INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

UNIVERSITY OF ALBERTA

CLIMATE CHANGE AND THE ARCTIC TREELINE

BY

Simon M. Landhäusser

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Department of Forest Science

Edmonton, Alberta
Spring 1994

0-612-22154-7

UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: Simon M. Landhäusser

TITLE OF THESIS: Climate change and the arctic treeline

DEGREE: Doctor of Philosophy

YEAR THIS DEGREE GRANTED: 1994

Permission is hereby granted to the UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves all other publication and other rights in association with the copyright in the thesis, and except as hereinbefore provided neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatever without the author's prior written permission.

Simon M. Landhäusser
Hünensand 45
49716 Meppen
Germany

April 22, 1994

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Climate Change and the Arctic Treeline submitted by Simon M. Landhäusser in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Dr. Ross W. Wein (Forest Science)

David Halliwell

Dr. Dave H. Halliwell (Geography)

Victor Lieffers

Dr. Victor J. Lieffers (Forest Science)

Ellen Macdonald

Dr. S. Ellen Macdonald (Forest Science)

G.P. Kershaw.

Dr. G. Peter Kershaw (Geography)

for

Dr. Keith Van Cleve (Forestry-Soils) U. of Alaska

April 22, 1994

DEDICATION

To my parents

ABSTRACT

In this thesis research, surveys and experimental studies were undertaken to test hypotheses related to the potential tree performance north of the present treeline. In order to determine whether a severe disturbance could result in tree establishment in former tundra areas, a severe fire which occurred in 1968 near Inuvik, Northwest Territories, was investigated. On paired burned-unburned study sites around the fire perimeter, plant cover and tree densities were determined and compared to results of an earlier survey, conducted in 1973. A second, more detailed survey investigated the establishment of tree species in former treed or non-treed areas within the burn. Trees at the arctic treeline appear to be distributed along a short-wave radiation input gradient. An experimental study at Inuvik tested the effect of short-wave radiation input in determining microsite conditions on growth of seedlings of the treeline tree species. In order to assess the potential of tree species to cope with environmental stresses, ecophysiological studies were undertaken to measure the response of *Betula papyrifera*, *Populus balsamifera*, and *Picea mariana* to different soil temperature and drought pre-conditioning treatments.

Revegetation surveys showed that after the severe fire, trees established in former tundra areas. The fast growing species *Betula papyrifera* and *Populus balsamifera* were successful in taking advantage the severe disturbance. The experimental study showed that short-wave energy input is not very strongly related to microsite conditions determining distribution pattern of the tree species. The ecophysiological studies of *Betula papyrifera*, *Populus balsamifera*, and *Picea mariana* under different soil temperature and drought pre-

conditioning regimes showed that *Populus balsamifera* and *Betula papyrifera* responded with higher net assimilation rates to higher soil temperatures than *Picea mariana*. *Betula papyrifera* and *Populus balsamifera* showed different strategies after drought pre-conditioning. *Betula papyrifera* decreased net assimilation rates and stomatal conductance compared to *Populus balsamifera* which responded with higher rates to the drought pre-conditioning treatment.

The results of the studies are interpreted in the light of changing environmental conditions due to increased disturbance regimes, predicted under the climate change scenarios in the energy limited northern ecosystems. If the insulating organic matter, which dominates most of these northern terrestrial ecosystems, is removed either slowly by decomposition or rapidly by disturbances like fire, mineral soil conditions will provide improved sites for more effecticve establishment and growth of the treeline tree species. It can be hypothesized that *Populus balsamifera* and *Betula papyrifera* could expand northwards, with each disturbance that removes the insulating organic matter. The coniferous species which require longer periods to reach maturity and which have less well developed seed dispersal systems might not be able to take full advantage of the new disturbance regimes.

ACKNOWLEDGEMENTS

I am grateful for the opportunity to come to Canada and see one of the most beautiful places on earth, the Arctic. I will always remember the land and the people of the North as an outstanding part of my life.

I like to thank my supervisor Dr. Ross W. Wein for providing the research subject and my committee members Drs. S. Ellen Macdonald, Victor J. Lieffers and Dave H. Halliwell for their support, help and stimulating discussions in this study. I also like to acknowledge the comments of the external reviewers Drs. Peter Kershaw and Keith Van Cleve. I have to thank Ross and his family for their great support, especially in the first months of my stay in a new country, giving me a good start, and trying to make sense of my spoken and written English at that time.

I thank my best friend Petra Lange who helped me through many difficult moments in a "researcher's life".

Many thanks also to the people who helped me as volunteers in my field studies especially Sue K. and Craig Olsen, Barbara Sander, Elke Kohler, Peter Engelfield, Laurie and Danny Wein, and Blair Stevenson.

I acknowledge the support and suggestions, not only in practical and theoretical problems in my research but also in every days obstacles, from my fellow graduate students, especially Uldis Silins, Ken Greenway, Michael H. Jones, Tim Conlin, and Barbara Thomas who made the office life endurable. I will miss the inspiring coffee breaks, we regularly had.

Logistical support is gratefully acknowledged from the Inuvik Research Centre of the Science Institute of the Northwest Territories and from the Polar Continental Shelf Project. I also thank Gary White and Les Kutny for assistance in the field. Research permits were received from Inuvialuit Development Corporation of Tuktoyaktuk, N.W.T. and the Science Institute of the Northwest Territories of Yellowknife, N.W.T.. I to acknowledge the use of a infra-red gas analyzer purchased with a NSERC Grant to Dr. S. Ellen Macdonald.

These studies have been supported financially with operating funds from two Boreal Alberta Research Grants from the University of Alberta to Simon M. Landhäusser, an Imperial Oil University Grant, and Natural Sciences and Engineering Research Council of Canada (NSERC) Operating Grants to Ross W. Wein and Dave H. Halliwell. Thanks also to the staff of the Department of Forest Science for their help and support.

TABLE OF CONTENTS

CHAPTER I

CHAPTER II

CHAPTER III

POST-FIRE VEGETATION RECOVERY AND TREE ESTABLISHMENT AT THE ARCTIC TREELINE: CLIMATE CHANGE - VEGETATION RESPONSE HYPOTHESES

CHAPTER IV

TREE SEEDLING RESPONSE RELATED TO SHORT-WAVE ENERGY INPUT AT THE ARCTIC TREELINE

CHAPTER V

GAS EXCHANGE AND GROWTH OF THREE ARCTIC TREELINE TREE SPECIES UNDER DIFFERENT SOIL TEMPERATURE AND DROUGHT PRE-CONDITIONING REGIMES

CHAPTER VI

LIST OF TABLES

TABLE PAGE

LIST OF FIGURES

CHAPTER I

GENERAL INTRODUCTION

General circulation models of the earth's atmosphere have been used to project climate changes as the atmospheric concentration of carbon dioxide doubles over the next 50 years. It is expected that the increase in global mean surface temperature on an annual basis will range from one to several degrees Celsius. Model projections for the past 100 years suggest a 0.3 - 1.0 °C increase in temperature and this appears to resemble closely the 0.3 - 0.7 °C change that has been measured (Bolin *et al.* 1986). It is further suggested that there will be an increase in the climate variability (Rind *et al.* 1989, Overpeck *et al.* 1990). This variability implies an increased frequency of drought and fire (Ryan 1989, Flannigan and Van Wagner 1991). On a more regional basis, studies have shown that, with the greenhouse effect, there will be a substantially greater temperature increase with increasing distance northward, especially in the winter season, whereas lower latitudes will have less pronounced warming in all seasons (Maxwell 1992). A warming in the Arctic could have a wide range of impacts on physical and biological mechanism (Maxwell and Barrie 1989, Chapin III *et al.* 1992). For the Mackenzie Delta, linkages between climate, physical and biological environments, resource users and economy have been hypothesized in Lawford and Cohen (1991). They predict changes in hydrology of the delta and lakes, melting permafrost, extended growing seasons, changes in vegetation composition and distribution, and changing animal migration and breeding patterns.

As climate changes, ecosystem components will be subjected to increasing ecological stress. This stress will be strongest at ecotones, where species are at the limit of their ranges. An example is the arctic treeline, which is the transitional zone between Boreal Forest in the south and Arctic Tundra in the north. This transitional zone has been much discussed in general terms (Larsen 1980) and is defined by Walter (1979) as "an area of ecological tension over which one type of vegetation is gradually replaced by another". Both vegetation types occur together in these zones under similar climatic conditions. Only local microclimatic conditions like relief and soil texture determine which vegetation type dominates on a specific site. There are many descriptions of northern ecotones (see review by Larsen 1989, Appendix A; Walter and Breckle 1986, 1991, Stevens and Fox 1991).

The forest-tundra of the western Northwest Territories spans an average of 150 km in width, increasing in width from northwest to southeast (Timoney *et al.* 1992), however, the circumpolar arctic treeline is a vast area covering about 30 million square kilometres of Eurasia and North America. Although covering this large amount of landmass, forest-tundra dynamics, in a circumpolar perspective, have not been studied intensively (Sirois 1992). Treeline dynamics in past and future has been of interest to many researchers around the northern hemisphere, however, studies were mainly on a regional scale. There have been a number of attempts to relate the position of the forest-tundra boundary to different climatic indices (e.g. Bryson 1966, Hare and

Ritchie 1972, Tukhanen 1980). However, all climatic indices developed do not give a satisfactory understanding of the forest-tundra boundary, chiefly because of limited ecological knowledge of tree species ecology (Sirois 1992).

The forest-tundra ecotone is dynamic, shifting continually and slowly in response to environmental changes as demonstrated in paleoecological studies over scales of thousands of years (Larsen 1971, Ritchie & Hare 1971, Nichols 1975, MacDonald *et al.* 1993). On a shorter time scale, more recent papers by Sirois and Payette (1989), Payette *et al.* (1989 a,b), Sirois and Payette (1990) and Cwynar and Spear (1991) provide an excellent understanding of fire and treeline dynamics over centuries for the humid boreal forest of Northern Québec. They have shown that there has been a northward shift in vegetation as climate has warmed over the historic time period.

There have been a number of earlier studies that have examined fire at the forest-tundra boundary of the lower Mackenzie Valley (Wein 1975, 1976, Black and Bliss 1978, 1980, Timoney and Wein 1991). All of the above studies focused on vegetation shifts under the prevailing conditions that were considered to be stable or changing very slowly; however, predicted climatic changes under the greenhouse effect may exhibit unprecedented rates of change in vegetation because of much faster changing climates. As a result, the studies mentioned above have limited value in making short-term predictions over one to three decades. Vegetation changes at the arctic treeline could be accelerated by the increased probability of disturbances predicted to accompany climate change (Viereck and Van Cleve 1984). Severe disturbances like fires, and subsequent thermokarst and erosion, which remove the insulating organic layer are the most important disruptions in low energy environments because they drastically alter the physical environment from an organic-soil dominated system to a mineral soil dominated system. Further, these disturbances remove vegetation types not well adapted to the changed site and climatic conditions, and provide new initiation points for better adapted species. At the arctic treeline it is critical for the tree species to gain these favourable sites in order to extend their range.

Not only distance of seed dispersal, amount of seed production, and seed viability, but also the microsite conditions are important factors affecting tree establishment and success at the treeline (Black and Bliss 1980). Sites with warm, well drained, and deep active layers are presently found only on steep south facing slopes and in the larger river valley flood plains, where organic layers are lacking or very thin. South facing slopes receive the most short-wave radiation and therefore have the warmest soils. In the river valleys warmer water from further south and early spring ice breakup and flooding events keep the active layer deep. With the predictions of climate change the amount of short-wave radiation received at the surface will not change significantly unless cloud cover changes significantly (Mitchell 1989). Long-wave radiation received will increase and, therefore, air and soil temperatures at the soil surfaces will increase. Soil temperature is probably the most prominent factor influencing performance and distribution of tree species at the treeline (Bonan 1992). With increasing air temperatures, accompanied by severe disturbances, soil temperatures will rise and less favourable sites for tree establishment could improve. A rise in soil temperature will change all biotic and abiotic processes that are directly or indirectly related to soil temperature. Active layers will be deeper, microbiological activity will increase, resulting in higher decomposition rates and increased nutrient availability (Sveinbjörnsson 1992, Nadelhoffer *et al.* 1992). On the other hand, higher evaporation rates could decrease soil moisture content (Oberbauer and Dawson 1992), which has presently not been considered to be a major factor controlling tree performance at the arctic treeline (Black and Bliss 1980). However, tree species presently occupying the well drained steep south facing slopes might suffer drought stress under the new climate conditions.

This dissertation research examines recent tree population changes at the arctic forest-tundra boundary and raises hypotheses about changes that are likely to occur as climate changes over the next several decades. In general, it is hypothesized that species abundance or composition at ecotones may change only slowly, unless a major environmental force such as a severe fire removes the plant community that is not well adapted to the new climatic conditions. Fire changes the organic matter-dominated soil system to a mineral soil-dominated system with strongly different nutrient and moisture conditions. This permits invasions, losses, and regrouping of species.

The SPECIFIC OBJECTIVES of this research were:

1) to document post fire plant cover and biomass accumulation and to determine if tree establishment in former tundra areas has occurred because of a recent severe fire

2) to experimentally determine the success of early tree seedling growth on different slopes and aspects and to relate this to the energy input

3) to experimentally determine, in growth chambers, the relative response of treeline tree species to different levels of soil temperature, drought pre-conditioning, and drought.

LITERATURE CITED

Black, R. A., and L. C. Bliss. 1978. Recovery sequence of *Picea mariana - Vaccinium uliginosum* forests after burning near Inuvik, Northwest Territories, Canada. Canadian Journal of Botany **56**: 2020-2030.

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

Bolin, B., B. R. Döös, J. Jäger, and R. A. Warrick (editors). 1986. The greenhouse effect, climate change and ecosystems. S.C.O.P.E. 29. John Wiley and Sons, Toronto.

Bonan, G. B. 1992. Soil temperature as an ecological factor in boreal forests. *In* Shugart H. H., R. Leemans, and G. B. Bonan. editors. System Analysis of the global boreal forest. Cambridge Press, Cambridge, p. 126-143.

Bryson, R. A. 1966. Air masses, stream lines, and the boreal forest. Geographical Bulletin **8**: 228-269.

Chapin III, F. S., R. L. Jefferies, J. F. Reynolds, G. R. Shaver, and J. Svoboda. 1992. Arctic plant physiological ecology in an ecosystem context. In: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver and J. Svoboda editors. Arctic ecosystems in a changing climate. An ecophysiological perspective. Academic Press, London, p 441-452.

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

Flannigan, M. D., and C. E. Van Wagner. 1991. Climate change and wildfire in Canada. Canadian Journal of Forest Research **21**: 66-72.

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

Larsen, J. A. 1971. Vegetation of Fort Reliance, N.W.T.. Canadian Field-Naturalist **85**: 147-178.

Larsen, J. A. 1980. The boreal ecosystem. Academic Press, New York.

Larsen, J. A. 1989. The northern forest border in Canada and Alaska. Ecological Studies 70, Springer Verlag, New York.

Lawford, R. G., and S. J. Cohen. 1991. The impacts of climatic variability and change in the Mackenzie Delta. *In*: Marsh P., and C.S.L. Ommanney editors. Proceedings of the Workshop on the Mackenzie Delta, 17-18 October 1989, Saskatoon. Environment Canada, Ottawa, Canada, p 155-172.

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

Maxwell, J. B. 1992. Arctic Climate: Potential for change under global warming. *In*: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver & J. Svoboda editors. Arctic ecosystems in a changing climate. An ecophysiological perspective. Academic Press, London, UK.

Maxwell, J. B., and L. A. Barrie. 1989. Atmospheric and climatic change in the Arctic and Antarctic. Ambio **18**: 42-49.

Mitchell, J.F.B. 1989. The "greenhouse" effect and climate change. Review of Geophysics **27**: 115-139.

Nadelhoffer, K. J., A. E. Giblin, G. R. Shaver, and A. E. Linkins. 1992. Microbiological processes and plant nutrient availability in arctic soils. *In*: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver & J. Svoboda editors. Arctic ecosystems in a changing climate. An ecophysiological perspective. Academic Press, London, p 281-300.

Nichols, H. 1975. Palynological and palaeoclimatic study of the recent late quaternary displacement of the boreal forest-tundra ecotone in Keewatin and Mackenzie N.W.T. Canada. Institute of Arctic and Alpine Research occ. Paper No. 15.

Oberbauer, S. F., and T. E. Dawson. 1992. Water relation of arctic vascular plants. *In* Chapin III, F. S., R. L. Jefferies, J. F. Reynolds, G. R. Shaver, and J. Svoboda. editors. Arctic ecosystems in a changing climate. Academic Press, London, p 259-280.

Overpeck, J. T., D. Rind, and R. Goldberg. 1990. Climate-induced changes in forest disturbances and vegetation. Nature **343**: 51-53.

Payette, S., C. Morneau, L. Sirois, and M. Desponts. 1989a. Recent fire history of northern Québec biomes. Ecology **70**: 656-673.

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

Rind, R., R. Goldberg, and R. Ruddy. 1989. Change in climate variability in the 21st century. Climate Change **14**: 5-37.

Ritchie, J. C., and F. K. Hare. 1971. Late Quaternary vegetation and climate near the arctic treeline of northwestern North America. Quaternary Research **1**: 331-342.

Ryan, K. C. 1989. Climate change, fire and natural vegetation: implications for wilderness areas. *In*: Walsch, D. editor. Wilderness and Wildfire. Miscellaneous Publication 50, Missoula, Montana, University of Montana School of Forestry. Montana Forest and Range Experiment Station, p. 18-21.

Sirois, L. 1992. The transition between boreal forest and tundra. *In* Shugart H. H., R. Leemans, and G. B. Bonan. editors. System Analysis of the global boreal forest. Cambridge Press, Cambridge, p. 196-215.

Sirois, L., and S. Payette. 1991. Reduced postfire tree regeneration along a boreal forest-forest-tundra transect in northern Québec. Ecology **72**: 619-627.

Sirois, L., and S. Payette. 1989. Post-fire black spruce establishment in boreal and subarctic Québec. Canadian Journal of Forest Research **19**: 1571-1580.

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

Sveinbjörnsson, B. 1992. Arctic treeline in a changing climate. *In*: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver & J. Svoboda editors. Arctic ecosystems in a changing climate. An ecophysiological perspective. Academic Press, London, p.239-258.

Timoney, K. P., G. H. La Roi, S. C. Zoltai, and A. L. Robinson. 1992. The High Subarctic forest-tundra of northwestern Canada: position, Width, and vegetation gradients in relation to climate. Arctic **45**: 1-9.

Timoney, K. P., and R. W. Wein. 1991. The areal pattern of burned tree vegetation in the subarctic region of northwestern Canada. Arctic 44: 223-230.

Tukhanen, S. 1980. Climatic parameters and indices in plant geography. Acta phytogeographica Suecica No.67. Uppsala.

Viereck, L. A., and K. Van Cleve. 1984. Some Aspects of Vegetation and Temperature Relationships in the Alaskan Taiga. *In*: McBeath, J. H. editor. The Potential Effects of Carbon Dioxide-Induced Climatic Changes in Alaska, School of Agriculture and Land Resource Management, University of Alaska, Miscellaneous Publication 83-1, pp. 129-142. Fairbanks, Alaska.

Walter, H. 1979. Vegetation of the earth and ecological systems of the geo-biosphere, Springer-Verlag New York.

Walter, H., and S.-W. Breckle. 1986. Ökologie der Erde. Spezielle Ökologie der gemässigten and arctischen Zonen Euro-Nordasiens: Zonobiom VI-IX. Volume 3, Fischer Verlag, Stuttgart.

Walter, H., and S.-W. Breckle. 1991. Ökologie der Erde. Spezielle Ökologie der gemässigten and arctischen Zonen ausserhalb Euro-Nordasiens: Zonobiom IV-IX. Volume 4, Fischer Verlag, Stuttgart.

Wein, R. W. 1975. Vegetation recovery in the arctic tundra and forest/ tundra after fire. A.L.U.R. 74-75-62. Indian Affairs and Northern Development, Ottawa, 81p.

Wein, R. W. 1976. Frequency and characteristics of arctic tundra fires. Arctic **29**: 213-222.

CHAPTER II

STUDY AREA DESCRIPTION

The location of the general study area was north of Inuvik along the eastern edge of the Mackenzie River Delta, the Caribou Hills and the Tuktoyaktuk Peninsula N.W.T. between latitudes 68°30' N and 69°30' N and longitudes 132°00' W and 134°00' W.

