

**POSTGLACIAL SPREAD OF SPRUCE AND PINE ACROSS WESTERN CANADA**

THE POSTGLACIAL POPULATION SPREAD OF *PICEA MARIANA*,  
*PICEA GLAUCA*, AND *PINUS BANKSIANA* ACROSS  
THE WESTERN INTERIOR OF CANADA

By

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A Thesis

Submitted to the School of Graduate Studies

in Partial Fulfilment of the Requirements

for the Degree

Master of Science

McMaster University

September 1991

MASTER OF SCIENCE (1991)  
(Geography)

MCMASTER UNIVERSITY  
Hamilton, Ontario

TITLE: The Postglacial Population Spread of *Picea mariana*, *Picea glauca*, and  
*Pinus banksiana* Across the Western Interior of Canada

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NUMBER OF PAGES: ix, 132

## ABSTRACT

In this thesis, the postglacial spread of three ecologically distinct species, *Picea mariana* (black spruce), *Picea glauca* (white spruce), and *Pinus banksiana* (jack pine), across the western interior of Canada are presented. The fossil pollen records from the sediments of thirteen lakes are used in reconstructing the population expansions of the three tree taxa. The objectives of this study are to examine temporal and spatial patterns in the growth of the populations and to determine if intraspecific and interspecific variations exist across a range of latitudes and elevations.

Pollen accumulation rates (PAR) are calculated from pollen grain counts and sedimentation rates throughout the early- to mid-Holocene, and are used to represent the population level at the time of pollen deposition. Exponential equations are used to calculate population growth rates. Three dimensional diagrams (time, space, abundance) are constructed to illustrate the spread of the populations.

The rates of population growth varied from south to north for all three species. Jack pine, on average had slower population growth rates, and its expansion across the region began over 3,000 years later than, and lasted approximately 1,000 years longer than the two spruce species. All three tree taxa experienced reduced rates of population growth at high elevation sites in the north. These variations are examined in light of the changing and static physical and botanical environmental conditions occurring during expansion.

## ACKNOWLEDGEMENTS

I would like to express my thanks to my supervisor, Glen MacDonald, for all his help, guidance, enthusiasm and humour throughout this undertaking. Assistance with the world of 3-D was given by Chi Chang to whom I am very grateful. My appreciation goes out to Chris Hanks and Angele Barnett for their field assistance and to James Ritchie, Robert Mott, and Thane Anderson for providing sediment samples.

Thanks to Julian Szeicz, Chris Larsen, and Katrina Moser - lab mates that made the days of toil over a microscope truly enjoyable - I realize now where the concept of chaos theory originated. A cajillion thanks to Susan Elliott for moral support and friendship beyond the call of duty. Ditto to John Pullen at the 'Cottage Cafe'. To Rebekah Pullen for some insightful discussions - amazing! Finally, a special thank-you to James Hamilton for knowledge, patience and understanding in dealing with this project, for use of his computer facilities and for always being aware of wonder.

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# CHAPTER I

## INTRODUCTION

### 1.0 Introduction to the Study

Most of the western interior of Canada was covered by ice during the late-Wisconsinan glacial maximum at 18,000 BP (Dyke and Prest, 1987). By approximately 14,000 to 12,000 BP climatic warming and glacial retreat began to provide the environmental conditions necessary for potential re-invasion of plants into western Canada. Species invasion consists of: initial arrival, establishment, and subsequent population increase to an environmentally determined carrying capacity. The study of arboreal invasion is difficult due to the longevity of trees. However, the preservation of pollen in lake sediment records changes in tree populations spanning millennia and therefore provides the opportunity to reconstruct postglacial invasions of tree species.

In this thesis, fossil pollen records obtained from lakes will be used to reconstruct the postglacial expansion of three ecologically distinct species - *Picea mariana* (Mill) B.S.P. (black spruce), *Picea glauca* (Moench) Voss (white spruce), and *Pinus banksiana* Lamb. (jack pine) in the western interior of Canada. The specific objectives of the study are to look at the temporal and spatial patterns of population growth of these trees. Particular attention will be given to variations in growth rates

between and within species across a range of latitudes and elevations. Intraspecific variations in population growth rates may result from differences in local environmental conditions, including differences in climate, soils, and competition as well as changes in the environment during invasion. Interspecific variations in population growth rates result from differences in ecological characteristics affecting colonizing ability, growth, reproduction and competitive ability and the individualistic response of a species to the changing environment.

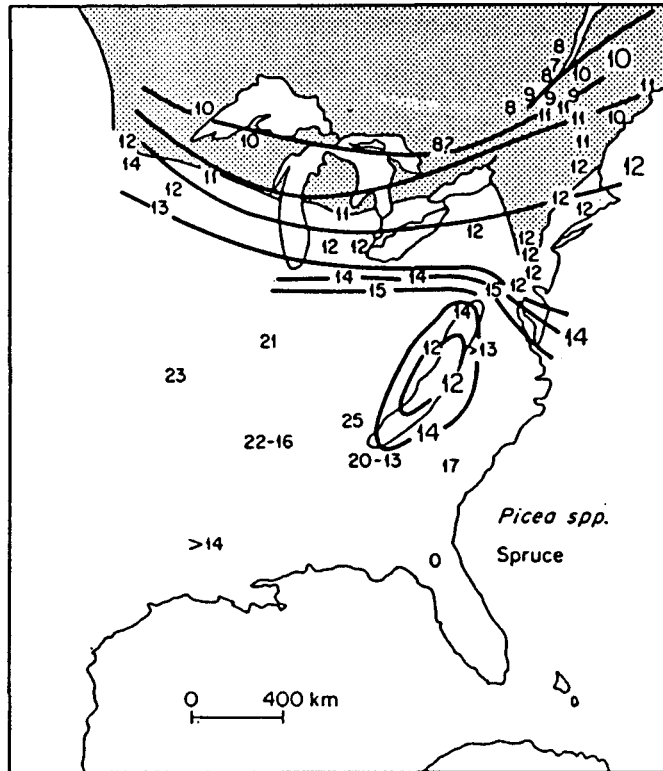
### **1.1 Range Expansion**

Species range extension is often termed migration in the palynological literature and is described in terms of the spatial pattern and rate of migration. Postglacial pollen records from across North America have shown both intraspecific and interspecific variation in the patterns and rates of migration. Eastern North America is an area that has been extensively studied and numerous pollen records have been obtained for this region. This has made it possible to produce regional isopoll and isochrone maps of postglacial plant invasion (Davis, 1981; Bernardo and Webb, 1977; Webb, 1987; Jacobson *et al*, 1987). Davis (1981) used isochrone maps (lines connecting points of equal arrival times for a given plant taxon) to illustrate that taxa migrated independently of one another and not as intact communities. *Picea* (spruce) migration occurred uniformly from the south to the north (Figure 1.1a), whereas *Pinus* (pine) migrated from the southeastern United States north along

the eastern seaboard and then west and north across the Great Lakes Region (Figure 1.1b). Bernardo and Webb (1977) used isopoll maps (lines connecting points of equal pollen percentage for a particular plant taxon at given point in time) to illustrate changing postglacial patterns of abundance. At approximately 11,000 BP spruces were present throughout the lower Great Lakes while pines were highly concentrated in Appalachia (Figure 1.2a). By 9,000 BP spruces experienced a reduction in abundance across its former range and were clustered along the southern edge of the receding ice sheet, yet pines had expanded throughout northeastern United States during the same period (Figure 1.2b).

