). In this thesis, a stem is any white spruce individual regardless of age or height. A seedling is defined as a stem younger than 13 years, i.e., the time of the 1968 Inuvik burn.

8. In this thesis, treeline, arctic treeline, and northern forest-tundra are used interchangeably, and refer to high latitude environments where trees are markedly contagious (i.e., patchy) and exist as big or small "islands" among communities dominated largely by ericoid associations. There is not, nor could be, an adequate quantitative definition for the northern limit of white spruce. Problems of scale make precision in such definitions an endlessly receding goal.

Literature Review

White Spruce Ecology

1. General autoecology

White spruce can survive a wide range of temperatures. Mean January temperatures of -51 degrees C have been recorded in the northern part of its range, and mean daily temperatures as high as 39 degrees C have been recorded near the southern limit (Nienstaedt, 1957). Higher temperatures undoubtedly occur.

White spruce seedlings have relatively slow growth rates. Day (1964) observed that 15 to 17 cm height is typical for 10-year-olds. Growth rates, however, can be much more rapid in newly-burned or scarified open sites. A consequence of relatively slow growth is that first-year seedling roots rarely penetrate more than 7.5 cm. Thus any seedbed that dries out to this depth would be unsuitable for establishment (Nienstaedt, 1957). The majority of the seed dispersal typically occurs in the autumn while most of the overwintering seeds germinate the following June or July (Zasada, 1971).

The pollen of white spruce can be dispersed many kilometers. Male strobili are usually located on branches in the central portion of the tree while female cones are located on higher branches.

White spruce can survive on a great variety of soils-- from clays to gravels-- but show best growth on loams. Sandy substrates are suitable if there is adequate moisture, i.e., a high water table (Nienstaedt, 1957). Sutton (1969) reported the optimal pH as being 5.0 to 7.0.

Fowells (1965) found that, in general, cone production began after 16 to 25 years, with maximum seed production at 150 to 250 years. Zasada (1971) stated that "good" seed production begins at approximately 40 years in interior Alaska.

There appears to be much variance in the quantity and quality of seed production from year to year. Large variance between mast years and poor seed production years is the norm (Zasada and Viereck, 1970; Stiell, 1976).

2. Seedbeds

Although white spruce can establish itself in almost any type of seedbed, the optimal seedbeds appear to be moist mineral soils with perhaps a thin veneer of duff (Lutz, 1956; Rowe, 1971; Dobbs, 1972; Zasada, 1971).

Stand-replacing fires or deep siltation events provide excellent seedbeds. The most important inhibitor of white spruce establishment is droughty soil conditions in the upper few centimeters. Germinants are relatively freely-transpiring succulents (Eis, 1965). Competition for water from vascular plants and cryptogams on the forest floor is one of the main causes of seedling mortality (Dobbs, 1972).

Fire removes the competition while often retaining some thickness of the highly water-retentive duff. Additionally, fire opens up the canopy and mobilizes nutrients which were incorporated in plant tissue, thus allowing for more rapid growth of the seedlings (Wein, 1975).

With respect to the distribution of this species, the emphasis must be on seedbeds. Although asexual reproduction does occur (Elliott, 1979; Viereck, 1979), it is rare. I found layered stems only on windy ridge-tops and spurs in the Caribou Hills, N.W.T.

3. Fire Ecology

Relative to other boreal forest tree species, white spruce is not particularly well-adapted to either survival of fire or rapid post-fire invasion. The optimality of burned areas as seedbeds is perhaps the only salient adaptation to fire (Zasada, 1971).

The thin bark of white spruce makes it vulnerable even to low-intensity ground fires (Lutz, 1956). The tendency of these stems in the northern forest-tundra to retain low branches increases this susceptibility.

There is no evidence of a seed-bank in white spruce (Johnson, 1975; Frank and Safford, 1970). The seed cannot remain dormant when moist (Jarvis et al., 1966). Mature seeds cannot survive a crown fire (Zasada, 1971).

Survival of some stems through fire is of paramount importance for white spruce (Viereck and Schandelmeier, 1980). Seed dispersal capacity is very low in this species. Animals are relatively unimportant in seed dispersal (Fowells, 1965). Nienstaedt (1957) stated that, in the southern portion of its range, the greatest distance seed could be dispersed by an "average" (undefined) wind was 99 m. Zasada (1971) in interior Alaska deemed the maximum dispersal distance to be about 60 m at a wind velocity of 10 km per hour. This does not take into account seeds scudding along the surface of snow or ice. To a great degree, the mean maximum wind-dispersed distance is a function of tree height. Roe (1967) in a study on dispersal in Engelmann spruce (Picea engelmannii), determined that the relation of seed rain density to distance from seed source showed a logarithmic decrease.

The importance of seed dispersal capacity can be offset by the magnitude of the seed rain, i.e., the ecological significance of the 5 percent of seeds travelling the farthest depends on the numbers involved in that 5 percent. Seed dispersal capacity should, therefore, be of more importance in the forest-tundra than in the interior of the range of white spruce.

As already mentioned, fire-generated seedbeds are often excellent for establishment. However, the more optimal seedbeds may be greatly dispersed across the landscape as fire intensity is markedly uneven over short distances in the forest-tundra (Wein, 1975).

Arctic Treeline Determination

1. Climate

Most of the work on arctic treeline in North America concerns black spruce in the Shield region of central Canada. In the Shield, black spruce typically extends farther north than white spruce. Consequently, many of the hypotheses concerning how climate delimits the northern range of trees are really dealing with controls on black spruce. It is often implicit in the arguments, however, that the same controls are operating also on white spruce (Black and Bliss, 1980; Larsen, 1980).

Bryson (1966) pointed out the rough correspondence between air mass frequencies and arctic treeline in North America. He asserted that the treeline is determined by the modal summer penetration of arctic air masses, and that the northern outliers of trees maintain themselves by virtue of the infrequent summers when the polar front is well north of its "normal" position. Nichols (1975) has gone a step further, suggesting that the northern outliers are Hypsithermal relicts which maintain themselves *in situ* primarily by asexual reproduction. Because of this, black spruce, which commonly layers at treeline, extends farther north in the Shield than does white spruce. Treeline in Keewatin is, then, in "disequilibrium" with present climate

(Nichols, 1975). Fires are so seldom followed by sexual reproduction that the Keewatin treeline is slowly being brought into equilibrium. Arctic treeline in Alaska and northwest Canada is already in equilibrium (Larsen, 1980), as indicated by the abruptness of the transition from forest-tundra to tundra (Ritchie, 1972).

Many authors working in the Holarctic have stressed the importance of low temperatures in determining arctic treeline: e.g., Mikola (1970) and Siren (1970) in Scandanavia, Kay (1978) and Mitchell (1973) in Keewatin, and Viereck (1979) in Alaska. However, as Hare and Ritchie (1972) point out, ". . . it is highly probable that the northern limits of forest growth and of individual tree growth are thermally determined, but ecologists cannot yet say in precisely what way. . . " It is worth noting that isolines of potential fire hazard correspond almost as well with treeline as do Bryson's isotherms (Simard, 1974). Were isolines of mean active layer depth available, they might also correspond well.

One line of inquiry involving the direct effects of low temperature focuses on a factor-complex comprised of low temperature, wind/ice blast, and desiccation (Hustich, 1953; Larsen, 1980). However, such damage typically results only in the death of shoots projecting above the snow (Wardle, 1974). Although of undoubted importance in combination with other factors, it is not likely to be of major importance in the more wind-sheltered sites.

A line of inquiry involving the indirect effects of air masses argues that the growing season (time of active layer thaw) is too short for adequate seed production (Tikhomirov, 1962; Ritchie, 1972; Sarvas, 1970; Mitchell, 1973; Kay, 1978). The popularity of this line of reasoning is matched only by the lack of evidence for it. I know of no published demographic study from the forest-tundra which includes the shorter stems. There are only qualitative statements about the apparent lack of cones, seeds, or seedlings. As mentioned above, white spruce is an intermittent seed producer even in the interior of its range.

The growing season argument assumes that the length of time in which the rooting zone is thawed is the main determinant. However, that thaw period has other effects. A short thaw interval will retard decomposition, so that nutrient availability may be a limiting factor (Haag, 1972; Sarvas, 1962). Additionally, shallow active layers may well have poor aeration in the rooting zone, an important factor in tree respiration and aerobic bacteria ecology (Larsen, 1980). Thus, depth of thaw may be as important as length of the thaw season. If so, texture and potential insolation, insofar as they help control depth of thaw, may play important roles in the local determination of the range of white spruce.

Another factor involving the substrate is drought during the growing season. The northern forest-tundra is quite dry, particularly when one considers that most of the precipitation will be lost in the spring as snowmelt run-off (Anderson and Mackay, 1974). However, given that evapotranspiration will be relatively low in these high latitudes, and that the active layer is usually thin enough in non-gravel soils for capillarity to provide a steady supply of moisture to the rooting zone, it seems likely that physiological drought is mostly of importance on the steep slopes and most coarse substrates.

2. Fire

It is generally assumed that fire frequency and intensity decrease with increasing latitude because of the decrease in lightning occurrences and fuel availability, and the shortness of the fire season (Wein, 1975; Kendrew and Currie, 1955; Van Wagner, 1979; Rowe et al., 1975). Tundra fires are easily halted by minor relief features so the percentage of burned area within a burned perimeter may also decrease as one moves north (Cochrane and Rowe, 1969; Wein, 1975). However, granted that fire frequency and intensity may be lessened in the northern forest-tundra, it is surprising that its role in treeline determination remains unexplored.

Black and Bliss (1980) speculated that black spruce is usually found farther north than white spruce because its semi-serotinous cones make it better adapted to fire. Lambert (1972) claimed that large sections of the northwest Canadian forest-tundra have been swept by fire. Citing palynological evidence, Nichols (1976) speculated that widespread fires are capable of causing sudden southward retreats of treeline in Keewatin. Van Wagner (1979) hypothesized that, since treeline fires are of low intensity, there may be inadequate optimal seedbed creation for species like white spruce.

Some authors have argued that seed production is so low at treeline that fire is primarily a destructive factor: post-fire regeneration is rarely adequate (Lutz, 1956; Hustich, 1966; Kryuchkov, 1968; Nichols, 1975; Larsen, 1965). Kryuchkov (1968) calls these burned treeline areas with little or no post-fire regeneration by tree species "pyrogenic tundras". Conversely, Marr (1948) and Cody (1965) report good post-fire regeneration by black spruce. In short, there are conflicting views as to the effects of fire in the forest-tundra and no detailed studies on the adequacy of the long-term seed production, the quality of the seedbeds being generated by fire, and the likelihood of survival of post-fire seed sources.

3. Succession

The local distribution of a species can only be understood with reference to temporal changes in its relative frequency, i.e., succession. There is, however, very little agreement on the nature of succession in the forest-tundra.

Heilman (1966, 1968) and Strang (1973) argued that on mesic sites, white spruce is seral. Lutz (1956) claimed that white spruce is the climax on the drier sites.

Many authors have argued for variants of a unidirectional cycling based on permafrost table flux (Drury, 1956; Benninghoff, 1952; Viereck, 1965). Viereck and Schandelmeier (1980) have proposed that succession in the north is a complex "web" of possible succession pathways dependent on fire frequency, fire intensity, seed-source proximity, and synecological considerations. However, Johnson (1981) reported no apparent significant changes with time in vascular plant composition on burned sites near Great Slave Lake.

Active Layer Depth

The study area is one of continuous permafrost. The comparative depth of the active layer on various sites is influenced primarily by vegetation: more specifically, moss depth and tree shade. A thicker bryophyte cover should tend to cause a shallower active layer because of the insulative properties of little-decomposed moss (Brown et al., 1969). Tree shade appears to be less important than bryophyte depth (Viereck, 1973).

In well-dissected terrain such as the Inuvik area, other factors may be as important as vegetation, e.g., comparative insolation, snow depth, time of snowmelt, soil texture, and albedo. In Alaska, Dingman and Koutz (1974) stressed the importance of potential insolation, i.e., a complex of slope angle, aspect, and latitude. However, Price (1971) in the Yukon Territory suggested that bryophytes are still of great importance even on mountain slopes.

Fire reduces the depth of the bryophytes and the amount of shade provided by taller species, and can cause short-term permafrost degradation (Brown, 1970). Additionally, the albedo change resultant upon fire should cause thicker active layers (Brown et al., 1969). Viereck (1973) showed that the degradation of the permafrost table is eventually reversed and that, after about 55 years, the active layer has returned to its "normal" thickness.

Mackay (1970) and Cody (1965) indicated that fire makes the ground more hummocky via thermokarst subsidence. Coarse soils are less prone to subsidence.

Problems Dealt With In This Thesis

Although there is much debate over the precise controls on arctic treeline, the broad causes agreed upon by many investigators are:

1) seed production and seedling establishment are too rare to allow for stand maintenance and/or radiation beyond the present treeline. Where stands are located in the most clement sites, long-term regeneration is barely able to keep pace with long-term mortality. Such a site can be said to be at equilibrium with present climate.

2) fire is primarily an agent of destruction as seed production is too low for adequate post-fire regeneration, and/or too little favorable seedbed is created.

This thesis concentrates on these two lines of inquiry, testing them in the Inuvik area. Other factors mentioned by various authors could have been the focus of this thesis--e.g., insect damage to matures and seeds; physiological drought in the summer; a winter mortality factor-complex comprised of wind, low temperature, and desiccation;

breakage of stems by snow accumulation-- but there is not as much agreement about their potential significance at arctic treeline. Initial reconnaissance in the Inuvik area indicated that some of these factors were certainly not of major importance there. Some of these secondary problems will, however, be discussed in Chapter 5.

Reconnaissance showed that the distribution of white spruce was markedly contagious, and that it could perhaps be best explained in terms of active layer depth and survival through fire.

The responses of white spruce to fire which were investigated included: pattern of survival through fire along a topographical gradient, the relative quality of fire-created seedbeds, the distribution of the more optimal seedbeds in the landscape (particularly in relation to likely surviving seed sources), and the typical seed dispersal capacity of the taller stems.

The responses of white spruce to active layer depth which were investigated included: reproductive and vegetative vigour, demographic structure, and seedling density in relation to site factors.

CHAPTER II

STUDY AREA

Introduction

This chapter will briefly describe the physical geography of the uplands of the Mackenzie Delta area. Compared to other areas in the low arctic or forest-tundra, the Mackenzie Delta area has been reasonably well-studied. However, much of this work is either a broad regional classification or is concerned with the Delta itself.

The main study area was located at Boot Creek Valley, 2 km east of Inuvik, N.W.T. (68 degrees and 21 minutes North; 133 degrees and 40 minutes West). This area is shown in Plates 1 and 2. A secondary study area was located in an unnamed valley near the southern end of the Caribou Hills escarpment (Figure 1). Part of this valley is shown in Plate 3. Initially, reconnaissance was conducted from Arctic Red River to Holmes Creek (about 40 km north of Reindeer Station), a north-south distance of approximately 130 km. The author is not aware of vigorous white spruce stands north of Holmes Creek (Plate 4). In the following sections, the discussion will be divided between specific

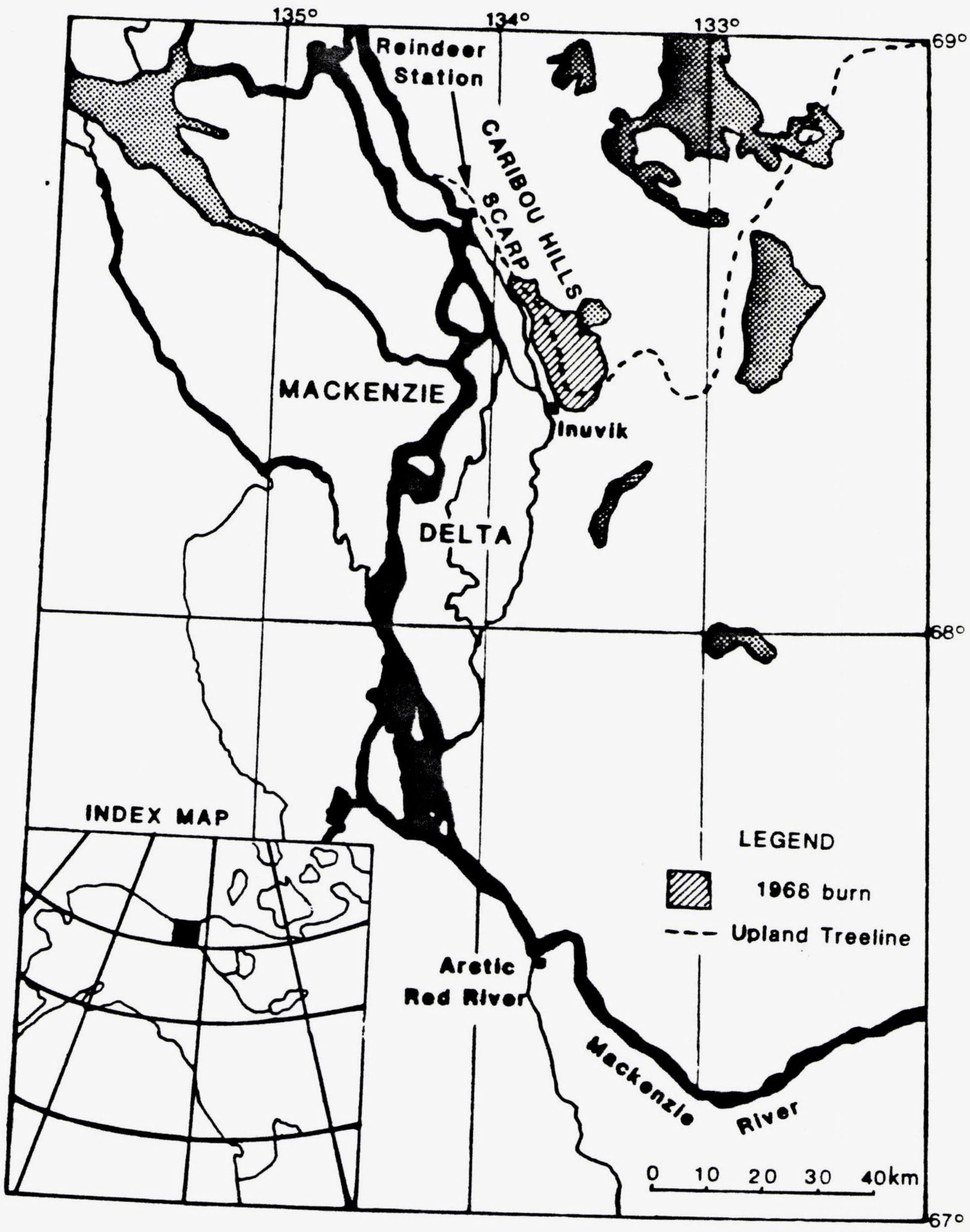


Figure 1. Map Showing the Location of the Study Area.

Plate 1. A South-facing Slope in Boot Creek Valley that was Burned in 1968.

Plate 2. An Unburned South-facing Slope in Boot Creek Valley that was Protected by a Fire-guard in 1968.

Plate 3. A South-facing Slope at the Caribou Hills Site.

Plate 4. Vigorous White Spruce in the Highly Sinuous Meander Lobes of Holmes Creek.

descriptions of the Caribou Hills site and the Boot Creek site. Where applicable, a more general discussion of the uplands of the Mackenzie Delta area is presented.

This area represents the transition between the northern forest-tundra and the tundra of the low arctic. The transition is much more abrupt here than in the Shield (Ritchie, 1972). From the Caribou Hills escarpment west to the Bering Strait, white spruce is the treeline species (with the exception of Populus balsamifera north of the Brooks Range.) East of the Caribou Hills escarpment, black spruce is usually the treeline species until, in Labrador, white spruce again forms the treeline (Elliott and Short, 1979).

For a general introduction to the Mackenzie Delta area, see Mackay (1963) and the regional monograph edited by Kerfoot (1972).

Geology

The Caribou Hills form a rolling tableland to the east of the Mackenzie Delta, rising as much as 300 m above it. The average elevation is 150 m above mean sea level (Young, 1978). Quaternary sediments (often quite thin) overlie Tertiary gravels, silts, sands, and lignite seams. Cretaceous shales are found in the southern portion of the

Hills (Rampton, 1972). Regionally, these Tertiary sediments dip gently 4 to 5 degrees towards the north (Young, 1978).