Geologically, the area is underlain by early deltas of the Mackenzie River with fluvial-marine deposits (Christie *et al.* 1972) except for the area of Inuvik and the Caribou Hills where to the north tertiary gravels and to the south shales are much older (Rampton 1971, 1972). The deposits and landforms result from at least two glaciations (Fyles 1966). The glacier of the last ice age (Wisconsin) did not cover the arctic coastal half of the Tuktoyaktuk Peninsula (Fyles 1967; Prest 1969).

Soils show little profile development compared to temperate regions and they are classified as Subarctic Orthic Regosols (Day and Rice 1964). The mineral soils are fine textured clays to silty-clay loams and are usually overlain with 10 to 20 cm of organic matter (Day and Rice 1964). The microrelief is hummocky as a result of frost action. Frost action is seen in features such as solifluction lobes on terraces in the uplands or the development of polygonal ground. These permafrost soils tend to be deficient in nitrogen and phosphorus (Brown 1970) because of the temperature restricted microbiological activity.

The upper horizons of the soils are acid but the lower layers are usually slightly acid to slightly alkaline (Brown 1970).

The climate of the study area ranges from the High Subarctic Ecoclimate Region to the Low Arctic Ecoclimate Region (CCELC 1989). Summers of about four months are cool, whereas winters are long and extremely cold. Mean annual temperatures range from -5 to -20 °C in the different regions, the average temperature in January is about -29.4 °C and in July about 13.3 °C. The total mean annual precipitation is 250 to 350 mm, with most falling in late summer and early fall (CCELC 1989) (Figure II-1). Snowmelt typically occurs in the later part of May, and first snowfall occurs in early September (Burns 1973). The climate has been conducive in the study area to continuous permafrost to depths >100 m (Brown 1970; Mackay 1978).

Fire is a major force that changes vegetation dynamics. The occurrence of fire in the northwestern area of the N.W.T. over the 1968 to 1973 period has been less than 1.5 fires per 1000 km^2 per year (Simard 1975). Murphy *et al.* (1980) noted an increase in the incidence of fire between 1950 and 1979 and there has been a further increase since then (CCFFM 1990). Fire at the forest-tundra ecotone does occur but with lower frequencies (> 100 years) than in the western boreal forest (50 to 100 years) (Wein and McLean 1983). Fire season in the northern boreal forest decreases in length with distance northwards (Simard 1975), with the main fire season occurring during the months of June, July and August (Murphy *et al.* 1980). In spatial terms Timoney and Wein (1991) observed greater incidence of fires, increasing from the Inuvik area to the Great Slave Lake region. The fire history of the Inuvik area has been documented to some extent (Wein 1975, 1976) but the full fire suppression record is on file with Renewable Resources G.N.W.T. Office in Inuvik. Of particular interest to the present study is a fire around the town of Inuvik, N.W.T. which burned from August 8 to August 18, 1968 and covered an area about 500 km² (Hill 1969). This fire was unusually severe and burned deeply into the organic soil after a prolonged drought. This fire is highly useful because it was a low frequency event that will likely become a higher frequency event under future climate change conditions. Therefore, this fire could provide a partial analogue of future fire effects.

The vegetation south of Inuvik is described by Rowe (1972) as a part of the Boreal Forest Region. *Picea mariana*[*] and *Picea glauca* are the characteristic species. Northwards with increasingly rigorous climate and soil conditions the vegetation becomes subarctic open lichen woodland and then tundra (Rowe 1972; Timoney 1988). More details on the plant communities in the forest-tundra ecotone of the Mackenzie River-Valley are given in Zoltai and Tarnocai (1974). North facing slopes are dominated by open crown *Picea mariana* stands with a well developed *Sphagnum* spp. layer and some lichen cover, dominated by *Cladonia* spp., which produces slowly decomposing organic material and provides insulation, resulting in a shallow active layer. The ground cover is dominated by ericaceous species such as *Ledum palustre* ssp. *decumbens*, *Vaccinium vitis-idaea* ssp. *minus*, *Vaccinium uliginosum* and *Empetrum nigrum* ssp. *hermaphroditum*. South facing slopes are characterized

---

[*] Nomenclature for all vascular plants follows Hultén (1968).

by *Betula papyrifera* and *Picea glauca*; the active layer is relatively thick due to lack of insulation. The ground cover contains *Vaccinium vitis-idaea* ssp. *minor*, *Ledum palustre* ssp. *decumbens* and *Rosa acicularis*. On dry areas the dominant community components are *Betula glandulosa* and low shrub ericaceous species. On poorly drained areas *Eriophorum vaginatum* ssp. *spissum* is a major species. Corns (1974) provides detailed physiognomy and floristic composition data for the tundra vegetation of the area east of the Mackenzie River. He recognized five major tundra vegetation types mostly on the basis of height of shrubs and abundance of herbs and heath species. Timoney (1988) working at a more landscape level observed that plant associations were correlated with soil pH and moisture. He described five major vegetation types along the forest-tundra boundary from the Yukon border to Hudson Bay. Acidic soils have: dwarf ericad/lichen cover on dry exposed areas, medium shrub/ericad on north-facing slopes and black spruce vegetation on south-facing slopes. Whereas on basic soils the dry exposed areas are covered with *Dryas*/lichen vegetation, the mesic north-facing slopes with medium shrub/*Dryas* and the south-facing slopes with white spruce vegetation. Wet areas with acidic or basic soils are covered with tussock-tundra vegetation.

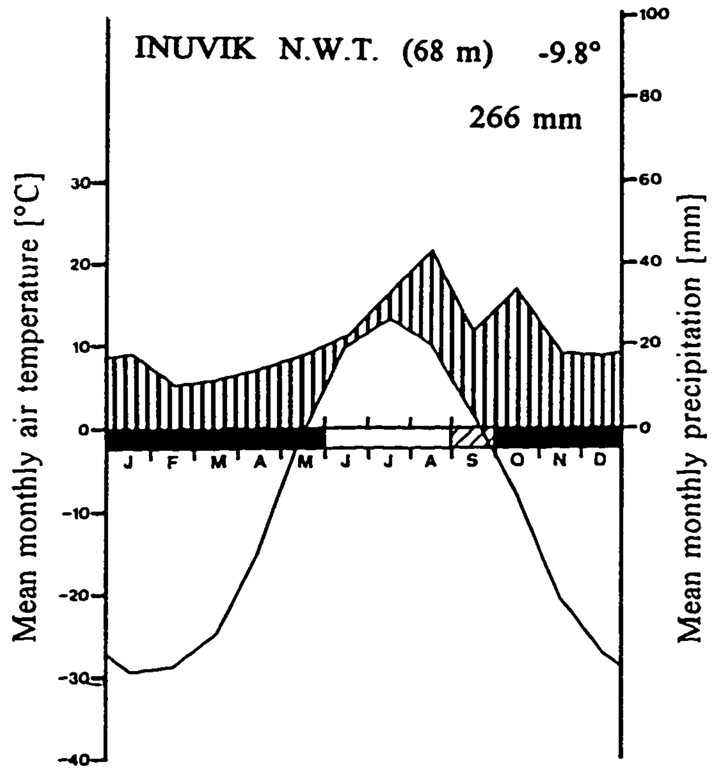

Figure II-1. Climate diagram of the High Subarctic Ecoclimatic Region (adapted from Ecoregions Working Group (CCELC) 1989).

LITERATURE CITED

Brown, R. J. E. 1970. Permafrost in Canada. University of Toronto Press.

Burns, B. M. 1973. The climate of the Mackenzie Valley-Beaufort Sea. Volume 1. Climatological Studies Number 24. Environment Canada, Atmospheric Environment, Toronto.

CCELC. 1989. Ecoclimatic Regions of Canada, first Approximation written and compiled by Ecoregions Working Group, Ecological Land Classification Series No. 23. Environment Canada.

CCFFM. 1990. Canadian Committee on Forest Fire Management, Reports, National Research Council Canada

Christie, R. L., D. G. Cook, W. W. Narsickuk, H. P. Trettin, and C. J. Yorath. 1972. The canadian Arctic islands and the Mackenzie region. XXIV international Geol. Congress, Montreal Quebec.

Corns, I. G. W. 1974. Arctic plant communities east of the Mackenzie Delta. Canadian Journal of Botany **52**: 1731-1745.

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

Fyles, J. G. 1966. Quaternary Stratigraphy, Mackenzie Delta and Arctic Coastal Plain. Geological Survey Canada **66-1**: 30-31.

Fyles, J. G. 1967. Mackenzie Delta and Arctic Coastal Plain. Geological Survey Canada **67-1A**: 34-35.

Hill, R. M. 1969. Review of the Inuvik forest fire August 8-18, 1968. Mimeograph on file at the Inuvik Research Laboratory of the Department of Indian and Northern Affairs (Government of Canada).

Hultén, E. 1968. Flora of Alaska and Neighbouring Territories. Stanford University Press. Stanford, California.

Mackay, J. R. 1978. Quaternary and permafrost features, Mackenzie Delta area. *In*: Young, F. G. editor. Geological and geographical guide to the Mackenzie Delta area. Canadian Society of Petroleum Geologists, Calgary, Alberta.

Murphy, P. J., S. R. Hughes, and J. S. Mactavish. 1980. Forest fire management in the N.W.T.. A review of 1979 forest fire. Department of Indian Affairs and Northern Development.

Prest, V. K. 1969. Retreat of Wisconsin and recent ice in North America (Map). Geological Survey Canada. Map 1257-A.

Rampton, V. N. 1971. Quaternary geology, Mackenzie Delta and Arctic Coastal Plain, District of Mackenzie. Geological Survey Canada 71-1A: 173-177.

Rampton, V. N. 1972. Quaternary geology, Arctic coastal plain. District of Mackenzie and Herschel Island, Yukon Territory. Geological Survey Canada 72-1A.

Rowe, J. S. 1972. Forest Regions of Canada. Canadian Forest Service. Publication No 1300. Reprint 1977.

Simard, A. J. 1975. Wildland fire occurrence, Environment Canada, Forest Service. Map with text, Ottawa.

Timoney, K. P. 1988. A geobotanical investigation of the subarctic forest-tundra of the N.W.T.. Ph.D. Thesis, University of Alberta.

Timoney, K. P., R. W. Wein. 1991. The areal pattern of burned tree vegetation in the subarctic region of northwestern Canada. Arctic **44**: 223-230.

Wein, R. W. 1975. Vegetation recovery in the arctic tundra and forest/ tundra after fire. A.L.U.R. 74-75-62. Indian Affairs and Northern Development, Ottawa, 81p.

Wein, R. W. 1976. Frequency and characteristics of arctic tundra fires. Arctic **29**: 213-222.

Wein, R. W., and D. A. MacLean. 1983. An overview of fire in northern ecosystems pp 1-18. *In*: Wein, R. W., and D. A. MacLean. editors. The Role of Fire in Northern circumpolar Ecosystems, Scope 18: John Wiley & Sons, Toronto.

Zoltai, S. C., and C. Tarnocai. 1974. Soils and Vegetation of hummocky Terrain. Environmental-Social Program Northern Pipelines Report **74-5**, Ottawa.

CHAPTER III

POST-FIRE VEGETATION RECOVERY AND TREE ESTABLISHMENT AT THE ARCTIC TREELINE: CLIMATE CHANGE - VEGETATION RESPONSE HYPOTHESES[*]

INTRODUCTION

Wildfire is an important, although infrequently occurring, event that influences vegetation composition (Timoney and Wein 1991; Sirois and Payette 1991) in the northern coniferous forest and forest-tundra region (Wein and MacLean 1983). At the climatically sensitive forest-tundra ecotone, where tree species are growing at the limit of their range, disturbances and/or climatic changes have caused major changes in vegetation patterns (Black and Bliss 1980; Payette and Filion 1985; Cwynar and Spear 1991). For the forest-tundra boundary in northern Québec (Payette and Gagnon, 1985) and for the Keewatin and Mackenzie regions, Northwest Territories (Nichols, 1976) it is recognized that the patchiness of vegetation is a direct result of historic fire events. Sirois and Payette (1991) found drastically reduced post-fire black spruce

---

[*] A version of this chapter has been published. Landhäusser S. M., and R. W. Wein. 1993. Journal of Ecology **84**: 665-672.

reestablishment on upland sites, which in turn led to more widespread tundra vegetation types.

General circulation models suggest that an increase in exceptionally warm and dry weather conditions will result in increased frequency and severity of fires (Flannigan and Van Wagner 1991). Given these predictions of changed fire conditions, it can be hypothesized that species abundance may change rapidly if fire removes plant communities that are poorly adapted to the new climatic conditions. In addition, it is recognized that not all fires have equal ecological consequences. It is the severe (deep burning) fires that are of special interest in low energy environments because they alter the soil-environment conditions from an organic soil dominated system to a mineral soil dominated system. Under mineral soil conditions tree seedling establishment and growth is enhanced by increased soil temperatures and nutrient availability (Viereck and Schandelmeier 1980; Van Cleve and Viereck 1981; Chapin *et al.* 1988; Komárková and McKendrik 1988).

Predictions of future vegetation changes are made more reliable if there is an understanding of the time scales involved. Dendrochronological or paleoecological studies predicting long-term (centuries or millennia) post-fire vegetation changes at the arctic treeline are common (e.g. Nichols 1976; Foster 1985; Payette and Gagnon 1985; Morneau and Payette 1989; Cwynar and Spear 1991; Sirois and Payette 1991). However, these types of studies have limited value in making predictions over short time scales unless the precision of measurement is within a very few years. Short-term (1-10 years) post-fire vegetation recovery patterns of burned forest-tundra and tundra vegetation are also well represented in the literature (Bliss and Wein 1972; Racine, Johnson and Viereck 1987; Ebersole 1987), but medium-term post-fire studies (ie. 10-30 years) that approach the time boundaries of the general circulation model exercises are few in number. Studies involving recovery of tree species after fire near the arctic treeline, have largely focussed on the long-lived *Picea* species. Less attention has been given to the short-lived tree species *Betula papyrifera*, *Populus tremuloides* and *Populus balsamifera*. These species are found well beyond the upland forests in soil-climate microrefugia along northward flowing rivers, where periodic disturbances like flooding and slumping create favourable microsites.

The objectives of this research were: (1) to remeasure, at permanent locations, post-fire plant cover and biomass on upland sites 22 years after a severe fire at the arctic treeline, (2) to determine the extent of tree reestablishment after fire within treeline forests and (3) to determine the extent of tree invasion into these upland tundra areas recovering after a severe fire.

MATERIALS AND METHODS

Study area

The study area is located in a 500 km² area north and east of Inuvik (68°18' N, 133°29' W), Northwest Territories between the latitudes 68°22' N and 68°35' N and longitudes 133°30' W and 134°00' W (Figure III-1) which burned from August 8 to August 18, 1968. The extent of the burn was limited in the west by the Mackenzie River Delta, in the south by a mechanically prepared fire guard and in the east and north by streams and lakes. Detailed fire histories are unavailable but fire frequencies in forest-tundra (Timoney and Wein 1991) and tundra vegetation (Wein 1976) are not as high as further south. However, fire scars on *Picea mariana* trees in the Inuvik area suggest a previous fire about 120 years ago.

In this gently rolling terrain, elevation ranges from 33 metres (Mackenzie River) to over 165 metres above mean sea level (Caribou Hills-located at the northern extent of the burn). The climate has been conducive to the development of continuous permafrost to depths >100 m (Brown 1970). Maximum active layers vary from 30 to 100 cm depending on slope and exposure. Summers are cool and short (about four months), whereas winters are long and extremely cold. Weather data have been collected continuously at the Inuvik airport only since 1958. Mean annual air temperatures range from -10 to -15 °C. The total mean annual precipitation is 250 to 350 millimetres, with the majority falling in late summer and early fall (Canada Committee on Ecological Land Classification 1989). From 1958 to 1992 the growing season climate has become slightly warmer and somewhat drier. There has been an increase in the annual sum of degree days (DD) greater than 0 °C for the months of June, July, and August ($DD=1023.7+2.83year$, $R^2=0.06$, $P=0.167$) and a slight decrease in annual precipitation (PR) during the growing season ($PR=104.3-0.44year$, $R^2=0.01$, $P=0.508$) since 1958 (Figure III-2).

The open boreal forest vegetation to the south of Inuvik is described by Rowe (1972) as part of the Boreal Forest Region. *Picea mariana* and *Picea glauca* are the dominant conifer species and *Betula papyrifera* is the dominant deciduous species. North of Inuvik, as the climate and soil conditions become more rigorous for plant growth, the vegetation becomes subarctic open woodland (Zoltai and Tarnocai 1974) and then tundra (Corns 1974). In the Mackenzie River delta and valley *Picea* forests are located approximately 50 kilometres further north than in the upland (Mackay 1963; Pearce, McLennan and Cordes 1988). We have located the additional tree species of *Populus balsamifera* and *Populus tremuloides* well north of this treeline. Relative to other parts of Canada, the latitudinal forest-tundra transition near Inuvik is narrow; the distance from open boreal forest to tundra is only 10 to 15 kilometres compared with approximately 100 kilometres in localities in the eastern Canadian Arctic (e.g. Payette *et al.* 1989). In some areas depending on elevational differences, the distance from the forested delta to the upland tundra can vary between only a few hundred metres and about 2 kilometres.

Vegetation recovery

In early August of 1973, 34 paired burned:unburned study sites were selected, on opposite sides of the narrow boundary of the fire perimeter, for both biomass and plant cover recovery estimates. Site pairs were chosen on the basis of having similar slope, elevation, and soil surface characteristics, and being separated by a fire guard or stream channel (Wein 1975). In August of 1990, 24 sites were relocated for measurements comparable to those made in 1973, restaked and numbered to ensure future relocation (Figure III-1). Ten sites were not revisited, because of their remote locations or because their vegetation types were not relevant to this study (e.g. white spruce delta vegetation types).

A pilot study was conducted in the unburned area along the perimeter of the fire to determine whether significant changes in cover and biomass accumulation had occurred in the 22 year period. Results showed that differences fell within the standard errors of the data collected in 1973, mainly due to variation within the plant community and among the quadrats randomly chosen along the transects both in 1973 and 1990. We believe that the changes in vegetation cover in the undisturbed sites were minor between 1973 and 1990: not surprisingly since the area had not been burned for 120 years and these undisturbed ecosystems, limited by energy and nutrients, change very slowly.

As a result of the pilot study, only the burned communities of the original pairs were remeasured in 1990. At each site a 50 metre base transect was located on a random azimuth and 20 quadrats (each 0.71 m x 0.71 m), were chosen randomly along each transect. Percent cover estimates were made within the quadrats for living vascular plants by species, total lichens, total mosses and bare ground. Additionally, the number of trees of each species was recorded in each quadrat for all transects.

Biomass of trees and shrubs (>50 centimetres), forbs (<50 centimetres), cryptogams, and dead plant material (litter), was removed sequentially on four randomly chosen quadrats (0.71 m x 0.71 m each) along the same base transect, used for estimating cover. After determining the total wet weight of biomass in the field, representative subsamples were transferred to the laboratory in plastic bags. In the laboratory the wet weight was determined; the samples were then dried at 80 °C to constant weight and the biomass extrapolated to a per square metre basis. The methods were identical to those used in 1973.

Cover and biomass data were analyzed by univariate analysis of variance procedures (Norusis 1988) to determine the differences between unburned and burned sites in 1973, both in the tundra (n=15 base transects) and in the forest-tundra (n=9 base transects) and also between unburned sites in 1973 and burned sites in 1990.

Tree establishment

A study area of 1 by 6 kilometres was established between Inuvik and Three Mile Lake in 1990 (Figure III-1) to determine post-fire tree establishment in time and space after the fire. Transects (10 x 50 metres) for each of the tree species *Betula papyrifera*, *Picea glauca*, *Picea mariana*, and *Populus balsamifera* were randomly established in upland sites. For *Picea mariana* and *Picea glauca*, six transects for each species were located in formerly (i.e. pre-fire) treed patches which contained a high density of stems (on average about 100 stems

500 m^{-2}) and extended outside the patches into low density areas (less than one stem 500 m^{-2}) as judged by the standing or fallen and still readily identifiable tree stems. For *Picea glauca*, the appearance and the distance of survivor trees adjacent to the chosen transect was noted because repeated recruitment from these adjacent survivor trees influenced seedling establishment. For *Betula papyrifera* six transects were established randomly in pre-fire high density stands (on average about 50 stems 500 m^{-2}) and six transects were established randomly in low density stands (less than one stem 500 m^{-2}). Since there were no *Populus balsamifera* trees in the study area prior to the 1968 fire, the six transects were randomly established and categorized as low density.