Using arrival times and the isochrone maps, the rates of migration of tree taxa across eastern North America have been calculated. Davis (1981) has illustrated that migration rates were as high as 400 m/yr for *Pinus banksiana/resinosa* (jack/red pine) and as low as 100 m/yr for *Castanea* (chestnut; Table 1.1). Spruce had a moderate rate of 250 m/yr. In contrast, Delcourt and Delcourt (1987) presented generally slower rates of migration for the boreal taxa and *Quercus* (oak) and *Ulmus* (elm) in eastern North America (Table 1.2). *Picea* had a migration rate of 141 m/year while *Pinus* varied from 135 m/yr for northern *Pinus* to 81 m/year for southern *Pinus*. In the British Isles and the European mainland the tree taxa show a great deal of diversity between taxa and within a taxon across sites (Table 1.3, Birks, 1989). For all the taxa reported, except *Tilia* (basswood), the migration rates were much faster on the European mainland than on the islands. The rates for pine vary from 100 to

(a)



(b)

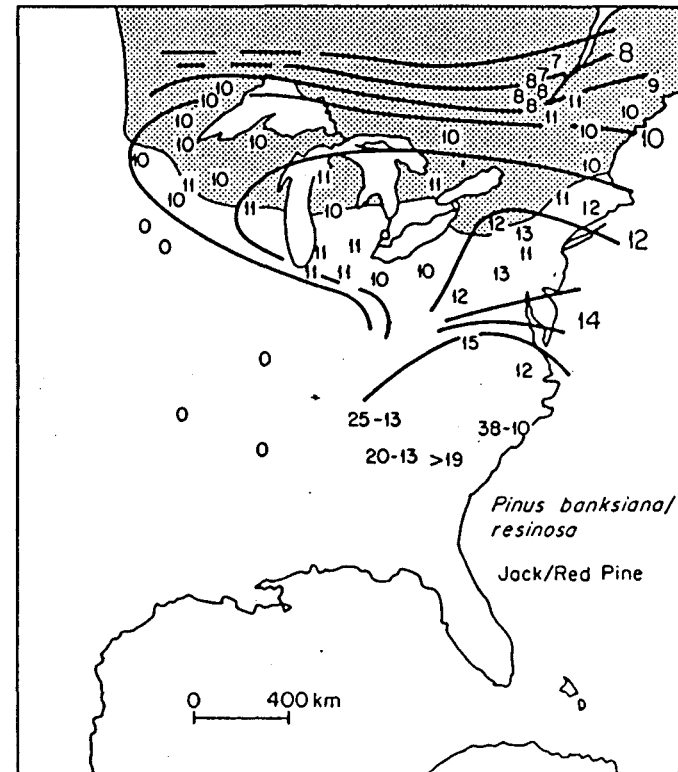


Figure 1.1 Migration maps for (a) *Picea* spp. (spruce), and (b) *Pinus banksiana/resinosa* (jack/red pine). The numbers refer to the radiocarbon age (in thousands of years) of the first appearance of the taxon at the site after 15,000 years ago. Isopleths were drawn to connect points of similar age; they represent the leading edge of the expanding population (Davis, 1981).

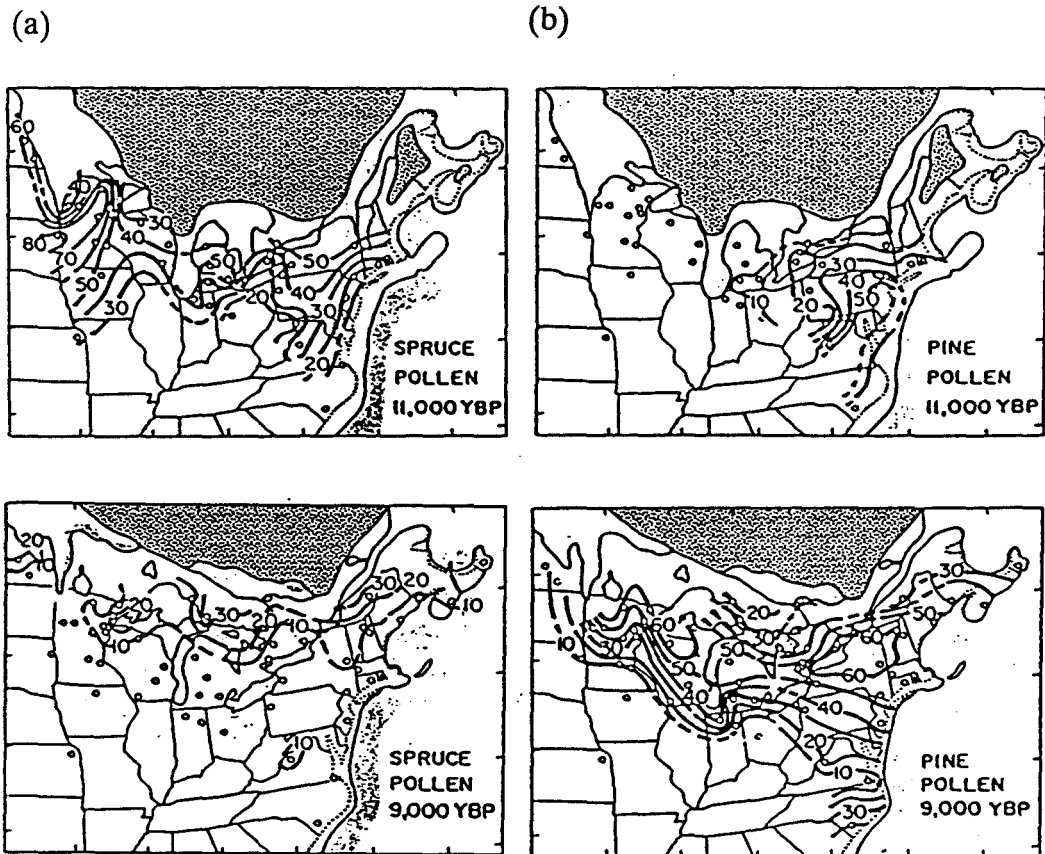


Figure 1.2. Isopoll maps illustrating the distribution of (a) *Picea* spp. (spruce) pollen, and (b) *Pinus* spp. (pine) pollen at 11,000 and 9,000 BP (from Bernardo and Webb, 1977).