The contact between the Hills and the Delta is a steep erosional escarpment which can rise as much as 250 m only 1.5 km east of the Delta. Generally, the escarpment is heavily dissected by very short streams (e.g., the valley of the Caribou Hills site is only 1 km long). These valleys terminate abruptly in the rolling tableland of the Caribou Hills. Exposures at the Caribou Hills site indicate only poorly consolidated sandstones with a few thin interbedded gravel layers.

Boot Creek Valley has no published stratigraphy. A nearby gravel quarry on the valley side exposed thick gravels with a silty overburden. However, there are no other exposures in the valley. Gravel was not encountered in any of the soil pits dug for this study.

Geomorphology

In the area of the Caribou Hills escarpment, ice retreat is thought to have begun about 12,000 BP. Mackay (1963) speculated that Boot Creek may have been a meltwater channel.

Fluvial erosion in this area is relatively rapid when one considers that total precipitation is only about 20 cm per year. Most of the sediment transportation by fluvial processes should occur during the spring snowmelt period (Kennedy and Melton, 1972). The poorly-consolidated sediments of the Caribou Hills escarpment are easily eroded, especially where steepened by undercutting of the East Channel of the Mackenzie Delta (Mackay, 1963). Gullying is both deep and common in the escarpment valleys. At the Caribou Hills site, the gullies are up to 12 m deeper than adjacent spur surfaces. Mass wasting is an important feature of the escarpment ecology. Almost all mature trees (white spruce and Betula papyrifera) on the south-facing slope show evidence of at least one tilting event, and many show evidence for repeated tilting (especially in the gully bottoms). At Boot Creek, evidence for tilting is much more uncommon because the slopes are less steep. In both valleys, the gullies are deeper on south-facing slopes than on north-facing slopes.

Slow mass wasting (frost creep and gelifluction) appears to be of greater importance on the north-facing slopes of both valleys, but is especially well-developed on the steep north-facing slope at the Caribou Hills site. There, the organic soils have a terraced appearence. The terracettes are small, having a maximum surface area of only a few square meters, and risers which average less than a meter. Gully bottoms on the south-facing slope of the Caribou Hills site also have small terracettes.

Evidence of rapid mass movements is common in both valleys. Many of the earthflows are associated with fire. At Boot Creek, Heginbottom (1972) counted 17 earthflows which occurred in the summer following the 1968 Inuvik burn. In an unburned portion of Boot Creek Valley, the present author found 2 charcoal layers in a single soil pit on a 15 degree slope. The lower charcoal layer (at 40 cm depth) was overlain by 10 cm of silty soil while the charcoal layer above it (at 30 cm depth) was also overlain by 30 cm of silty loam and organic surface material. It is possible that the overlying material represents in both cases an earthflow or gelifluction. Aeolian deposition seems an unlikely explanation since the spruce needles in the charcoal layers are clearly recognizable.

Both study sites are located in asymmetrical valleys. In each case, the north-facing slope is steeper than the south-facing slope, and the creek lies on the southern side of the valley (Figure 2). North of the creek is a relatively flat area; south of the creek, the steep north-facing slope begins almost immediately. Kennedy and Melton (1972) speculated that material deposited from the more poorly vegetated south-facing slopes forced the creek southwards, thus oversteepening the north-facing slope.

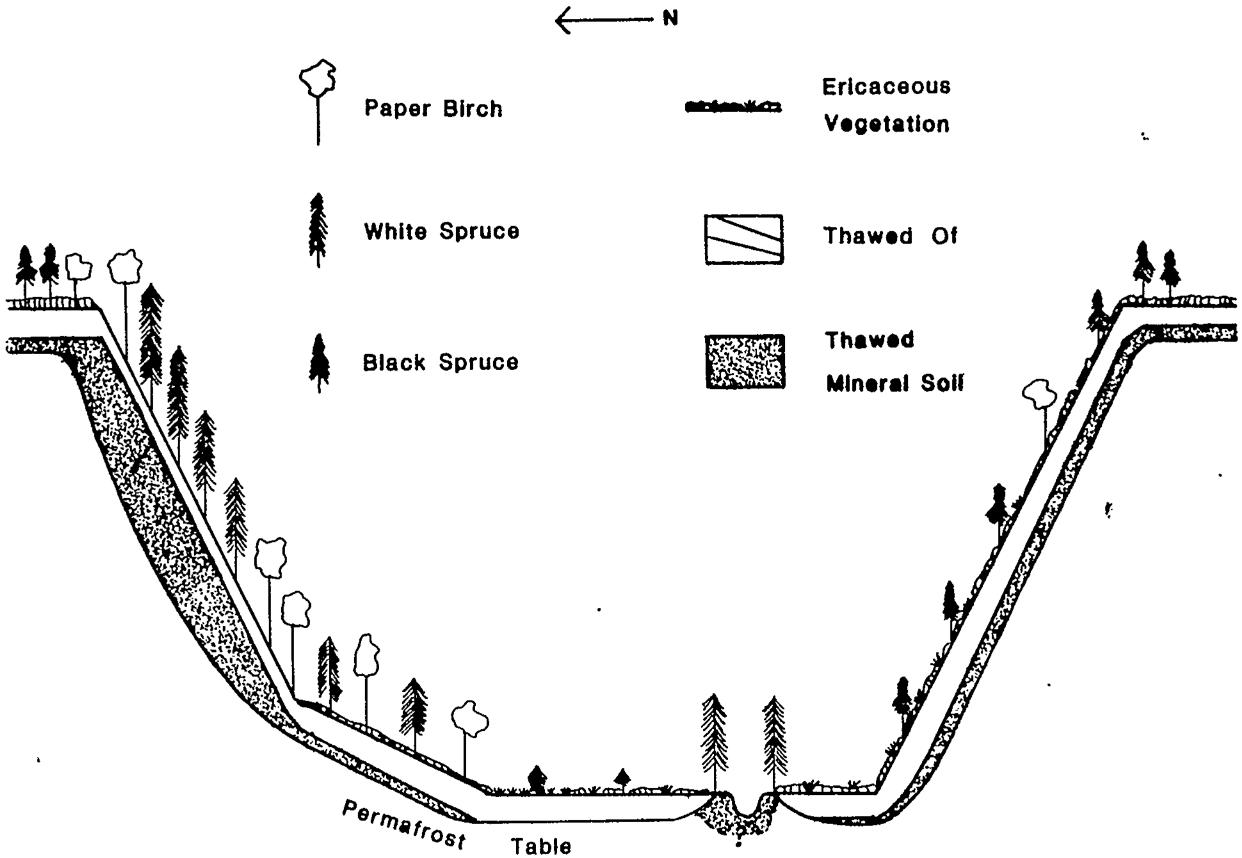


Figure 2. Idealized Topographic Relationships Between Of Depth, Slope Angle, Active Layer Depth, Aspect, and Vegetation.

Tundra polygons were not found in either valley although they occur in the tableland above the valleys. Nivation hollows were not of apparent importance at either valley although, again, they were noted in the adjacent tableland.

Hummocky ground was concentrated on the flat alluvial/colluvial areas on the valley bottoms. This hummocky micro-relief reached a maximum of 70 cm, but averaged about 35 cm. More subdued hummocks were found on north-facing slopes. There appears to be a broad inverse relationship between the magnitude of the hummocky micro-relief and the depth of the active layer, i.e., hummocky ground is most common on the poorly drained sites (French, 1976).

Active Layer Depth

Much of the work on permafrost/vegetation relationships in this area has been concerned with the Delta and is therefore of little value to the present study (Gill, 1971; Smith, 1975). The more detailed studies of permafrost/vegetation relationships in the uplands were focused on the 1968 burn.

Hummocky ground (i.e., the coincidence of shallow active layers and non-coarse materials) occupies 80 percent of the Inuvik area (Pettapiece et al., 1978). The vast majority of white spruce stems are segregated into the remaining 20 percent of this area.

In the Mackenzie Delta area, the increase in active layer depth after about August 1 is very minimal (Mackay, 1970; Haag and Bliss, 1974; Zoltai and Pettapiece, 1973). Haag and Bliss (1974) estimated that 85 percent of the summer thaw had occurred by July 25 at a tundra site north of the Caribou Hills escarpment.

Younkin and Hettinger (1978) examined snow road construction near the Inuvik airport. They noted that small changes in bryophyte depth produced no apparent change in active layer depth. (Note: in this thesis, active layer depth measurements will always include any organic epipedon present.) There must be, then, some threshold of bryophyte insulation value below which permafrost table degradation will proceed.

Sakai et al (1979) noted that there was a broad correspondence between active layer depth and vegetation community type in this area. They concluded that vegetative vigour (height and diameter of bole) in white spruce was severely curtailed on shallow active layers.

Janz (1973) in a tundra area of the Caribou Hills concluded that the moisture-retentive organic layer was very important in determining active layer depth. Depth of thaw and density of the organic layer decreased downslope, while the organic layer depth increased downslope. That is, the Of becomes an increasingly larger component of the organic layer downslope. The organic layer, then, responding to a moisture gradient, helps determine active layer depth through its high insulative value and its relatively high ice content.

The 1968 Inuvik burn lasted from August 8 to 18. The fire began after an 86 day drought and it burned 350 square km of both tundra and forest-tundra communities. The fire swept through the central portion of Boot Creek Valley and ranged northward to within a few km of the Caribou Hills site where it was extinguished by a light rain (Heginbottom, 1972). Mackay (1970) concluded that the actual heat of the burn was unimportant in the subsequent permafrost degradation; removal of the vegetation was the most important factor.

Heginbottom (1972) compared the burn with adjacent unburned stands. By the summer of 1970, active layers in the burned area were deeper than in the unburned. Mackay (1977) showed that for the first 8 years after the fire, the rate of increase in total thaw depth at some permanent plots was leveling off at a roughly exponential rate. Active layer thickening appears to be delayed until a few years after a fire (Zoltai, 1975).

Climate

The climate of this area is transitional between the arctic and subarctic (Mackay, 1963). A detailed compilation of the regional climatic mensuration was presented by Burns (1973).

Selected climatic normals for the Inuvik area are presented in Table 1. These data are taken from Environment Canada (1982).

The Mackenzie Delta area is one of transition from subarctic to arctic environments. This area experiences cold winters and cool summers. The number of degree days is low. Precipitation values are also very low.

Gill (1971) carried out a study of leaf phenology, and suggested that the Delta has a longer growing season than the adjacent uplands because flooding subsequent to break-up (early June usually) rapidly removes the snow-cover from the flooded area, thus allowing soil thaw to begin earlier than in the uplands. The sample size in that study was very small. However, Don McLennan (pers. comm.) in 1982 conducted a study which indicated that there are no significant phenological differences within shrub species located on both deltaic and upland sites. Tarnocai (pers. comm., 1983) has data showing that over a five-year

Table 1. Climatic Normals for Inuvik, N.W.T., 1951-1980.

	Month												
	J	F	M	A	M	J	J	A	S	O	N	D	Year
Mean Daily Max Temp (°C)	-24.7	-23.7	-18.8	-7.9	4.2	16.2	19.4	15.9	7.1	-4.6	-16.2	-22.4	-4.6
Mean Daily Min Temp (°C)	-34.4	-34.1	-31.1	-20.6	-5.7	4.1	7.8	5.4	-1.1	-11.6	-25.3	-31.9	-14.9
Mean Daily Temp (°C)	-29.6	-28.9	-25.0	-14.3	-0.8	10.1	13.6	10.7	3.1	-8.1	-20.7	-27.2	-9.8
Mean Rainfall (mm)	0.1	0.0	0.0	T	0.9	5.9	24.5	25.4	9.5	1.2	0.0	0.0	67.4
Mean Snowfall (cm)	20.4	12.6	15.0	17.0	13.0	2.2	0.5	3.3	12.0	37.2	22.6	20.8	176.6
Total Precip (mm)	17.9	10.5	12.0	14.8	17.6	23.5	33.6	43.6	23.9	33.4	17.9	17.4	266.1
Degree Days Above 5°C	0.0	0.0	0.0	0.1	17.6	165.3	270.0	182.0	29.6	0.6	0.0	0.0	665.2

(Source: Environment Canada, 1982)

period, a group of upland sites in this area thawed more rapidly than did two Delta sites.

Palynological reconstruction for this area by Ritchie (1972) suggested that tundra communities were replaced by forest-tundra communities (including Picea) around 11,500 RCYBP (radiocarbon years before present). This forest-tundra community remained until about 8,500 RCYBP, when it was replaced by a closed-canopy forest of spruce and paper birch (Betula papyrifera). Invasion by alder (Alnus) began about 5,500 RCYBP. From 4,000 RCYBP to the present there was a decline in spruce pollen. This record is similar to pollen studies carried out in the Shield region by Nichols (1976). The palynological records from Alaska are, however, much less straightforward (Colinvaux, 1967).

Burns (1973) showed that fluctuations in temperature values for this area in the twentieth century have been greater for mean January than mean July temperatures. Mackay (1975) calculated that a 3 degrees C warming would thicken the active layer in the northern Mackenzie Valley by 20 to 50 per cent. Fluctuations exceeding 3 degrees C for periods a few years long have been common during the twentieth century (Burns, 1973).

Hydrology

Hydrological investigations have been carried out in Boot Creek Valley by Anderson and Mackay (1973, 1974). They found that in apparently average years, the peak run-off occurs with the spring snowmelt in late May or early June. There is little direct run-off following summer storms as 95 percent of the rain is held in depressions and in the peat. The run-off pattern can, however, be almost reversed when a droughty winter is followed by an unusually rainy summer (Anderson, 1974).

Boot Creek is perennial while the gullies on the steep south-facing slope feeding it contain running water for only a few weeks during and after snowmelt. The creek at the Caribou Hills site is "ephemeral" in that it contains water only a few cm deep during most of the summer. This water is derived from active layer thaw in the higher portions of the catchment area. At a similar valley on the Caribou Hills escarpment, Kennedy and Melton (1972) noted the relatively clear water in the summer flow and they speculated that most of the sediment transport takes place during the spring snowmelt.

The creeks at Boot Creek Valley and the Caribou Hills site are both incised and their beds are clayey silts. The incision at Boot Creek is about three times as deep as at the CH site. Conversely, valley side gullies are much deeper and wider at the Caribou Hills site.

Inter-hummock depressions have a higher moisture content than do the hummock-tops (Pettapiece et al., 1978). Masses of almost pure ice are often found in the depressions under a thin veneer of bryophytes. Active layers are thicker under hummock-tops than under adjacent depressions, even after fire (Mackay, 1977).

Soils

Deep active layer sites tend to be occupied by Static Cryosols (Canadian System of Soil Classification, 1978). On a gradient of increasing moisture, the coarser soils typically range from Regosolic to Orthic to Brunisolic Static Cryosols. Shallow active layer sites are dominated by Turbic and Organic Cryosols depending on the depth of the organic material. Gleying is common.

It should be noted that fire can change soils from one Great Group to another by removal of organic material and/or deepening of the active layer. For example, fire can turn an Organic Cryosol into a Turbic Cryosol by removal of enough organic material. Fire can also change the soil designation at the Order level, e.g., from a Regosolic Static Cryosol to a Regosol, by deepening the active layer.

Cryoturbation is common in the hummocky areas (Pettapiece et al., 1978). As noted above, such sites tend to have shallow active layers. In all soils in this area, structure is weakly developed, translocation of clays is minimal, and organic accumulation is often in excess of bacterial decomposition (Zoltai and Tarnocai, 1974; Janz, 1973).

In permafrost terrain, moisture/topographic relationships should be less straightforward than elsewhere. Except at the coarsest deep active layer sites, soil thaw should always be producing water which can move within the rooting zone by capillarity.

For more detail on northern soils and cryopedogenic processes in this area, see Tarnocai (1973), Pettapiece et al (1978), Zoltai and Tarnocai (1974), Janz (1973), and Day and Rice (1964).

Vegetation

Only the vegetation at Boot Creek and the Caribou Hills site will be discussed in this section. For detailed discussion of the composition and distribution of the plant communities which are common in this area, see Mackay (1963), Lambert (1972), Cody (1965), and Corns (1972). Wein (1975) discussed revegetation of the 1968 Inuvik burn.

The plant communities in the valleys of Boot Creek and the Caribou Hills site can most conveniently be divided according to whether they occur on deep or shallow active layer sites (Figure 2). Hydric sites would confound this dichotomy but they are not of importance in this thesis.

Generally, shallow active layer sites are dominated by species which rely primarily on vegetative reproduction. Deep active layer sites are dominated by species which rely primarily on sexual reproduction.

1. Deep Active Layer Sites

Deep active layer sites include steep south-facing slopes, sites with near-surface gravels, and narrow areas along water-bodies. Where the site is extremely xeric-- e.g., a steep sandy spur-- vegetation is lacking or consists of scattered individuals of such drought-tolerant species as *Vaccinium vitis-idaea* and *Juniperus communis*.

On moderately drained south-facing slopes, the canopy is dominated by paper birch. White spruce is usually only a minor canopy component except along creeks and gully sides. Tall shrubs include alder (*Alnus crispa*) and willows (*Salix* spp.), especially on the wetter sites. Low shrubs include wild rose (*Rosa acicularis*) and *Shepherdia canadensis*. Prostrate vascular plants and cryptogams include *Vaccinium* vitis-idaea, Linnea borealis, Hylocomium splendens, and Eurhynchium pulchellum.

Where deep active layer sites have been recently burned, the early recolonization depends on the proximity of seed sources and the depth of burn. Light-seeded species such as paper birch, fireweed (Epilobium angustifolium), and Calamagrostis canadensis can have quite high densities on sites where there is little Of remaining. Alder and willow species along gullies and creeks often remain unburned or are able to sucker from surviving roots (Wein, 1975). Bryophyte diversity is much reduced: Ceratodon purpureus is often the sole bryophyte.

2. Shallow Active Layer Sites

These sites include north-facing slopes, gently sloping south-facing slopes, poorly drained flat areas, and the rolling tablelands above the valleys. Typically, the only tree species is black spruce, although sometimes there are isolated dense stands of paper birch. Stunted white spruce can be relatively numerous on such sites only if they are in close proximity to deep active layer sites. Black spruce are numerous at Boot Creek Valley and often achieve very high densities of thin stunted stems. Many of these black spruce stems are the result of layering. At the Caribou

Hills site only a few stunted black spruce clones were noted.

Tall shrubs are usually absent from such sites. Low shrubs are typically ericoid species such as Betula glandulosa, Vaccinium uliginosum, Rubus chamaemorus, Arctostaphylos rubra, and Ledum decumbens. Creeping vascular plants include the ubiquitous Vaccinium vitis-idaea and Empetrum nigra. There is a rich diversity of mosses with Sphagnum teres and Aulacomnium palustre often dominating the cover. Hummock tops and inter-hummock depressions tend to have different micro-communities, although the distinction is frequently blurred by the great asymmetry of most hummocks.

Colonization following fire depends on the depth of the remaining Of. Where the burn only skims the surface, the ericoids return via suckering. Where there is little or no Of remaining, colonization is primarily by the light-seeded species more commonly associated with the deep active layer sites. Even in a burn of low intensity, the bryophytes usually must colonize from adjacent unburned areas. Polytrichum strictum is often the first moss to colonize the lightly burned areas.

Evidence of Human Disturbance

At the Caribou Hills site there was no evidence of human interference of any kind. At Boot Creek, although the edge of the town of Inuvik is only a few hundred meters away, there is also little evidence of important human interference. The Inuvik townsite is new (late 1950s) and was not previously occupied by either Indians or Inuit (pers. comm. with local inhabitants). The only apparent human disturbance at the study area are a few skidoo trails, two long-unoccupied dug-outs, a few trees which have been cut, and a fire-guard bulldozed in 1968.

The degree to which Inuvik limits its environmental interaction to only the delta, the airport, and the road south, is remarkable. During an entire summer of research, the author did not see a single non-scientist in the burned area east of Airport Road.

Airport Road was built in the 1960s and Boot Creek was forced to flow through a wide culvert under the road. Whether this causes greater than ordinary ponding upstream of the road during snowmelt is not documented. Certainly, there is no apparent difference in density or vegetative vigour between the white spruce stems near the road and those found on similar sites elsewhere in the area.

Summary

This chapter briefly examined the literature dealing with the uplands in the Mackenzie Delta area, with a particular focus on the valleys of the two study sites: Boot Creek and the Caribou Hills site. The climate is cold and dry, and the growing season curtailed. This is an area of continuous permafrost, and periglacial geomorphic processes predominate.

Soils at Boot Creek and the Caribou Hills site are silty loams and sandy loams, respectively. The hydrological cycle is characterized by a run-off peak during the spring snow-melt.