On all transects, measurements made in the summer of 1990 included dead tree densities, live seedling densities and seedling age as determined by terminal bud scars or tree rings. *Populus balsamifera* was often found in clones with two or more ramets. Clones were treated as one individual, and the oldest ramet was used to determine the age and year of establishment. Tree seedling densities and establishment data were analyzed using non-parametric Wilcoxon's signed-ranks comparison test (Norusis 1988) for two groups, namely pre- and post-fire tree densities.

RESULTS

Vegetation cover

Five years following the severe fire the forest-tundra and the tundra vegetation showed similar patterns of recovery. Vascular plant cover had reached about 65 percent of the pre-fire condition and there was still 17 percent bare soil (Table III-1). Twenty-two years after the fire the average vascular plant cover was 17 percent higher in the burned sites than in the unburned sites in 1973 allowing the total plant cover to reach 124 percent by 1990 (Table III-1).

Although the cryptogam communities were almost completely destroyed by the fire in the forest-tundra and tundra the bryophyte cover increased by 1973 to an average of 25.4 percent in the forest-tundra and 23.7 percent in the tundra but showed little further increase. *Marchantia polymorpha* L. and *Ceratodon purpureus* (Hedw.) Brid. accounted for most of this recolonization (Table III-2). Lichens which made no contribution to the total percentage cover in 1973, increased by 1990 to an average of 8.4 percent in the forest-tundra and 6.0 percent in the tundra. Cover values of the cryptogams were still significantly lower in 1990 in both locations (Table III-2).

Several differences were evident between the forest-tundra and tundra sites. In the forest-tundra sites the vascular plant cover after 22 years reached similar values to those in 1973 of the unburned vegetation. *Picea mariana* and *Vaccinium vitis-idaea* had not yet recovered to the unburned level reaching only about 33 and 45 percent, respectively, of the cover values prior to the fire. *Betula papyrifera* increased in cover about three times to 3.9 percent cover after the fire. Shrub species like *Salix* spp., *Betula glandulosa* and *Alnus crispa* had reached pre-fire cover values. Herbaceous plant species such as *Calamagrostis canadensis* and *Epilobium angustifolium* had decreased, from high cover values of 11.6 and 6.8 percent, respectively, 5 years after the fire, to almost pre-fire levels of 1973 with 7.6 and 1.2 percent, respectively, in 1990.

On tundra sites the total vascular plant cover was more than double on the burned area when compared to the unburned sites. This increase was primarily due to *Ledum palustre* and *Betula glandulosa* which increased 11.7 percent and 8.8 percent, respectively, over the control (Table III-2). Invader species like *Calamagrostis canadensis*, *Carex Bigelowii*, and *Arctagrostis latifolia* which had high cover values in 1973 were still well represented in the tundra sites in 1990 with cover values of 11.4, 1.5, and 1.4 percent respectively. Only *Epilobium angustifoli*um decreased to pre-fire values of 0.7 percent cover. *Empetrum nigrum* and *Arctostaphylos rubra* with present cover values of 1.1 and 1.9 percent respectively had recovered to only 18 and 42 percent of pre-fire levels (Table III-2).

Trees were not well represented in any of the burned forest-tundra or tundra sites. The cover of *Betula papyrifera* and *Picea mariana* on the burned forest-tundra sites was 0.7 and 0 percent, respectively, in 1973. By 1990 *Betula papyrifera* increased to 3.9 percent (almost four times the pre-fire level) in forest-tundra sites and was about 0.2 percent in burned tundra sites. *Picea mariana* did not reach the pre-fire cover levels; it was significantly lower in cover in forest-tundra sites and was not found in tundra sites (Table III-2).

Biomass

The total biomass by 1990 in both burned forest-tundra and burned tundra vegetation was still significantly lower (about 50 percent) than that in the unburned vegetation due mostly to the low cryptogam biomass of the tundra sites and cryptogam and forb biomass of the forest-tundra sites (Table III-2). The biomass of the forb layer (< 50 centimetres in height) of the tundra sites was mostly composed of *Ledum palustre*, *Eriophorum vaginatum*, and *Calamagrostis canadensis*. The litter in burned forest-tundra and tundra sites showed increases of 280 and 230 percent, respectively, over the unburned sites in 1990. Leaf material from grasses and sedges, especially *Calamagrostis canadensis* and *Eriophorum vaginatum*, made up the largest proportion of the litter. Tree and shrub biomass (> 50 centimetres in height) in burned forest-tundra sites reached about 62 percent of unburned sites mainly because of a high density of *Betula papyrifera* (the only significant tree species) and shrub species. In unburned tundra sites trees and shrubs did not contribute to biomass. The appearance of such biomass at the burned tundra sites between 1973 and 1990 was mainly due to *Betula glandulosa* and to a lesser extent to *Salix* spp. and *Alnus crispa* (Table III-2).

Tree density

The revegetation surveys measuring cover in 1973 and 1990 also included measurements of tree densities. The density of *Betula papyrifera* in the burned forest-tundra sites had increased about five times, from 0.08 to 0.4 stems m^{-2}, compared to the unburned sites. *Populus balsamifera* was found only after the fire and had a density of 0.02 stems m^{-2}. *Picea mariana*, at 0.2 stems m^{-2} on the burned sites was about 50 percent lower than on the unburned sites (Table III-3).

The more detailed study between Inuvik and Three Mile Lake showed similar results. Post-fire *Betula papyrifera* and *Populus balsamifera* seedling density increased over pre-fire levels and also expanded into former treeless areas (Table III-4). In sites occupied by *Betula papyrifera* before the fire (treed), the post-fire tree density doubled. Out of six transects only one showed lower tree densities after the fire. All transects in low density sites (non-treed) for *Betula papyrifera* showed higher post-fire population densities; the density increased from one to about nine trees 500 m^{-2}. *Picea* species, however, did not expand into the tundra (Table III-4). Within burned *Picea* clumps post-fire seedling density for both species *Picea glauca* and *Picea mariana* was significantly lower than the pre-fire densities of trees. For *Picea glauca*, where survivor trees were located within 50-200 metres of the transect, seedling density reached an average of 53 percent of the pre-fire densities within the clumps (Table III-4).

The age distribution of *Betula papyrifera* and *Picea glauca* seedlings showed an even annual establishment throughout the 22 years; however, *Picea glauca* seedlings establishment showed peaks approximately every three or four years (Figure III-3). The age distribution of *Picea mariana* seedlings showed a steady increase in number of seedlings that established in the post-fire period from 1968 to 1976; after 1976 the establishment rate declined. Establishment of *Populus balsamifera* seedlings after the fire was sporadic (Figure III-3).

DISCUSSION

As indicated earlier, the climate of the Inuvik area has shown a slight warming trend since the 1968 fire; therefore this study might be considered as a partial analogue of how post-fire vegetation of the treeline in the western Canadian Arctic might change in 10 to 30 years as a result of the warmer and drier conditions predicted by climate change. Most of the vascular plant cover in the early post-fire revegetation stages of both the forest-tundra and the tundra was dominated by nitrophilous invader species such as *Epilobium angustifolium* and *Calamagrostis canadensis*. Subsequently, forbs and low shrubs including *Petasites frigidus*, *Ledum palustre*, and *Vaccinium uliginosum* sprouted from surviving rhizomes or rootstocks and after which such plants accounted for most of the cover, as found in a number of other post-fire recovery studies (e.g. Wein and Bliss 1973, Racine 1981, 1987; Johnson and Viereck 1983; Racine, Johnson and Viereck 1987).

Twenty years after the fire, patterns of plant cover in the burned forest-tundra and tundra have become different. In the burned tundra, tall shrubs and deciduous trees have become dominant compared to the previously treeless cover dominated by low shrubs. However, some early invader species, especially *Calamagrostis canadensis*, maintained cover values due to the still open conditions in tree and shrubless sites. In the forest-tundra, early vascular plant invaders decreased in cover to the low pre-fire levels. However, understorey species like *Ledum palustre*, *Vaccinium vitis-idaea*, *Rubus chamaemorus*, and *Petasites frigidus* had still not reached pre-fire levels 22 years after the fire, probably a result of shading by the dense shrub and tree vegetation which was 3 to 6 metres tall.

Biomass accumulation followed the trend in total vascular plant cover. Accumulation of litter was particularly high compared to pre-fire levels in both forest-tundra and tundra sites. Wein (1975) estimated that a minimum biomass of about 1500 grams m^{-2} was necessary to carry the fire through the shrub-dominated tundra in 1968. Parts of the burned area have again reached this level and although the combustible material has changed from pre-fire mosses, lichens and organic soil deposits to post-fire forbs, grasses and woody organic matter, these latter materials would probably support fire spread, particularly under severe drought conditions.

Spatial changes in vegetation patterns were also evident in the post-fire succession patterns. Early invader species like *Calamagrostis canadensis* and *Epilobium angustifolium* can colonize over long distances via their wind-disseminated seeds. These species grow vigorously, especially after severe fires expose mineral soil, and dominate the vegetation for 10 or more years. Deciduous tree species, with their resprouting potential, ability to produce seeds at an early age, and long range seed dispersal, are effective in invading formerly treeless areas under increased disturbance regimes. A lack of viable seeds, especially in *Picea glauca*, and the short distances over which seeds are dispersed appears to have restricted re-establishment of this species. Similar observations were made in the eastern Canadian Arctic (Elliott 1979; Sirois and Payette 1991), where fire occurrence has been linked to the patchiness of conifer trees within the wide treeline zone (Payette and Gagnon 1985).

With greater increases in temperature and drought, as predicted under global warming, and the anticipated polar amplification of temperature, there may be even more profound effects on vegetation patterns than measured in the present study. Some environmental factors with which the performance of plants is positively correlated, like soil temperature and nutrient availability, will increase; however, other factors which are negatively correlated, like drought and frequency of fires, are also likely to increase. With increased mean annual air temperature, the fertility, viability, and availability of seeds of all tree species will probably increase. However, lack of long range seed dispersal in *Picea* species will limit their chances of re-establishment under warmer climate scenarios. The longer-lived character of coniferous species will be of limited value if fire frequency increases since they will be removed before they can dominate the forest system. Drought-tolerant species with efficient seed dispersal over a wide geographic range and vigorous resprouting ability will be well suited to invade tundra areas rapidly, especially after fires (Viereck and

Van Cleve, 1984). The present study established that *Betula papyrifera* and *Populus balsamifera* invaded burned tundra areas. Under climate warming scenarios, this invasion would be more effective if fire frequency increases and occurs over larger areas.

We hypothesize that the treeline in the western Canadian Arctic will move northwards, step-wise with each severe fire that removes the insulating organic matter, exposes mineral soil, promotes thawing of the permafrost, and provides seedbeds conducive to tree establishment. Present-day heath tundra areas could become dominated by tall shrubs until trees emerge over the shrub layer. The movement of deciduous trees will be particularly evident in areas where the forest-tundra ecotone is narrow and where the major northward flowing river valleys, such as the Mackenzie, Anderson and Horton, protect small outlier forests and scattered trees. Both will provide a source of propagules for the invasion of the tundra. This prediction probably applies to other sites adjacent to circumpolar northward flowing rivers.

Table III-1. Mean (± SE) percentage cover values for the combined forest-tundra and tundra communities for total vascular plants, cryptogams, total plant cover, and bare soil on 24 burned:unburned paired communities after a forest-tundra and tundra fire in 1968 near Inuvik, N.W.T..

	UNBURNED	BURNED	
	1973	1973	1990
Vascular Plants	77.4 ± 3.4	50.2 ± 3.5**	94.7 ± 3.5*
Cryptogams	57.7 ± 4.2	24.3 ± 3.4**	29.4 ± 3.3**
Total Plant Cover	135.1 ± 4.5	74.5 ± 4.4**	124.1 ± 8.3
Bare Soil	1.2 ± 0.5	17.0 ± 4.6**	5.1 ± 0.7

* $P < 0.05$. ** $P < 0.01$ for $F_{(1, 69)}$, $\alpha=0.05$. comparing between unburned and burned 1973 and undburned and burned 1990.

Table III-2. Mean (± SE) percentage cover and biomass accumulation (g m^{-2}) of dominant species of vascular plants, cryptogams and bare ground estimated for forest-tundra and tundra vegetation that burned in 1968. Only species showing differences among treatments are reported.

	FOREST-TUNDRA (n=9)			TUNDRA (n=15)		
	UNBURNED	BURNED		UNBURNED	BURNED	
	1973	1973	1990	1973	1973	1990
Percentage cover (subsample = 20)						
Vaccinium vitis-idaea	16.7 ± 2.7	2.2 ± 0.6**	7.5 ± 2.2**	14.8 ± 2.4	2.4 ± 0.5**	13.4 ± 2.1
Picea mariana	2.8 ± 1.0	0**	0.7 ± 0.3*	0.5 ± 0.5	0	0
Betula papyrifera	1.1 ± 0.9	0.7 ± 0.3	3.9 ± 1.7	0	T	0.2 ± 0.2
Betula glandulosa	7.2 ± 5.6	0.6 ± 0.3	5.7 ± 2.2	6.2 ± 2.6	0.6 ± 0.3	15.0 ± 2.2**
Alnus crispa	5.0 ± 2.4	1.1 ± 0.6	7.7 ± 5.3	7.1 ± 1.9	1.5 ± 0.5**	5.8 ± 1.4
Salix spp.	3.4 ± 1.4	2.2 ± 1.1	8.0 ± 3.3	2.2 ± 0.7	0.8 ± 0.3*	1.5 ± 0.4
Calamagrostis canadensis	3.5 ± 1.5	11.6 ± 4.2	7.6 ± 2.3	1.5 ± 0.4	10.1 ± 2.0**	11.4 ± 2.1**
Epilobium angustifolium	0	6.8 ± 2.4**	1.2 ± 0.6	0	5.8 ± 2.9*	0.7 ± 0.2
Eriophorum vaginatum	4.3 ± 3.3	5.0 ± 5.0	3.9 ± 2.3	6.3 ± 2.5	6.1 ± 1.7	7.8 ± 2.5
Ledum palustre	18.5 ± 2.1	4.4 ± 1.2**	16.3 ± 4.7	15.1 ± 2.2	6.4 ± 1.2	26.8 ± 2.7**
Carex Bigelowii	0	T	0	0	0	1.5 ± 0.7**
Arctagrostis latifolia	0	4.7 ± 4.0	1.4 ± 0.7	T	1.4 ± 0.5*	1.4 ± 0.6*
Empetrum nigrum	1.9 ± 0.6	0.2 ± 0.2	1.4 ± 0.8	5.8 ± 1.7	1.1 ± 1.0**	1.1 ± 0.4**
Arctostaphylos rubra	0.6 ± 0.6	T	2.0 ± 2.0	4.5 ± 1.6	1.9 ± 0.7	1.9 ± 0.7
Vascular Plants	79.1 ± 6.9	51.7 ± 5.1*	79.9 ± 13.4	76.4 ± 3.9	49.4 ± 5.1**	103.6 ± 7.3**
Mosses	34.2 ± 4.7	25.4 ± 5.1	20.2 ± 5.1	31.7 ± 5.1	23.7 ± 4.7	23.9 ± 2.6
Lichens	17.5 ± 6.3	0**	8.4 ± 2.8	29.6 ± 6.4	0**	6.0 ± 1.5**
Bare Ground	2.2 ± 1.1	25.3 ± 6.7**	6.2 ± 1.2	0.5 ± 0.3	12.0 ± 6.2**	4.4 ± 0.8
BIOMASS (g m^{-2}) (subsample = 4)						
Trees & Shrubs (> 50 cm)	663 ± 379	0	413 ± 142	0	0	280 ± 80**
Forbs (< 50 cm)	414 ± 62	147 ± 16**	193 ± 39**	657 ± 132	104 ± 27**	401 ± 33*
Cryptogams	1239 ± 187	0**	69 ± 26**	2008 ± 624	6 ± 6**	137 ± 25**
Litter	190 ± 98	7 ± 5	532 ± 107**	161 ± 50	10 ± 6*	367 ± 82**
Total Biomass	2506 ± 554	154 ± 18**	1208 ± 163*	2826 ± 564	120 ± 27**	1174 ± 150**

Trace < 0.1

* $P < 0.05$, ** $P < 0.01$ for $F_{(1,16)}$ for forest-tundra and $F_{(1,41)}$ for tundra, $\alpha = 0.05$

Table III-3. Mean (± SE) tree population densities (stems m^{-2}) in unburned and burned forest-tundra determined in the revegetation surveys of 1973 and 1990 (n=9).

	UNBURNED	BURNED	
SPECIES	1973	1973	1990
Picea mariana	0.4 ± 0.12	0	0.2 ± 0.1
Betula papyrifera	0.08 ± 0.03	0.2 ± 0.1	0.4 ± 0.13
Populus balsamifera	0	0	0.02 ± 0.02

Table III-4. Mean (± SE) pre-fire (number of dead stems) and post-fire (number of seedlings) tree density (number 500 m^{-2}) on sites which were treed or non-treed before the fire (n=6).

	TREED		NON-TREED	
SPECIES	Pre-fire	Post-fire	Pre-fire	Post-fire
Picea mariana	161.6 ± 12.3	18.6 ± 5.5*	0	0
Picea glauca survivor trees[a]	103.3 ± 10.9	54.7 ± 20.1*	0	T
Picea glauca no survivor trees[a]	55 ± 10.4	0.7 ± 0.7	0	0
Betula papyrifera	51.3 ± 13.3	112.3 ± 42.7	0.5 ± 0.3	9.2 ± 1.7*
Populus balsamifera	NA	NA	0	2.5 ± 0.7

* significant differences between pre- and post-fire densities (Wilcoxon's signed-ranks comparison test, $\alpha = 0.025$).
T = Trace < 0.5.
[a] see text for explanation.

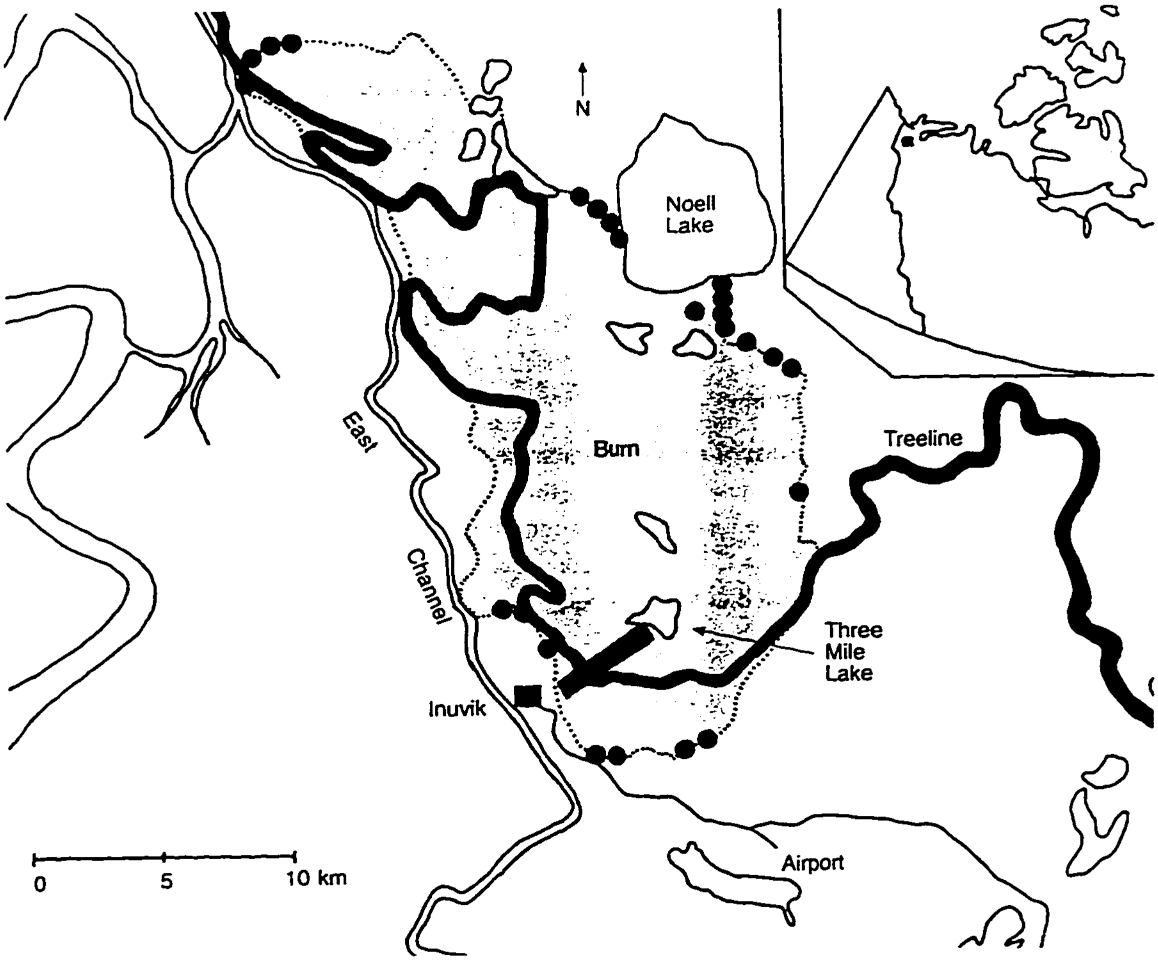

Figure III-1. The study area was located north and east of Inuvik (68°18' N, 133°29' W) Northwest Territory, Canada. The 24 points shown along the perimeter of the 1968 burn are locations sampled for post-fire vegetation recovery in 1973 and 1990. The rectangle represents the tree-recovery study area of 6 km^2.