700 m/yr within the British Isles and reach up to 1500 m/yr on the mainland. Both, variation between species and variation within a species in the rates of migration are seen to exist. Delcourt and Delcourt (1987) illustrate this by measuring the rates of migration along five transects running south to north in eastern North America (Figure 1.3).

Though these data provide some information on expansion, the use of migration patterns and particularly migration rates is complicated by difficulties

**Table 1.1.** Average rates of Holocene range extensions in eastern North America (from Davis, 1981).

<b>Taxon</b>	<b>Migration Rate (m/yr)</b>
<i>Pinus banksiana/resinosa</i>	400
<i>Pinus strobus</i>	300-350
<i>Quercus</i>	350
<i>Picea</i>	250
<i>Larix</i>	250
<i>Ulmus</i>	250
<i>Tsuga</i>	200-250
<i>Carya</i>	200-250
<i>Abies balsamea</i>	200
<i>Acer</i>	200
<i>Fagus</i>	200
<i>Castanea</i>	100



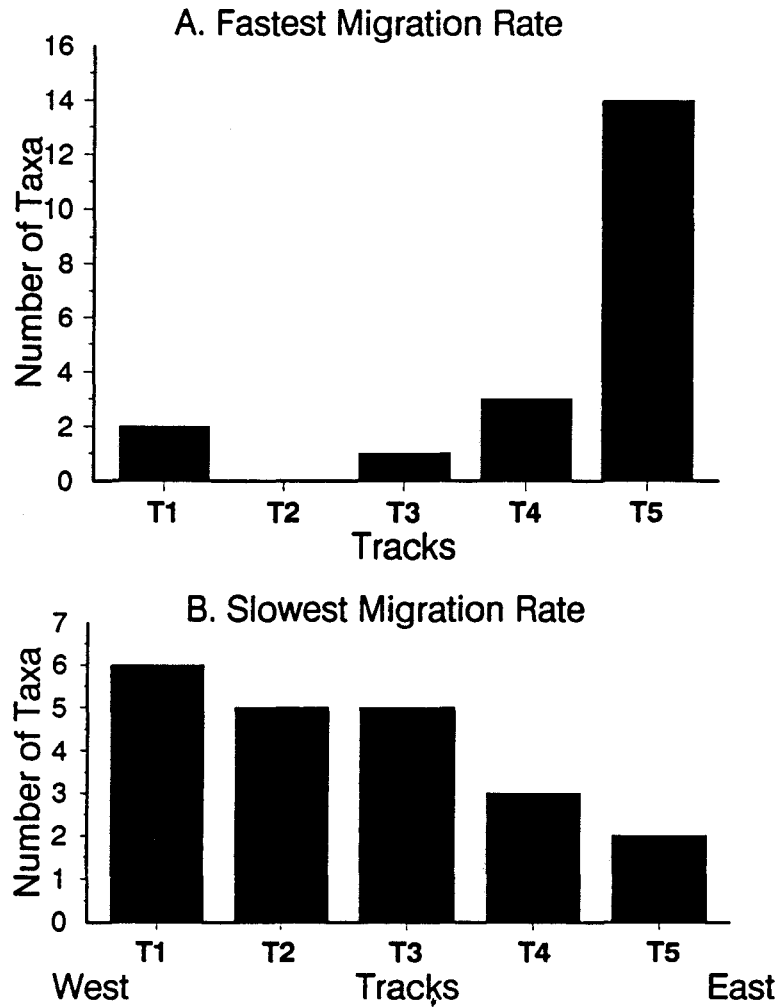


Figure 1.3. A. Geographic patterns in number of taxa with fastest migration rates (tracks run south to north across eastern North America).  
 B. Geographic patterns in number of taxa with slowest migration rates (Delcourt and Delcourt, 1987)

related to accurately determining arrival times. Limitations in the spatial and temporal resolution of pollen records make it difficult, if not impossible, to determine the exact time when a taxon first arrives at a site. Low levels of pollen may indicate; either the presence of a few individuals at a site, or that the pollen may be due to long-distance transport from distant sources. The area represented by the pollen record of a site cannot be precisely defined. This applies in particular to the influx of pine which has a small aerodynamically shaped pollen grain (Prentice, 1985; MacDonald, 1988). The exact time of first arrival is also hard to define. Except when using annually laminated lake sediments, most pollen counts are from samples taken at intervals which may represent tens or hundreds of years of sedimentation (Bennett, 1983; Tsukada and Sugita, 1982). Assigning a date to each interval is also problematic due to the availability of datable material and the accuracy and resolution of the dating technique.

Researchers have used different methods to estimate the arrival times of plants based on pollen records. Davis (1981), Watts (1973), and Tallantire (1977) use sharp increases in the pollen influx as an indication that a given taxon is locally present at the site. Bennett (1985) suggests that when using small lakes (5-20 ha) most of the pollen is from local sources and very small populations may be undetected in the pollen record. The first detection of pollen in the record may result from an increase in the pre-existing population to a level that can be observed

**Table 1.2.** Migration rates for the leading (northern) edge of distribution (from Delcourt and Delcourt, 1987).

<b>Taxon</b>	<b>Migration Rate (m/yr)</b>
<i>Salix</i>	287
<i>Populus</i>	263
<i>Betula</i>	212
<i>Tilia</i>	209
<i>Tsuga</i>	202
<i>Larix</i>	189
<i>Fagus</i>	169
<i>Abies</i>	159
<i>Picea</i>	141
<i>Juglans</i>	140
Northern Cupressacea	138
<i>Pinus</i> (Northern)	135
<i>Ulmus</i>	134
<i>Acer</i>	126
<i>Quercus</i>	126
<i>Fraxinus</i>	123
<i>Carya</i>	119
<i>Pinus</i> (Southern)	81
<i>Nyssa</i>	70
Southern Cupressacea	45

in the fossil pollen record. Bennett (1986) models the expansion of a species range illustrating the actual range extension compared to that which is theoretically

detectable in the pollen record (Figure 1.4). In the above model the apparent rate of migration may vary from the actual rate of range extension due to abundance/distance gradients and the rate of population growth.

**Table 1.3.** Estimated rates of spread (m/yr) of trees in the British Isles and on the European mainland (from Birks, 1989).