Vegetation can be roughly characterized in terms of active layer depth. Sexual reproduction is more important on deep active layers than on shallow active layers. White spruce is much more common on sites with deep active layers. Fire can cause short-term yet drastic changes in active layer depth.

CHAPTER III

METHODS

Introduction

The methodology was selected to emphasize a comparison of certain aspects of vegetative and reproductive vigour along transects in burned and unburned areas in relation to selected site factors. Amongst the site factors, soil conditions were included so as to check on which soil factors might be important in short-term or long-term occupancy of sites.

Vascular plant species were identified using the flora of Porsild and Cody (1980). The bryophytes were identified by D. Vitt of the University of Alberta. The lichens were identified by J. Case of the University of Calgary.

Statistics

Statistical analyses consisted only of linear regressions and difference of means tests. The variables used in these regressions will be discussed in the text.

It should be noted that the observations in the regressions represent averages. This of course inflates the r square values. However, the emphasis will be on comparing the r square values for various predictors rather than on the statistical significance derived from the F tests. Averaging of observations is common in ecology. For example, averages of monthly climatic data are extremely common in fields such as dendrochronology (Fritts, 1976). In some instances averages are the only meaningful way of dealing with the data. For example, if one wishes to predict tree height using active layer depth, then a single active layer measurement at the base of the tree is absurd. Given the distribution of the root system of the tree, only an averaging of local active layer depths would be ecologically meaningful.

Vegetation and Active Layer Depth

1. Boot Creek

The study area at Boot Creek consisted of burned and unburned areas at the southwest corner of the 1968 Inuvik burn (Figure 1, and Plates 1 and 2). Two subjectively chosen transects were run from the creekbottom upslope to the rolling tableland above the south-facing slope, one being in the non-burned area (Transect 1), and one in the burned area (Transect 2). Each transect was run approximately north to south. A fireguard lay between the two transects. Transect 1 is about 50 m west of the fire-guard; Transect 2 is about 150 m east of the fire-guard.

Stands (10 m square) were sampled every 20 m along each transect for slope angle, altitude, and percent cover for each plant species present. Slope angle and altitude were measured in the center of each stand. Percent cover was estimated separately for different height strata. These strata were cryptogams, 0 to 30 cm, 30 cm to 1 m, and greater than 1 m.

Four 1 m square quadrats were located at the corners of each stand. The Of, Om, Oh, or LFH depths were recorded for each quadrat. The organic horizon designation was made qualitatively in the field using the Von Post Scale of Decomposition (Canadian System of Soil Classification, 1978).

Active layer depths were measured with a calibrated steel rod at each quadrat. All active layer depth measurements were made in the period August 3 to August 6, 1982, so that the results would be comparable. As mentioned above, these measurements should represent the great majority of active layer thaw for the year (Haag and Bliss, 1974).

At Transect 1, all white spruce stems greater than 3 m in height were cored, and their dbh (diameter at breast height), height, and evidence of cone production or chlorosis recorded. This was done for all tall stems inside or outside of stands on the transect. Sections of Transect 1 (10 by 30 m along the alluvial flat, and 10 by 20 m on the steep south-facing slope) were intensively sampled for white spruce. In these intensively sampled areas, all white spruce stems were aged regardless of height. For white spruce greater than 3 m tall, cores were taken 30 cm above the apparent root collar. Stems less than 3 m but greater than 30 cm tall were aged by disks taken at the apparent root collar. The very smallest stems were aged by counting the terminal bud scars.

In the burned area, a 50 ha section adjacent to the fireguard was studied for the distribution of white spruce survivors and seedlings. For the seedlings, 12 equidistant 10 m wide transects were walked parallel to the creek. The location of seedlings and their distance from a tall potential seed source were recorded to determine the relative distribution of seedlings. Survivors greater than 5 m tall were mapped with binoculars from the opposite slope.

Seedlings within the burn were randomly sampled for age determination using a random numbers table. The sampling sites were 10 m square. Additionally, subjectively chosen seedlings from the southeast corner of the burn, from the fireguard, and from recent mudflows were aged.

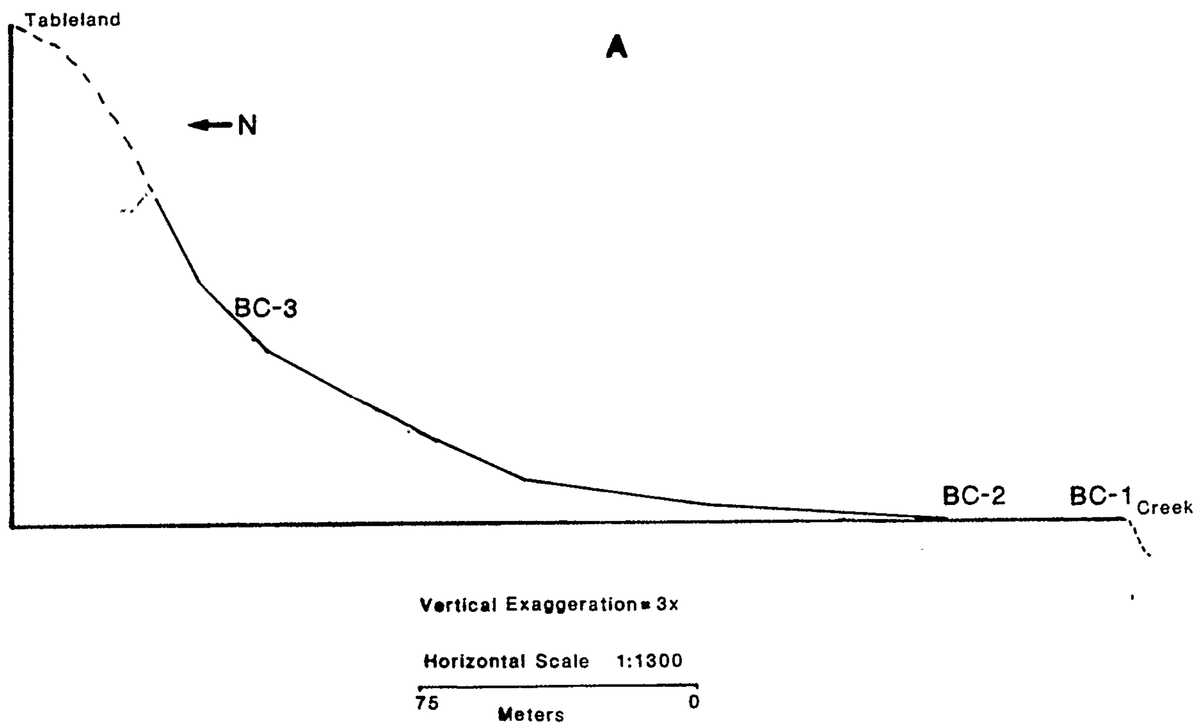
In the area not burned by the 1968 fire, it was apparent that a fire had taken place some time in the recent past. This old burn was approximately dated and partially mapped using cores from paper birch, white spruce, and black spruce, in combination with the presence or absence of surficial charcoal. The stems for coring were subjectively chosen: the criterion was that they appeared to be the oldest stems in areas of surficial charcoal.

Five soil pits were dug. At Transect 1, a pit was located at the edge of the creek, on the alluvial/colluvial flat, and on the steep slope (Figure 3A). At Transect 2, pits were located only on the steep slope and alluvial/colluvial flat since the creekside site did not burn (Figure 3B). The methodology for studying the soils is given below.

2. Caribou Hills

At the Caribou Hills site, a transect was run north-south across the valley (perpendicular to the east-west trending creek) from ridge to ridge. General vegetation data was compiled in the same manner as at Boot Creek.

Permafrost data were collected as at Boot Creek. The active layer at each quadrat was measured in late June and early August.



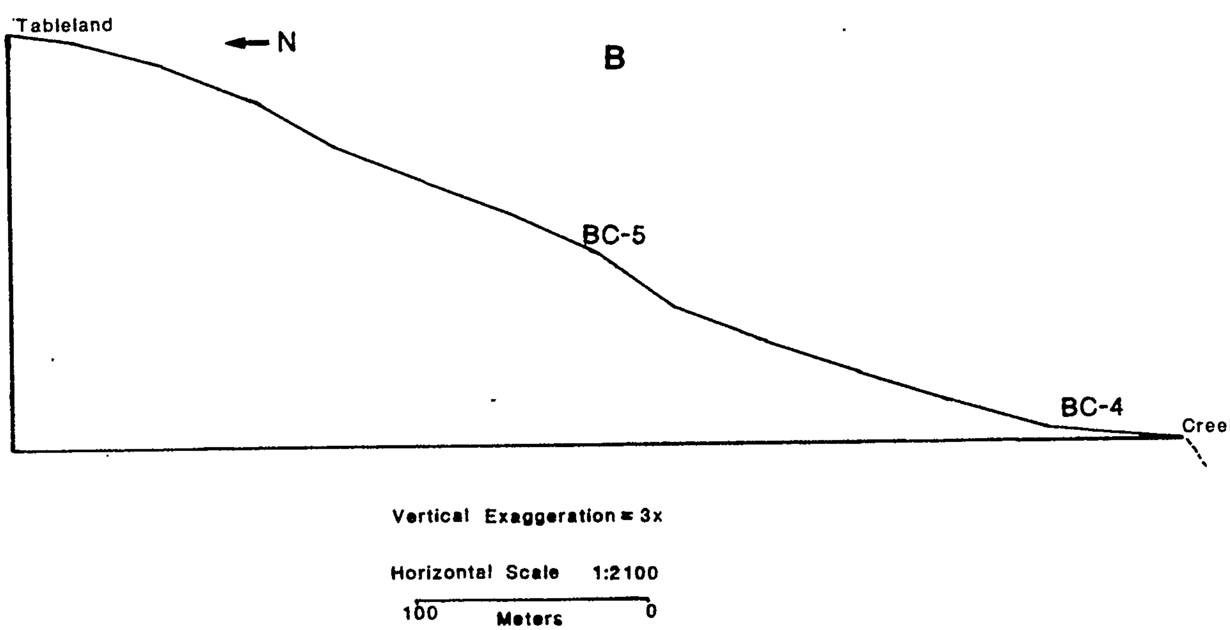


Figure 3. Location of the Five Soil Pits in Boot Creek Valley Along the Unburned (A) and Burned (B) Transects.

The major difference between the investigations at Boot Creek and the Caribou Hills site is that no demographic data were collected on either seedlings or mature white spruce stems at the Caribou Hills site. Only a few tall trees were cored in an effort to get a rough idea of the ages of the stands. Height data for trees were only recorded for the three tallest trees in each stand. The dbh was not recorded.

Only a single soil pit was dug at the Caribou Hills site. The samples from this pit were analyzed in the same manner as those at Boot Creek (see below).

Two km to the south, at the northwest edge of the 1968 burn, seedlings were sampled for age. The seedlings were taken from an earthflow which, although it lies in the burned area, predated the burn.

Methodology for Soils

In this thesis, the soils terminology is that of the Canadian System of Soil Classification (1978). At each pit, the following data were recorded: depth of the organic layer, evidence for gleying and cryoturbation, depth of rooting, and depth to permafrost. Samples from each apparent horizon were analyzed in the laboratory for pH; extractable calcium, magnesium, sodium, and potassium; particle size distribution; water holding capacity at 1/3 and 15 bars; percent organic matter; percent free iron oxides; extractable ammonium and nitrates; and rubbed and unrubbed fiber content. All soil pits were dug between August 3 and 10.

Bulk density data were not obtained during this study. In order to compare nutrients on a volume basis, it was decided to take average bulk density values from the published literature. Data were taken from pedological studies in permafrost areas in the northern Mackenzie River Valley by Zoltai and Pettapiece (1973). Problems associated with greater than "normal" densities in permafrost terrain can perhaps be alleviated by using only permafrost sites (Hollingshead et al., 1978). The values used for the horizons were (in g per cm cubed): Of = 0.25; Om = 0.40; L,F,H = 1.00; A = 1.40; and B and C = 1.9.

The following tests were performed at the soils laboratory in the Department of Geography at the University of Calgary:

1. pH was analyzed using a Fisher model 525 digital pH/ion meter. The slurry consisted of two parts distilled water to one part soil.
2. Particle size distribution was determined by the pipette method (Day, 1965). Organic matter was removed with

hydrogen peroxide. Calgon was used as a dispersant. The U.S.D.A. particle size limits were used, i.e., the sand/silt boundary at .05 mm, and the silt/clay boundary at .002 mm.

3. Rubbed and unrubbed fiber content were determined as in McKeague (1976).
4. The percentage of free iron oxides was determined with the titration method of Olson (1965).
5. Water holding capacity at 1/3 and 15 bar was determined with the pressure plate extraction method (McKeague, 1976).
6. Organic matter percentage was calculated via the titration method of Walkley and Black (1934).

The following analyses were performed by the Soils Testing Laboratory of the Alberta Agriculture Department in Edmonton. These methods (or variants) are described in detail in McKeague (1976).

7. Ammonium was extracted with 1 N KCl and determined on an autoanalyzer.
8. Nitrate and phosphorus were extracted by the weak Bray method and color developed on an auto analyzer.

9. Calcium, magnesium, sodium, and potassium were extracted with 1 N ammonium acetate and the analysis carried out on a plasma emission spectograph.

Summary

Vegetation and soils data were collected from two transects at Boot Creek, and from a single transect at the Caribou Hills site. The methodological design allows for the expression of differences in soil chemistry and vegetation on sites which are clearly different in terms of such parameters as texture, recent fire history, active layer depth, Of depth, and potential insolation. The focus of this study is on the regeneration and distribution of white spruce in relation to these parameters.

CHAPTER 4

SOILS AND ACTIVE LAYER DEPTH

Introduction

In this chapter, local variation in soil characteristics and active layer depth are examined. As the results will be used to try to understand the plant community ecology, particular attention is given to nutrient availability and rate of soil thaw, and these will be discussed in relation to stand history. Determinants of active layer depth are also examined. In this and the succeeding chapter, the central role of the organic layer in forest-tundra ecology is stressed.

Soils

The data from the soil samples from the six soil pits are presented in Tables 2 through 7. The five soils from Boot Creek Valley are named BC-1 through BC-5. These five soils were located on the two transects at Boot Creek. Their topographic locations are depicted in Figure 3. The pit at the Caribou Hills site is called CH-1. This section

Table 2. Soil Data for BC-1.

			Texture			Water Retention				Extractable Nutrients (g/m^2)							
	Depth							Organics	Fe_2O_3	Cations				Anions			
Horizon	(cm)	pH	Clay	Silt	Sand	1/3 bar	15 bar	(%)	(%)	Ca	Mg	Na	K	P	NH_4	NO_3	Comments
L,F	0-1	6.87	Not	Done		120.9	9.0	37.5	1.58	27.2	5.2	0.2	1.6	0.1	0.1	0.3	5YR 3/2; Rooty.
H	1-26	6.43	24	65	11	89.3	7.4	25.5	1.26	1136	300	5.5	22	0.5	2.9	0.5	10YR 4/3; Rooty to 26 cm.
AC	26-50	6.57	18	71	11	84.2	7.5	11.6	1.9	1035	254	9.1	31	1.3	2.8	0.4	7.5YR 3/2.
ACz	50^+																

Soil Classification: Regosolic Static Cryosol. Stand Information: 2 km east of Inuvik; 2 m north of Boot Creek. Slope angle is 0 degrees. Vegetation: a white spruce stand older than 300 years; no sign of fire; tall alder (*Alnus crispa*) and willow (*Salix* spp.); virtually no understory or ground-cover. Active Layer Depth: (early August) 80 cm at edge of creek and 50 cm 2 m from creek.

Table 3. Soil Data for BC-2.

Horizon	Depth (cm)	pH	Texture			Water Retention		Organics (%)	Fe_2O_3 (%)	Extractable Nutrients (g/m^2)							Comments
										Cations				Anions			
			Clay	Silt	Sand	1/3 bar	15 bar			Ca	Mg	Na	K	P	NH_4	NO_3	
Of	0-18	6.63		Not Done		308.7	17.5	72.4	Not Done	207	43.3	6.3	22.7	1.0	2.3	0	2.5YR 3/2; Rooty.
Om	19-20	6.48		Not Done		220.0	10.7	51.7	Not Done			Not	Done				Moderate to well-decomposed mosses just above the degrading ice.
Omz	20^+																

Soil Classification: Organic Cryosol (probably). Stand Information: 2 km east of Inuvik; about 20 m north of Boot Creek. Slope angle is 2 degrees. This area is moderately frost-heaved; the pit is located mid-way between a depression and a hummock-top. Vegetation: dominated by mosses and ericaceous shrubs. There are a few stunted white spruce (*Picea glauca*). There is no sign of recent fire.

Table 4. Soil Data for BC-3.

Horizon	Depth (cm)	pH	Texture: Clay	Texture: Silt	Texture: Sand	Water Retention: 1/3 bar	Water Retention: 15 bar	Organics (%)	Fe_2O_3 (%)	Extractable Nutrients (g/m^2) Cations: Ca	Mg	Na	K	Anions: P	NH_4	NO_3	Comments
L,F,H/ Of	0-7	6.43	Not Done			148	15.2	79.1	0.9	422	91	2.2	43.8	2.0	1.2	1.1	10YR 3/2; Rooty; Charcoal Present.
Ae	7-10	6.48	5	60	35	59.6	5.7	6.7	1.9	251	70	0.6	5.8	0.2	1.0	0.1	10YR 4/4; Few Roots.
Bf	10-16	6.72	0	75	25	48.9	4.8	4.9	5.6	517	124	1.6	10.7	0.6	0.9	0.0	2.5Y 6/4.
Cu	16-53	7.02	0	67	33	43.4	4.6	4.9	1.5	2325	435	11	43.3	3.9	2.6	0.0	10YR 4/4; Moderate Gleying.
L,F,Hb	30-32	7.01	0	70	30	67.9	6.1	11.6	1.3	96	15	0.4	1.0	0.1	0.1	Trace	7.5YR 3/2; Buried in Cu Horizon; Charcoal Present.
L,F,Hb	40-41	7.11	1	77	22	115.0	10.8	10.9	1.1	48	8	0.2	0.4	0.1	0.1	Trace	7.5YR 3/2; Buried in Cu Horizon; Charcoal Present.
Cuz	53^+																

Soil Classification: Orthic Static Cryosol. Stand Information: 2 km east of Inuvik; about 100 m north of Boot Creek. Slope angle is 12 degrees. This area burned in 1880 (note the surficial charcoal). Vegetation: dominated by *Picea glauca* and *Betula papyrifera* which seeded in after the fire. Burnt stems indicate dominance by these species for the last 300 years.

Table 5. Soil Data for BC-4.

Horizon	Depth (cm)	pH	Texture			Water Retention		Organics (%)	Fe_2O_3 (%)	Extractable Nutrients (g/m^2)							Comments
										Cations				Anions			
			Clay	Silt	Sand	1/3 bar	15 bar			Ca	Mg	Na	K	P	NH_4	NO_3	
Of	0-25	6.42	Not Done			768	20.0	92.5	Not Done	504	96	11.6	34.8	1.0	9.3	0.1	10YR 7/4; Rooty; Charcoal at 2 cm.
Cgy	25-29	6.51	Not Done			59	9.0	9.3	0.79	224	49	1.8	7.2	0.1	1.2	0.1	5YR 4/4; Gleyed.
Of	29-35	6.42	Not Done			333	22.3	85.8	Not Done	118	16	1.2	1.9	0.2	1.3	Trace	2.5YR 2/2.
Oz	35+																

Soil Classification: Organic Cryosol. Stand Information: 3 km east of Inuvik; 25 m north of Boot Creek. The slope angle is 3 degrees. The stand burned in 1968. Vegetation: both before and after the burn, the vegetation has been dominated by ericaceous shrubs and bryophytes.

Table 6. Soil Data for BC-5.