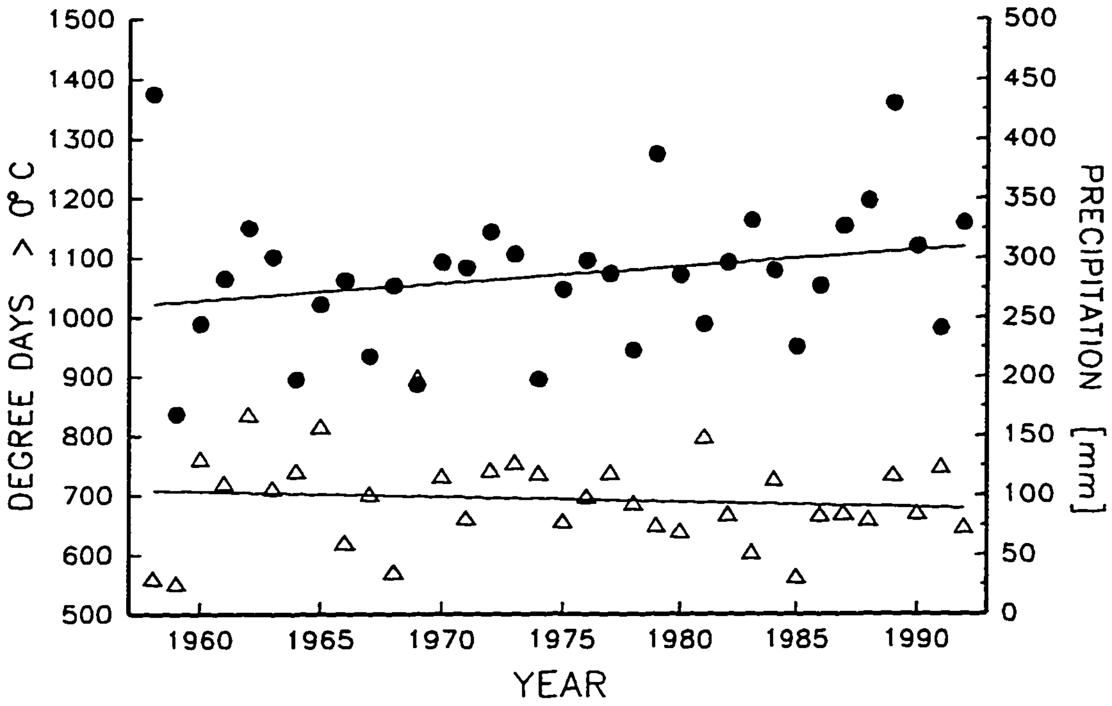

Figure III-2. Annual sum of Degree Days (DD) greater than zero degree (●) and total precipitation (PR) (△) during the months of June, July, and August, based on data obtained from Atmospheric Environment Canada at the airport in Inuvik, between 1958 and 1992.

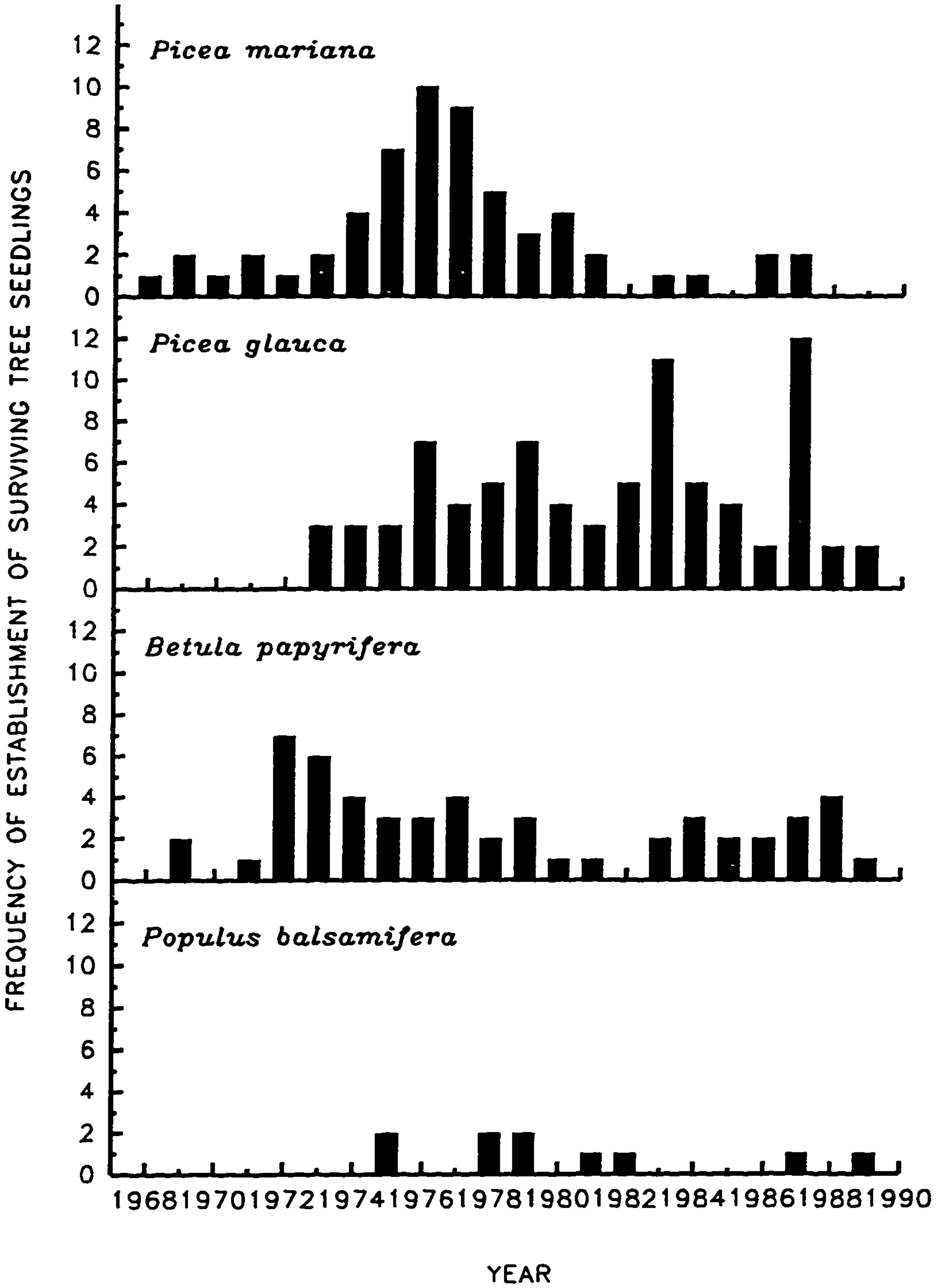

Figure III-3. Annual establishment of seedlings of tree species after a 1968 burn based on six transects of 500 m^2 each, for a total area of 3000 m^2.

LITERATURE CITED

Black, R. A. and L. C. Bliss. 1980. Reproductive ecology of *Picea mariana*, at the treeline near Inuvik N.W.T., Canada. Ecological Monographs **50**: 331-354.

Bliss, L. C., and R. W. Wein. 1972. Plant community responses to disturbances in the western Canadian Arctic. Canadian Journal of Botany **50**: 1097-1109.

Brown, R. J. E. 1970. Permafrost in Canada. University of Toronto Press, Toronto, Canada.

Canada Committee on Ecological Land Classification (CCELC). 1989. Ecoclimatic Regions of Canada, First Approximation, written and compiled by Ecoregions Working Group, Ecological Land Classification Series No. 23, Environment Canada, Ottawa, Canada.

Chapin, F. S. III., N. Fetcher, K. Kielland, K. R. Everett, and A. E. Linkins. 1988. Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing soil water. Ecology **69**: 693-702.

Corns, I. G. W. 1974. Arctic plant communities east of the Mackenzie Delta. Canadian Journal of Botany **52**: 1731-1745.

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

Ebersole, J. J. 1987. Short-term vegetation recovery at an Alaskan arctic coastal plain site. Arctic and Alpine Research **19**: 442-450.

Elliott, D. L. 1979. The current regenerative capacity of the northern Canadian trees, Keewatin, N.W.T., Canada: some preliminary observations. Arctic and Alpine Research **11**: 243-251.

Flannigan, M. D., and C. E. Van Wagner. 1991. Climate change and wildfire in Canada. Canadian Journal of Forest Research **21**: 66-72.

Foster, D. R. 1985. Vegetation development following fire in *Picea mariana-Pleurozium* forest of south-eastern Labrador, Canada. Journal of Ecology **73**: 517-534.

Johnson, L. A., and L. A. Viereck. 1983. Recovery and active layer changes following a tundra fire in northwestern Alaska. Permafrost Fourth International Conference Proceedings, 17-22 July 1983, University of Alaska, Fairbanks, Alaska, pp. 543-547. National Academic Press, Washington, D.C.

Komárková, V., and J. D. McKendrick. 1988. Patterns in vascular plant growth forms in arctic communities and environment at Atkasook, Alaska. *In*: Werger, M. J. A., P. J. M. van der Aart, H. J. During, and J. T. A. Verhoeven. editors. Plant Form and Vegetation Structure, pp. 45-70. SPB Academic Publishing, The Hague.

Mackay, J. R. 1963. The Mackenzie Delta area, N. W. T. Geographical Branch Memoir No.8, Department of Mines and Technical Surveys, 202 pp. Ottawa, Canada.

Morneau, C., S. and Payette. 1989. Postfire lichen-spruce woodland recovery at the limit of the boreal forest in northern Québec. Canadian Journal of Botany **67**: 2770-2782.

Nichols, H. 1976. Historical aspects of the northern Canadian treeline. Arctic **29**: 38-47.

Norusis, M. J. 1988. SPSS/PC+ V 2.0 Base manual. SPSS Incorporation, Chicago, U.S.A..

Payette, S., and L. Filion. 1985. White spruce expansion at the treeline and recent climate change. Canadian Journal of Forest Research **15**: 241-251.

Payette, S., and R. Gagnon. 1985. Late Holocene deforestation and tree regeneration in the forest-tundra of Québec. Nature **313**: 656-673.

Payette, S, C. Morneau, L. Sirois, and M. Desponts. 1989. Recent fire history of northern Québec biomes. Ecology **70**: 656-673.

Pearce, C. M., D. McLennan, and L. D. Cordes. 1988. The evolution and maintenance of white spruce woodlands on the Mackenzie Delta, N. W. T., Canada. Holarctic Ecology **11**: 248-258.

Racine, C. H. 1981. Tundra fire effects on soils and three plant communities along a hill-slope gradient in the Seward Peninsula, Alaska. Arctic **34**: 71-84.

Racine, C. H. 1987. Fire. *In*: Walker, D. A., D. Cate, J. Brown, and C. H. Racine editors. Disturbance and recovery of arctic alaskan tundra terrain: A review of recent investigations. U.S. Army Cold Region Research and Engineering Laboratory, Report 87-11, pp. 13-14. Hanover, New Hampshire, U.S.A..

Racine, C. H., L. A. Johnson, and L. A. Viereck. 1987. Patterns of vegetation recovery after tundra fires in northwestern Alaska, U.S.A.. Arctic and Alpine Research **19**: 461-469.

Rowe, J. S. 1972. Forest Regions of Canada. Canadian Forest Service Publication 1300. Canadian Department of Environment, Ottawa, Canada.

Sirois, L., and S. Payette. 1991. Reduced postfire tree regeneration along a boreal forest-forest-tundra transect in northern Québec. Ecology **72**: 619-627.

Timoney, K. P., and R. W. Wein. 1991. The areal pattern of burned tree vegetation in the subarctic region of northwestern Canada. Arctic **44**: 223-230.

Van Cleve, K., and L. A. Viereck. 1981. Forest succession in relation to nutrient cycling in the boreal forest of Alaska. *In*: West, D. C., H. H. Shugart, and D. B. Botkin. editors. Forest succession: concepts and application, pp. 185-211. Springer Verlag, New York.

Viereck, L. A., and L. A. Schandelmeier. 1980. Effects of fire in Alaska and adjacent Canada - a literature review. U. S. Department of Interior Bureau Land Management. Technical Report 6. 124 pp. Fairbanks, Alaska, U.S.A..

Viereck, L. A., and K. Van Cleve. 1984. Some Aspects of Vegetation and Temperature Relationships in the Alaskan Taiga. *In*: McBeath, J. H. editor. The Potential Effects of Carbon Dioxide-Induced Climatic Changes in Alaska, School of Agriculture and Land Resource Management, University of Alaska, Miscellaneous Publication 83-1, pp. 129-142. Fairbanks, Alaska.

Wein, R. W. 1975. Vegetation recovery in the arctic tundra and forest-tundra after fire. Arctic Land Use Research 74-75-62. Indian Affairs and Northern Development, Ottawa, Canada.

Wein, R. W. 1976. Frequency and characteristics of arctic tundra fires. Arctic **29**: 213-222.

Wein, R. W., and L.C. Bliss. 1973. Changes in arctic Eriophorum tussock communities following fire. Ecology **54**: 845-852.

Wein, R. W., and MacLean, D. A. 1983. An overview of fire in northern ecosystems. *In*: Wein, R. W. and D. A. MacLean. editors. The Role of Fire in Northern circumpolar Ecosystems, pp. 1-18. Scientific Committee on Problems of the Environment, 18, Wiley, New York, U.S.A..

Zoltai, S. C., and C. Tarnocai. 1974. Soils and vegetation of hummocky terrain. Environmental-Social Program Northern Pipelines Report 74-5, Ottawa, Canada.

CHAPTER IV

TREE SEEDLING RESPONSE RELATED TO SHORT-WAVE ENERGY INPUT AT THE ARCTIC TREELINE[**]

INTRODUCTION

The polar regions are low-energy environments with the arctic treeline and forest-tundra zone receiving approximately 700 - 800 MJ m^{-2} $year^{-1}$ of net radiation; this value decreases to about 300 - 400 MJ m^{-2} $year^{-1}$ in the High Arctic (Hare and Thomas 1974). A characteristic of the high latitudes is the relatively low solar altitude and long day-length during the growing season. The mean and maximum solar noon intensities of the direct solar beam in the Arctic from May to July are typically slightly lower but occasionally greater than those at lower latitudes because of higher transparency of the atmosphere due to low dust and moisture content (Gavrilova 1966). Further, the daily total radiation inputs during the growing season are as high as in temperate regions due to long day length.

[**] A version of this chapter has been submitted for publication by Landhäusser, S. M., D. H. Halliwell, and R. W. Wein, April 1994.

It is well known that phytomass accumulation differs strongly with slopes and aspects, with the greatest difference between low phytomass north-facing and high phytomass south-facing slopes (Dolgin 1970). In alpine areas microclimatic gradients are steep and the treeline is abrupt; in low relief arctic areas the treeline is more gradual. Due to the low position of the sun, differences of short-wave radiation received among slopes and aspects are enhanced in the arctic region (Corbet 1972; Bonan and Shugart 1989) when compared to the temperate regions.

At present, the four arctic treeline tree species occupy distinct habitats, which should be strongly related to the energy input. *Populus balsamifera* is found on steep, south facing slopes with deep active layers and high short-wave energy inputs, *Betula papyrifera* and *Picea glauca* are found on most slopes and aspects, however, *Picea mariana* is found most commonly on north and northeast facing low energy slopes and on valley bottoms where organic layers are deep and, as a result, active layers are shallow.

The objective of this study was to use a model to explore the short-wave radiation inputs over a range of different slopes and aspects at the western arctic treeline and to verify the model with field data. It was hypothesized that short-wave energy input plays an important role in determining the growth of the four treeline tree species *Picea mariana, Picea glauca*, *Betula papyrifera* and *Populus balsamifera.*

MATERIAL AND METHODS

Study Area

In 1990, an experimental area was established on spoil piles in an abandoned borrow pit close to the arctic treeline near Inuvik, Northwest Territories (68°18' N, 133°29' W). The site was especially useful because the spoil piles provided a range of slopes and directions and no surrounding vegetation shaded or otherwise influenced the experimental site, since it had been burned in 1968 and was now of low stature (up to 2 m in height). A total of 51 plots were established on the borrow pit spoil piles with three replicates each of a horizontal surface plus the eight cardinal and sub-cardinal directions with slopes of 15 and 30 degrees. The plots were 100 x 100 x 20 cm deep and underlain by black plastic foil to prevent upward movement of salts from the spoil during evapotranspiration. Small drainage holes were cut in the foil and plots were filled with a mixture of peat and surface mineral soil (collected nearby) in a 1 : 5 ratio. The texture of the mineral soil was clay to clay/loam with approximately 10% organic matter. The soil was treated with 750 g limestone to raise the pH to near neutral.

Weather data for the Inuvik region, which have been collected continuously at the Inuvik Airport since 1958, indicate a mean temperature during the growing season of June, July and August of about 13 °C and a mean precipitation of about 90 millimetres (Canada Committee on Ecological Land Classification 1989). The weather during the growing season, when the research was conducted, was close to this average, with an air temperature of 12.6 °C and 73 millimetres of precipitation.

Energy Input

The model used (Oke 1987), calculated the total solar radiation received as the sum of the direct radiation, diffuse sky radiation, and reflected (ground) radiation. Contributions of diffuse sky and reflected radiation were determined for each slope using a sky view factor (Oke 1987). The direct radiation for each slope was determined by calculating the angle between direct radiation and the normal of a slope (Oke 1987). Due to measurement errors of the pyranometer, readings of less than 2 W m^{-2} on the horizontal surface were not incorporated into the calculations for the modelled values for the different slopes and aspects.

To verify the model, the half-hourly modelled values for the four 90 degree slopes (N,S,E,W) were compared with measured values at the borrow pit (Figure IV-1). The model provided underestimations of about 15 % for each of the four slopes. For a horizontal surface, the calculations predicted the field measurements accurately, since these values were the measurements. This suggests that the error increases at a uniform rate as the slope angle increases. A more complex calculation might reduce the error, but is unlikely to have much effect on the relative ranking of the different slopes. For this reason, the simple model was deemed acceptable for the intended study.

To verify the amount of short-wave radiation a surface receives, microclimatic measurements were taken during the period of June 28 to August 21 in the summer of 1992 at the borrow pit. Measurements included total incoming solar radiation on a horizontal surface and at slopes of 90 degrees facing the cardinal directions. Reflected and diffuse radiation were also recorded at the site. Total radiation on horizontal and sloped surfaces was measured with five Licor Pyranometers (Licor, LI200S Pyranometer, Lincoln, Nebraska) mounted on a wooden block. Reflected ground radiation was determined using an inverted Licor Pyranometer mounted at a height of 100 cm above the soil surface. A Kipp and Zonen pyranometer with a shade ring was used to measure diffuse radiation. Direct radiation was calculated by subtracting the amount of diffuse radiation from the amount of total radiation received on a horizontal surface. All data were collected by a CR 7 Campbell Scientific datalogger (Campbell Scientific, Logan, Utah), collecting half hourly means of readings every 10 seconds. In 1993, measurements of soil temperatures were taken during the course of one clear day. Soil temperature was measured at a depth of 5 cm on the three replicates of plots of the four cardinal directions with slopes of 30 degrees with a hand held electronic thermometer. Ten measurements were taken in each plot, to ensure a better estimate of the soil temperature present. During the summer of 1993 radiation inputs were also measured using the same methods described above.