Taxon	Rate of Spread *	Rate of Spread **
<i>Betula</i>	250	>2000
<i>Corylus</i>	500	1500
<i>Ulmus</i>	550 (100 near northern limit)	500-1000
<i>Quercus</i>	350-500 (50 near northern limit)	150-500
<i>Pinus</i>	<100-700 (England), 150 (Scotland), 150-200 (Ireland)	1500
<i>Alnus</i>	500-600 (50-150 near northern limit)	500-2000
<i>Tilia</i>	450-500 (50-100 near northern limit)	300-500
<i>Fraxinus</i>	50-200	200-500
<i>Fagus</i>	100-200	200-300

\* British Isles

\*\* European Mainland

That a plant taxon may be present at a site before its pollen is recorded in lake sediments is confirmed by the occurrence of dated macrofossils which precede

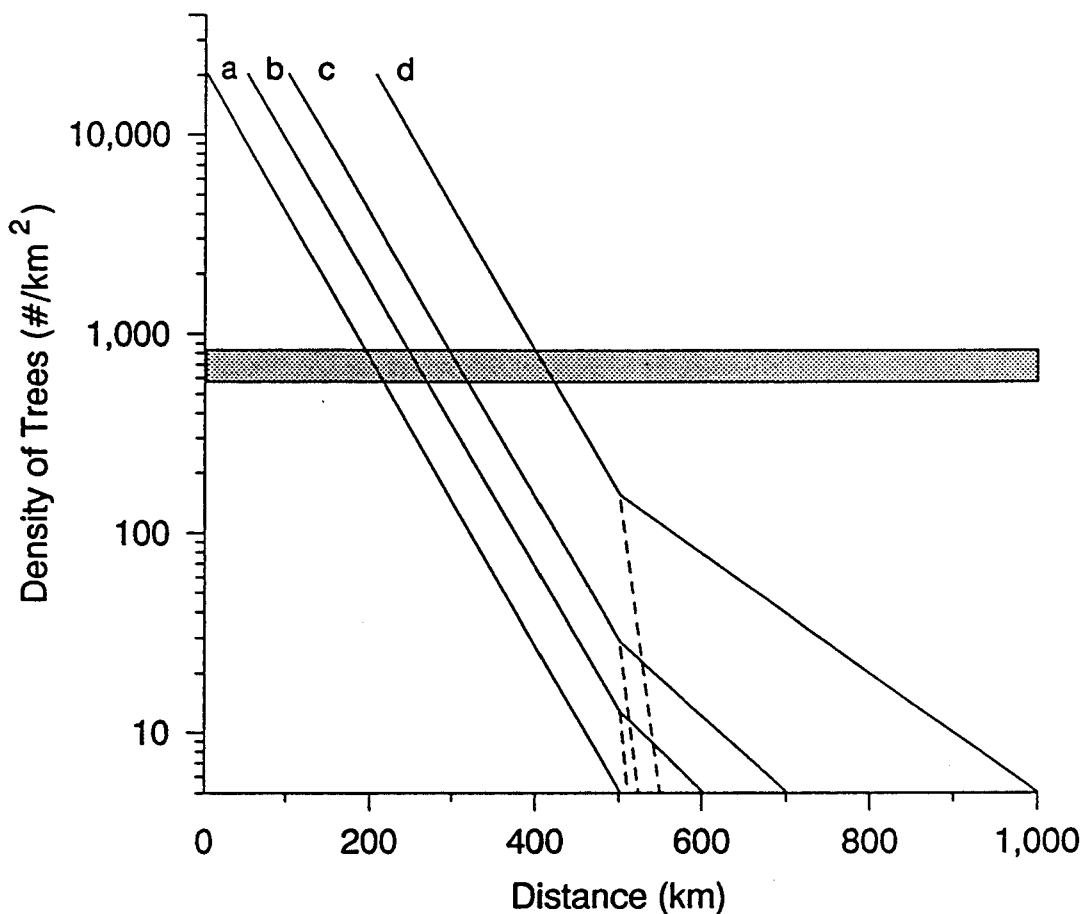


Figure 1.4. Hypothetical section across the margin of a species range.  $a=0$ ,  $b=100$ ,  $c=200$ ,  $d=500$  years since expansion began. Population densities double every hundred years, while the margin of the range is advancing at 100m/yr (dashed line) or 1000m/yr (solid line). The level of abundance at which the taxon would normally be detected by routine pollen analysis is shaded (Bennett, 1986).

the pollen rise. In small basins, macrofossil transport into a lake is limited to local sources. Pennington (1986) found macrofossils of *Betula* (birch) below the level of sustained high pollen abundance. Bush and Hall (1987) found *Alnus* (alder) macrofossils in an ancient fen in England before its pollen was continuously recorded in lake sediments. The difficulties in using pollen to determine the presence of a plant taxon suggest that migration rates may not be accurate measurements of expansion and that the earliest detection of pollen is only a minimum approximation of arrival. Measured arrival times would only approach actual arrival times when there is a rapid rate in population growth after arrival (Bennett, 1986). Reconstructed patterns of migration may only be accurate if the rate of initial population increase and the time from arrival to detection in the pollen record is similar at all sites across a region (Birks, 1989).

In light of these problems many researchers (Bennett, 1983, 1985, 1986; Birks, 1989; Ritchie and MacDonald, 1986) use the initial point of continuous pollen deposition by a plant taxon as an indication that the taxon is established at the site. The spatial sequence of taxon establishment across a region indicates the spread of population growth. Though spread may not always represent true range extension, if there is a consistent, sequential nature to the spread there is probably a strong component of arrival and establishment in the data.

In conceptual modelling of the postglacial spread of plant species, Delcourt and Delcourt (1987) present three possible strategies for migration (Figure 1.5).

These strategies are based on the proposed evolutionary species strategies presented by MacArthur and Wilson (1967). The first model describes the *r-migration strategist*, which is short-lived, shade intolerant, quickly reaches the reproductive stage, produces abundant propagules that are widely dispersed, and can germinate and grow in nutrient-poor soils (Figure 1.5a). Typically this strategist is an early-successional taxon. It enters a area and quickly increases in numbers, obtaining temporary domination of the site. This is followed by a decrease in population levels. The *K-migration strategist* is long-lived, needs nutrient-rich soils, is shade tolerant, grows slowly and produces a few large propagules (Figure 1.5b). This strategist is typically a late-successional taxon. The form of spread reflects slow initial establishment with a slow rise in population levels. The *fugitive strategist* is a rare taxon that exists only in isolated habitats (Figure 1.5c). The area studied by Delcourt and Delcourt (1987) was eastern North America where many of the taxa used in the models, such as *Picea*, are not now dominant taxa. *Picea* was described as an r-migration strategist but based on the data used it is uncertain if this is a good model of spruce expansion in more northerly areas where it is now the dominant tree.