Horizon	Depth (cm)	pH	Texture: Clay	Texture: Silt	Texture: Sand	Water Retention: 1/3 bar	Water Retention: 15 bar	Organics (%)	Fe_2O_3 (%)	Extractable Nutrients (g/m^2) Cations: Ca	Cations: Mg	Cations: Na	Cations: K	Anions: P	Anions: NH_4	Anions: NO_3	Comments
Of1	0-3	6.75	Not Done			282	14.5	79.1	Not Done	60	10	0.6	8.3	0.7	0.7	0.4	7.5YR 3/2; Rooty;
Of2	3-5	6.96	3	69	28	101	9.3	Not Done	Not Done	21	3	0.2	2.3	0.5	Not Done	0.1	10YR 3/2; Rooty; Charcoal.
C1	5-11	6.76	20	55	25	36	6.3	6.1	1.9	217	184	1.8	20.3	1.0	0.5	Not Done	10YR 4/2; Rooty.
C2	11-31	6.76	21	58	21	31	5.7	4.9	1.4	1241	235	9.1	50.2	6.1	0.5	0.8	10YR 4/2; Rooty Down to 17 cm.
Cg1	31-80	7.07	20	57	23	34	7.0	3.8	1.6	3215	468	19.6	148.9	12.1	1.7	0.0	10YR 5/1; Gleyed with Mottling.
Cg2	80-90	7.08	25	55	20	32	6.3	Not Done	1.7	733	167	5.7	46.2	1.3	Not Done	0.2	10YR 2/2; Gleyed with Mottling.
Cgz	90^+																

Soil Classification: Regosolic Static Cryosol. Stand Information: 3 km east of Inuvik; about 80 m north of Boot Creek. The slope angle is 7 degrees. This stand burned in 1968. Vegetation: Dominated by *Betula papyrifera* and *Epilobium angustifolium* which seeded in after the fire. Vegetation prior to the burn is not known but neither *B. papyrifera* nor *Picea glauca* were present.

Table 7. Soil Data for CH-1.

Horizon	Depth (cm)	pH	Texture			Water Retention		Organics (%)	Fe_2O_3 (%)	Extractable Nutrients (g/m^2)							Comments
										Cations				Anions			
			Clay	Silt	Sand	1/3 bar	15 bar			Ca	Mg	Na	K	P	NH_4	NO_3	
Om	0-3	6.07		Not Done		150	10.9	61.0	0.6	14	5.4	0.8	7.9	0.5	0.9	0.5	10YR 4/4; Rooty.
C	3-50	6.18	8	30	62	29	2.1	1.2	0.3	185	69.7	5.4	41.1	21.4	3.7	21.4	2.5Y 6/2; Rooty Until 10 cm.
Cz	50^+																

Soil Classification: Regosolic Static Cryosol. Stand Information: 30 km north of Inuvik near the southern end of the Caribou Hill escarpment; .5 km east of the East Channel. Slope angle is 7 degrees. Located between edge of *Picea glauca* stand and unvegetated spur. Vegetation: *Ledum decumbens* and *Vaccinium vitis-idaea* with very poor vigour. This site probably has not burned for at least 150 years.

begins with a discussion of the histories of the stands around each pit.

Stand History

BC-1 (Table 2) is a Regosolic Static Cryosol in an old white spruce stand with dominant trees exceeding 300 years in age. Tall (greater than 3 m) willow and alder are present. The canopy cover is 85%, and there is virtually no ground-cover. There is no evidence of fire during the last few centuries. Siltation, however, is probably a recurrent disturbance. Large, rotted roots of the dominant, living white spruce are found at a depth of 40 cm at the edge of Boot Creek. The sedimentation rate, then is probably less than 20 cm in 300 years. However, sedimentation itself may be a common event on this reach of Boot Creek as the organic matter content remains quite high to a considerable depth, yet there are no clearly defined buried organic horizons.

BC-2 (Table 3) is either an Organic Cryosol or a Turbic Cryosol. It is located on a one degree slope. The Of extends down to the ice-rich permafrost. This site is dominated by ericaceous shrubs and bryophytes, and there is no evidence of recent fires. This area is probably flooded at times.

BC-3 (Table 4) is the only soil showing distinct horizonation. This soil is an Orthic Static Cryosol.

Although protected by the fire-guard in 1968, this site burned in 1880. This date was determined by using the demography of black spruce, white spruce, and paper birch, coupled with the presence of surficial charcoal. Additional charcoal layers were found at depths of 30 and 40 cm. As explained in Chapter 2, there is good reason to suppose that the two lower charcoal layers are each overlain by earthflows or soliflucted material. Therefore, both fires and mass wasting are important recent processes in the stand history. Paper birch and white spruce presently dominate the site, and these species appear to have dominated the site for quite some time. The burned white spruce and paper birch boles on the ground (killed in 1880) have diameters as large as the oldest white spruce in the area. Occupancy of this site by these two species should extend back at least to near the beginning of the most recent neo-glacial event (about 600 years BP).

BC-4 (Table 5) is a deep Of site on flat ground in the 1968 burn. The soil is an Organic Cryosol. Both prior to and after the fire, it has been dominated by ericaceous shrubs and bryophytes. The shrubs have recolonized predominantly by root suckers.

BC-5 (Table 6) is a Regosolic Static Cryosol on a 7 degree slope in the area burned in 1968. It is presently dominated by paper birch seedlings and fireweed. It is difficult to say precisely what vegetation was dominant here prior to the fire. Boles of burnt paper birch are very common nearby, but not on this site. A charcoal-rich, thin (5 cm) Of layer is found here. It is possible that ericaceous shrubs dominated this site, but were killed outright by the fire. This, however, is pure speculation.

CH-1 (Table 7) is a Regosolic Static Cryosol in an open area at the border between a dense white spruce stand and the unvegetated spur. The vegetation cover at the soil pit itself consists of ericaceous shrubs with poor vigour. The slope angle is 7 degrees. The spruce stand nearby is at least 150 years old. There is no clear evidence of recent fires in this valley in the Caribou Hills escarpment, although one charred, white spruce bole was found.

To summarize the stand histories, BC-1, BC-2, and CH-1 are the only sites to have gone longer than 150 years without a fire. BC-1 has been repeatedly disturbed by mild siltation events. BC-3 was burned in 1880, and shows evidence of repeated burning. BC-4 and BC-5 were burned in 1968. BC-1 and BC-3 are the only sites which have clearly maintained vigorous white spruce forest for at least 300 years.

All six of the soils were in the Cryosol order (i.e., permafrost was found within 100 cm of the surface). Some nearby areas would have been classified in the Regosol order because the depth of the active layer exceeded 100 cm. Such areas include sandy spurs at the Caribou Hills site and the steepest south-facing slopes at the burned portion of Boot Creek Valley.

Three of the four shallow Of soils (BC-1, BC-5, and CH-1) are Regosolic Static Cryosols. The fourth shallow Of soil (BC-3) is an Orthic Static Cryosol.

BC-2 and BC-4 are deep Of sites. The Great Group for each is probably Organic Cryosol. This is not known for certain because the control section at BC-2 is not deep enough.

Physical Properties

The CH-1 soil is a sandy loam. Sandy and sandy loam soils predominate in the southern part of the Caribou Hills escarpment. All of the Boot Creek soils are silty loams. In Boot Creek Valley, the percentage of silt is relatively constant, whereas the percentages of sand and clay change from soil to soil. Stones were absent from all soil pits except BC-3 where a few small rocks were found.

Cryturbation was found only at BC-4. This is one of the two deep Of sites. Earth hummocks were pronounced only in these two organic soils. The micro-relief was as great as 70 cm, but more typically was about 35 cm. More subdued frost-heaving was found on the seven degree slope in the burned area (BC-5), where the micro-relief averaged about 20 cm. The other soils did not show hummocks.

Gleying was evident in the lowest sections of the two soils on the south-facing slope in Boot Creek Valley (BC-3 and BC-5). It was more pronounced at BC-5, where mottling was present. Gleying was evident in the cryoturbated C horizon in the deep Of soil at BC-4. Reducing conditions are undoubtedly common through much of the summer in both the organic soils.

Aside from organic-mineral soil interfaces, distinct horizonation was only found at BC-3. Presumably, this lack of horizonation is due to the slowness of mechanical and chemical breakdown of soil particles, and to the low amount of precipitation.

Soil structure is weakly defined in all these soils. The relative lack of wetting and drying cycles may explain the poorly developed structure.

Chemical Properties

1. General

pH does not greatly differ between deep and shallow Of sites, nor between burned and unburned sites. One might have expected relatively more acidic conditions in the deep Of sites, and in those stands going the longest without fire (Wells, 1979). Generally, the pH is neutral to slightly acid. Most of the soils show a tendency toward increasing alkalinity with increasing depth, especially where the drainage is good. The lowest horizon at the BC-5 site (a Cg2 horizon) is the only one which reacted with 2 N HCl.

Organic matter is surprisingly high in virtually all mineral soil horizons. Assumedly, this is due to the slow rate of decomposition by microbial activity in these northern ecosystems (Tedrow, 1977). As one might expect, water-retention at one-third and 15 bars shows a somewhat positive logarithmic relationship with organic matter content.

Incipient podzolization was found at BC-3. The border between the dark yellow Ae and the underlying light yellow Bf is sharply defined. This thin (6 cm) Bf horizon is not, however, thick enough to be classed as a Podzolic B horizon (Canadian System of Soil Classification, 1978).

2. Nutrient Availability

This thesis is ultimately concerned with plants. Consequently, nutrient availability in the primary rooting zone (i.e., traditionally the upper 30 cm) is presented in Table 8. The units used are grams per meter square per 30 cm.

One would expect the extractable nutrients (other than nitrogen) to increase somewhat following fire (Wells, 1979).

Table 8. Extractable Nutrients in the Upper 30 Centimetres for Six Soils (in g · m^{-2}).

Stand	Nutrients								Stand Age
	Ca	Mg	Na	K	P	NH_4	NO_3	N	
BC-1	1346	349	7.3	29.1	0.8	3.5	0.9	4.4	>300 yr
BC-2	230	49	7.0	25.2	1.1	2.5	0.0	2.5	>300 yr
BC-3	2148	290	8.9	78.1	4.4	4.2	1.2	5.4	100 yr
BC-4	747	147	13.6	42.3	1.1	10.7	0.2	10.9	14 yr
BC-5	1538	431	11.7	81.1	8.3	2.0	2.4	4.4	14 yr
CH-1	121	46	3.9	31.5	12.8	3.1	12.8	15.9	>150 yr

In other words, those sites which have gone the longest without fire (i.e., BC-1, BC-2, and CH-1) should have the lowest amounts of extractable nutrients other than nitrogen (Heilman, 1968).

In general, this expectation is met. These three sites have the lowest amounts of extractable calcium, sodium, and potassium. CH-1 and BC-2 are the lowest in magnesium. BC-1 and BC-2 are the lowest in phosphorus. Exceptions can be found though, e.g., BC-1 has a high amount of magnesium, and CH-1 has a very high amount of phosphorus.

Given that each test was only run once, and that the bulk density values are a generalization from local work by Zoltai and Pettapiece (1973), it is not surprising that exceptions should be found. Also, the effects of fire depend greatly on parameters such as fuel characteristics and fire intensity (Viereck and Schandelmeier, 1980). There is, however, a broad trend in Table 8. The oldest stands tend to have the lowest available amounts of non-nitrogenous nutrients. It would appear that stand age is more important than either drainage or vegetation type in determining nutrient availability.

Nitrogen can be lost during fire through volatization (Armson, 1977). Conversely, available nitrogen often increases following fire because of increased microbial activity (Lutz, 1956). One might expect though that the oldest stands should have less available nitrogen as increasing amounts are "locked" into the biomass compartment (Heilman, 1966). Indeed, BC-1 and BC-2 do have the lowest amount of available nitrogen. However, CH-1 has the highest amount. Why this should be is not known. Virtually all of the extractable nitrogen at this site is found in the sandy loam C horizon, yet this horizon has the lowest organic matter content (1.2%) found at any soil pit. The slope (7 degrees) and the texture should insure adequate leaching downslope. There is no apparent explanation for the high amounts of phosphorus and nitrogen at CH-1.

In summary, there is a broad trend toward decreasing nutrient availability with increasing stand age. BC-2 is the only stand which has consistently low levels of each nutrient. BC-2 is a deep Of site with no evidence of fire in hundreds of years.

Van Cleve et al. (1981) show that a flat permafrost site had more extractable nutrients than a nearby, steeper permafrost-free site. Conversely, the non-permafrost site had greater productivity. Both sites were black spruce stands in central Alaska. Their explanation for the apparent anomaly is that nutrients are less likely to be leached out of the stand with the poorer drainage. Secondarily, soil temperature was lower at the permafrost site, thus relatively hampering uptake of nutrients by plants. This trend is the opposite of that seen in Table 8. This may be because the Alaskan stands were young (about 60 years since fire) and even-aged.

Active Layer Depth

Figure 4 is a scattergram of active layer depth versus Of depth. Each observation represents the stand average of four quadrats. These averages are tabulated in Table 9. The observations come from the two transects in Boot Creek Valley and the single transect at the Caribou Hills site. Thus, they include a wide variety of sites differing markedly in such factors as slope angle, fire history, vegetation, Of depth, amount of shade, soil texture, albedo, and soil moisture.

The Of depth predicts active layer thickness in a linear regression with an r of -0.78 (n = 37). This is significant at .001.

However, slope angle predicts active layer depth with an r of 0.18 (n = 37). This is not significant at .05. It must be remembered that the significance levels should not be taken especially seriously since the correlation coefficients are inflated by the stand averaging process. One can, however, regard the gross differences in the predictive prowess of the two independent variables as worthy of attention.

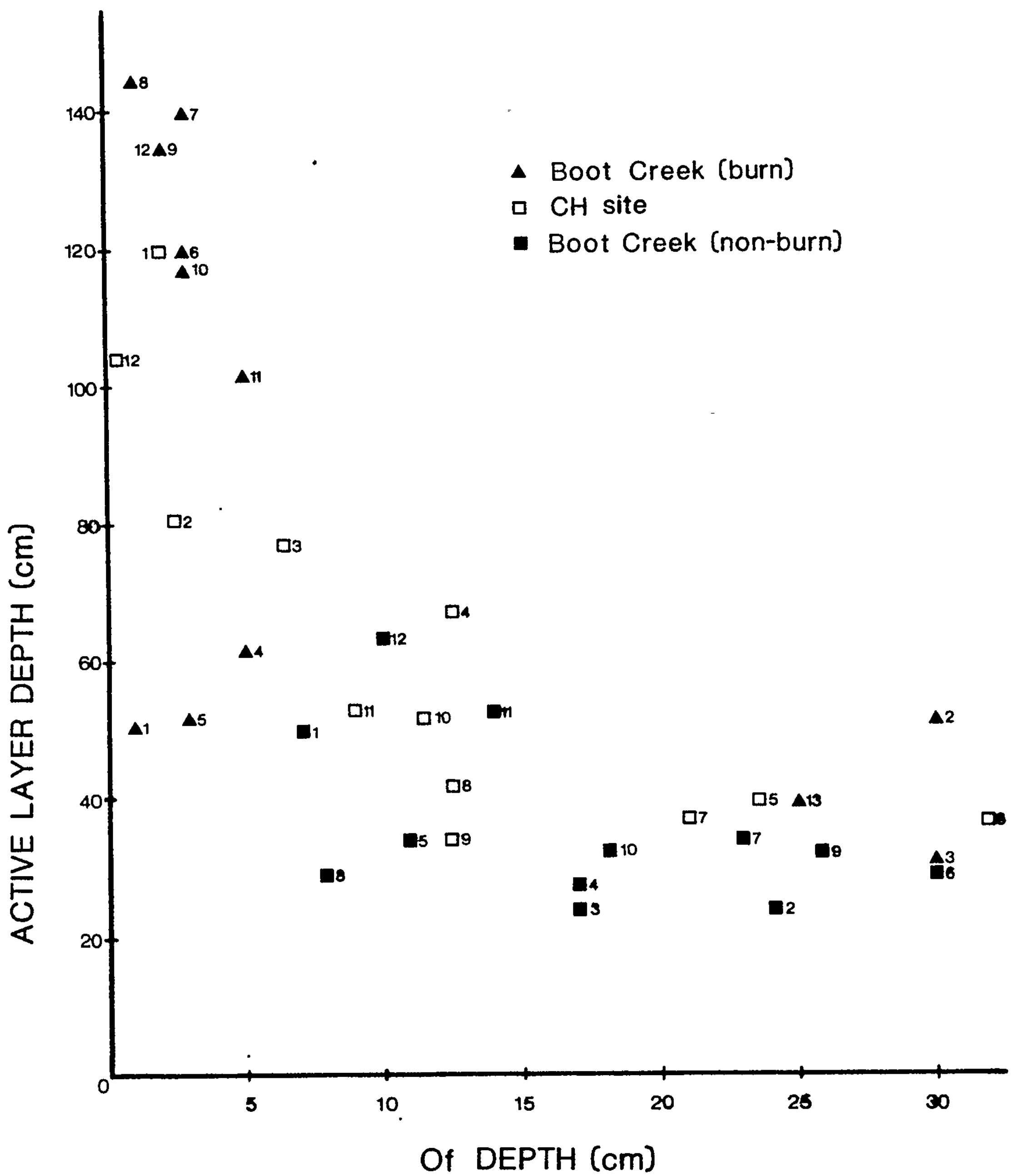


Figure 4. Scattergram of Of Depth and Active Layer Depth.

Table 9. Averages of Active Layer Depth, Of Depth, and Slope Angle Measured at 37 Stands.

	Stand	Of Depth (cm)	Slope (°)	Active Layer Depth (cm)	Texture	Aspect
Caribou	1	2	8	120	SL	Ridge-top
Hills	2	2.5	28	81	SL	South
Transect	3	6.5	30	77	SL	South
	4	12.5	14	67	SL	South
	5	23	5	40	SL	South
	6	32	1	36	SL	South
	7	21	3	39	SL	North
	8	12.5	14	42	SL	North
	9	12.6	19	39	SL	North
	10	11.5	29	52	SL	North
	11	9	19	53	SL	North
	12	0.2	2	105	SL	Ridge-top
Boot Creek	1	7	0	50	SiL	Edge of Creek
Transect	2	24	0	24	SiL	South
(Unburned)	3	17	1	24	SiL	South
	4	17	1	28	SiL	South
	5	15	1	34	SiL	South
	6	30	2	30	SiL	South
	7	23	3	34	SiL	South
	8	26	8	29	SiL	South
	9	26	9	33	SiL	South
	10	18	10	33	SiL	South
	11	14	15	53	SiL	South
	12	10	21	64	SiL	South
Boot Creek	1	1	1	51	SiL	Edge of Creek
Transect	2	30	2	52	SiL	South
(Burned)	3	30	5	30	SiL	South
	4	5	6	62	SiL	South
	5	2.5	6	52	SiL	South
	6	2.5	7	120	SiL	South
	7	3	12	140	SiL	South
	8	1	8	144	SiL	South
	9	2	7	135	SiL	South
	10	3	7	117	SiL	South
	11	5	10	102	SiL	South
	12	2	7	135	SiL	South
	13	25	3	40	SiL	Tableland

Equivalent latitude is a measure of potential insolation based on latitude, slope angle, and aspect (Dingman and Koutz, 1974). It is calculated by the equation:

$$\theta' = \sin^{-1} (\sin k \cos h \cos \theta + \cos k \sin \theta)$$

where θ' equals the equivalent latitude, θ equals the actual latitude, k equals the slope angle in degrees, and h equals the aspect in degrees. In a linear regression, equivalent latitude predicts active layer depth with an r of -0.19 (n = 37). This is not significant at .05. There are only 5 observations which are not south-facing slopes (numbers 7 through 11 at the Caribou Hills site) so it is not surprising that the correlation coefficients for slope angle and equivalent latitude are almost equal (although opposite in sign).

Relative to potential insolation (i.e., equivalent latitude), Of depth is a good predictor. That it predicts so well across such a variety of sites is surprising.