In order to determine the amounts of radiation on the sloping surfaces it was assumed that the diffuse radiation was equal on all slopes and aspects (isotropic). Radiation inputs for the differing 16 slopes and aspects were modelled by using the total radiation measurements taken for the horizontal surface, the reflected (ground radiation, and the diffuse radiation measurements.

Plant growth responses

Tree seedlings of the four treeline tree species were used in a phytometer approach to express plant response to the short-wave energy environment. Seeds of *Picea mariana*, *Picea glauca*, and *Betula papyrifera* and branch cuttings of *Populus balsamifera* were collected locally during the autumn of 1990. Seedlings were raised in growth chambers from the seeds and the branch cuttings, to be available for planting in the following spring. Germination and growing period conditions (for both seedlings and cuttings) were similar to Inuvik summer conditions. For three months the treatments were 24 hour light, a temperature of 18 °C and a relative humidity of approximately 60%. For induction of bud set and hardening, the conditions were changed to 8 hours high intensity light, a day temperature of 10 °C and a night temperature of 6 °C for six weeks. The seedlings were exposed to six hours low intensity light and temperatures of 2 °C in a refrigerator for further hardening during a period of six weeks.

Due to the different amounts of planting material available for each of the four tree species, four specimens of *Betula papyrifera*, six specimens of *Populus balsamifera*, six specimens of *Picea mariana* and one specimen of *Picea glauca* were planted in each field plot in June of 1991. To exclude the effect of drought, periodic watering of the plants was necessary for the duration of the experiment. Garden beans grown in each plot identified water deficiency when the leaves wilted. Plots were checked daily, and if necessary the seedlings were watered. For the winter of 1991/1992 snow fences provided a deep snow cover to lessen desiccation and frost heaving of the seedlings in the spring. Mortality during the experiment was low. Only a few seedlings of *Picea mariana* were killed due to frost heaving. No measurements were taken during 1991 because seedlings were recovering from transplanting shock. In August 1992, leader elongation and dry total aboveground biomass for *Picea mariana*, *Picea glauca*, *Betula papyrifera* and *Populus balsamifera* were determined. Aboveground biomass for *Populus balsamifera* included only the shoots and leaves which were produced during the growing season of 1992, due to the use of branch cuttings. Leader elongation and aboveground biomass relative to the largest amounts of elongation and biomass were calculated in order to enable a comparison among species.

Linear regression analysis was undertaken with relative leader elongation and dry aboveground biomass as dependent variables and energy input as the independent variable.

RESULTS

Energy input

The modelled values of short-wave radiation input suggested that north facing, 30 degree, slope received about 650 MJ/m^2 during the investigation period of June 28 to August 21, 1992. This is about one third less solar radiation than a 30 degree south-facing slope which received about 980 MJ/m^2 during the same period. Figure IV-2 shows a polar plot of the modelled radiation for the eight plot orientations. This figure shows only seasonal totals, but the ratio of solar radiation among slopes and exposures was constant throughout the investigation period. The distribution of short-wave radiation for the west and east facing slopes was not exactly symmetrical along the north-south axis, resulting in somewhat smaller amounts of radiation received by east-facing slopes (Figure IV-2). The differences were the result of variations in the sky conditions between the morning and evening hours, due to afternoon cumulus cloud formation.

During the course of a clear day in mid July 1993, east-, south-, and west-facing slopes all had similar short-wave radiation input patterns in the form of a bell-shaped curve (Figure IV-3). The only major difference was the time of day during which these aspects received maximum solar energy. The west-facing slope was a mirror image of the east-facing slope, with a morning of diffuse radiation and an afternoon of direct radiation. The depression during the period of peak radiation on the east slope is due to some morning clouds. A

30 degree north-facing slope received direct radiation all day, since solar elevation exceeded 30 degrees at solar noon. At solar midnight, when the sun was below the horizon the north slope received only diffuse radiation as for all the other surfaces (Figure IV-3).

The soil temperature at five centimetres depth for the south and west-facing slopes followed closely the diurnal pattern of the radiation input, reaching maximum at solar noon and 3 pm respectively (Figure IV-3). The soil temperature at the same depth on the east slope reached its maximum (close to ambient temperature) at about solar noon, when it still received some direct solar radiation and the air temperature was close to its maximum. At 6 pm, soil temperatures on north slopes reached the maximum (Figure IV-3).

Plant growth response

All four tree species had a significant, positive relationship between short-wave radiation input and relative leader elongation. The slopes of the regression lines ranged from 0.0012 for *Picea glauca* to 0.0007 for *Populus balsamifera*. The short-wave radiation input accounted for 14 percent of the variability for *Populus balsamifera* and 34 percent of the variability for *Picea mariana* of the relative leader elongation during the growing season of 1992. There were no statistical differences among the slopes of the regression lines for the four species. The weaker relationship between short-wave radiation input and the performance of *Populus balsamifera* could probably have been due to differences in root systems and types of buds (producing long and short-shoots) among the different cuttings (Figure IV-4).

The relationship between relative biomass and energy input tended to be weaker than between relative growth and energy input especially for *Populus balsamifera* where no significant relationship was found (Figure IV-5); but, in general, the relative biomass data followed the trend given for the relative leader elongation. There were no statistical differences among slopes of the regression lines for the relative biomass for the four tree species.

DISCUSSION

During the investigation period at the experimental site, the frequency of clear, cloudy and overcast sky conditions showed a greater number of clear days in the early part of the growing season (June to mid July) than towards mid August when the sky was mainly overcast. The average daily sunshine hours in June, July, and August were 12.3, 11.9, and 6.7 hours, respectively (pers. comm. Environmental Atmospheric Services, Inuvik). These overcast sky conditions resulted in smaller differences among slopes, by reducing the amount of direct radiation while increasing diffuse radiation. The short-wave radiation inputs for the eight week investigation period were somewhat higher than the generalized annual short-wave radiation limits (628 - 837 MJ/m^2) reported in Larsen (1980) and Hare and Thomas (1974) for the forest-tundra region. This suggests a slightly higher short-wave radiation input in the Inuvik region during 1992 than the annual average.

Due to a sun angle greater than 30 degrees during the growing season in the Inuvik area, the trees, since they are vertical regardless of slopes, received direct radiation. Therefore, light quantities on all slopes and aspects during the investigation period should have been sufficient to support normal photosynthetic rates.

As mentioned earlier, the four tree species occupy distinct habitats potentially related to the energy input. In contrast to this long-term development of the landscape tree patterns, the experimental study did not show statistical differences among tree species in the relative leader growth as a function of total short-wave radiation input. Only about one quarter of the growth response of tree seedlings could be explained by the short-wave radiation input. Therefore, we must reject the original hypothesis that short-wave radiation input plays an important role in determining the success of the four treeline tree species measured as relative leader growth and biomass increase. It is likely that a large amount of the response in leader length growth rates and biomass accumulation are linked to soil temperature. On a clear day, when soil temperatures should show the greatest differences, soil temperatures under the experimental soil conditions were not very different. On average the soil temperature were about 20 °C on the south and west facing slopes and 16 °C on the north and east facing slopes at an average air temperature of about 15 °C. The mineral soil of the experimental plots promoted heat conduction into the soil. The soil temperatures in the experimental site were relatively high compared to similar slopes and exposures on the landscape; however, the responses of the tree species in the experiment could indicate how mineral soil conditions could effect the performance of the tree species. On the other hand, leader length may also be pre-determined by previous year's weather and therefore the period of two growing seasons might not be enough time to detect differences.

At present, a majority of the soils at the arctic treeline are overlain by a moss-lichen-organic layer. Due to the insulating effect of the organic layer soil temperatures are significantly cooler than bare mineral soils (Van Cleve *et al.* 1983). The depth of the organic layer varies with slope and aspect; generally only steep south south-west facing slopes have bare mineral soil conditions and north facing slopes have the deepest organic layers. After severe disturbances soil organic layers could be removed and soil temperatures will increase (Van Cleve *et al.* 1983) resulting in increased performance of the tree species.

Under an enhanced-greenhouse climate the short-wave radiation input will not change unless other attributes of climate such as the cloud cover changes to influence direct radiation from the sun (Mitchell 1989). Therefore short-wave radiation should not change soil energy budgets. Future climate scenarios predict that the greatest amount of warming in northern regions will be due to the transport of warm air masses from more southern regions (French 1986; Maxwell and Barrie 1989; Etkin 1990). These changes in air temperature will increase the net energy inputs into northern soils (Bonan 1992). Under these changed climatic conditions, tree species should increase their growth. With increases in disturbance frequencies and severity predicted under the climate change scenarios (Flannigan and Van Wagner 1991; Wotton and Flannigan 1993), soil organic layers could be removed. This could enhance tree seedling establishment and could favour tree expansion into former tundra areas (see also Chapter III).

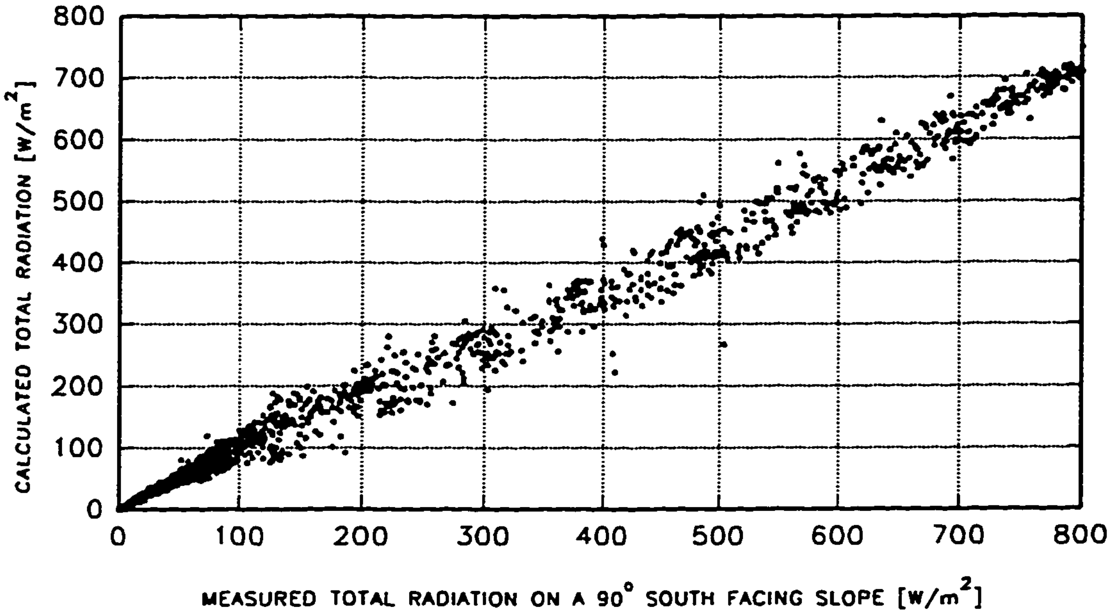

Figure IV-1. Comparison of half-hourly measured and modelled values for a 90 degree south facing slope during the period of June 28 to August 21, 1992.

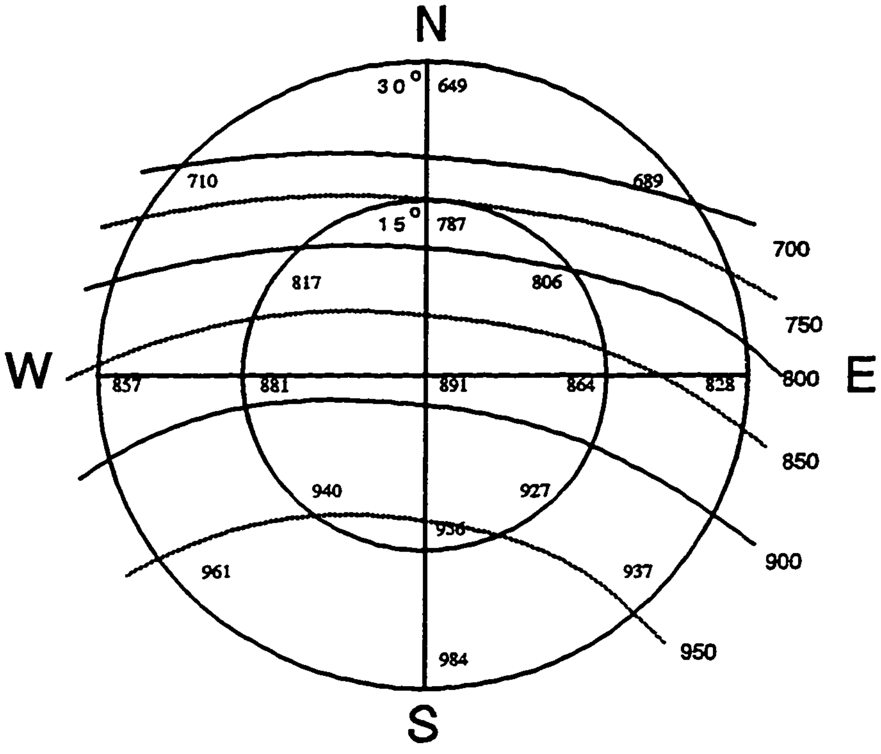

Figure IV-2. Polar plot showing the modelled seasonal totals for the eight plot directions and two different slope angles at a borrow pit near Inuvik, Northwest Territories. The angle is the slope aspect/azimuth, the radius the slope angle (0-30 degree), and isoradiation lines have been superimposed..

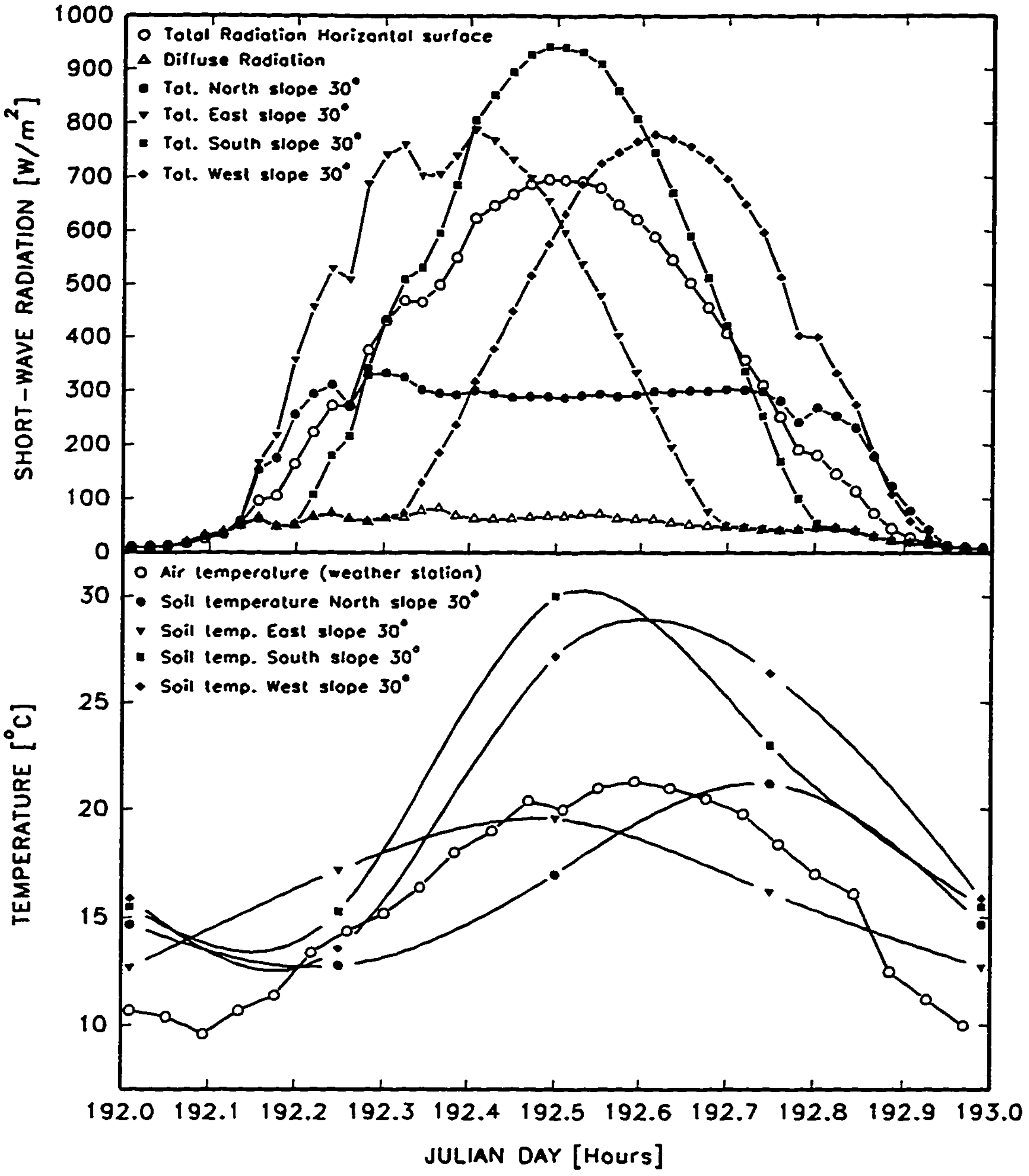

Figure IV-3. Total and diffuse radiation (upper part) and soil temperature (5 cm depth) trends on 30 degree slopes facing the cardinal directions during the course of a clear day (July 10, 1993) at the experimental site at Inuvik, Northwest Territories.

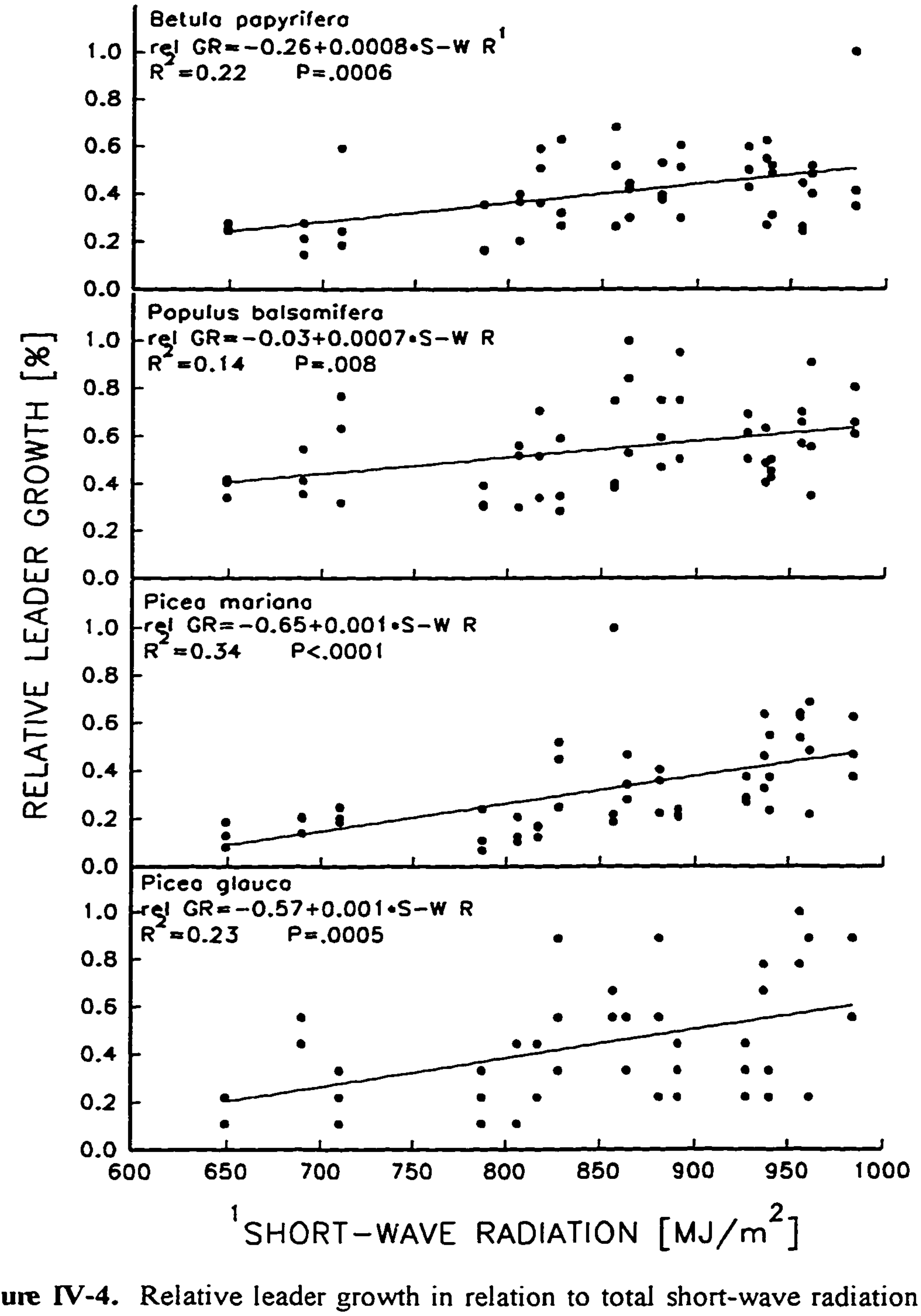

Figure IV-4. Relative leader growth in relation to total short-wave radiation input during the growing season of 1992 for *Betula papyrifera*, *Populus balsamifera*, *Picea mariana*, and *Picea glauca* (n=51).