In contrast Bennett (1985), Cwynar and MacDonald (1985), Pennington (1986), Prentice (1986), Walker (1982), and Watts (1973) all suggest that the spread of invading plants may take place by the establishment of low density populations or patches of trees established at some distance from the main populations. These individuals would act as nuclei for further population expansion. In addition, Davis

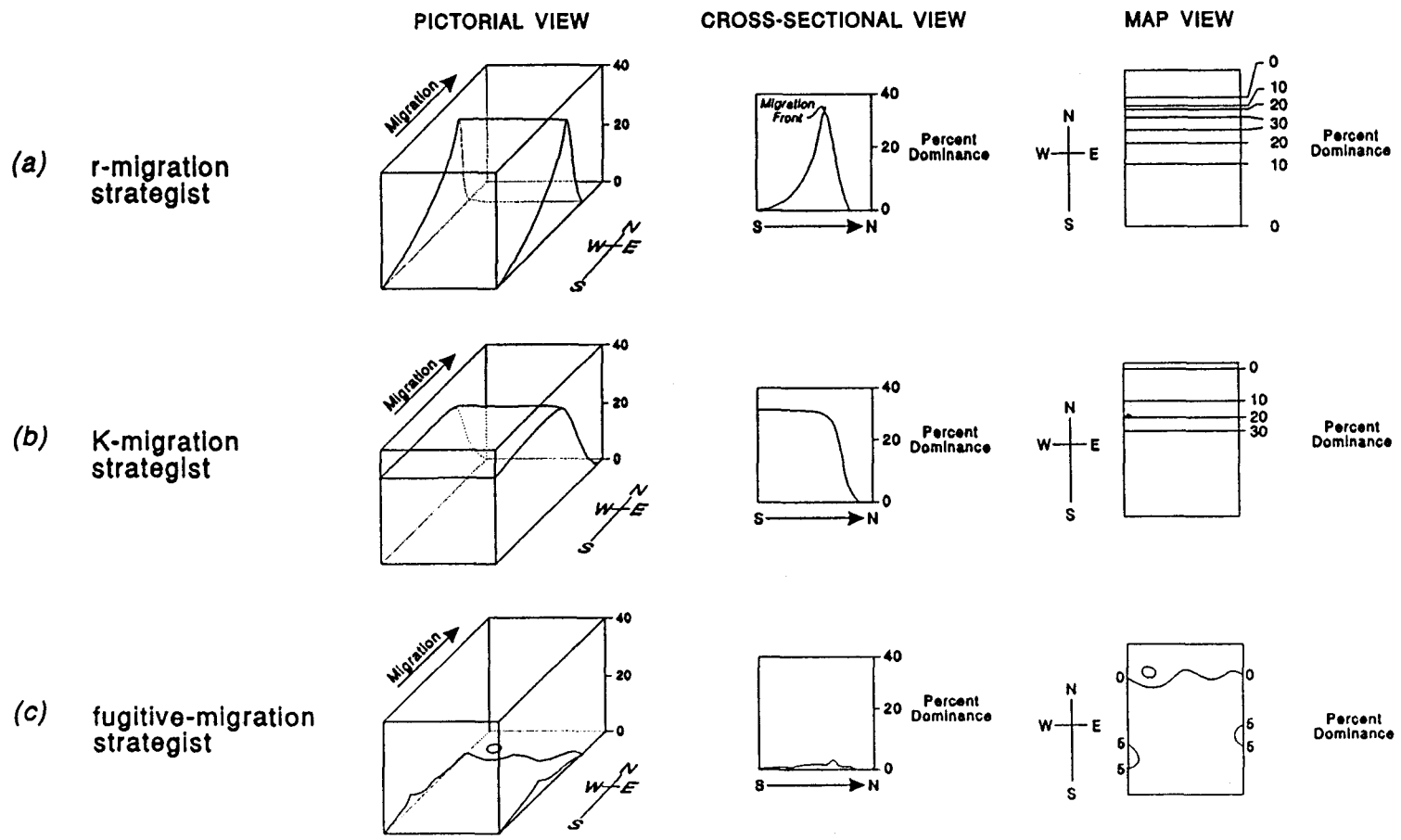


Figure 1.5. Hypothetical models of population expansion during a time of environmental change (Delcourt and Delcourt, 1987).



*et al* (1986) found that in the area of northern Michigan, *Tsuga* (hemlock) first appeared synchronously at a number of separated sites. This indicates that small outlying colonies were initially established and became the source for further population increase, supporting the concept of low density population spread.

## 1.2 Expansion Within a Site

The use of palynological data to study population changes at a site assumes that there is a direct relationship between population growth and increases in the pollen abundance recorded in lake sediments. It has been shown that modern pollen deposition does reflect the composition of the existing vegetation and that recent changes in the vegetation are discernable in the pollen records (eg., Birks and Birks, 1980; Delcourt and Delcourt, 1987). Though the relationship between pollen influx and the population of a given taxon is complex, population growth rates, as well as spatial intraspecific and interspecific variations in these rates, have been calculated at a number of sites.

Increases in pollen abundance, related to population growth at a site, have been modelled by exponential and logistic growth curves. Bennett (1983) used both methods to approximate the postglacial growth of seven tree taxa in Norfolk, England. For five of the taxa, *Betula* (birch), *Ulmus* (elm), *Quercus* (oak), *Tilia cordata* (small-leafed lime), and *Alnus glutinosa* (European alder), exponential curves were used and for *Corylus avellana* (hazel) and *Pinus sylvestris* (scots pine) logistic

curves were used. Tsukada and Sugita (1982) working on postglacial population change in Washington, used logistic models. Tsukada (1983) used logistic growth curves to model the postglacial increase in *Picea* pollen in Japan but the subsequent population decline of *Picea* was exponential. It appears that both models were equally well suited to describe past population increases.