In Figure 5, an exponential curve has been fitted for the observations in Figure 4. For this curve, the r value increases only from -0.78 (the linear regression) to -0.79. One reason for this small change is the break in the line between 15 and 18 cm of Of depth. At Of depths less than

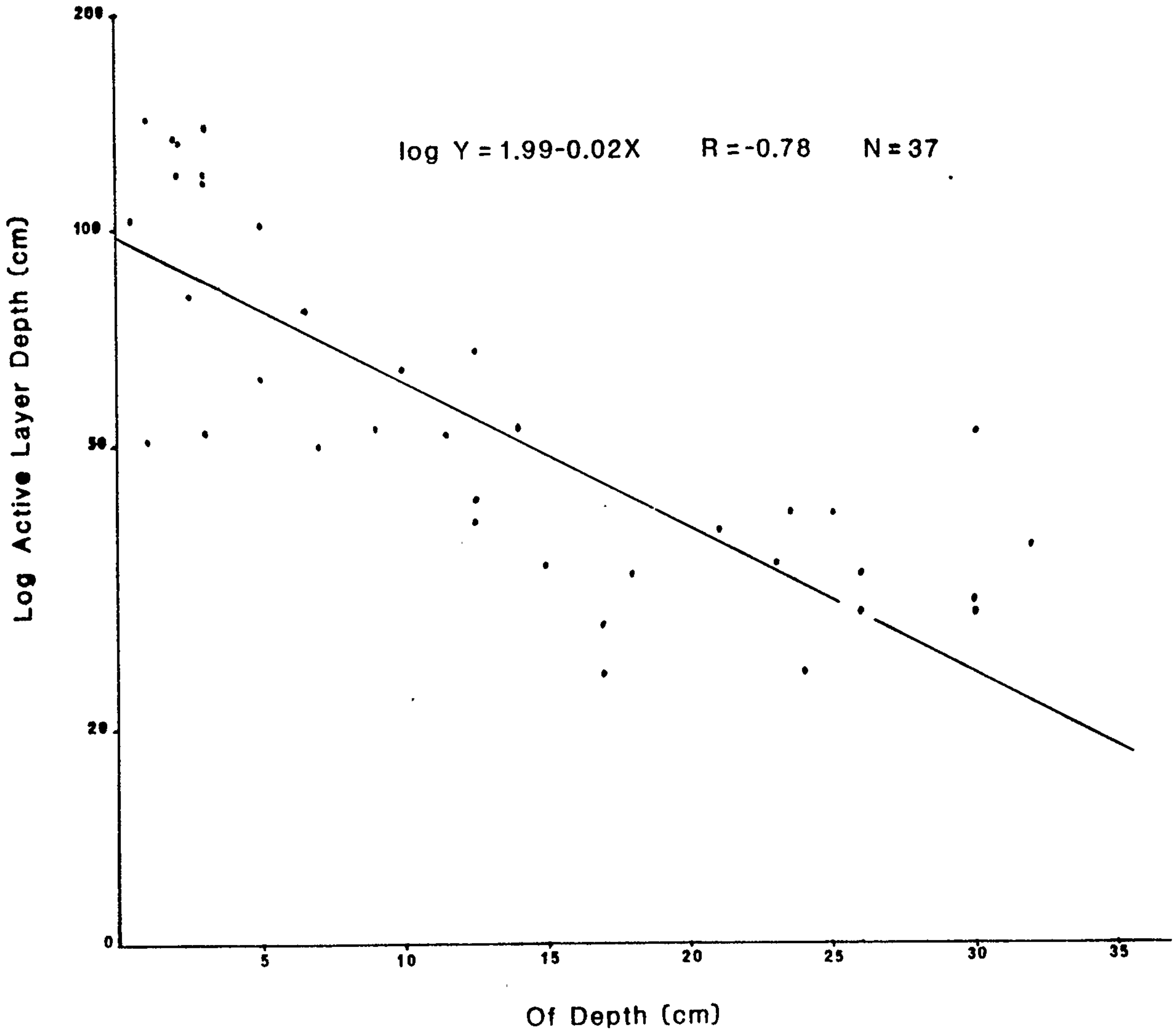


Figure 5. Of Depth Plotted Against the Log of Active Layer Depth.

15-18 cm, the observations are roughly exponential (i.e., straight on semi-log paper). Above 15-18 cm of Of depth, there is little or no change in active layer depth with increasing Of depth.

One explanation for this lack of change at Of depths greater than 15-18 cm is that, given the local climate in the summer of 1982, this value represents an equilibrium between air temperature and the insulative properties of the Of. That is, it does not matter whether the Of depth is 15 cm or 15 m, the local climate (for that summer) will thaw the soil to a depth of about 25 cm.

Further evidence for this interpretation lies in the differences in texture and fire history between the transects. There are not enough observations greater than 15 cm of Of depth (see Figure 4) to permit difference-of-means tests between transects on that portion of the curve. Qualitatively, one can however say that differences between lightly burned and unburned stands are not of apparent importance where the Of depth exceeds 15-18 cm. There does appear to be some difference between silty loams and sandy loams (the Caribou Hills site) on this portion of the curve. It may be that the underlying texture exerts an effect by limiting the amount of moisture in the Of. Reduced moisture content would effect a lower diffusivity value (Oke, 1978).

This Of depth of 15-18 cm represents a critical value given the climate at Inuvik during 1982. One imagines that the critical value would fluctuate with year to year changes in the climatic variables, but the degree of variation remains to be determined.

Of depth explains 61% of the variance in Figure 5. It is noteworthy that much of the loss of explanatory power occurs in the part of the curve to the right of the critical 15 cm value. The virtual lack of slope in this portion of the curve is causing a reduction in the value of the correlation coefficient. It is paradoxical that the part of the line where Of is most predominant is where it predicts the poorest. If one plots a regression for all observations greater than 15 cm of Of depth, the correlation coefficient is 0.06 (N = 14). This is not significant at .05. If one plots a separate regression for all observations less than 18 cm of Of depth, the correlation coefficient is -0.84 (N = 26). This is significant at .001 (Figure 6).

The rest of the unexplained variance in Figure 4 is presumably to be apportioned among factors such as sampling error, potential insolation, soil moisture (insofar as it is not perfectly intercorrelated with Of depth), snow depth and duration, and albedo.

By the first week in June in the Caribou Hills escarpment, snow was only noted (by aerial reconnaissance)

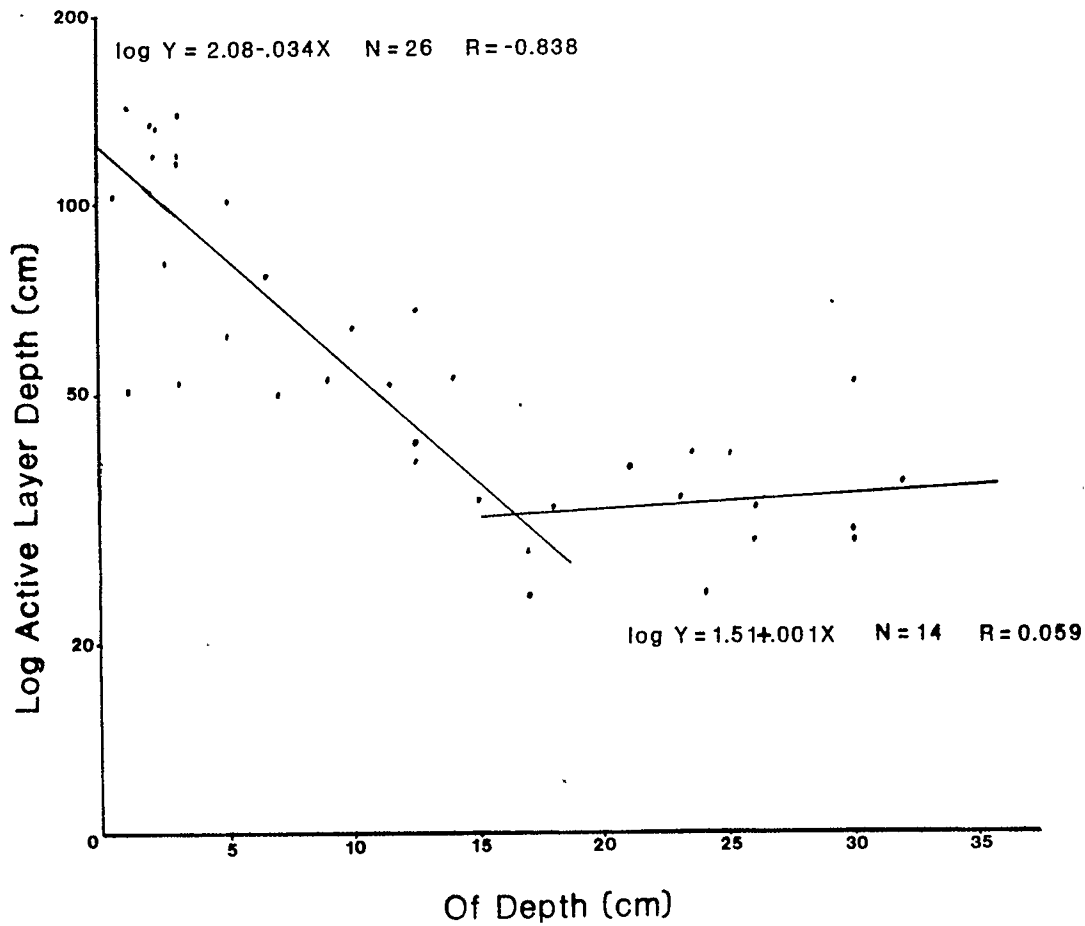


Figure 6. Separate Regressions of Of Depth on the Log of Active Layer Depth.

in nivation hollows on the edges of the tableland above the escarpment valleys. By 25 June, the (eventual) deep active layer soils were already much more deeply thawed than the (eventual) shallow active layer soils. The mineral soils (steep south-facing slopes) had an average active layer depth of 22.6 cm. This is 25% of the total thaw in early August. More gentle slopes and north-facing slopes averaged 9.8 cm on 25 June. This is 23% of the total thaw in early August. Thus, even at the beginning of soil thaw in the early summer, the deep active layer soils were twice as deep on average as the shallow active layer soils. This differential rate of thaw in ice-rich and ice-poor sediments has also been reported by Bliss and Wein (1971) and Van Cleve et al. (1981). As shown below in Chapter 5, this difference in rate of thaw may have tremendous consequences for the distribution of white spruce in the northern forest-tundra.

Given roughly equal time for loss of snow cover, it is likely that the rate of thaw is controlled primarily by ice content. At some sites, running water is also of importance. Ice content, in turn, is controlled primarily by Of depth, texture, and drainage. As already pointed out, where Of depth exceeds a critical depth, it tends to over-ride the effect of texture. This is because of the very high water retention capacity of the Of (see Figures 2 through 7). Nor does Of respond to drainage (i.e., a moisture gradient) in a simple manner. Deep Of layers can be found on 10 degree south-facing slopes on Transect 1 at Boot Creek. Intuitively, Of depth is also governed by fire frequency and intensity, and by plant synecological variables such as leaf fall and cover value.

One might guess that snow depth and duration would be important factors in the rate of thaw in the spring and early summer. At Boot Creek, however, snowmelt appeared to occur at approximately the same time on all slopes. The snow appeared (qualitatively) to be deeper on south-facing slopes than on north-facing slopes. The snow melted more rapidly on the south-facing slope because of, presumably, greater insolation. Snow depth and duration are perhaps not then of major importance in explaining the differential thaw in the Inuvik area.

Potential insolation appears to be much less important than ice content in determining the rate of thaw. It must be remembered that June thawing occurs when insolation values for north-facing and south-facing slopes are not greatly different (Huovila, 1970).

Deep active layers near the edges of perennial creeks are the result of three factors. First, flowing water hastens the thaw of the bank sediments. Second, as discharge decreases and the bank is exposed, longwave radiation can penetrate the bank both from the upper surface and from the side. Third, the leaf fall of alders and willows, coupled with sedimentation events, retard the build-up of an appreciable Of layer. Active layer depths decline radically with increasing distance from the creek. Within 80 cm of the bank edge, the active layer depth is 80 cm. Two meters from the edge, the active layer is 50 cm deep. Five meters from the edge, the active layer is 28 cm deep and the Of layer is thick.

In summary, it appears that drainage (insofar as it correlates with Of depth) is more important than texture in determing local active layer depths. Texture is only a factor where drainage is good. In either case, soil moisture is the key factor.

Soil moisture affects active layer depth by requiring greater amounts of inputs of energy to effect the change of state from ice to water or water to vapour. Secondarily, high soil moisture values abet the development of a thick Of. This organic layer in turn may act like a sponge, keeping the soil moisture values high. The capacity for deep Of layers to develop on the steeper slopes should be a function of soil texture, evapotranspiration, fire history, and plant synecological relationships. For example, frequent, intense burns or heavy deciduous leaf fall can retard the development of a thick Of layer on a steep south-facing slope. Conversely, light, infrequent fires may promote the development of a thick Of layer by removing the source of the litter fall without greatly changing the substrate (i.e., the developing Of layer). It is interesting that steep, north-facing slopes typically have deep Of layers, whereas steep, south-facing slopes typically do not. Because of lessened evapotranspiration, the north-facing slope should offer a wetter substrate. The relationship between Of thickness and micro-site drainage should be, then, synergistic. Consequently, fires following drought may be less intense on the north-facing slope. In the 1968 burn, mineral soil was often exposed by the fire on south-facing slopes. Such mineral soil exposure was, by contrast, rare on the deep Of north-facing slopes. There are no studies in the forest-tundra which indicate whether mineral exposure is more frequent on the south-facing slope because more of the ground-cover was burned or because it was simply thinner prior to the burn.

Summary

The soils examined in this area are Cryosols. Static Cryosols correspond with deep active layers, lower soil moisture, shallow or absent Of layers, and they are usually found on steep south-facing slopes or by the edges of perennial streams.

Organic Cryosols (or Turbic Cryosols where the organic layer is too thin to qualify as an Organic soil) correlate with shallow active layers, high soil moisture, pronounced frost heaving, and deep Of layers. They are usually found on north-facing slopes and on the more gentle south-facing slopes.

There appears to be a broad correspondence between nutrient availability and stand age. The deep Of site that had gone at least 250 years without fire showed the least extractable nutrients in the horizons.

The depth of the Of explains 61% of the variance in active layer depths across a wide variety of sites. Fifteen to 18 cm of Of depth appears to represent a critical equilibrium value, given the climate during 1982. At that Of depth, effects of texture, drainage, or potential insolation become much less important.

One might speculate that rate of thaw is governed mainly by ice content. Where drainage is good, texture is an important variable. In either case, soil moisture is the ultimate cause.

Chapter 5

WHITE SPRUCE ECOLOGY

INTRODUCTION

In this chapter, the vegetative and reproductive vigour of white spruce stems is examined in relation to substrate characteristics. Additionally, the fire ecology and seed dispersal capacity of northern forest-tundra white spruce are examined. The summary at the end of the chapter serves to sythesize the arguments introduced in this and the preceding chapter.

White Spruce Reproductive Ecology

1. Vegetative vigour of matures.

Sakai et al (1979) pointed out an apparent correspondence between active layer depth and vegetative vigour in both white spruce and black spruce in the Inuvik area. The small sample size used, the wide range of time in which active layer depth measurements were made, the wide variance in tree ages, and the lack of information concerning the history of the stands, made their study less than substantive.

The relationship of active layer depth to height and diameter of stems for Transect 1 at Boot Creek is shown in Table 10. Only the stems in the age classes 50 to 95 years are used for the comparison as it is pointless to compare mensuration for stems of widely differing ages. Ninety-five years is used as a cut-off point because it was determined that the steep slope and footslope of Transect 1 were inside a burn perimeter dated at approximately 1880 (see below). These ages are uncorrected: the variance in growth to 30 cm is too great for fixing an exact or "somewhat exact" age. Rather than apply some averaged correction factor, it was decided to present the uncorrected ages. No stems aged by disks at the apparent root collar or by terminal bud scars are used in Table 10.

Table 10 shows that there are greater height and diameter values for stems on deep active layers. This differential vegetative vigour cannot be merely an artifact of increased potential insolation because the stems along the creek show roughly the same height growth as the steep slope stems. Regressing the original observations (n = 53) rather than the averages of Table 10, active layer predicts tree height with an r of 0.688, whereas slope angle predicts tree height with an r of 0.567. The difference between the two predictors could have been much greater if the sampling

Table 10. Tree Mensuration From Transect 1 for the Uncorrected Age Classes 50 to 95 Years. *

	Creek	Alluvial flat	Colluvial flat	Footslope	Steep slope
Average Slope (°)	0	0.75	4.3	9	18
Average depth of Of or LFH (cm)	3	20	27	24	13
Average active layer depth: Aug. 4, 1982 (cm)	50	27	30	28	58
Number of Trees (50 to 95 years)	3	6	3	23	18
Average height of stems (m) (50 to 95 years)	9.8	2.5	5.0	6.3	11.0
Density of stems per m^2	0.02	0.015	0.004	0.03	0.02
Evidence of recent burning	none	none	none	surficial charcoal	surficial charcoal
% of trees (2m) with no evidence of cones on branches or near base (all ages)	8	68	100	62	0
% of cone-bearing stems with long axis of cone 2.5cm (all ages)	92	19	0	50	96
chlorotic needles (all ages)	no	common	common	uncommon	no

*Uncorrected age equals the age at 30cm. Stems cut at the base are not included.

design had been stratified: only three creekside stems are included.

Suppression of growth by shadeing should only be a major factor along the creek where the cover value of tall shrubs and trees (80 percent) is greatest. The canopy white spruce along the creek are older than 300 years. By contrast, cover values on the flat average only a few percent. Differences in shadeing, then, only serve to accentuate the differences in height between stems on shallow versus deep active layers.

Density-related poor vegetative vigour should be most important on the steep slope and footslope where the densities are quite high. Both areas burned in the 1880 fire. As with shadeing, density-dependent curtailment of vegetative vigour only highlights the differences between shallow and deep active layers sites.

Regression on dbh indicates that active layer depth is, again, a better predictor than slope angle. Taking stand averages for the 50 to 95 year-old stems (n = 11) at Transect 1, active layer depth predicts dbh with an r of 0.909, while slope angle predicts with an r of 0.644.

When age classes are disregarded and the average height of the three tallest stems in each stand is examined, then active layer still explains more of the variance than does slope angle. This is not a local artifact. Using observations from Transect 1 (silty loam) and the Caribou Hills site (sandy loam), active layer depth predicts the averaged height with an r of 0.69, while slope angle predicts with an r of 0.338. For both regressions, N = 20.

Reconnaissance showed that the taller stems along creek edges and on steep south-facing slopes were almost always taller than the flat site (shallow active layer) stems.

Dead and dying stems are more common on the shallow active layer sites. Dead stems constitute 38 percent of all stems greater than 3 m tall on the shallow active layer stands of Transect 1. None of the taller stems on the deep active layers sites were dead. This is not a result of stand age. The flat and creekside stands appeared to have escaped the 1880 fire and the tallest stems in both areas were over 300 years old. Both the footslope and steep slope stands originated in 1880, yet stems were already dying on the footslope. None of the post-1880, steep slope stems were dead.

As detailed above, potential insolation is not the chief factor governing the vegetative vigour of these stems. The soils data in Chapter 4 do not indicate any important difference between deep and shallow active layer sites in terms of pH. Parent material is held relatively constant at Boot Creek. The differences in vegetative vigour are best explained in terms of nutrients, soil temperature, rate of thaw, and aeration.

Effectively, the shallow and deep active layer soils can be regarded as organic and mineral soils, respectively. Examination of the soils data in Chapter 4 indicates a concentration of available nutrients in the upper horizons of the mineral soils and throughout the profile of the organic soils. The rooting zone (including the largest roots) of white spruce in the mineral soils appeared to be confined to the upper 25 cm of the profile, with the greatest concentration in the upper 10 cm. For the seedlings, the greatest concentration of fine roots was found in the upper four cm: the O or LFH horizons. This is typical of conifers (Armson, 1977). Safford and Bell (1972) found that over 50 percent of the fine roots in a white spruce plantation were concentrated in the upper 5 cm (FH). The reason for this is that this is the zone of the greatest density of nutrients, and of the more optimal temperature and aeration regimes (Armson, 1977).

By contrast, it appeared that most of the fine roots of the seedlings on the organic soils were concentrated between 5 and 12 cm below the surface. The upper surface of the organic soils dries out rapidly in the intervals between summer rain because of the lack of shade and wind-breaks. Further, the extremely low bulk density of the upper few cm should enhance the rate of evaporation. The living mosses themselves transpire quite freely when water is available. Given the low summer precipitation in the forest-tundra, it is reasonable to assume that the upper 10 cm of organic soils are much drier than the corresponding depth in the nearby mineral soils. The upper 10 cm of the organic soils may well contain large amounts of extractable nutrients but they are perhaps not available during much of the summer.

In Chapter 4, it was shown that thawing at the Caribou Hills site began at roughly the same time in early June for north-facing and south-facing slopes, and for flat areas. But by late June the mineral soils on the steep slopes were already much more deeply thawed than the organic soils on the shallow active layer sites. Given the relative distribution of fine roots in mineral soils versus organic soils, it follows that mineral soils provide, effectively, a longer growing season than do the organic soils. The difference may be as great as 3 or 4 weeks. Given that the growing season is only about 3 months long, a 3-week difference could be crucial.

The primary rooting zone is displaced downward in organic soils, and, likewise, the horizon of greatest decomposition rates may be displaced downward. The effective season for bacterial action at this depth will be less than at the upper horizons of the mineral soils.