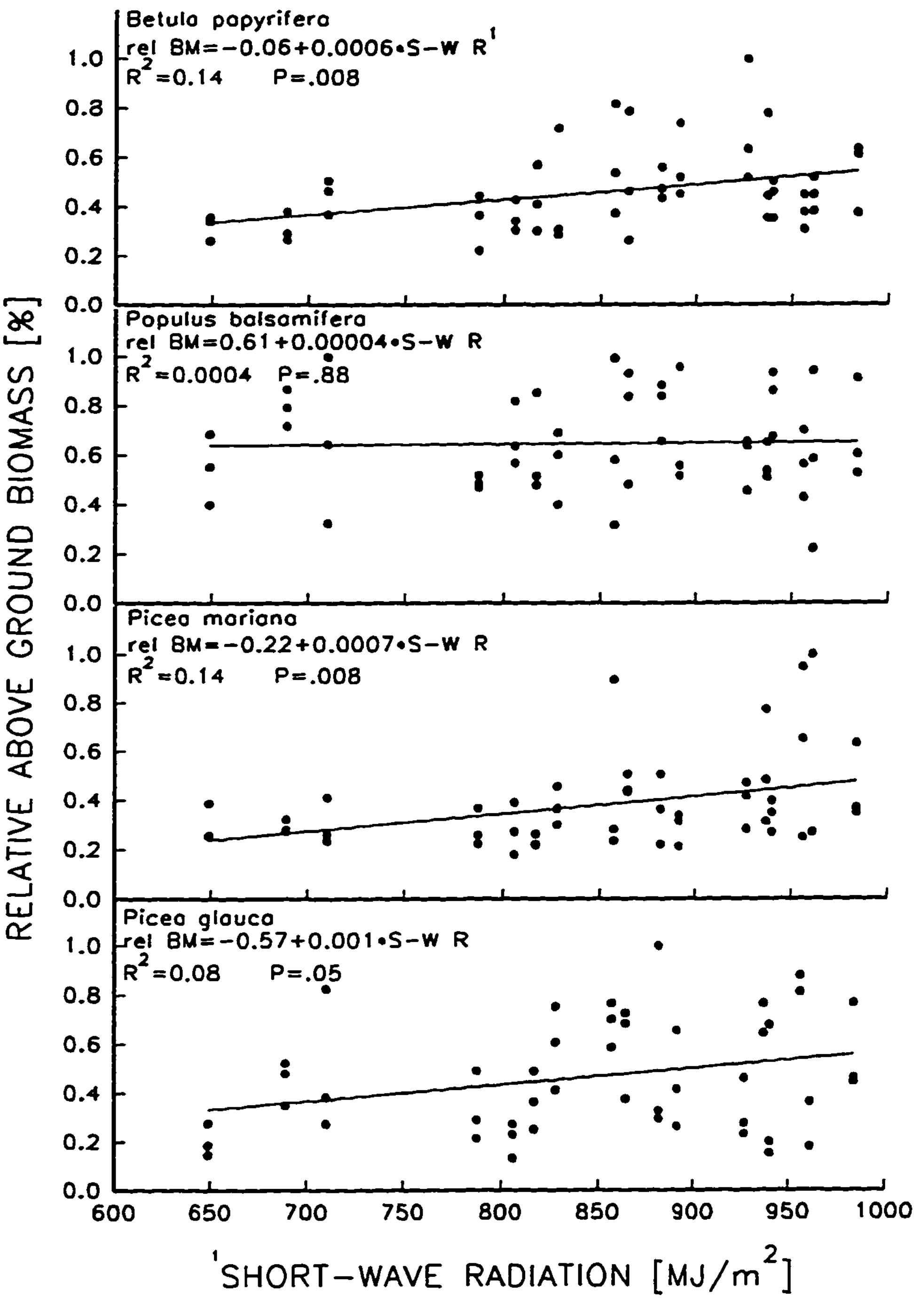

Figure IV-5. Relative above ground biomass in relation to total short-wave radiation input during the growing season of 1992 for *Betula papyrifera*, *Populus balsamifera*, *Picea mariana*, and *Picea glauca* (n=51).

LITERATURE CITED

Bonan, G. B. 1992. Soil temperature as an ecological factor in boreal forests. Pages 126-143 *in*: H. H. Shugart, R. Leemans, and G. B. Bonan, editors. A system analysis of the global boreal forest. University Press, Cambridge, UK.

Bonan, G. B., and H. H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. Annual Review of Ecology and Systematics **20**:1-28.

Canada Committee on Ecological Land Classification (CCELC). 1989. Ecoclimatic Regions of Canada, first Approximation written and compiled by Ecoregions Working Group, Ecological Land Classification Series No. 23, Environment Canada, Ottawa, Canada.

Corbet, P. S. 1972. The microclimate of arctic plants and animals, on land and in fresh water. Acta Arctica Fasc XVIII, Kopenhagen, Denmark.

Dolgin, I. M. 1970. Subarctic meteorology. Pages 41-61, *in*: Ecology of the Subarctic Region. Proceedings of the Helsinki Symposium. UNESCO, Paris, France.

Etkin, D. A. 1990. Greenhouse warming: Consequences for arctic climate. Journal of Cold Region Engineering **4**: 54-66.

Flannigan, M. D. and C. E. Van Wagner. 1991. Climate change and wildfire in Canada. Canadian Journal of Forest Research **21**: 66-72.

French, H. A., editor. 1986. Impact of climatic Change on the Canadian arctic. Atmospheric Environment Service, Canadian Climate Centre, Downsview, Ontario, Canada.

Gavrilova, M. K. 1966. Radiation climate of the Arctic. Translated from russian. Edited by M. I. Budyko. Israel Program for Scientific Translation, Jerusalem, Israel.

Hare, F. K. and M. K. Thomas. 1974. Climate Canada. Wiley Publisher of Canada Limited, Toronto.

Larsen, J. A. 1980. The Boreal Ecosystem. Academic Press New York, USA.

Maxwell, J. B., and L. A. Barrie. 1989. Atmospheric and climatic change in the Arctic and Antarctic. Ambio **18**: 42-49.

Mitchell, J F.B. 1989. The "greenhouse" effect and climate change. Review of Geophysics **27**: 115-139.

Oke, T. R. 1987. Boundary layer climates. Methuen, New York, USA.

Van Cleve, K., L. Oliver, R. Schlentner, L. A. Viereck, and C. T. Dyrness. 1983. Productivity and nutrient cycling in taiga forest ecosystems. Canadian Journal of Forest Research **13**: 747-766.

Wotton, B. M., and M. D. Flannigan. 1993. Length of the fire season in a changing climate. Forestry Chronicle **69**: 187-192.

CHAPTER V

GAS EXCHANGE AND GROWTH OF THREE ARCTIC TREELINE TREE SPECIES UNDER DIFFERENT SOIL TEMPERATURE AND DROUGHT PRE-CONDITIONING REGIMES[***]

INTRODUCTION

Low air and soil temperatures (including permafrost) are prominent factors determining vegetation in northern boreal forest ecosystems and especially at the energy limited boreal forest-tundra boundary (Bonan and Shugart 1989). The forest floor of these forests, composed of lichens, mosses, and/or thick organic layers is an important feature which controls soil temperature and permafrost, nutrient cycling, and soil moisture. These site factors determine the establishment and success of the tree species. Increasing thickness of the organic layer causes low soil temperatures (Van Cleve and Viereck 1981, Van Cleve *et al.* 1983a, b). Viereck (1979) suggested that soil temperature is a more limiting factor for plant performance than air

---

[***] A version of this chapter has been submitted for publication to the Canadian Journal of Botany Landhäusser, S. M., R. W. Wein, and P. Lange. January 1994.

temperature, in reducing plant growth (Sveinbjörnsson 1991) and driving distribution patterns (Van Cleve *et al.* 1983a, Larsen 1989). In the summer months, although air temperatures are high, a dry surface layer of the organic forest floor will interrupt the thermal transport processes into deeper soil layers, resulting in slower warming of the soils.

Cold soil temperatures decrease biological activity of plants by restricting water uptake due to increased root resistance and water viscosity (Lawrence and Oechel 1983, Lopushinsky and Kaufmann 1984, Goldstein *et al.* 1985). Other physiological processes, affected by low soil temperatures, are nutrient uptake due to decreased root metabolism and also nutrient availability (Heininger and White 1974, Chapin 1983), decreased substrate synthesis and translocation necessary for growth (Lopushinsky and Kaufmann 1984), and impaired growth hormone production (Anderson and McNaughton 1973, Chapin 1983). As a result of these impairments, transpiration and net assimilation rates of plants are reduced under cold soil conditions (Kaufmann 1975, Lippu and Puttonen 1991)

Natural or human caused disturbances in the northern boreal forest are a major force in changing abiotic conditions. Fire, a common disturbance, can remove considerable depths of the insulating organic matter resulting in warmer soil temperatures and deeper active layers (Chapin and Shaver 1981, Dyrness 1982, Viereck 1982). Following disturbance, especially in low energy environments, improved growth performance can be related changes in the soil environment (Sirois 1992). These improved conditions can also be beneficial for tree establishment in areas which could not support trees before the disturbance (see also Chapter III). The success of established tree seedlings is very dependent on the micro-environmental conditions created by the disturbance at the site and the ability of the seedling to cope with these site conditions. At the arctic treeline, where tree species are at the limit of their range, soil temperature and related drought conditions are two important factors determining tree seedling success (Black and Bliss 1980).

With increasing air temperatures, due to elevated concentrations of greenhouse gases in the earth's atmosphere (Bolin *et al.* 1986, Maxwell 1992), and with a higher climatic variability predicted under the climate change scenarios (Overpeck *et al.* 1990) stresses for tree species could increase. Drought has not been considered a major stress factor for trees at the arctic treeline despite low annual precipitation levels (Walter 1979, Black and Bliss 1980). Under a warmer climate, more moisture could be supplied by the melting out of permafrost (Peterson *et al.* 1984), however, the increased water availability could only be temporary, as deeper active layers develop. Lower precipitation levels may fail to recharge the soil (Oberbauer and Dawson 1992). The importance of drought as a factor increases for tree species at the seedling stage, and desiccation is thought to be one of the most important threats to the survival of seedlings (Grossnickle 1988).

The ability of tree seedlings to tolerate different levels of drought is very dependent on the past life history of the seedling in having previously experienced drought stresses (Levitt 1980). An exposure of a seedling to repeated drought stresses can not only result in a higher tolerance of more severe drought stresses, but also to an increased tolerance of other environmental stresses (Levitt 1980). Drought pre-conditioning is thought to improve drought, freezing, and heat tolerance (Levitt 1980). Water stress affects almost every aspect of plant physiology and morphology (Kozlowski *et al.* 1991).

At the arctic treeline, *Populus balsamifera* and *Populus tremuloides* appear to tolerate periodic drought stress since they are the only species presently found on the extremely steep south-facing, warm, and dry slopes. On the other hand *Betula papyrifera* is found on mesic but well drained sites at the western arctic treeline, over a broad range of soil temperatures. Under a possible drier climate, these tree species could be exposed to increased drought stress. This research will examine whether both deciduous tree species show tolerances for drought and dehydration. The results will be used to make predictions about the potential distribution of the tree species under climate conditions, with increased temperatures and drought stresses, predicted for the near future.

This research determined experimentally how soil temperature affects relative above and below ground biomass, root shoot ratio, and gas exchange of the arctic treeline tree species *Picea mariana*, *Betula papyrifera*, and *Populus balsamifera*. Further, it was investigated how drought affects relative above and below ground biomass, root shoot ratio, and the photosynthetic rates of *Betula papyrifera*, and *Populus balsamifera* at different levels of drought pre-conditioning by withholding water.

MATERIAL AND METHODS

To prepare the planting medium, sand was screened for a particle size between 1.2 and 6 mm and dried peatmoss was shredded and screened using a 6 mm mesh. The peat moss was moistened to about 300% (on dry weight basis) before it was thoroughly mixed with sand in a volume ratio of 1:1. The bottom openings of the planting tubes (Conetainer, (Steuwe & Sons, Corvallis, Oregon) were plugged with a ball of polyester fibres. The planting tubes were then filled with approximately 200 ml of the soil mixture. All containers were filled in the same manner to ensure similar compaction and weight. After drying the soil to constant weight at 80 °C, the dry weight of each container was determined and after saturation the wet weight at field capacity was determined. The average dry weight of soil plus container was 175.15 g ± 4.9 g and the average soil water content at saturation was 42.54 g ± 2.65 g per container.

Seeds of *Betula papyrifera*, *Populus balsamifera*, and *Picea mariana* were collected locally near Inuvik during the spring and autumn 1991. About three pre-germinated seeds were planted in each planting tube. After one week the plants were thinned to one individual per planting tube. The seedlings were fertilized by watering on a weekly basis with a solution of 0.5 g l^{-1} of a commercial fertilizer (N:P:K 20:20:20) with chelated micronutrients. The seedlings were watered every two days to field capacity and allowed to drain freely. During the growth period the planting tubes were moved to different bench positions and rotated weekly. The tree seedlings were grown for 55 days to ensure successful seedling establishment prior to the treatment application.

The growth chamber conditions during the establishment period were 24 hours light, air temperature of 21 °C and night temperature of 16 °C (18 h/ 6 h). The relative humidity was about 60 percent. Light intensity was about 320 µmol m^{-2} s^{-1} photosynthetic active radiation (PAR). After 55 days, drought pre-conditioning and soil temperature treatments were applied. The weight of the planting tube including soil, which was watered to field capacity, and the tree seedling were determined. Initial heights of the seedlings were measured to account for variability in seedling height. Growth chamber conditions during the experimental period were the same as during the establishment period.

In order to control soil temperature the containers were placed in racks, which are designed for the planting tubes, in water baths (69x63x21cm). Each bath accommodated the planting tubes randomly assigned within the racks. A closed water circulation system was developed (Figure V-1). Water was cooled to the desired temperature in a common reservoir and then pumped with a flow of about 12 litres min^{-1}, to each of three water baths. Even and steady distribution of cooled water entering the boxes was attained through perforated hoses attached at the bottom of the water baths. All hoses carrying water to the baths were well insulated to minimize warming. An overflow pipe returned the warmer surface water back to the cooling unit (Figure V-1).

For the soil temperature experiment a set of nine plants (one plant per planting tube), for each of the three species, were treated with three different soil temperature (3, 10 and 15 °C). The soil temperature treatments were replicated three times to a total of 243 planting tubes. The soil temperature treatment was applied for a period of five weeks. The plants were watered every second day to about field capacity, which was determined by weighing the planting tube and adding an amount of water, which was the difference to the initial weight at field capacity. To control soil moisture for the different soil temperature, the dark soil surface in the planting tubes was covered with 10 g of white sand to increase albedo and insulate the soil surface. The bottoms of the planting tubes were sealed by slipping a balloon over the tubes before placing in the water baths that reached within one centimetre of the container rim (Figure V-1). Gas exchange of *Populus balsamifera*, *Betula papyrifera*, and *Picea mariana* was determined at the different soil temperatures.

In a second experiment, conducted at a soil temperature of 15 °C, three replicates of eight *Betula papyrifera* and *Populus balsamifera* seedlings were pre-conditioned with two day (control), four day, and six day watering cycles each. The watering regimes were established in a pilot study where seedlings showed signs of wilting after six days, but recovered without leaf loss. Before each watering to field capacity, the planting tubes were weighed and the water loss determined; then the weight deficit was replenished by adding water. During the experimental period, the four and six day water cycles were repeated six and four times, respctively. After four weeks of the different levels of pre-conditioning *Populus balsamifera*, and *Betula papyrifera* seedlings were subjected to a drought period of six days. During these six consecutive days, four different seedlings of each of the two species and the three levels of drought pre-conditioning were measured for photosynthetic performance, for each day.

Gas exchange was determined using an infra-red gas analyzer (LCA-3, Analytical Development Cooperation ADC, Hoddesdon, England) and a conifer cuvette. Ingoing humidity was maintained at 0%. Photosynthesis reached equilibrium within 1 to 2 minutes. A projector light (Quartz Halogen, 300 W) was used to provide a light quantity of about 1100 μmol m^{-2} s^{-1} PAR. The flow rate of air in the cuvette was 400 ml min^{-1}. The CO_2 concentration, relative humidity in and out of the cuvette, and air temperature in the cuvette were monitored continually during the measurement period. Projected leaf area was determined using an area meter (Li-Cor, LI-3100, Lincoln, Nebraska). Net assimilation [μmol m^{-2} s^{-1}], stomatal conductance to water vapour [mmol m^{-2} s^{-1}], residual conductance to CO_2 [mmol m^{-2} s^{-1}], and water use efficiency were calculated for the species (Caemmerer and Farquhar 1981).

In the soil temperature experiment, analysis of variance was performed on the gas exchange data, using SAS (Joyner 1985). Net assimilation, stomatal conductance to water vapour and residual conductance to CO_2 were the dependent variables, soil temperature and species the fixed independent variables. In the drought pre-conditioning experiment, analysis of variance was performed with net assimilation, stomatal conductance to water vapour and residual conductance to CO_2 as dependent variables, and drought pre-conditioning, species, and day of water withheld as independent variables. Planned comparisons were used to interpret interactions, and differences among treatments and species.

After completion of the gas exchange measurements, biomass measurements of seedling root and shoot dry weight were used to calculate root-shoot ratios. In order to compare among species, measures of root and shoot mass were calculated relative to the largest individual mass for each of the species. Analyses of covariance were performed with relative root, relative shoot mass, and root:shoot ratio as dependent variables. The independent variables were soil temperature and species and drought pre-conditioning treatment and species, with relative initial height as the covariate.

RESULTS

Morphological responses

The Analysis of Covariance (Table V-1) showed that soil temperature had a significant influence, by increasing relative root mass, and root : shoot ratio of the seedlings of the three species with increasing soil temperature. The maximum values measured for dry root mass were 1.43, 1.48, and 0.04 g for *Betula papyrifera*, *Populus balsamifera*, and *Picea mariana.* respectively. Further, there were significant differences among species. Relative shoot mass was not significantly affected by soil temperature; however, there were significant differences between the deciduous species and *Picea mariana*, especially at soil temperatures of 3 °C and 15 °C (Figure V-2a). The maximum values measured for dry shoot mass were 1.87, 1.81, and 0.12 g for

Betula papyrifera, *Populus balsamifera*, and *Picea mariana*, respectively. Relative root mass almost doubled from 3 °C to 15 °C soil temperature in all three species. Differences in relative root mass among species were greatest under the cold soil temperature conditions, where *Betula papyrifera* (at 35%) was significantly higher than *Picea mariana* (at 20%) (Figure V-2b). Root:shoot ratio increased more rapidly with increasing temperature in the deciduous tree species (from 0.50 at 3 °C to 0.82 at 15 °C) than in *Picea mariana*, which increased from 0.15 at 3 °C to 0.34 at 15 °C , resulting in a significant soil temperature and species interaction (Table V-1). In all soil temperature treatments, the deciduous tree species had significantly higher root:shoot ratios (about 0.68) compared to *Picea mariana* (about 0.25) (Figure V-2c).