Using either method to model expansion, rates of fossil pollen increase can be calculated and the time required for the pollen abundance levels to double can be used as a measure to compare population growth rates. Bennett (1983) presented doubling times that ranged from 35 years for *Corylus avellana* to 176 years for

**Table 1.4.** Doubling times of various taxa in Britain (from Bennett, 1983).

Taxon	Doubling Time (yrs)
<i>Betula</i>	59
<i>Pinus sylvestris</i> *	73
<i>Pinus sylvestris</i> **	58
<i>Corylus avellana</i> *	46
<i>Corylus avellana</i> **	35
<i>Ulmus</i>	67
<i>Quercus</i>	141
<i>Tilia cordata</i>	99
<i>Alnus glutinosa</i>	174

\* Results of analysis of  $\ln(N)$  against age (exponential growth)

\*\* Results of analysis of  $\ln(K-N)/N$  against age (logistic growth)

*Quercus* (Table 1.4). The doubling times for pine ranged from 58 to 73 years. Doubling times calculated from the growth rates presented by Tsukada and Sugita (1982) ranged from 52 years to as long as 462 years (Table 1.5). *Pinus contorta* ssp *contorta* (lodgepole pine) had doubling times of 107-173 years. Work done by MacDonald and Cwynar (in press) in western Canada shows a wide variation in the doubling times of *Pinus contorta* ssp *latifolia* (lodgepole pine) from as low as 80 years to as high as 1100 years (Table 1.6).

**Table 1.5.** Doubling times of taxa from Mineral Lake, Washington. Derived from r-values listed in Tsukada and Sugita (1982) using the equation  $\ln 2/r$  (exponential growth).

Taxon	Doubling Time (yrs)
<i>Pinus contorta</i>	107-173
<i>Picea</i>	177
<i>Abies</i>	408
<i>Tsuga mertensiana</i>	462
<i>Alnus</i>	112
<i>Pseudotsuga</i>	52
<i>Thuja plicata</i>	231

The timing of post glacial expansion into high latitude and high elevation sites shows considerable delay for some species. MacDonald and Cwynar (in press) have found that the expansion of *Pinus contorta* across a south to north transect of western

Canada has continued throughout the Holocene and reflects a slow rate of spread into northern areas (Table 1.6). In the Adirondack Mountains, Jackson and Whitehead (1991) using macrofossil and pollen records, found that increases in *Abies* (fir), *Pinus strobus* (white pine), and *Tsuga* occurred later in the Holocene at higher elevations compared to lower elevations. Van Leeuwaarden and Janssen (1987) found that postglacial increases of *Betula*, *Pinus*, *Corylus* (hazel), *Quercus*, *Ulmus*, *Tilia*, and *Alnus* into valley bottom sites in the Netherlands preceded expansion onto nearby ridges by several hundred years.

**Table 1.6.** Results of *Pinus* pollen based on first continuous presence of *Pinus* pollen (from MacDonald and Cwynar, in press).

Site	Start of Increase (yr BP)	End of Increase (yr BP)	PAR Doubling Time (yrs)	Range of Doubling Time (yrs)
Goldeye Lake (1st increase)	12,000	10,380	276	192-489
Goldeye Lake (2nd increase)	9,000	6,370	796	581-1,268
Goldeye Lake (total increase)	12,000	6,370	797	651-969
Lone Fox Lake	10,200	5,100	608	556-670
Snowshoe Lake	10,250	6,750	396	335-483
Lac Ciel Blanc	7,850	3,000	1,100	922-1,363
Hail Lake	5,760	4,900	80	65-103
Kettlehole Pond	4,360	1,090	364	321-421
Flamingo Lake	2,490	260	425	357-524

### 1.3 Controls on Expansion

The expansion of any taxon depends on seed production and dispersal, seedling survival and growth to reproductive maturity. In general, the early successional trees (r-strategists) such as *Salix* (willow), *Populus* (poplar), *Alnus* (alder), and *Betula*, should be able to expand and spread faster than late-successional trees (K-strategists), such as *Quercus*, and *Tsuga*. This is due to the production of large numbers of easily transported seeds and subsequent rapid growth and early reproduction (Brubaker, 1986). However, spatial variations in the realized expansion and spread cannot be explained solely by a taxon's potential capabilities. The spread and expansion of postglacial populations must be in part controlled by physical and biological factors acting on reproductive, growth and colonizing abilities.

Climate change associated with the end of the Wisconsinan was the ultimate cause of expansion of trees during the Holocene (Davis, 1981, 1986; Ritchie, 1987). Davis (1981) documented the arrival of *Pinus strobus* (white pine) in Minnesota at approximately 7,000 BP. Further westward spread was curtailed by the increasingly arid climate. Cooler and moister conditions within the last 1,000 years stimulated further expansion to the west. In Michigan, a western range limit was established for *Fagus* (beech) by approximately 2,500 BP and was maintained for 1,500 years. Davis *et al* (1986) suggested that climatic change stimulated spread further west between 1,000 and 500 BP. Tallentire (1972, 1977) suggested that the spread of *Picea abies* (Norway spruce) in Fennoscandia in the last 2000 years was controlled and stalled by

climate, particularly by the severity of winters and early summer drought.

In the above cases it has been suggested that the populations were in equilibrium with climate. Climate change may alter the carrying capacity of an area for a particular taxon and the taxon may respond with changes in range and or abundance. Variations in expansion and spread are thus due to variations in the rates of climate change (Davis, 1984; MacDonald and Cwynar, in press). Climate changes in the Holocene were often rapid, so that extensive areas would quickly become available for colonization. If a taxon is unable to respond as quickly as the rate of climate change the equilibrium with climate is lost and the taxon is said to lag behind climate change. There are two possibilities: (i) the taxon may be in quasi-equilibrium with climate such that the initial invasion is controlled by climate but subsequent rates of population expansion are influenced by other factors; (ii) the taxon may be in complete disequilibrium with climate with realized spread and population expansion controlled by other factors (MacDonald and Cwynar, in press). When taxa lag behind climate change other environmental factors may influence variations in spread and population expansion, including static physical environmental conditions (differences between sites in static climatic conditions, topography and soils) and biological conditions (differences in vegetation; Ritchie, 1987).

The late postglacial appearance of *Betula* at various sites in Britain showed differences in timing of 500 to 1,500 years (Pennington, 1986). These differences in the timing of appearance occurred within a region of similar climate. Pennington

(1986) suggested that this variation was due to differences in soils and in soil development. These soil variations resulted from differences in the substratum, relief and drainage which in turn affected organic matter accumulation and soil development. Soils may also have affected the competitive balance between plant taxa. *Pinus* increased at sites in Scotland approximately 8,000 years ago and quickly dominated the sites investigated. *Quercus* increased later and was only able to compete with *Pinus* on the more favourable, less acidic soils (Pennington, 1986). The influence of soils on competition is due to varying tolerances among taxa of soil moisture, organic matter and mineral nutrient contents (Brubaker, 1975). In upper Michigan, *Pinus strobus* dominated both the fine textured till and less coarse outwash sites during the early- to mid-postglacial. After 5,000 BP, climatic conditions became more mesic and soil moisture increased allowing the invasion of deciduous trees on the fine textured tills. The range of white pine became restricted to the moderately coarse outwash soils (Brubaker, 1975). This example illustrates that soils may become limiting only under certain climatic conditions.