Consequently, there may be less available nutrients in the organic soils than in the mineral soils. This may explain the consistently low levels of nutrients found at the deep Of soil pit BC-2 (Chapter 4). Time since fire is an important factor, but rate of thaw and mean soil temperature may also be important. Table 10 indicates how widespread chlorosis is in the leaves of the white spruce on the organic soils. Chlorotic leaves can be caused by a number of deficiencies including nitrogen. Nitrogen has been shown to be extremely limiting for the growth of tundra and forest-tundra species on shallow active layers because of low soil temperature (Haag, 1972).

The lowest portion of the active layer in organic soils may also be a poor environment for white spruce roots. Lees (1972) concluded that poor aeration strongly limits the vegetative vigour of Picea sitchensis seedlings in peaty soils. Root development was concentrated in the better aerated horizons of the soil. Heikurainen (1982) showed that fertilized and artificially well-drained peat soils in Finland produced Picea abies seedlings which were as vigorous as those on fertilized mineral soils. Thus, the few cm of soil profile in the perched water table immediately above the degrading ice is a very poor environment for a period of time during the growing season.

In summary, it appears that stems on deep active layer sites (mineral soils) have greater vegetative vigour than do stems on shallow active layer sites (organic soils). A complex of factors is involved. An important factor is that the effective growing season length is shorter on the shallow active layer sites. Additionally, available nutrients, and/or the ability to take up these nutrients, may be less because of, ultimately, lower soil temperatures. Another factor is the poor aeration in the lower portion of the active layer on organic soils.

2. Vegetative vigour of seedlings.

Table 11 depicts the relationship between site characteristics and vegetative vigour in seedlings. For each site-type in Table 11, only the 10 tallest seedlings were used. Only the age classes 8, 9, and 10 years old are used in the table. It seemed more sensible to average the 10 tallest rather than average the total sample for each site because density-dependent mortality at the most densely-populated sites will assuredly remove the smaller stems during the next few years. Thus, averages of the 10 tallest seedlings allows one to compare the vigour of those seedlings most likely to survive. Another reason to take the taller stems is that the optimal sites would have the poorest average vigour if one included all seedlings in the

Table 11. Seedling Mensuration at Boot Creek Valley.

	Ave ht (cm)	Ave diameter (cm) at root-collar	Ave Of depth (cm)	Highest density per 10 m square	Cover (%) of tall shrubs & trees	Chlorotic needles common
Non-burn gentle slope	14.5	0.2	20	6	1	yes
Non-burn steep slope	17.0	0.5	12	5	40	no
Burn steep slope	31.0	0.8	1	90	0	no
Post-1968 earthflows	17.0	0.5	0	23	0	no
Pre-1950 earthflow*	7.0	0.3	7	19	1	no
Fire-guard	7.0	0.2	0	34	0	no

* This is the only site not located at Boot Creek Valley. It is found at the northwest corner of the 1968 Inuvik burn.

mean: even a poorly growing seedling can survive a few years on an optimal site. A nine-year-old only a few cm long could not survive on the deep Of because of the necessity of extending leaves above the mosses, and of extending roots below the most desiccated surface layer.

The differences in vigour between sites is similar to the differences noted for matures. The height of seedlings above the root collar is much greater for seedlings on deep active layers-- especially in the burn area.

Differences in seedling diameter at the root collar are also marked. Seedlings at the burned sites have much greater diameter growth than do seedlings at unburned sites. The non-burn seedlings on the steep slope may have low diameter values because they endure high cover values (40 percent). No seedlings were found in the creekside stand where the cover value is 85 percent.

The seedlings on the non-burn shallow active layer sites have very low diameter values. Certainly, the discussion (see above) on the nutrient, temperature, and aeration regimes of shallow versus deep active layer sites is germane. The root collars of the non-burn shallow active layer sites tended to be a few cm below the surface of the Of. It seems reasonable that the seed commonly germinates a few cm below this low bulk density surface. In the root classification scheme of Wagg (1967), the root system form commonly displayed on this site is an elongated taproot. This is the typical form for white spruce on the best drained sites where there is no subsurface impediment (Wagg, 1967). As detailed previously, the primary roots must penetrate relatively deeply to secure summer-long moisture and nutrients. Conversely, the stem must extend upward a few cm before the cotyledons are exposed to direct insolation. This rate of stem extension must be greater than the rate of Of aggradation. The seedlings are, then, elongate but very thin. Such demands are costly: there are no sites in the non-burn where seedling density is nearly as great as in the burn (where density values can be as high as 90 seedlings per 10 m square) or on recent earthflows.

Table 11 only hints at the differences in vigour between seedlings on burned deep active layer sites versus non-burn shallow active layer sites. Qualitatively, the number of leaves on the burn seedlings is very much higher than the number on the deep Of non-burn seedlings of the same age. Some of the non-burn seedlings have only a few chlorotic leaves and a few thin lateral roots. Holding age constant, the tallest non-burn seedlings never appeared to have as many leaves as the shortest burn seedlings.

The mobilization of nutrients subsequent to burning is of tremendous consequence in vegetative vigour for at least the first few years after fire (Wein, 1975). Further, the increase in near-surface soil temperatures may accelerate decomposition (Rowe and Scotter, 1973). In addition to the lack of shade, these factors may explain the difference in vigour between seedlings on burn and non-burn deep active layers.

Seedlings on earthflows can have quite high densities if seed sources are nearby. Earthflow toes remain damper than most sites in this area. The toes, however, often have a dense cover of Equisetum. By contrast, competition for light, nutrients, and soil moisture is low on the earthflow channels. The channel surface can, however, be quite dry: most of the earthflow channels examined had mudcracks on the surface.

The "old" earthflow (at least pre-1948 in origin) at the northwest corner of the burn had a thin rivelut of running water during most of the summer. This water was supplied by active layer thaw upslope. The moss depth was only a few cm. Vigour was poorer on this old earthflow than on the more recent flows because, perhaps, of problems associated with aeration.

Common features of earthflows in the Mackenzie Delta area are high "levees" along the perimeter. These heaped-up areas are composed of sediment in a matrix of shrubs and tree trunks. The bulk density of these levee soils is, on the whole, very low. Hollow spaces are common. Seedlings were never found on the levees. Possibly, these sites are too dry for good establishment. Similarly, no seedlings were found on the heaped-up edges of the fire-guard. The common vegetation on both the levees and the bulldozer-created mounds is wild rose and fireweed.

Table 12 shows the relationship between age at 30 cm and site characteristics. In all cases, these data probably represent much better than average growth for each site. For the non-burn sites, the stems with the poorest growth are less likely to survive and, thus, be available for sampling. For the burned sites, only the tallest 7 seedlings had reached 30 cm.

The difference between sites in Table 12 is clear: stems on the burn grow to 30 cm about 3 times as fast as those on any site in the non-burn. The standard deviation within sites is great, especially for the non-burn shallow active layer. Partially, this is simply a function of sample size, but spatial and temporal differences in micro-site characteristics and in stand history are undoubtedly also of importance. As can be seen in Table 12, attempts to derive correction factors and arrive at exact ages for cored stems are pointless.

Table 12. Age at 30 cm for Immature White Spruce.

	Ave age at 30 cm ht	Ave age of sample stems	# of stems used	stan. dev. of age at 30 cm	cover (%) of tall trees & shrubs	Ave active layer depth (cm)	Ave slope angle (°)
Boot Creek non-burn gentle slope	22.2	44.5	4	21.3	1	25	1
Boot Creek non-burn steep slope	20.8	42.2	5	8.3	40	58	17
Boot Creek (tallest seed-lings in burn)	8.7	9.1	7	0.5	0	91	12
CH site steep slope	25.3	30.0	3	6.8	60	74	15

3. Cone production.

As there was virtually no cone crop during the investigation, conclusions about differential reproductive capacity for stems on deep versus shallow active layers must rely on indirect evidence and be regarded, therefore, as very tentative. However, the local distribution of stems leads to the conclusion that the more vegetatively vigorous stems are responsible for a disproportionately large share of the seedling establishment.

The taller trees (i.e., on the deep active layers) have many more open cones evident around their bases than do the more stunted stems on the shallow active layer sites. The stunted stems commonly show much smaller cones (Table 10). Old opened cones still clinging to branches are much more common on the taller trees.

Although the seed crop in conifers is typically inversely correlated with vegetative growth during and for some time after the crop, the relationship between vegetative vigour and long-term reproductive activity is usually positive (Kozlowski, 1971). The great differences between the vegetative vigour of seedlings and matures on deep versus shallow active layer sites has been discussed above. Environmental conditions that favor rapid vegetative growth in conifers tend to induce earlier flowering (Schmidtling, 1969). The more vegetatively vigorous individuals tend to have earlier reproduction (Harper and White, 1974), and larger seed crops (Larson and Schubert, 1970; Fowells and Schubert, 1956). For an even-aged white spruce stand in Manitoba, Waldron (1965) showed that the more vigorous stems produced far more seeds than the shorter suppressed stems. Sarvas (1962) showed that *Pinus sylvestris*, a European treeline species, has increased seed production and flowering as soil fertility increases. Poor seed production in conifers is typical of stems on nutrient-poor sites (Kozlowski, 1971).

If stems on the shallow active layer sites produced seeds as readily as those on the deep active layer sites, then it follows that isolated stunted stems (e.g., more than 100 m from a deep active layer site) should show local densities and/or age structures similar to that found on the deep active layer sites. Nothing like this appears to occur in the Inuvik area. Invariably, the isolated white spruce stem (e.g., on the tableland or north-facing slope) has no other stems nearby. Such isolated stems appear to be the product of relatively long-range chance dispersal by deep active layer stems. Dense, yet stunted stands were only found in close proximity to tall trees located on deep active layers, e.g., on narrow sections of alluvium/colluvium between a steep south-facing slope and a creek.

4. Demography in non-burned areas.

Figure 7 depicts the ages for the (smaller) stems from Transect 1 (unburned) which were cut at the apparent root collar or aged via terminal bud scars. Because of extreme variability in early growth in treeline white spruce, these stems more closely approximate exact ages than do the stems cored at 30 cm. However, because of problems such as adventitious rooting, and missing or false rings, the stems in Figure 7 should not be interpreted as exact ages. They should be, however, on average within a year or two of the exact age.

The youngest age classes (less than about 4 years old) are undoubtedly underestimated as these youngest seedlings are, given the methodology, difficult to find in deep moss. On the one occasion where a small plot of ground was examined, a few first-year germinants were found. These individuals are not included in the demography.

As can be seen in Figure 7, seedling establishment has been common during the last 70 years. Even if one assumes that elimination of all sources of error in ageing the stems would increase the intervals between establishment, the error is probably no more than a year or two on average; thus, the intervals would still be quite short. Assumptions

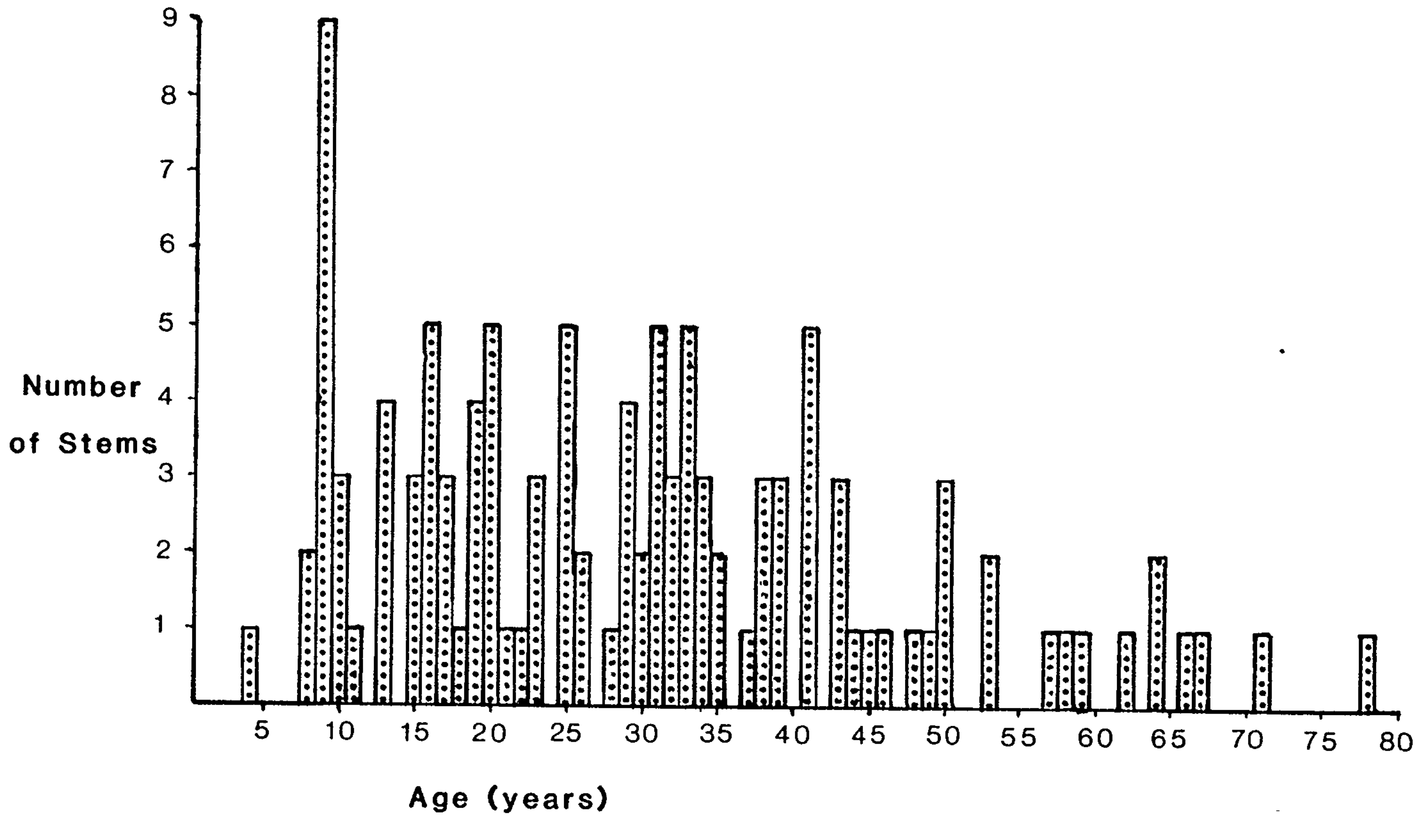


Figure 7. Demography of Stems Cut at the Root Collar or Aged by Terminal Bud Scars.

of perfect synchrony in flowering, or of increasingly long seed production intervals with increasing latitude, are perhaps unwarranted (Hagner, 1965).

The average establishment interval for the stems cored at 30 cm is much longer than that shown in Figure 7. That is expected though as the cored stems range up to 325 years of age. As pointed out above, the data from the cored stems are less persuasive because of the great variability in growth to 30 cm.

Figure 7 emphasizes that, in this area at least, seedling establishment intervals are not especially long. One would guess that seed production intervals should be even shorter than the seedling establishment intervals. The magnitude of the seed production interval indicated here would not be considered unduly long in the interior of the range of white spruce. It is unlikely then that the length of the seedling establishment interval is an important determinant of white spruce treeline in this area. One might argue that it is the magnitude of the seed rain which is of prime importance. This argument is examined in the following section.

White Spruce Fire Ecology

1. Seedling demography.

The number of white spruce seedlings younger than 13 years old which were aged was 185. Of these seedlings, 94.1 percent germinated in the 3-year period 1971, 1972, and 1973. The year 1971 had 15.7 percent of the total seedlings, 1972 had 49.2 percent, and 1973 had 29.2 percent. This temporal distribution was not a local artifact but was similar for burned areas at the southeast and northwest corners of the burn, for recent and pre-burn earthflows, and for non-burned areas on both deep and shallow active layers (Figure 7).

These data should not be misinterpreted as evidence of differential seed production preceding the germination years. Survivorship curves are not known.

A problem with these data is that the very youngest age classes are undoubtedly being relatively underestimated. Given the sampling methodology, 1982 germinants and slightly older seedlings are very difficult to perceive as one walks. On the virtually unvegetated surfaces of earthflow channels, the very youngest stems should be easy to see. The temporal distribution on earthflows is, however, much the same as on other sites. Perhaps the underestimation is not very great.

Paper birch and black spruce seedlings in the burn and non-burn were also aged in the expectation that they might help in interpretation of the white spruce seedling demography. Paper birch seedlings were more varied in their age class distribution. Only 15 of the taller seedlings were (subjectively) sampled. The number in each class from 1969 to 1974 was about equal. By contrast, 88.5 percent of the black spruce seedlings (n = 62) germinated in the period 1969 to 1972. The percentage breakdown was 1969 (14.5 percent), 1970 (27.4 percent), 1971 (30.6 percent), and 1972 (16.0 percent). This temporal distribution is in rough agreement with Wein (1975).

It is tempting to look to meteorological data to ascertain the causes of the 3-year burst of white spruce recruitment in the early 1970s. Such an attempt would be misguided. Sexual reproduction and germination represent a 3-year process with bud differentiation in the first summer, seed maturation in the second, and germination in the third summer (Zasada et al., 1978). The optimal meteorological conditions for success at each stage may not be identical. Mortality curves are not known. It would be impossible to disentangle the optimal climatic configuration.

It seems likely that optimal conditions for bud formation and seed maturation are similar (i.e., conditions causing relatively high amounts of photosynthate.) If one hypothesizes that the same conditons are, at least, reasonably good for germination-- or that germination success is primarily dependent on seed size-- the contagiousness of the temporal distribution is not hard to interpret. Conversely, there may be simply no marked synchrony in flowering in these northern forest-tundra stands. Many scenarios are possible. With the data presented here, all such scenarios are hopelessly speculative.

Ignoring the underrepresentation of the very youngest seedlings, there are, for the period 1969 to 1980, three good years of recruitment. Together with the demographic structure presented in Figure 7, these data reinforce the idea that these northern outliers are not the reproductive cripples the literature so often suggests. If the fecundity of these stands is a local anomaly, no one has advanced a plausible explanation for it. The concept of very low (or an utter lack of) recruitment in northern forest-tundra stands has become a commonplace. Yet there is not a single published demography for either white spruce or black spruce at treeline which includes the youngest stems. Elliott (1979) claims to have demographic data which demonstrates the lack of recent recruitment in both black and white spruce at treeline; these data have still not been published.

The magnitude of the seed rain per stem is undoubtedly lower here than in the interior of the species' range, yet densities as high as 90 per 10 m sq (Table 11) are evidence that the seed rain is ample for regeneration. These seedlings average 9 years old; one might guess that much of the density-independent mortality has already taken place. Such densities for 9 year-old seedlings would not be considered low by foresters working in the heart of this species' range. Such high densities are, however, rarely achieved in the burn. The problems of seedbed quality and seed dispersal capacity are detailed in the next two sections.

2. Spatial distribution of seedlings in the burn.

The seedlings in the burn were contagiously distributed. In the 50 ha study area at Boot Creek, most of the 470 seedlings censused were found in about 10 clusters.

The average O depth at the base of each seedling at one of these clusters was 7 cm (n = 73). The average O depth for quadrats on Transect 2 was 9 cm (n = 48). A difference of means test shows that this is not significant at .05. However, the average O depth at the most lightly burned stands of Transect 2 was 33 cm (n = 8). A difference of means test between O depths at the cluster of seedlings and at the lightly burned portion of Transect 2 is significant at .001. No seedlings were found in any quadrat on Transect 2. Given the discussion in Chapter 1 on the optimality of mineral seedbeds, one wonders why the low O areas of Transect 2 (primarily steep slopes) do not have seedlings. Seedling clusters in the burn were found on earthflows, fire-guards, virtually unvegetated slopes, and in the most deeply burned areas of the alluvial/colluvial flats. These clusters were commonly associated with dense stands of fireweed and vigorous paper birch seedlings. As explained above, a deep Of layer should be a poorer seedbed than shallow Of layer.

Much of the burned steep slopes have little or no Of, yet they are uncolonized by white spruce. The explanation for this lies in the poor seed dispersal capacity of the surviving white spruce.

Examination of the spatial distribution of seedlings showed that 96 percent of the 470 seedlings were within 30 m of a tall survivor, and that approximately 80 percent were within 15 m. Seedling densities tended to be greatest near the greatest densities of tall survivors. Of the 470 seedlings, 72 percent were near the creek, 25.5 percent near the gullies, and only 2.5 percent in the inter-gully steep slope areas. As detailed in the following section, 100 percent of the tall survivors were found near gullies or by the creek.

One wonders whether the main reason for the lack of colonization of the inter-gully areas is droughtiness rather than distance from a seed source. I think xeric substrates are an unlikely explanation because:

1) the inter-gully areas were densely colonized by light-seeded species such as fireweed and paper birch. Seedlings of these two species were almost always found in association with white spruce seedlings where nearby seed sources for the latter were present.