The drought pre-conditioning treatment affected significantly the relative shoot mass and root:shoot ratio, by reducing the shoot mass and increasing the root:shoot ratio with increasing drought pre-conditioning levels. Statistical differences between *Betula papyrifera* and *Populus balsamifera* were not detectable (Table V-2). Relative shoot mass of *Populus balsamifera* decreased significantly from about 55 % for the control to about 44 % under severe drought conditions, however, not for *Betula papyrifera*, where no differences were detectable (Figure V-3a). Relative root mass did not show a significant drought treatment effect (Figure V-3b). At the highest level of drought pre-conditioning, *Betula papyrifera* significantly increased the root:shoot ratio from about 0.82 to 0.9 (Figure 3c). There were no statistical differences between species, however, root:shoot ratios tended to be higher in *Populus balsamifera* (0.94) than in *Betula papyrifera* (0.82). The maximum values measured in

Betula papyrifera and *Populus balsamifera* were for the dry shoot mass 1.87 and 1.48 g, respectively and for the dry root mass 1.43 and 1.81, respectively.

Gas exchange

Analysis of Variance of gas exchange data revealed a significant effect of soil temperature and significant differences among the three species (S) (Table V-1). The net assimilation (NA) generally increased with increasing soil temperature (T) but there was a significant T x S interaction (Table V-1). NA at 15 °C, of the deciduous species, about 3.7 µmol m^{-2} s^{-1}, was significantly higher than in *Picea mariana* with NA of about 2.4 µmol m^{-2} s^{-1} (Figure V-4a) . NA increased steadily in *Populus balsamifera* from 1.6 µmol m^{-2} s^{-1} at 3 °C to about 4.1 µmol m^{-2} s^{-1} at 15 °C. There was no statistical difference in NA for *Betula papyrifera* between 3 °C and 10 °C; however, NA increased significantly 2.3 to 3.4 µmol m^{-2} s^{-1} between soil temperatures of 10 °C and 15 °C, respectively. In *Picea mariana* NA increased from 1.2 µmol m^{-2} s^{-1} to 2.6 µmol m^{-2} s^{-1} between soil temperatures of 3 °C and 10 °C, but a further increase at a soil temperature of 15 °C was not detectable (Figure V-4a). Stomatal conductance to water vapour (g_s) for all species increased significantly with increasing soil temperatures (Figure 4b). *Picea mariana* had the highest conductance of the three species with about 44.0 mmol m^{-2} s^{-1} at 3 °C and 85.9 mmol m^{-2} s^{-1} at 15 °C. *Betula papyrifera* had the lowest g_s with about 21.3 mmol m^{-2} s^{-1} at 3 °C which increased at a slower rate compared to *Picea* *mariana* and *Populus balsamifera* with increasing soil temperature to about 43.6 mmol m^{-2} s^{-1} at 15 °C (Figure V-4b). Soil temperature had a significant effect on residual conductance. The residual conductance (g_m) followed closely the statistical results of NA (Table V-1). Similar to NA, the three tree species performed significantly different with soil temperature treatments (Figure V-4c). g_m showed a steady increase in *Populus balsamifera* with increasing soil temperatures, while *Betula papyrifera* showed an increase of g_m only at 15 °C soil temperatures. The *Picea mariana* g_m increased between soil temperatures of 3 °C and 10 °C, and no further increase was detected to 15 °C (Figure V-4c).

Analysis of Variance of the gas exchange data showed that *Betula papyrifera* and *Populus balsamifera* responded differently in net assimilation (NA) to the drought pre-conditioning treatment (P) and the day of water withheld (D). There were no statistically significant differences in NA between *Betula papyrifera* and *Populus balsamifera* (Table V-3). During the course of the six consecutive days of drought, NA decreased significantly towards the end of the watering cycle. Drought pre-conditioning resulted in somewhat higher NA rates at the sixth day of drought compared to the plants without pre-conditioning, especially in *Populus balsamifera* (Figure V-5a). Overall, *Betula papyrifera* showed little difference in the NA rates after different levels of drought pre-conditioning, however, *Populus balsamifera* tended to increase the NA rates with increasing levels of drought pre-conditioning from about 4.7 µmol m^{-2} s^{-1} with no pre-conditioning to about 5.7 µmol m^{-2} s^{-1} at high drought pre-conditioning. *Populus balsamifera* maintained higher levels of NA during the course of the six days of drought than *Betula papyrifera*. The difference increased with increasing levels of drought pre-conditioning.

Stomatal conductance to water vapour (g_s) was significantly different for *Betula papyrifera* and *Populus balsamifera*, reacting differently to day and to the drought pre-conditioning (Table V-3). Higher g_s in *Populus balsamifera* is maintained over a longer time period with increasing drought pre-conditioning treatments compared to *Betula papyrifera*. g_s in *Betula papyrifera* tended to decrease with increased drought pre-conditioning, on the other hand g_s increased slightly in *Populus balsamifera* (Figure V-5b). On average the difference in g_s between both species ($g_{s\,(Pop.\,bal.)} - g_{s\,(Bet.\,pap.)}$) over the six day drought period increased with higher levels of drought pre-conditioning from an average of -1.2 mmol m^{-2} s^{-1} to 24 mmol m^{-2} s^{-1}. Similar to NA, *Betula papyrifera* and *Populus balsamifera* responded differently in residual conductance to CO_2 (g_m) to the pre-conditioning treatment and during the course of the six day drought treatment (Table V-3). Statistical differences in g_m between species were not detectable. Overall, g_m followed a similar pattern to the NA rate (Figure V-5c).

DISCUSSION

Soil temperature had significant effects on the performance of the treeline tree seedlings The slower growing *Picea mariana*, which is found on cold and wet sites, showed small positive changes in biomass and net assimilation with increasing soil temperatures. In net assimilation the strongest increases were detectable between 3 and 10 °C. The data show some evidence, that root mass and subsequently root:shoot ratio increased with higher soil temperatures in *Picea mariana*. Similar results were obtained in a *Picea mariana* stand where soil temperature was artificially increased by 9 °C over the ambient temperature (Van Cleve *et al.* 1983).

The faster growing, deciduous species (*Betula papyrifera* and *Populus balsamifera*), which are presently found at the treeline on medium to well drained sites, with thin organic layers and warmer soil conditions, responded positive to increased soil temperatures. *Betula papyrifera* which presently occurs over a broad spectrum of site conditions, ranging from cool to warm and moist to mesic site conditions (see also Chapter IV), maintained a more conservative position in reacting to changing soil temperatures. Stomatal conductance in *Betula papyrifera* was always lower than in *Populus balsamifera* and *Picea mariana*, while maintaining a somewhat higher assimilation rate at the lower soil temperatures compared to *Populus balsamifera* and *Picea mariana*. NA of *Betula papyrifera* at higher soil temperatures was lower than in *Populus balsamifera*.

The results suggest that *Betula papyrifera* could cope with cool site conditions, however, it responds well to improvements in soil temperatures. *Populus balsamifera*, on the other hand, showed strong response to increased soil temperature, however, at low soil temperature its performance is significantly decreased. Due to the stronger response of *Populus balsamifera* to higher soil temperatures, it could be inferred that on warm sites *Populus balsamifera* could have some advantage over *Betula papyrifera*.

The results of drought pre-conditioning suggest that *Betula papyrifera*, not previously subjected to any drought stress, can endure a single drought event better than *Populus balsamifera*, due to lower stomatal conductances during the earlier part of the drought period. However, subjected to mild and severe drought pre-conditioning, *Populus balsamifera* responded stronger than *Betula papyrifera* with increased NA rates and while maintaining high stomatal conductances. *Betula papyrifera* responded differently to the drought pre-conditioning treatments, by reducing stomatal conductance to water vapour while decreasing NA rates.

The specific reasons for drought tolerance can differ among species and are often difficult to identify (Kozlowski *et al.* 1991). Among the factors affecting the drought tolerance are the root system size, stomatal responsiveness, cuticular transpiration, water storage and tolerance of dehydration. The morphological responses to the drought pre-conditioning experiment showed significant increases in root:shoot ratio in *Betula papyrifera* and slight increases in *Populus balsamifera* with increased severity of pre-conditioning. Similar observations have been made for lobolly and Scotch pine seedlings (Kaufmann 1968).

The results of this study suggest that *Populus balsamifera* is better adaptable to repeated drought stresses than *Betula papyrifera*, which should enable *Populus balsamifera* to grow on sites with periodic drought stresses. *Betula papyrifera* will probably be more successful in areas with mesic moisture conditions. Under frequent drought occurrences, *Betula papyrifera* will be able to cope with these conditions, however, *Populus balsamifera*, if present at the same site, could be a strong competitor.

Under a warming climate, soil temperatures will increase slightly and the result will be slightly increased growth rates of the tree species at the arctic treeline. If insulating organic matter, which dominates most of the arctic ecosystems, is removed either slowly by decomposition or rapidly by disturbance these new mineral soil conditions will provide improved sites for growth of tree species (Chapin *et al.* 1988, Komárková and McKendrik 1988). Slow removal of the organic matter will maintain cool soil conditions. These conditions would mostly favour *Picea mariana*. If, however, most of the organic layer is removed by a disturbance like fire, the stands could be dominated by the deciduous tree species *Betula papyrifera* and *Populus balsamifera*. The present study suggests that *Betula papyrifera* could occupy a wide range of sites after disturbance at the treeline, and even colonize the cooler sites. Viereck and Van Cleve (1984) proposed an increased dominance of *Betula papyrifera* in stands presently dominated by *Picea mariana* under a warming climate. Under a warming and drier climate the fast growing *Populus balsamifera* could perform well in early succession on a wider array of south facing slopes, which will have higher soil temperatures and more frequent drought episodes.

Table V-1. Summary of ANCOVA for morphological responses and ANOVA for ecophysiological responses of *Betula papyrifera*, *Populus balsamifera*, and *Picea mariana* to different soil temperatures. (P > F) for data presented in Figure V-2 and Figure V-4.

Response variable	Source of variation			
	Temperature (T)	Species (S)	T x S	Relative initial Height
Relative root mass[1]	< 0.001	0.031	0.976	0.021
Relative shoot mass	0.808	0.003	0.972	< 0.001
Root : shoot ratio	< 0.001	< 0.001	< 0.001	0.026
Net Assimilation[2]	< 0.001	0.002	0.014	N/A
Stomatal conductance	< 0.001	< 0.001	0.622	N/A
Residual conductance	< 0.001	0.008	0.012	N/A

[1] For morphological responses, degrees of freedom for T, S, T x S, and relative initial height were 2, 2, 4, and 1, respectively (n=27).

[2] For ecophysiological responses, degrees of freedom for T, S, T x S were 2, 2, and 4, respectively (n=27).

Table V-2. Summary of ANCOVA for morphological responses of *Betula papyrifera* and *Populus balsamifera* to different levels of drought pre-conditioning. (P > F) for data presented in Figure V-3.

Response variable	Source of variation			
	D[1]	S[2]	D x S	rel. initial height
Relative root mass[3]	0.788	0.816	0.179	0.458
Relative shoot mass	0.039	0.346	0.085	0.002
Root : shoot ratio	0.013	0.108	0.117	0.001

---

[1] D = Water withhold

[2] S = Species

[3] For morphological responses, degrees of freedom for D, S, D x S, and relative initial height were 2, 1, 2, and 1, respectively (n=18).

Table V-3. Summary of ANOVA for ecophysiological responses of *Betula papyrifera* and *Populus balsamifera* subjected to six days of drought after pre-conditioning with different levels of drought. (P > F) for data presented in Figure V-5.

Response variable	Source of variation						
	P[1]	S[2]	D[3]	P x S	P x D	S x D	P x S x D
Net assimilation[4]	0.002	0.061	< 0.001	0.051	0.484	0.037	0.825
Stomatal conductance	0.080	< 0.001	< 0.001	0.012	0.592	0.003	0.857
Resididual conductance	< 0.001	0.067	< 0.001	0.054	0.577	0.037	0.814

[1] P = Drought Pre-Treatment

[2] S = Species

[3] D = Day since watering

[4] For ecophysiological responses, degrees of freedom for P, S, D, F x S, P x D, S x D, and P x S x D were 2, 1, 5, 2, 10, 5, and 10, respectively (n=108).

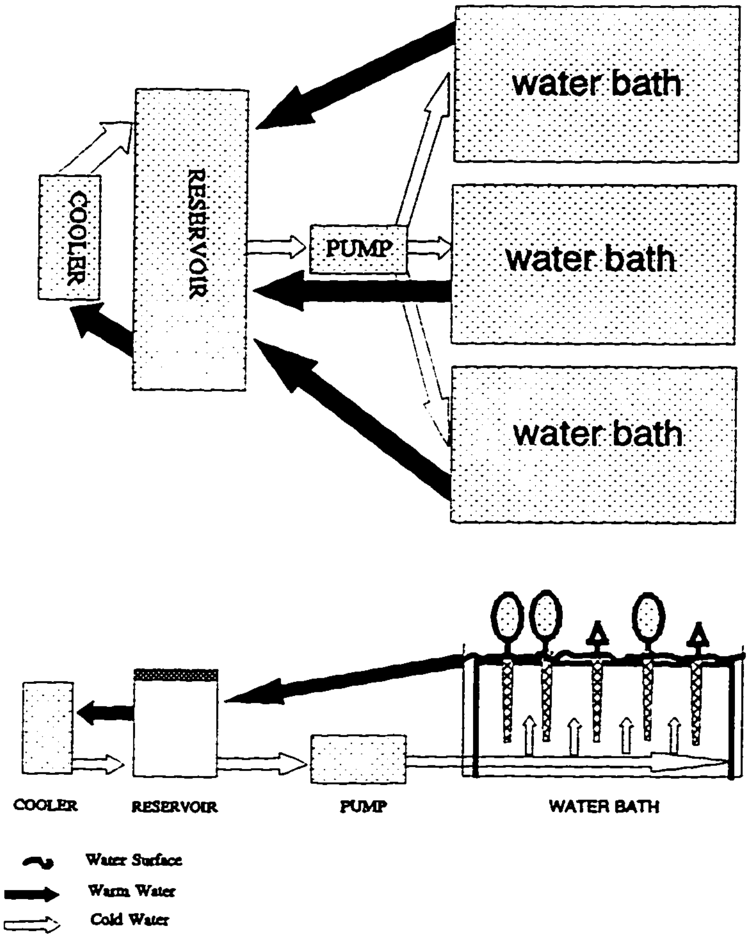

Figure V-1. Diagram of the closed cooling system for one soil temperature and the placement of the containers with the seedlings in the water baths.

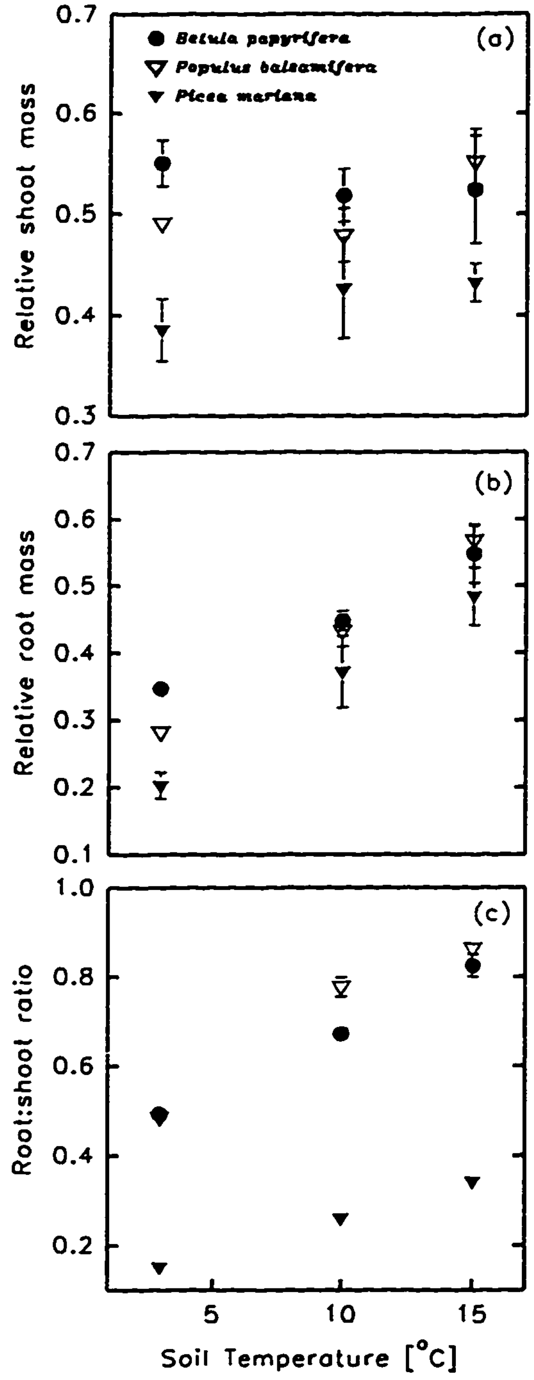

Figure V-2. Morphological responses (mean ± SE) of *Betula papyrifera*, *Populus balsamifera*, and *Picea mariana* at three soil temperatures regimes. (a) Relative shoot mass, (b) Relative root mass, and (c) Root:shoot ratio.

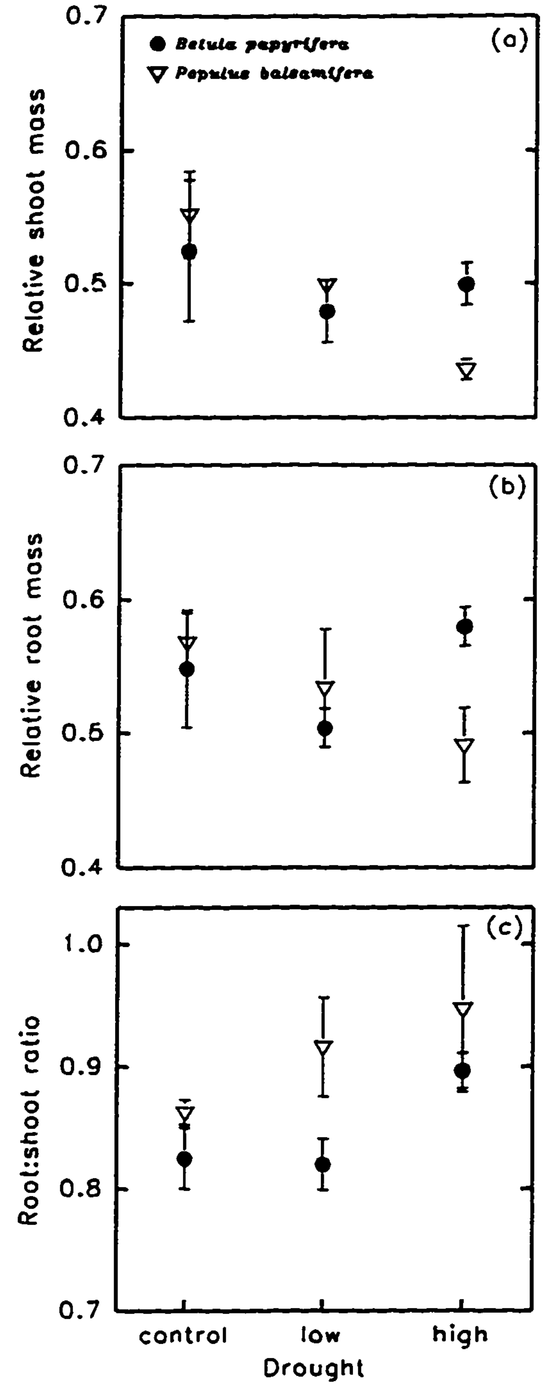

Figure V-3. Morphological responses (mean ± SE) of *Betula papyrifera*, and *Populus balsamifera* at three levels of drought. (a) Relative shoot mass, (b) Relative root mass, and (c) Root:shoot ratio.