Existing vegetation can also affect invading species by competing for limited resources including space, soil nutrients, and light. However, existing vegetation may produce conditions favourable for the invasion of other taxa. Jacobson (1979) found that the oak savannas and oak forests of Minnesota around 4,000 years ago were prime sites for white pine expansion. The understories had low levels of humus accumulation which is favourable for white pine germination and growth. Once

established, white pine persisted. Its heavy litter strongly inhibits growth of other plants by increasing soil acidity, decreasing bacterial decomposition, and providing a physical barrier to seeds needing to reach the mineral soil to germinate.

Spread and population expansion may be affected by fire intensity and frequency. Certain species such as *Pinus banksiana* and *Pinus contorta*, depend on fire to open serotinous cones and release the seeds, to prepare a seedbed for their germination and to open the canopy to allow sufficient light for growth. Other taxa such as *Betula* and *Populus* are shade intolerant and with rapid growth rates can also quickly invade burned sites. A high fire frequency may facilitate expansion of fire-tolerant or fire-dependant trees while retarding the expansion of late-successional, less fire tolerant taxa (Brubaker, 1975; Fowells, 1965).

Feedback loops characterize the linkages among these factors. Climate affects fire frequency, soil moisture, and vegetation composition. Where climatic conditions become stressful some of the other factors may exercise an important role in determining abundance and distribution of vegetation. Fire affects vegetation while vegetation composition in turn affects the amount of combustible material altering the fire cycle (Rowe, 1970). Soil fertility affects vegetation composition but the vegetation contributes to soil fertility.

This thesis will examine patterns of spread, and the timing and rates of population expansion at sites across western Canada for three ecologically distinct species; *Picea mariana* (black spruce), *Picea glauca* (white spruce), and *Pinus*



*banksiana* (jack pine). Although much information on continental patterns of plant migration exists, there is no similar data on continental patterns of plant population expansion. The focus is to reveal any significant interspecific and intraspecific differences in population growth rates and determine if these differences have any geographic pattern, particularly with respect to latitude and elevation. If variations are found, the results will be examined in light of the changing and static physical and botanical environmental conditions occurring during expansion.

## **CHAPTER II**

### **REGIONAL CHARACTERISTICS**

#### **2.0 Introduction**

Pollen records from thirteen lakes are used in this study. The sites are located along two north-to-south transects in central Canada (Figure 2.1). The area includes the District of Mackenzie, Northwest Territories, the northern part of the province of Alberta, northeastern British Columbia, and northern Saskatchewan. The first group of sites (sites 1 to 10) cross the western range of black spruce and white spruce in the northern Interior Plains. The second transect (sites 4, 5, 6, 11, 12, 13) crosses the western range of jack pine, running from the Mackenzie River near Great Bear Lake in the northern Interior Plains to north-central Saskatchewan in the western Canadian Shield. This chapter briefly outlines the geology, geomorphology, climate (modern and Holocene), soils, and vegetation (modern and Holocene) of the study region.

#### **2.1 Geology and Geomorphology**

##### **Bedrock Geology**

The majority of the sites are located in the Interior Plains with the following exceptions; sites 11, 12 and 13 are in the Canadian Shield and site 3 is in the Franklin

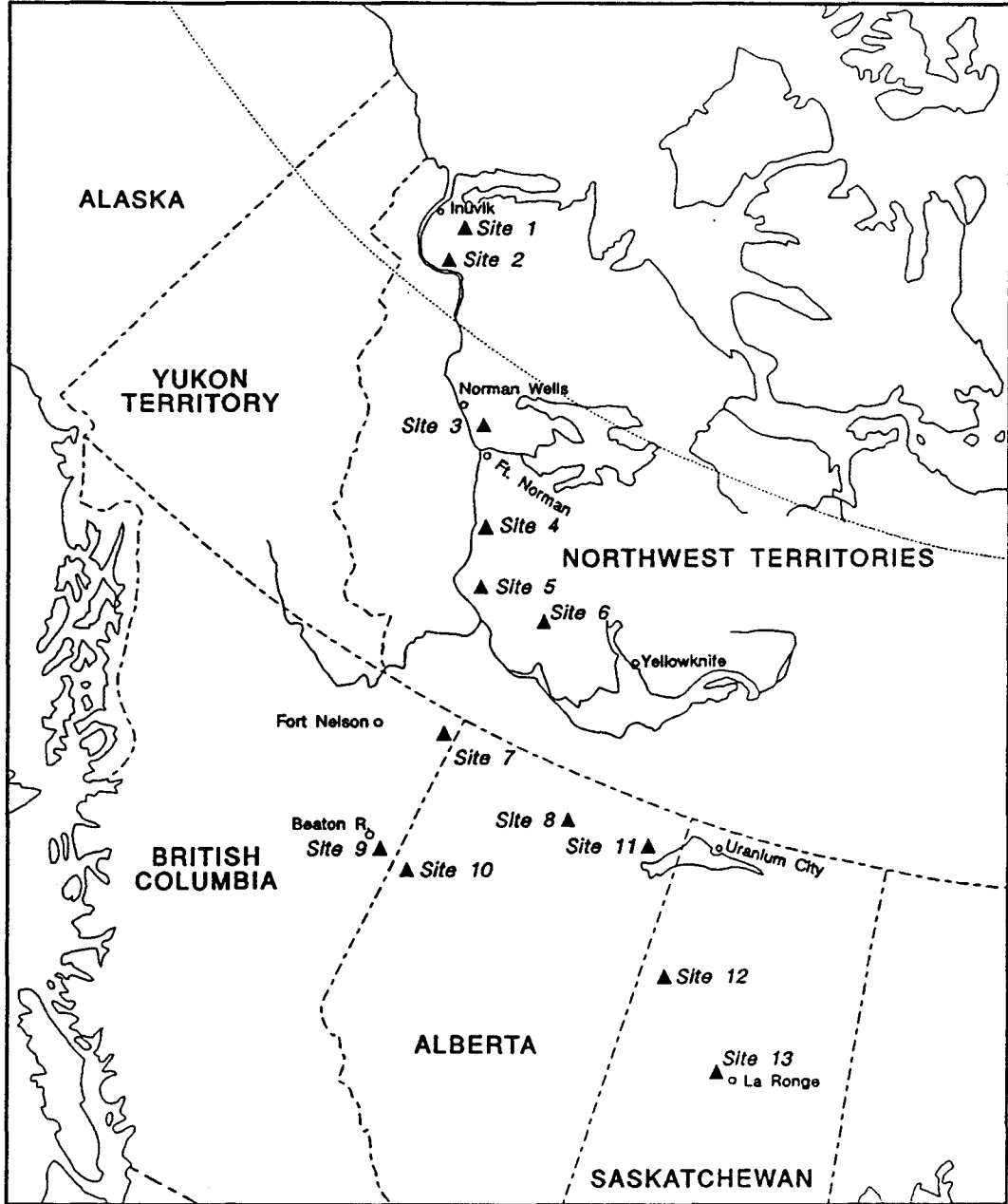
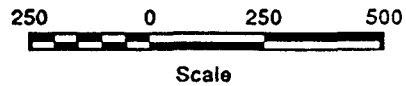