2) the taller of the white spruce seedlings in the inter-gully areas were as vigorous as the taller seedlings found near a gully or creek.

3) burned stems with good vigour prior to the burn can be found in the inter-gully areas.

Droughtiness in the inter-gully areas at Boot Creek may be a problem but there is no evidence to indicate that it is nearly as critical a factor as proximity to seed sources. As pointed out in Chapter 1, for most wind-dispersed species, seed dispersal capacity is closely related to tree height (Harper, 1977); dispersal in conifers is typically limited to within a horizontal distance of twice the tree height (Viereck and Schandelmeier, 1980). Given that the tallest trees here average about 15 m tall, the figure of 96 percent of seedlings within 30 m of a tall survivor does not seem unreasonable. Therefore, the seed dispersal capacity of white spruce is severely curtailed in these treeline stands.

On the lightly burned deep Of sites on the flat, no seedlings were found. One might guess that this is because the sampling method did not allow the area to be scrutinized as closely as the intensive section of Transect 1. Conversely, where the burn is of low intensity on deep Of, vegetative reproduction by (primarily) ericoids is vigorous, and white spruce seedlings may find themselves rapidly outcompeted for light. One might speculate that, given nearby seed sources, the total density of white spruce seedlings on lightly burned deep Of may be less than on unburned deep Of.

On the mildly burned parts of the steep slope, willow species and (especially) alder return vigorously through root suckering. White spruce seedlings were not found in the shade of these already tall shrubs. Again, competition for light may be important.

In summary, it would appear that the optimal seedbeds for both high densities and good vigour in the ninth year can be tentatively defined. These optimal seedbeds have less than 10 cm of Of, have had a burn intense enough to prevent suckering, and have seed sources within 30 m. From a distance one would see this seedbed only as a red cover of fireweed near some tall surviving conifers. From a few meters away, one would mainly note the vigorous (over 1 m tall in many cases) paper birch seedlings. It would require very close examination to reveal the white spruce seedlings. Many investigators claim that, qualitatively, there was no apparent regeneration after burning. One wonders how closely they looked, or if they looked at areas close by surviving conifers.

These optimal seedbeds are not often near the base of a survivor, i.e., where the seed rain is likely to be the greatest. There are no fire-scars. It would appear that the tree either burns and dies or it does not burn at all. Survival requires that the burn does not reach the tree. Consequently, the immediate area near the tree did not burn, or did so only lightly. This was especially true near the creek: the greatest seedling densities were found between about 10 and 20 m away from the seed sources.

3. Survival of matures through fire.

The seed dispersal capacity of this species at treeline is low. It follows that continued occupancy of treeline valleys (or disjunct sections of valleys) is greatly dependent on survival through fire.

In the 50 ha burned area studied at Boot Creek, 100 percent of the surviving tall stems were found within 10 m of the creek or gullies. Four out of five south-facing slope gullies had tall survivors (though sometimes only a few stems). Of the surviving 245 tall stems, 12 percent were clustered along the gullies and 88 percent along the creek.

The methodology employed for mapping survivors allows enumeration of only the taller stems, i.e., approximately greater than 5 m in height.) Extremely stunted, surviving stems were sometimes found away from the gullies or creek in the dense shade of alder which had not burned at all. The importance of these stems as future contributors to the seed rain is very questionable.

The distribution of tall survivors at Boot Creek is similar to that found at a recent (late June, 1982) burn about 30 km southeast of Inuvik. At this recent burn, fire seldom could burn down the steeper south-facing slopes. Slope angle on south-facing slopes seemed to control the likelihood of burning. Steep north-facing slopes were more commonly burned than south-facing slopes. The tableland, a black spruce/lichen woodland, was extensively burned. This new burn was probably quite mild compared to the 1968 Inuvik fire. In 1968, the fire followed an 86-day drought (Wein, 1975).

Given the low seed dispersal capacity, the distribution of survivors at these two burns helps explain the tendency of white spruce stems to be restricted to or near steep south-facing slopes and the edges of water-bodies. Mean fire return intervals are, perhaps, too short to allow a great deal of colonization of the high fire frequency areas. It is unlikely that the ephemeral nature of fire-created seedbeds is an important factor. After 150 years wind-throw of senescent paper birch stems should be common. Prior to that, wind-throw of burned stems will be common. Wind-throw depressions are ideal, though very disjunct, seedbeds.

As there are no fire-scars, potential survival through fire should be greatest where fire frequency is lowest. Intuitively, such sites should include:

1.) near water. This includes sites which are either perennial or (when deeply incised) ephemeral. Water is an obvious fire break. Even shallow ephemeral water channels constitute a fire break if there is plentiful subsurface drainage toward the channel: the local vegetation should be less flammable during the prolonged droughts which likely precede the most intense fires.

2.) on or below a steep slope. All fires have relative difficulty burning downhill. Downhill spread of fire appears to be especially difficult for the low intensity fires that characterize the northern forest-tundra.

3.) near areas which are bare of vegetation because of very low soil moisture.

Any point on the landscape where one or more of these three conditions are effective should have relatively low fire frequency. One might deem such areas examples of a "peninsula effect". It follows that white spruce should be most common where the peninsula effect is great and where the total area of such affected sites is large. However, given the low seed dispersal capacity of these stems, the total area should not be greatly disjunct. Reconnaissance in the uplands of the Mackenzie Delta area indicates that the great majority of white spruce stems are restricted to or very near areas of low fire frequency. Examples are appended below.

At Boot Creek Valley, white spruce survivors are restricted to the creek and the more deeply incised (about 1 to 3 m) south-facing gullies (Plates 1 and 2). About .75 km east of the fire-guard in Boot Creek Valley, the south-facing slope becomes more gentle, there are no gullies, and there are no burned stems to indicate that white spruce has occupied this area in the last few hundred years. The Of remains deep, suckering shrubs dominate the vegetative recovery, and there are no white spruce seedlings.

As mentioned above, the June 1982 fire southeast of Inuvik rarely burned down into the steeper south-facing slopes. The average slope angle on these south-facing slopes appeared to be greater than at Boot Creek. White spruce stems on the south-facing slope and at the bottom of the steep-sided narrow valleys were seldom burned.

About 15 km south of Campbell Lake (i.e., about 30 km south of Inuvik), a burn which occurred in 1968 (not the Inuvik burn), often left the creekside white spruce untouched. The gentle plain around the creek was dominated by black spruce prior to the fire and is now dense with black spruce seedlings. Survival of black spruce matures was rare.

The heavily-dissected Caribou Hills escarpment represents a north-trending salient of dense vigorous white spruce stands. The northern edge of the 1968 Inuvik burn rarely penetrated downslope into the southern part of the escarpment. Slope angles of 25 degrees are common in the southern half of the escarpment, The gullies in the valley sides are deep (Chapter 2) with the inter-gully areas (i.e., sharp spurs) frequently bare of vegetation. Tall white spruce are confined to the gully-sides and bottoms on the south-facing slope (Plate 3). They are found along the (typically ephemeral) creeks only in a few of the escarpment valleys. Given the steep slope at the top of the gullies, and the bare slopes on the adjacent spurs, fire can only approach easily from one direction. These gullies are like very narrow peninsulas. Where the escarpment becomes markedly more gentle (about 9 km north of Reindeer Station), white spruce are rare. Further north, the escarpment again become steep, and white spruce are, again, common. Beyond this area (about 20 km north of Reindeer Station) the escarpment becomes very gentle and the air photos taken during this investigation no longer indicate tall white spruce stands along the western edge of the Caribou Hills.

About 50 km north of Reindeer Station lies the mouth of Holmes Creek. A few km east of the creek-mouth, tall dense stands of white spruce are common within the tight meander lobes of the creek (Plate 4). This creek has very high sinuosity and is margined by relatively steep terraces. I have seen this creek only from the air but one would guess that the active layers are relatively deep because the creek is perennial, and because the lobes are dense with willow and alder. The leaf-fall of willow and alder helps suppress Of development (personal observation). Flooding/siltation also aid in moss suppression.

Other Factors

1. Low soil moisture.

Droughtiness is important locally in determining the distribution of white spruce. The steep sandy spurs of the Caribou Hills escarpment are frequently bare of vegetation. Salt crusts are common on these bare areas. Prostrate drought-tolerant shrubs such as _Juniperus communis_ surround the bare areas. Where the spur becomes more gentle, or in the adjacent gullies, soil moisture increases and the vegetation is dominated by tall paper birch and white spruce.

Tarnocai (1978) pointed out that, in the low arctic at least, mean active layer depth should decrease with increasing latitude. Independent of fire cycles, the deepest active layers in this area are found on coarse bare slopes. These sites are unavailable to white spruce because of the very low soil moisture. Optimal sites for white spruce should become more narrowly defined with increasing latitude. The deep active layer sites are increasingly droughty (Tarnocai, 1978). The shallow active layer sites have increasingly shorter thaw seasons, i.e., effective growing seasons.

2. Wind.

Wind-- in reality a factor-complex of desiccation, snow blast, and low temperature-- does not appear to be as important as the other factors discussed in the preceding sections. Verticils are rare. There is little evidence of flagging except on exposed ridge-tops. Such sites are poor sites for white spruce regardless because of low soil moisture.

It is possible that on the gently rolling sandy terrane of the Caribou Hills tableland, wind is an important factor. Species which are common to both the tableland and the adjacent, more sheltered escarpment valleys, are shorter on the tableland. The upper shoots of the tableland shrubs are often dead and, apparently, scoured by snow blast. The rare white spruce stems on the tableland show the same effect. Wind, however, cannot be the only factor rendering the tableland unsuitable for white spruce. The slope angle change from escarpment to tableland is often abrupt. Tall trees in the upper gullies are within reasonable seed dispersal distance of the tableland, yet seedlings are rarely found. Because of the snow cover, tableland seedlings should be relatively unaffected by any destructive effects associated with high winds.

3. Animal predation.

I have seen no evidence that animal predation on white spruce is important in this area. Although they must exist, I saw no piles of shucked cones. I saw or heard only two tree squirrels (*Tamiasciurus hudsonicus*) at Boot Creek, and only one in the Caribou Hills. I saw only a single arctic ground squirrel (*Spermophilus parryii*). That so few were seen or heard makes one guess that their densities are quite low. No white-winged crossbills (*Loxia leucoptera*) were seen. Perhaps these low densities of the typical seed predators are due to deleterious habitat modification by the 1968 burn. It is difficult to say.

It seems unlikely that species which rely primarily on conifer seeds (such as those listed above) and are found at the northern limit of conifers, could maintain appreciable densities. The low densities of stems and seeds, the disjunct local distributions of the two conifer species, and the normal pattern of frequent poor seed production years in white spruce, combine to keep seed predator populations, assumedly, very low.

Summary: the Local Distribution of White Spruce

In this section, the results from both Chapters 4 and 5 are summarized. The main constraints on the local range of white spruce are:

1. Depth of the active layer. White spruce is restricted to the deeper active layer sites because shallow active layer sites have:
    a) poorer aeration above the degrading ice.
    b) shorter effective growing seasons.

c) decreased supply of available nutrients (although time since fire plays an important role).

d) a higher probability of mortality through fire without the subsequent creation of the more optimal seedbeds.

e) poorer vegetative growth and, therefore, poorer seed dispersal capacity.

f) reduced reproductive vigour (probably).

g) desiccation in the upper few cm throughout much of the summer.

2) Fire. Given the relatively low seed dispersal capacity and (one would guess) low magnitude of the seed rain in the northern forest-tundra, fire constrains via:

a) restricting white spruce to areas of relatively low fire frequency. These areas must occupy some minimal total area in terms of likely dispersal; otherwise white spruce will be removed probabilistically. An ideal site only a quarter hectare in extent but surrounded for a great distance by flat terrain (i.e., high fire frequency) is useless for long-term occupancy.

b) poor seedbed creation. On balance, fire is probably a "destructive" factor for white spruce at treeline (Wein, 1975). Although good seedbeds are often created, such seedbeds are useless unless surviving matures are nearby. Fire is likely a "contructive" factor only where the probability of local survival is very high (e.g., the Caribou Hills escarpment). High fire frequency might be "constructive" in the sense that the Of layer is kept so shallow that good seedbed creation becomes a general feature. However, this phenomenon is likely to be of more value to light-seeded species such as paper birch and fireweed rather than white spruce.

3) Xeric soil conditions. Low soil moisture prohibits white spruce establishment on some sites. Although such sites have, intuitively, the very lowest local fire frequencies, white spruce cannot take advantage of it. In coarse terrane,

droughtiness should become an increasingly important constraint with increasing latitude.

CHAPTER SIX

CONCLUSIONS

General Conclusions

The local (and regional) distribution of white spruce is apparently constrained by fire regime, Of depth, and droughtiness. However, other factors are undoubtedly involved, and their importance will vary in space and time.

As discussed in Chapter 1, many authors-- e.g., Nichols (1976), Larsen (1980), Bryson (1966), and Ritchie (1972)-- have looked for palynological and pedological evidence of treeline flux to support arguments about changes in arctic air-mass frequencies. Effectively, they assert that a change in treeline of n km equals a change in mean annual temperature of n degrees C. The lag period is undefined. This straightforward relationship presupposes two facts. First, we must be able to adequately define "treeline". Given the tremendous dispersal capacity of spruce pollen (see Chapter 1), and the manner in which site characteristics can be more important than potential insolation, one wonders whether such exact definition is available to palynologists. As Colinvaux (1967) points out, palynology is, in the north, a very blunt instrument. Second, the argument assumes that "treeline" must march in lock-step with arctic air mass frequency (allowing for a lag period). Given the constraints outlined in this paper, one doubts that this must necessarily be true. Must fire frequency and intensity, for example, change in a facile manner with changes in arctic air mass frequency? There is absolutely no data to support such an assumption either way. Given the importance of site characteristics, it seems one must redefine arctic treeline as a broad zone which is, perhaps, hundreds of kilometers in width. Latitudinal migration of such a broad zone is difficult to monitor palynologically except in the most general sense.

An important point in this thesis is that establishment events are by no means unusual for this species in this area. Yet the literature suggests that such events must be exceedingly rare. Additionally, it is thought that treeline recruitment patterns should be very sensitive to short-term changes in climate (Elliott, 1978). In essence, treeline stands are barely able to produce enough photosynthate to provide for self-maintenance (Kay, 1979; Mitchell, 1973). Accordingly, recruitment events are quite rare and they reflect the abnormal departure from arctic air mass dominance during the summer. As pointed out earlier, there are no demographic studies prior to this thesis which include the younger stems. Is there something anomylous about the Inuvik area? Is there some reason why, as Larsen (1980) suggests, the western forest-tundra is in "equilibrium" with present climate whereas the Keewatin treeline is a Hypsithermal relict? Elliott and Short (1979) reported reasonable recruitment for white spruce at treeline in Labrador. Marr (1948) reported good post-fire recruitment near Hudson Bay. These qualitative descriptions remain minority reports. One does not doubt that investigators have found white spruce stands where, qualitatively, there were no seedlings or saplings. Such stands are undoubtedly common. Yet virtually all of the forest-tundra remains unexplored in terms of forest ecology. In particular, sites dominated by white spruce have been neglected. White spruce seedlings are both difficult to see and very contagiously distributed (especially in recent burns). Might there not be many scattered hectares of well-dissected terrain where regeneration is adequate? It seems likely. But adequate recruitment is not a guarantee of long-term occupancy. These optimal sites may not support white spruce in the long-term because, given their small extent, the species will be probabilistically removed by fire.

It is interesting that white spruce is the arctic treeline conifer in the more heavily dissected areas of

North America. From the Mackenzie Delta west to the Bering Strait (Viereck, 1979), and in Labrador (Elliott and Short, 1979), white spruce forms the conifer treeline. In the intervening area, from the Caribou Hills escarpment to Labrador, i.e., essentially the Canadian Shield, black spruce is the common treeline species. One might intuitively argue that the white spruce treeline areas are, in sum, more heavily dissected than is the Shield. Black spruce is better adapted to fire than is white spruce because of such traits as semi-serotiny and layering (Black and Bliss, 1980; Larsen, 1980). It is impossible to disentangle clearly the relative contribution of fire regime, soil temperature, rate of thaw, Of seedbeds, soil aeration, and drought in the determination of white spruce treeline in the Inuvik area or across the continent. All these variables are inter-correlated. The argument presented here does, however, make clear that fire has been underestimated as a treeline determinant in the literature. This importance of fire is, likely, the only conclusion reached in this thesis which will surprise anyone. Wein (1975) sent out a questionaire on fire in the tundra and forest-tundra. Most respondents were not aware of fires ever occurring so far north. Yet everywhere the present author went during the field season, there was evidence of fire. In the valley of the Caribou Hills site, in the three charcoal layers in the soil pit at Boot Creek, in the tundra-dominated tableland above the valleys, at sites along the Dempster Highway south of Inuvik-- evidence for old fires is commonplace if one makes some effort to look for it. This often requires digging or looking closely at the root collars of shrubs. Dating these fires where trees are absent or rare may well be impossible. But this methodological problem should not prevent us from seeing that fire, although less frequent with increasing latitude, is not necessarily of less consequence.

Suggestions for Further Research

Studies of white spruce stands in other treeline areas are necessary to corroborate the conclusions reached in this thesis. Ideally, these future studies would be more narrowly focused than the present study. Each of the conclusions listed in the summary of Chapter 5 could serve as a separate study and occupy an investigator for many field seasons.

The aggradation of the Of layer should be a pivotal feature in any future investigation of forest-tundra or Low Arctic plant ecology. As this thesis detailed, the fire regime, rate of thaw, late-summer active layer depth, soil moisture content, and vegetation composition are all influenced by it. The most intractable problem is the relationship between the fire regime and Of aggradation.

Imagine an idealized experiment where one begins with two bare slopes which are identical. Seed dispersal is postulated as unimportant. One slope sustains a fire frequency which is greater than "normal", while the other slope sustains a fire frequency which is less than "normal". Subjecting the two slopes to differing fire frequencies for, say, 1000 years, one could end with an ericaceous assembledge on one slope and a boreal forest assembledge on the other. Of aggradation would be the key to this differentiation. These vegetation assembledges might well be (more or less) self-regenerating if the fire frequencies were then returned to "normal". In this thought experiment, it is assumed that there is some threshold value of Of depth. (Note: this hypothesized threshold should not be confused with the Of/permafrost threshold identified in Chapter 4.) Above this threshold, the "normal" fire regime cannot reduce the Of layer to some minimum depth which the boreal assembledge (taken as a whole) can tolerate-- either as seed producers or as seedlings. This hypothesized Of threshold would be an interesting line of inquiry for a series of graduate students to pursue. Experimental burning and careful examination of Of aggradation after fires of known age would help detail this relationship.

REFERENCES

Anderson, J. C. 1974. Hydrological studies at Boot Creek and Peter Lake basins during 1974. In: Further Hydrological Studies in the Mackenzie Valley. Env. Soc. Comm. for North. Pipeline Devel., Rep. No. 74-35, Canada. P. 25-61.

-------, and D. K. Mackay. 1973. Preliminary results from Boot Creek and Peter Lake watersheds, Mackenzie Delta region, N.W.T. In: Hydrologic aspects of Northern Pipeline Development. Env. Soc. Comm. for North. Pipeline Devel., Rep. No. 73-3. Canada. P. 71-111.

---------------------. 1974. Progress of hydrologic studies at Boot Creek and Peter Lake watersheds, N.W.T., during 1973. In: Hydrologic Aspects of Northern Pipeline Development. Env. Soc. Comm. for North. Pipeline Devel. Rep. No. 74-12. P. 203-225.

Armson, K. A. 1977. Forest Soils. Univ. of Toronto Press. 390 p.

Benninghoff, W. 1952. Interaction of vegetation and soil frost phenomena. Arctic 5: 34-43.

Black, R. A., and L. C. Bliss. 1980. Reproductive ecology of Picea mariana (Mill.) BSP., at treeline near Inuvik, Northwest Territories, Canada. Ecol. Monogr. 50 (3): 331-354.

Bliss, L. C., and R. W. Wein. 1971. Changes to the active layer caused by surface disturbance. In: Proceedings of a Seminar on the Permafrost Active Layer, 4 and 5 May, 1971. Nat. Res. Council of Can., Tech. Memo. No. 103. Canada. P. 37-48.

Brown, J., W. Rickard, and D. Vietor. 1969. The effect of disturbance on permafrost terrain. U. S. Army Corps Eng., Cold Regions Res. Eng. Lab, Spec. Rep. 138. 9 p.