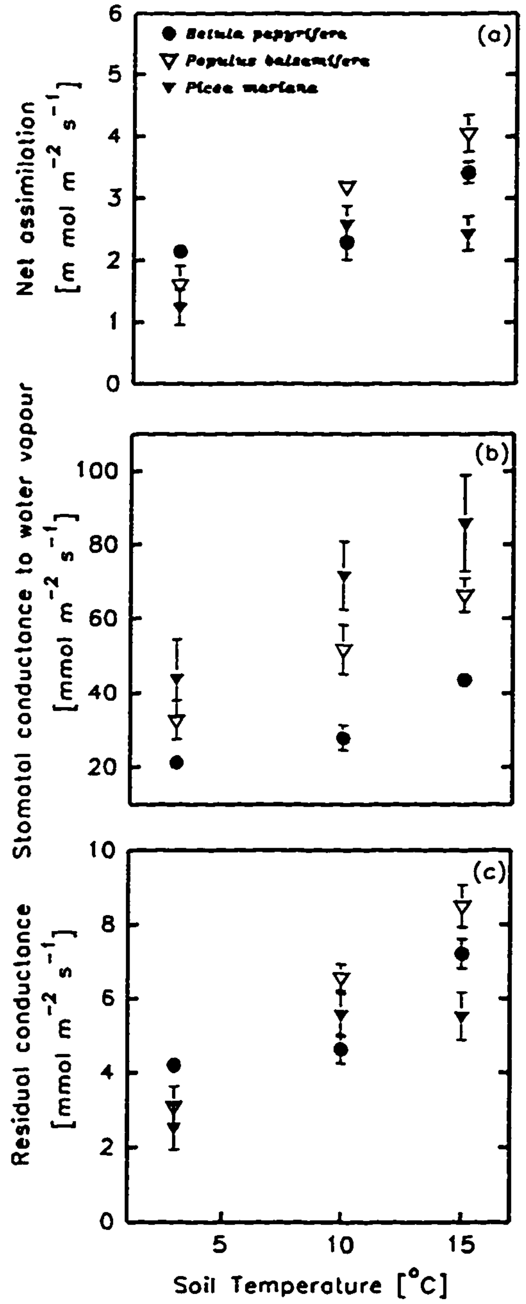

Figure V-4. Ecophysiological responses (mean ± SE) of *Betula papyrifera*, *Populus balsamifera*, and *Picea mariana* at three soil temperatures regimes. (a) Net assimilation, (b) Stomatal conductance to water vapour, and (c) Residual conductance.

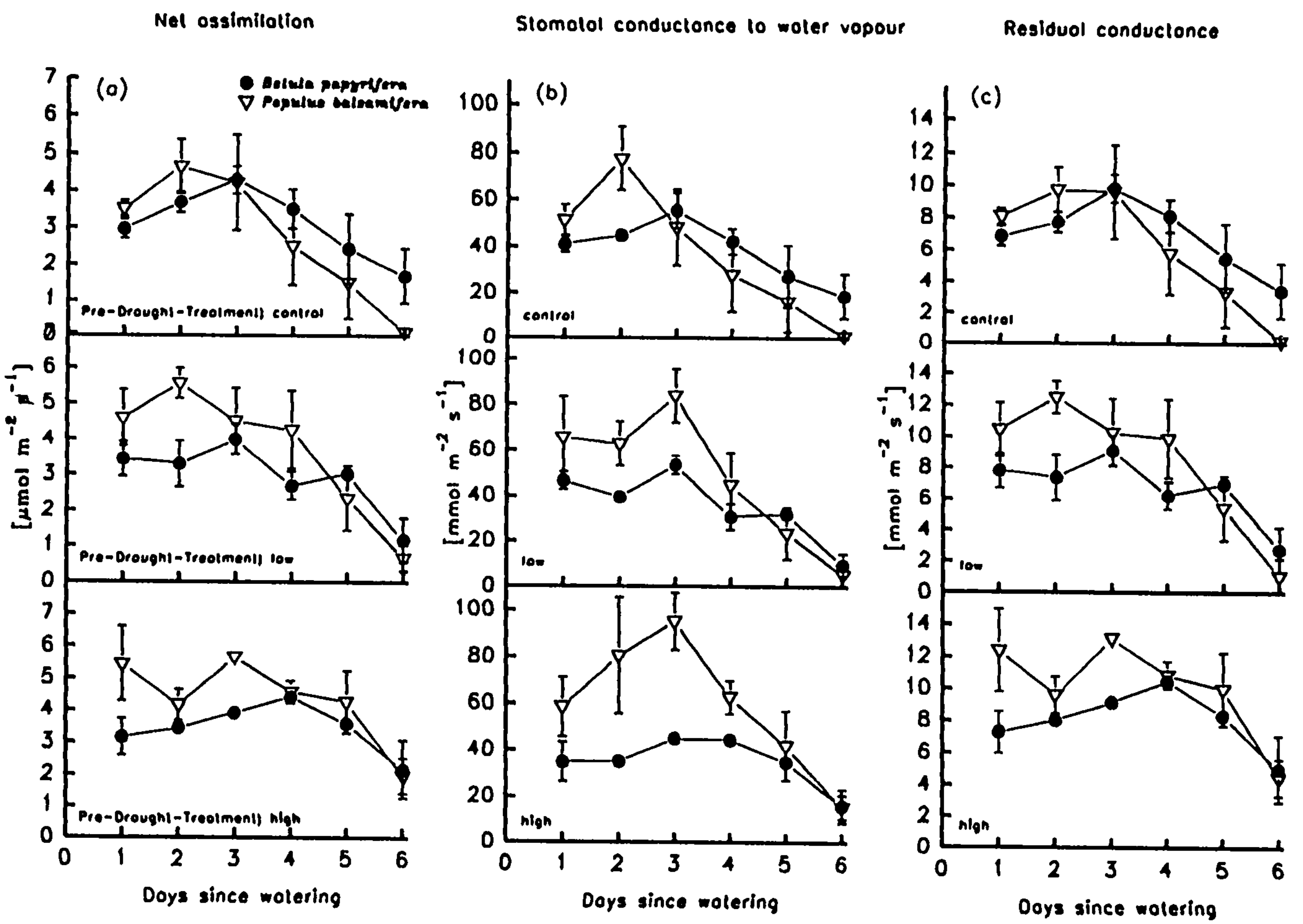

Figure V-5. Ecophysiological responses (mean ± SE) of *Betula papyrifera* and *Populus balsamifera*, pre-treated with three different drought levels during six days of water withhold. (a) Net assimilation, (b) Stomatal conductance to water vapour, and (c) Residual conductance.

LITERATURE CITED

Anderson, J. E., and S. J. McNaughton. 1973. Effects of low soil temperature on transpiration , photosynthesis, leaf relative water content, and growth among elevationally diverse plant populations. Ecology **54**: 1220-1233.

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

Bolin, B., B. R. Döös, J. Jäger, and R. A. Warrick (editors). 1986. The greenhouse effect, climate change and ecosystems. S.C.O.P.E. 29. John Wiley and Sons, Toronto.

Bonan, G. B., and H. H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. Annual Review of Ecology and Systematics **20**:1-28.

von Caemmerer, S., and G. D. Farquhar. 1981. Some relationships between the biochemistry of photosynthesis and gas exchange of leaves. Planta **153**: 376-387.

Chapin III, F. S. 1983. Adaptation of selected trees and grasses to low availability of phosphorus. Plant and Soil **72**: 283-287.

Chapin III, F. S., and G. R. Shaver. 1981. Changes in soil properties and vegetation following disturbance of alaskan arctic tundra. Journal of Applied Ecology **18**: 605-617.

Chapin, F. S. III., N. Fetcher, K. Kielland, K. R. Everett, and A. E. Linkins. 1988. Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing soil water. Ecology **69**: 693-702.

Dyrness, C. T. 1982. Control of depth to permafrost and soil temperature by the forest floor in black spruce/feathermoss communities. U.S. Forest service Research Note PNW-369.

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

Grossnickle, S. C. 1988. Planting stress in newly planted jack pine and white spruce. 1. Factors influencing water uptake. Tree Physiology **4**: 71-84.

Heininger, R. L., and D. P. White. 1974. Tree seedlings growth at different soil temperatures. Forest Science **20**: 363-367.

Joyner, S. P., editor. 1985. SAS/STAT guide for personal computers, Version 6 edition. SAS Institute, Inc. Cary, North Carolina, USA.

Kaufmann, M. R. 1975. Leaf water stress in Engelmann spruce. Influence of the root an shoot environments. Plant physiology **56**: 841-844.

Komárková, V., and J. D. McKendrick. 1988. Patterns in vascular plant growth forms in arctic communities and environment at Atkasook, Alaska. *In*: Werger, M. J. A., P. J. M. van der Aart, H. J. During, and J. T. A. Verhoeven. editors. Plant Form and Vegetation Structure, pp. 45-70. SPB Academic Publishing, The Hague.

Kozlowski, T. T., P. J. Kramer, and S. G. Pallardy. 1991. The physiological ecology of woody plants. Academic Press, New York.

Larsen, J. A. 1989. The northern forest border in Canada and Alaska. Ecological Studies 70, Springer Verlag, New York.

Lawrence, W. T., and W. C. Oechel. 1983. Effects of soil temperature on the carbon exchange of taiga seedlings. II Photosynthesis, respiration, and conductance. Canadian Journal of Forest Research **13**: 850-859.

Levitt, J. 1980. Responses of plants to environmental stresses. 2nd edition. Academic Press, New York.

Lippu, J., and P. Puttonen. 1991. Soil temperature limitations on gas exchange in 1-year-old *Pinus sylvestris* (L.) seedlings. Scandinavian Journal of Forest Research **6**: 73-78.

Lopushinsky, W., and M. R. Kaufmann. 1984. Effects of cold soil on water relations and spring growth of Douglas-fir seedlings. Forest Science **30**: 628-634.

Maxwell, J. B. 1992. Arctic Climate: Potential for change under global warming. *In*: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver & J. Svoboda editors. Arctic ecosystems in a changing climate. An ecophysiological perspective. Academic Press, London, UK. pp. 11-34.

Oberbauer, S. F., and T. E. Dawson. 1992. Water relation of arctic vascular plants. *In* Chapin III, F. S., R. L. Jefferies, J. F. Reynolds, G. R. Shaver, and J. Svoboda. editors. Arctic ecosystems in a changing climate. Academic Press, London, p 259-280.

Overpeck, J. T., D. Rind, and R. Goldberg. 1990. Climate-induced changes in forest disturbances and vegetation. Nature **343**: 51-53.

Peterson, K. M., W. D. Billings, and D. N. Reynolds. 1984. Influence of water table and atmospheric CO_2 concentration on the carbon balance of arctic tundra. Arctic and Alpine Research **16**: 331-335.

Sirois, L. 1992. The transition between boreal forest and tundra. *In* Shugart H. H., R. Leemans, and G. B. Bonan. editors. System Analysis of the global boreal forest. Cambridge Press, Cambridge, p. 196-215.

Sveinbjörnsson, B. 1992. Arctic treeline in a changing climate. *In*: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver & J. Svoboda editors. Arctic ecosystems in a changing climate. An ecophysiological perspective. Academic Press, London, p.239-258.

Viereck, L. A. 1979. Characteristics of treeline plant communities in Alaska. Holarctic Ecology **2**: 228-238.

Viereck, L. A. 1982. Effects of fire and firelines on active layer thickness and soil temperatures in interior Alaska. *In*: Proceedings of the Fourth Canadian Permafrost Conference, pages 123-135. National Research Council of Canada, Ottawa.

Viereck, L. A., and K. Van Cleve. 1984. Some Aspects of Vegetation and Temperature Relationships in the Alaskan Taiga. *In*: McBeath, J. H. editor. The Potential Effects of Carbon Dioxide-Induced Climatic Changes in Alaska, School of Agriculture and Land Resource Management, University of Alaska, Miscellaneous Publication 83-1, pp. 129-142. Fairbanks, Alaska.

Van Cleve, K., and L. A. Viereck. 1981. Forest succession in relation to nutrient cycling in the boreal forest of Alaska. *In*: West, D. C., H. H. Shugart, and D. B. Botkin. editors. Forest succession: concepts and application, pp. 185-211. Springer Verlag, New York.

Van Cleve, K., L. Oliver, R. Schlentner, L. A. Viereck, and C. T. Dyrness. 1983a. Productivity and nutrient cycling in taiga forest ecosystems. Canadian Journal of Forest Research **13**: 747-766.

Van Cleve, K., C. T. Dyrness, L. A. Viereck, J. Fox, F. S. Chapin, and W. Oechel. 1983b. Taiga ecosystems in interior Alaska. Bioscience **33**: 39-44.

Walter, H. 1979. Vegetation of the earth and ecological systems of the geo-biosphere, Springer-Verlag New York.

CHAPTER VI

GENERAL DISCUSSION AND CONCLUSIONS

Surveys, 20 years after a severe fire near Inuvik, Northwest Territories, at the western arctic treeline showed that deciduous tree species *Betula papyrifera* and *Populus balsamifera* had established in former tundra areas. The conifer species *Picea glauca* and *Picea mariana* recovered to a certain extent; however, the species did not show evidence of expanding their range after the severe fire. Deciduous tree species have the ability to produce seeds at an early age, and have long range seed dispersal, which could make them effective in invading formerly treeless areas after disturbance.

Picea species with their short-range seed dispersal, appear to have been restricted in re-establishment. Similar to observations have been made in the eastern Canadian Arctic (Elliott 1979; Sirois & Payette 1991), where fire occurrence has been linked to the patchiness of trees at treeline (Payette & Gagnon 1985). In other circumpolar areas, local expansion of treeline and increased seedling establishment have been observed (e.g. Sonesson and Hoogesteger 1983; Morin and Payette 1984; Payette and Filion 1985; Scott *et al.* 1987). These conflicting results show that the climate-vegetation relationship of the northern boreal forest ecotone is still poorly understood, due to a lack of knowledge of the ecophysiology of the treeline tree species (Oechel and Lawrence 1985).

In the area investigated, the four treeline tree species occupy distinct habitats, which initially seemed to be strongly related to the short-wave radiation input. *Populus balsamifera* occupies south facing slopes with deep active layers. *Betula papyrifera* and *Picea glauca* are found on well drained mesic to moist sites with shallow organic layers. *Picea mariana* is found on cold sites, where organic layers are deep and active layers are shallow. The growth response of seedlings of the tree species over a range of short-wave radiation inputs revealed that short-wave radiation input directly accounted for only about one-quarter to one-third of the growth performance. These results suggest that other factors, probably directly or indirectly related to short-wave energy input, played important roles in tree growth. It was hypothesized that a large amount of the growth response could be linked to soil temperature. Mineral soil conditions used in the experiment promoted heat conduction into deeper layers of the soil, therefore the soil temperature in the experimental site was higher, compared to the surrounding landscape. This experiment gave an indication that other factors might be more relevant, influencing seedling growth at the treeline, than short-wave radiation input.

The ecophysiological responses at several soil temperatures, suggested that *Betula papyrifera* could grow in cool site conditions. *Populus balsamifera*, on the other hand, showed a strong response to increased soil temperature, and at low soil temperatures its performance was reduced to low levels. The strong response of *Populus balsamifera* to higher soil temperatures could suggest that *Populus balsamifera* might have some advantage over *Betula papyrifera* on sites with warmer soil temperature. *Picea mariana* responded only moderately to increasing soil temperatures.

Moisture availability, another important factor determining microsite conditions, revealed that *Populus balsamifera* was better adapted to repeated drought stresses than *Betula papyrifera*. This suggests that *Betula papyrifera* will probably be more successful in areas with mesic moisture conditions. Under more frequent drought occurrences, *Betula papyrifera* could probably cope with these conditions, however, *Populus balsamifera*, if present at the same site, would be a strong competitor. This thesis research represents the first study in its kind comparing ecophysiology among the different treeline tree species.

Undisturbed vegetation, especially in the nutrient-and energy-limited northern ecosystems, shows little change over time if there is no disturbance. Even under gradually increased air temperature, it is expected that vegetation changes would be difficult to detect over a few years (Davis and Botkin 1985; Solomon 1986; Payette *et al.* 1989). Slightly increased growth and reproductive capacities could be interpreted as early responses to a change in climate. Widespread soil surface organic matter conditions are not conducive to significant tree seedling establishment in the forest-tundra ecotone. Changes from the present in distribution and occurrence of the treeline tree species will only be enhanced, if the distribution of microsites suitable for tree establishment will change, favouring one tree species over another. It is hypothesized that the insulating organic matter could decrease in depth only slowly by decomposition and/or disturbances (fires) of low severity and frequency. Under this scenario the physical and chemical soil environment will change only slowly even if the air temperature is increased. Tree establishment and growth could increase only slowly, and long-lived tree species like *Picea mariana* and to a certain extent *Picea glauca* which can tolerate cold, deep organic matter soils could establish successfully under these conditions. There would be a slow increase in their dominance in the landscape, due to slightly improved growth and reproduction capacity. However, increased air temperature combined with low soil temperatures could also result in increased drought stress, which could have negative effects (Kozlowski 1991).

If disturbances increase in frequency and severity throughout the forest-tundra ecotone, the insulating organic matter would be removed and the mineral soil would be exposed. This second hypothesized scenario would lead to improved microsite conditions for the success of tree species, under the mineral soil conditions. The deciduous tree species, *Populus balsamifera* and *Betula papyrifera* which disseminate propagules over wide areas, have high light requirements, have rapid growth and strong competitiveness, and reach maturity quickly, might have an advantage over the coniferous tree species. However, microsite conditions will largely determine which of the tree species could be successful. The ecophysiological studies suggested that *Populus balsamifera*, which is capable of adjusting quite well to drier conditions, could occupy a wide array of south slopes with higher soil temperatures and more frequent drought episodes under a changing climate. *Betula papyrifera* seems to be the tree species capable of growing in a wider range of dry to moist environments. Sites presently dominated by *Picea glauca* could be changed quickly under increased disturbance frequencies and severities, to be dominated by the faster growing and more competitive *Betula papyrifera*. *Picea glauca* could continue to occupy sites with lower fire frequencies like river valleys and along streams and lakes. *Picea mariana* could probably be found in the cold and wet organic soil dominated areas with low to moderate fire frequencies and severities, where successful dissemination is guaranteed by its semiserotinous cones, the capability of germinating on organic soils, and the tolerance of cold soils.

In conclusion, this thesis research gave greater insight into the post fire plant cover and biomass accumulation at the forest-tundra boundary. The research documented tree establishment in former tundra areas following a severe fire which removed much of the soil surface organic matter. Further, the research showed that the success of early tree seedling growth is determined only partly by short-wave energy input. This research added to the knowledge of the ecophysiology of treeline tree species, by experimentally comparing the response of treeline tree species to important site factors of soil temperature and drought. It further determined that drought pre-conditioning, can be of importance for the deciduous tree species at the arctic treeline.

LITERATURE CITED

Davis, M. B., and D. B. Botkin. 1985. Sensitivity of cool-temperate forests and their fossil pollen record to rapid temperature change. Quaternary Research **23**: 327-340.

Elliott, D. L. 1979. The current regenerative capacity of the northern Canadian trees, Keewatin, N.W.T., Canada: some preliminary observations. Arctic and Alpine Research **11**: 243-251.

Kozlowski, T. T., P. J. Kramer, and S. G. Pallardy. 1991. The physiological ecology of woody plants. Academic Press, New York.

Morin, A., and S. Payette. 1984. Expansion récente du mélèze à la limite des forêts (Québec nordique). Canadian Journal of Botany **62**: 1404-1408.

Oechel, W. C., and T. W. Lawrence. 1985. Taiga. *In* Chabot, B. F., and H. A. Mooney. editors. Physiological ecology of the North American plant communities. Chapman & Hall, New York. p. 66-94.

Payette, S., and L. Filion. 1985. White spruce expansion at the treeline and recent climate change. Canadian Journal of Forest Research **15**: 241-251.

Payette, S., and R. Gagnon. 1985. Late Holocene deforestation and tree regeneration in the forest-tundra of Québec. Nature **313**: 656-673.

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

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

Sirois, L., and S. Payette. 1991. Reduced postfire tree regeneration along a boreal forest-forest-tundra transect in northern Québec. Ecology **72**: 619-627.

Solomon, A. M. 1986. Transient response of forest to CO_2-induced climate change: simulation modelling experiments in eastern North America. Oecologia **68**: 567-579.

Sonesson, M. and J. Hoogesteger. 1983. Recent treeline dynamics (*Betula pubescens* Ehrh. ssp. *tortuosa* (Ledeb.)Nyman) in northern Sweden. Nordicana **47**: 47-54.