Bryson, R. A. 1966. Air masses, streamlines, and the boreal forest. Geog. Bull. 8 (3): 228-269.

Burns, B. M. 1973. The climate of the Mackenzie Valley-Beaufort Sea. Vol. 1. Climatological Studies No. 24, Env. Canada, Ottawa. 227 p.

Canadian System of Soil Classification. 1978. Res. Branch, Can. Dept. of Agri. Publ. No. 1646. 164 p.

Cochrane, G. R., and J. S. Rowe. 1969. Fire in the tundra at Rankin Inlet, N.W.T. Annual Tall Timbers Fire Ecology Conference. April 10-11. Tall Timbers Res. Sta., Tallahassee, Florida. P. 61-74.

Cody, W. J. 1965. Plants of the Mackenzie River Delta and reindeer grazing preserve. Can. Dept. Agri., Plant Res. Inst. 56 p.

Colinvaux, P. A. 1967. Quaternary vegetation history of arctic Alaska. In: Hopkins, D. M. (ed.), The Bering Land Bridge. Stanford Univ. Press, Stanford, California. P. 205-231.

Corns, I. G. W. 1972. Plant communities in the Mackenzie Delta region. In: Bliss, L. C., and R. W. Wein (eds.), Man Modified Habitats in the Eastern Mackenzie Delta Region and the Arctic Islands. Arctic Land Use Research Program, Dept. Indian and North. Affairs, ALUR Rep. No. 71-72-14. Canada. P. 4-46.

Day, J. H., and H. M. Rice. 1964. The characteristics of some permafrost soils in the Mackenzie Valley, N.W.T. Arctic 17: 223-236.

Day, P. A. 1965. Particle fractionation and particle-size analysis. In: Black, C. A. (ed.), Methods of Soil Analysis. Amer. Soc. of Agron., Madison, Wisconsin. P. 545-567.

Day, R. J. 1964. The microenvironments occupied by spruce and fir regeneration in the Rocky Mountains. Can. Dept. For. Publ. No. 1037. 25 p.

Dingman, S. L., and F. R. Koutz. 1974. Relations among vegetation, permafrost, and potential insolation in central Alaska. Arc. and Alp. Res. 6 (1): 37-42.

Dobbs, R. C. 1972. Regeneration of white and Engelmann spruce: a literature review with special refernce to the British Columbia interior. Pac. For. Res. Cen., Can. For. Serv. Info. Rep. BC-X-69. 77 p.

Drury, W. H., Jr. 1956. Bog flats and physiographic processes in the Upper Kuskokwin River region, Alaska. Harvard Uinv. Contrib. Gray Herb. 178. 130 p.

Dyrness, C. T. 1982. Control of depth to permafrost and soil temperature by the forest floor in Black Spruce/Feathermoss communities. U.S.D.A. Pac. NW For. and Range Exp. Sta. Res. Note PNW-396. 19 p.

Eis, S. 1965. Development of white spruce and alpine fir seedlings on cut-over areas in the central interior of British Columbia. For. Chron. 41: 419-431.

Elliott, D. L. 1979. The current regenerative capcity of the northern Canadian trees, Keewatin, N.W.T., Canada: some preliminary observations. Arc. and Alp. Res. 11 (2): 243-251.

--------, and S. K. Short. 1979. The northern limit of trees in Labrador: a discussion. Arctic 32: 201-206.

Environment Canada. 1982. Canadian Climate Normals, vols. 2, 3, and 4. Atmo. Env. Serv. Canada.

Fowells, H. A. 1965. Silvics of forest trees of the United States. U.S.D.A. Handbook No. 271. Washington, D. C. 764 p.

--------, and G. H. Schubert. 1956. Seed crops of forest trees in the pine region of California. U.S.D.A., For. Serv. Tech. Bull. 1150.

Frank, R. M., and L. O. Safford. 1970. Lack of viable seeds in the forest floor after clearcutting. J. For. 68:776-778.

French, H. M. 1976. The Periglacial Environment. Longman Group Ltd. 309 p.

Fritts, H. C. 1976. Tree Rings and Climate. Academic Press, New York. 567 p.

Gill, D. 1971. Vegetation and environment in the Mackenzie River Delta, N.W.T.-- a study in subarctic ecology. Unpublished Ph.D. dissertaion, Dept. of Geography, Univ. of Brit. Columbia.

Haag, R. W. 1972. Limitations to production in native plant communities in the Mackenzie Delta region. In: Bliss, L. C., and R. W. Wein (eds.), Man Modified Habitats in the Eastern Mackenzie Delta Region and the Arctic Islands. Arctic Land Use Research Program. Dept. North. and Indian Affairs, ALUR Rep. No. 71-72-14. Canada. P. 69-142.

-------, and L. C. Bliss. 1974. Energy budget changes following surface disturbance to upland tundra. J. Appl. Ecol. 11: 355-374.

Hagner, S. 1965. Cone crop fluctuations in Scots Pine and Norway Spruce. Stud. For. suec. Skogshogski, Stockholm, 33: 1-21.

Hare, F. K., and J. C. Ritchie. 1972. The boreal bioclimates. Geogr. Rev. 62: 333-365.

Harper, J. L. 1977. Population Biology of Plants. Academic Press, New York. 892 p.

-------, and J. White. 1974. The demography of plants. Ann. Rev. Ecol. Syst. 5: 419-463.

Heginbottom, J. A. 1972. Some effects of a forest fire on the permafrost active layer at Inuvik, N.W.T. In: Kerfoot, D. E. (ed.), Mackenzie Delta Area Monograph. 22 Int. Geog. Cong., Brock Univ., St. Catharines, Ontario. P. 149-157.

Heikurainen, L. 1982. Development of seedling stands on drained peatlands. Silva Fennica 16 (3): 287-323.

Heilman, P. E. 1966. Change in distribution and availability of nitrogen with forest succession on north slopes in Interior Alaska. Ecology 47: 825-831.

-------. 1968. Relationship of availability of phosphorus and cations to forest succession and bog formation in interior Alaska. Ecology 49: 331-336.

Hollingshead, G. W., L. Skjolingstad, and L. A. Rundquist. 1978. Permafrost beneath channels in the Mackenzie Delta, N.W.T., Canada. In: Proceedings of the Third International Permafrost Conference. Vol. 1. P. 406-413.

Huovila, S. 1970. Some features of the microclimate within hilly regions in Finland. In: Ecology of the Subarctic Regions, Proceedings of the Helsinki Symposium. UNESCO. P. 63-67.

Hustich, I. 1953. The boreal limit of conifers. Arctic 6: 149-162.

-------. 1966. On the forest-tundra and the northern tree-lines. Ann. Univ. Turku., A, II, 36 (Rep. Kevo Subarctic Sta. 3), P. 7-47.

-------. 1979. Ecological concepts and biogeographical zonation in the North: the need for a generally accepted terminology. Holarc. Ecol. 2: 208-217.

Janz, A. 1973. Topographic influence on soil and plant nutrients. In: Bliss, L. C. (ed.), Botanical Studies of Natural and Man Modified Habitats in the Mackenzie Valley, Eastern Mackenzie Delta, and the Arctic Islands. Env. Soc. Comm. for North. Pipeline Devel., Rep. No. 73-43. P. 25-49.

Jarvis, J. M., G. A. Steneker, R. M. Waldron, and J. C. Lees. 1966. Review of silvicultural research, white spruce and trembling aspen cover types, Mixed-wood Forest Section, Boreal Forest Region, Alberta-Saskatchewan-Manitoba. Can. Dept. of For. and Rural Devel., For. Branch Publ. No. 1156. 189 p.

Johnson, E. A. 1975. Buried seed populations in the subarctic forest east of Great Slave Lake, Northwest Territories, Canada. Can. J. Bot. 53: 2933-2941.

-------. 1981. Vegetation organization and dynamics in the Northwest Territories, Canada. Ecology 62 (1): 200-215.

Kay, P. A. 1978. Dendroecology in Canada's forest-tundra transition zone. Arc. and Alp. Res. 10 (1): 133-138.

Kendrew, W. G., and B. W. Currie. 1955. The climate of central Canada. Queen's Printer, Ottawa. 194 p.

Kennedy, B. A., and M. A. Melton. 1972. Valley asymmetry and slope forms of a permafrost area in the Northwest Territories, Canada. In: Polar Geomorphology. Inst. of Brit. Geomorph. Alden Press, London. P. 107-120.

Kerfoot, D. E. (ed.). 1972. Mackenzie Delta Area Monograph. 22nd Int. Geog. Cong., Brock Univ., St. Catharines, Ontario. 174 p.

Kozlowski, T. T. 1971. Growth and Development of Trees. I. Seed Germination, Ontogeny, and Shoot Growth, 443 p. II. Cambial Growth, Root Growth, and Reproductive Growth, 520 p. Academic Press, New York.

-------. 1979. Tree Growth and Environmental Stresses. Univ. of Washington Press, Seattle, Washington. 192 p.

Kryuchkov, V. V. 1968. Soils of the far north should be conserved. Priroda 12: 72-74.

Lambert, J. D. W. 1972. Vegetation patterns in the Mackenzie Delta area, N.W.T. In: Kerfoot, D. E. (ed.), Mackenzie Delta Area Monograph. 22nd Int. Geog. Cong., Brock Univ., St. Catharines, Ontario. P. 51-69.

Larsen, J. A. 1965. The vegetation of the Ennadai Lake area, N.W.T.: studies in subarctic and arctic bioclimatology. Ecol. Monogr. 35: 437-459.

-------. 1980. The Boreal Ecosystem. Academic Press, New York. 500 p.

Larson, M. M., and G. H. Schubert. 1970. Cone crops of ponderosa pine in central Arizona, including the influence of Albert squirrels. U.S.D.A. For. Serv. Res. Pap. RM-58. 15 p.

Lees, J. 1972. Soil aeration and sitka spruce seedling growth in peat. J. Ecol. 60: 343-349.

Linnel, K. A., and J. C. F. Tedrow. 1981. Soils and Permafrost Surveys in the Arctic. Oxford Univ. Press. 279 p.

Lutz, H. J. 1956. Ecological effects of forest fires in the interior of Alaska. U.S.D.A. Tech. Bull. No. 1133. 121 p.

Mackay, J. R. 1963. The Mackenzie Delta area, N.W.T. Can. Dept. Mines Tech. Surv., Geog. Branch Memo. 8. 202 p.

-------. 1970. Disturbances to the tundra and forest tundra environment of the western arctic. Can. Geotech. J. 7: 420-432.

-------. 1975. The stability of permafrost and recent climatic change in the Mackenzie Valley, N.W.T. Geol. Surv. Can., Paper 75-1B. P. 173-176.

-------. 1977. Changes in the active layer from 1968 to 1976 as a result of the Inuvik fire. Geol. Surv. Can., Paper 77-1B. P. 273-275.

McKeague, J. A. (ed.). 1976. Manual on soil sampling and methods of analysis. Soil Res. Inst., Agri. Canada. Canada. 212 p.

Marr, J. W. 1948. Ecology of the forest-tundra ecotone on the east coast of Hudson Bay. Ecol. Monogr. 18: 118-144.

Mikola, P. 1970. Forests and forestry in subarctic regions. In: Ecology of the Subarctic Regions, Proceedings of the Helsinki Symposium. UNESCO. P. 295-303.

Mitchell, V. L. 1973. A theoretical treeline in central Canada. Ann. Assoc. Amer. Geog. 63 (3): 296-301.

Nichols, H. 1975. The time perspective in northern ecology: palynology and the history of the Canadian boreal forest. In: Circumpolar Conference on Northern Ecology, Proceedings. Canada. P. 155-167.

-------. 1976. Historical aspects of the northern Canadian treeline. Arctic 29 (1): 38-47.

Nienstaedt, H. 1957. Silvical characteristics of white spruce (*Picea glauca*). U.S.D.A., For. Serv. Paper No. 55. 23 p.

Oke, T. R. 1978. Boundary Layer Climates. Wiley and Sons, New York. 372 p.

Olson, R. V. Free iron oxides. In: Black, C. A. (ed.), Methods of Soil Analysis. Two Volumes. Amer. Soc. of Agron., Madison, Wisconsin. Publ. No. 9. P. 967-973.

Pettapiece, W. W., C. Tarnocai, S. C. Zoltai, and E. T. Oswald. 1978. Guidebook for a tour of soil, permafrost, and vegetation relationships in the Yukon and Northwest Territories of northwest Canada. Tour 18. 11th Cong., Int. Society of Soil Sci., Edmonton, Alberta, June, 1978.

Porsild, A. E., and W. J. Cody. 1980. Vascular Plants of the Continental Northwest Territories, Canada. Nat. Mus. Canada. 667 p.

Price, L. W. 1971. Vegetation, microtopography, and depth of active layer on different exposures in subarctic alpine tundra. Ecology 52 (4): 638-647.

Rampton, V. 1972. An outline of the Quaternary geology of the Lower Mackenzie Region. In: Kerfoot, D. E. (ed.), Mackenzie Delta Area Monograph. 22nd Int. Geog. Cong., Brock Univ., St. Catharines, Ontario. P. 7-15.

Ritchie, J. C. 1960. The vegetation of northern Manitoba. IV. The Caribou Lake Region. Can. J. Bot. 37: 185-197.

-------. 1972. Pollen analysis of late-Quaternary sediments from the arctic treeline of the Mackenzie River Delta region, N.W.T. In: Kerfoot, D. E. (ed.), Mackenzie Delta Area Monograph. 22nd Int. Geog. Cong., Brock Univ., St. Catharines, Ontario. P. 29-51.

Roe, A. L. 1967. Seed dispersal in a bumper spruce seed year. U.S.D.A. For. Serv., Res. Paper INT-39. 10 p.

Rowe, J. S. 1971. Spruce and fire in northwest Canada and Alaska. In: Proceedings of the Annual Tall Timbers Fire Ecology Conference, 20-21 August, 1970. Tall Timbers Res. Sta., Tallahassee, Florida. P. 245-255.

-------, and G. W. Scotter. 1973. Fire in the boreal forest. J. Quat. Res. 3: 444-464.

-------, D. Spittlehouse, E. Johnson, and M. Jasieniuk. 1975. Fire studies in the upper Mackenzie Valley and adjacent precambrian uplands. Dept. Indian and North. Affairs, Canada. INA Publ. No. QS-8045-000-EE-A1.

Safford, L. O., and S. Bell. 1972. Biomass of fine roots in a white spruce plantation. Can. J. For. Res. 2: 169-172.

Sakai, A., S. Yoshida, M. Saito, and S. C. Zoltai. 1979. Growth rate of spruce related to the thickness of permafrost active layer near Inuvik, Northwestern Canada. Low Temp. Sci., Ser. B 37: 19-32.

Sarvas, R. 1962. Investigations of the flowering and seed crop of Pinus sylvestris. Commun. Inst. Forst. Fenni. 53: 1-198.

Schmidtling, R. C. 1969. Reproductive maturity related to height of loblolly pine. U.S.D.A. For. Serv. Res. Note SO-94.

Simard, A. J. 1974. Forest fire weather zones of Canada. Can. For. Serv., Env. Can., Canada.

Siren, G. 1970. Remarks on current silvicultural research in the Subarctic of Finland. In: Ecology of the Subarctic Regions. Proceedings of the Helsinki Symposium. UNESCO. P. 343-349.

Smith, M. W. 1975. Microclimate influences on ground temperature and permafrost distribution, Mackenzie Delta, N.W.T. Can. J. Ear. Sci. 12: 1421-1438.

Stiell, W. M. 1976. White spruce: artificial regeneration in Canada. For. Manag. Inst., Ottawa, Ontario. Info. Rep. FMR-X-85. 275 p.

Strang, R. M. 1973. Succession in unburned arctic woodlands. Can. J. For. Res. 3: 140-143.

Sutton, R. F. 1969. Silvics of white spruce. Can. Dept. Fish. and For., For. Branch, Publ. No. 1250. 57 p.

Tarnocai, C. 1973. Soils of the Mackenzie River area. Env. Soc. Comm. for North. Pipeline Devel., Canada. Rep. No. 73-26. 136 p.

-------. 1978. Distribution of soils in northern Canada and parameters affecting their utilization. 11th Int. Cong. of Soil Sci. Transact. Vol. 3, Symp. Papers. P. 332-347.

Tedrow, J. C. F. 1977. Soils of the Polar Landscapes. Rutgers Univ. Press, New Brunswick, New Jersey. 638 p.

Tikhomirov, B. A. 1962. The treelessness of the tundra. Polar Record 11 (70): 24-31.

Van Cleve, K., R. Barney, and R. Sclentner. 1981. Evidence of temperature control of production and nutrient cycling in two interior Alaska black spruce ecosystems. Can. J. For. Res. 11: 258-273.

Van Wagner, C. E. 1979. Fire behavior in northern conifer forests and shrublands. In: Fire in Northern Circumpolar Ecosystems, Symposium, Univ. of New Brunswick, 22-24 October, 1979. Fredricton, New Brunswick, Canada.

Viereck, L. A. 1965. Relationship of white spruce to lenses of perennially frozen ground, Mt. McKinley N.P., Alaska. Arctic 18: 262-267.

-------. 1973. Ecological effects of river flooding and forest fires on permafrost. In: The North American Contribution to the Second International Conference on Permafrost. Nat. Acad. of Sci., ISBN-0-309-02115-4. Washington, D. C. P. 60-67.

-------. 1979. Characteristics of treeline plant communities in Alaska. Holarc. Ecol. 2: 228-238.

-------, and L. A. Schandelmeier. 1980. Effects of fire in Alaska and adjacent Canada-- a literature review. Dept. Inter., Bureau Land Manag. Tech. Rep. 6. 124 p.

Wagg, J. W. 1967. Origin and development of white spruce root-forms. Can. Dept. Fish. For., For. Branch Publ. No. 1192, Canada. 45 p.

Waldron, R. M. 1965. Cone production and seedfall in a mature white spruce stand. For. Chron. 41 (3): 316-329.

Walkley, A., and T. A. Black. 1934. An examination of the Degtjareff method for determining soil organic matter and a proposed modification of the chromic acid titration method. Soil Sci. 37: 29-38.

Wardle, P. 1974. Alpine timberlines. In: Ives, J. D., and R. G. Barry (eds.), Arctic and Alpine Environments. Methuen Press, London. P. 371-403.

Wein, R. W. 1975. Vegetation recovery in arctic tundra and forest-tundra after fire. Arctic Land Use Research Program, Dept. Ind. and North. Affairs, Canada, ALUR Rep. No. 74-75-62.

Wells, C. G. (ed.). 1979. Effects of fire on soil: a state-of-knowledge review. National Fire Effects Workshop. April 1978, Denver, Colorado. U.S.D.A. For. Serv., Gen. Tech. Rep. WO-7. 34 p.

Young, F. G. 1978. The Caribou Hills. In: Young, F. G. (ed.), Geological and Geographical Guide to the Mackenzie Delta Area. Can. Soc. Petroleum Eng., Calgary, Alberta. P. 52-57.

Younkin, W. E., and L. H. Hettinger. 1978. Assessment of the effects of snow road construction and use on vegetation surface elevations and active layers near Inuvik, N.W.T. In: Proceedings of the Third International Conference on Permafrost. Vol. 1. P. 480-489.

Zasada, J. C. 1971. Natural regeneration of interior Alaska forests-- seed, seedbed, and vegetative reproduction considerations. In: Slaughter, C. W., R. J. Barney, and G. M. Hansen (eds.), Prodeedings, Fire in the Northern Environment, a Symposium. Fairbanks, Alaska, April 13-14, 1971. Pac. NW For. and Range ExP. Sta., U.S.D.A. For. Serv., Portland, Oregon. P. 231-246.

-------, and L. A. Viereck. 1970. White spruce cone and seed production in interior Alaska 1957-1968. U.S.D.A. For. Serv. Res. Note PNW-129. 11 p.

-------, M. J. Foote, F. J. Deneke, and R. H. Parkerson. 1978. Case history of an excellent white spruce cone and seed crop in interior Alaska. U.S.D.A. For. Serv. Gen. Tech. Rep. No. PNW-65. 53 p.

Zoltai, S. C. 1975. Tree ring record of soil movements on permafrost. Arc. and Alp. Res. 7 (4): 331-340.

-------, and W. W. Pettapiece. 1973. Studies of vegetation, landforms, and permafrost in the Mackenzie Valley. Env. Soc. Comm. for North. Pipeline Devel., Rep. No. 73-4. Canada. 105 p.