Figure 2.1. Study Region

- ▲ Pollen Sites
- Climate Stations



Mountains of the Cordillera. The Canadian Shield consists of Precambrian igneous and metamorphic rocks: granite, gneiss and greenstone dominate the outcrops. The Shield dips southwestwardly beneath the Interior Plains; an unconformable contact separates the Precambrian from the overlying sedimentary strata of the Interior Plains (Douglas *et al*, 1970). Westward in the subsurface of the Interior Plains and outcropping within the orogen are thick Precambrian quartzites, carbonates and shales of Helikian age, overlying the crystalline basement. The bulk of the strata in the Interior Plains are gentle southwesterly dipping sedimentary rocks that increase in thickness toward the orogen. The Phanerozoic succession of the Northern Interior Plains is divisible into two main parts (Meijer Drees, 1989; Douglas *et al*, 1970). The lower part is made up of early Cambrian to Silurian sandstones, shale, anhydrite, and carbonates. It is absent in the southern areas of the study region. The upper part of the succession is a thick sequence of Devonian evaporites, carbonates and shales. The contact between the two divisions is unconformable. In the south where the lower division is absent, the Devonian rests directly on Precambrian. In the northeastern section of the Alberta Plateau (sites 7 and 9) the Palaeozoic is capped by minor Permian and Carboniferous carbonates. Over most of the Interior Plains the Paleozoic is overlain by Cretaceous shales and sandstones. The Cretaceous is absent in some topographic lows; in those areas outcrops are usually Devonian. In the eastern portion of the Cordillera (e.g. site 3), the majority of the outcrop is Paleozoic; the Precambrian quartzites and carbonates are seen farther to the west.

## **Geomorphology**

The geomorphology of the Canadian Shield and Interior Plains reflects repeated glaciation in the Pleistocene. To the west in the Cordillera, tectonic and fluvial activity have also had a major role in landscape development.

The Kazan Region of the Canadian Shield is rolling with numerous glacially scoured lakes and streamlined bedrock landforms (Bostock, 1970; Prest, 1970). Glacial deposits are generally thin although subglacial and proglacial fluvial features such as eskers, drumlins, and outwash are common. Though local relief is generally less than 60 to 90 metres the undulating bedrock features influence microclimates, drainage, soil development and vegetation patterns (Ritchie, 1987).

The Interior Plains are an extensive area of low relief, with abundant lowlands, and gently rolling plateaux or hills (Bostock, 1970; Prest, 1970). The hills and plateaux are usually erosional remnants of Cretaceous strata (e.g. site 6: Horn Plateau). In the Interior Plains most of the area is draped in unconsolidated materials with glacial sediments accounting for the bulk of the surficial mantle. Ice marginal sedimentation accounts for the end and hummocky moraine forms which are common in this area. Additionally, deposition into proglacial lakes produced wide areas of lacustrine sediments in lowlands. Extensive outwash systems associated with deglaciation are observed in the region. Major river systems, including the Mackenzie, Liard and Peace Rivers have carved out protected valleys, leaving floodplain, terrace and deltaic deposits.

## **2.2 Ecoclimatic Regions**

In this section, the climatic variables that are discussed are those which affect the abundance and distribution of vegetation, particularly trees. Climate will therefore be described in terms of ecoclimatic regions used by the Ecoregions Working Group (1989), Hare and Thomas (1979), and Ritchie (1987), with reference to climate normals from nearby stations.

### **High Subarctic**

This climatically severe region is located just south of the Arctic zone and includes sites 1 and 2 (Table 2.1). Climatic conditions at Inuvik airport (Figure 2.2a) typify this area; mean annual temperature is  $-9.8^{\circ}\text{C}$  and an annual precipitation of 266 mm with most falling in the late summer and early fall. The growing season is short, approximately four months long.

### **Low Subarctic**

Site 3 occurs within this region, an area closer to the Boreal ecoclimatic zone. Climatic conditions from Norman Wells (Figure 2.2b), typical of this area, indicate that temperatures are slightly higher and the growing season is slightly longer, lasting between four and five months. Mean annual temperature is  $-6.4^{\circ}\text{C}$  and annual precipitation is 328 mm.

### **Subhumid High Boreal**

This region encompasses five sites (sites 4, 5, 6, 8, and 11) but generally summers are cool with a growing season of approximately 5 months. Mean annual

temperatures are around  $-5^{\circ}\text{C}$  and average precipitation ranges from 300 to 500 mm.

**Table 2.1** Physical characteristics of the study areas.

Site	Ecoclimatic Region <sup>1</sup>	Permafrost Zone <sup>2</sup>	Soil Types <sup>3</sup>	Vegetation Zone <sup>4</sup>	Wetland % <sup>5</sup>
1, 2	High Subarctic	Continuous	Cryic Regosol Cryic Fibrisol	Forest-Tundra	1-4
3	Low Subarctic	Widespread	Eutric Brunisol	Northwestern Transition	3-4
4, 5	Subhumid High Boreal	Widespread	Cumulic Regosol	Upper Mackenzie	1 (site4), 23 (site5)
6	Subhumid High Boreal	Widespread	Eutric Brunisol Cryic Fibrisol	Northwestern Transition	23
7	Subhumid Mid-Boreal	Sporadic	Cryic Fibrisol Orthic Gray Luvisol	Hay River	78
8	Subhumid High Boreal	Sporadic	Cryic Fibrisol Orthic Gray Luvisol	Lower Foothills	28
9, 10	Boreal Southern Cordilleran	Sporadic	Orthic Gray Luvisol, Cryic Fibrisol	Lower Foothills	14-20
11, 12, 13	Subhumid High Boreal (11) Subhumid Mid-Boreal (12, 13)	Sporadic	Orthic Humo-Ferric Podzol, Cumulic Regosol (site 11), Fibrisol Rockland	Upper Mackenzie, Northern Coniferous (sites 12 and 13)	6-8

1. Ecoregions Working Group, 1989

2. Harris, 1986

3. Clayton *et al*, 1977

4. Rowe, 1972

5. National Atlas of Canada, 1973

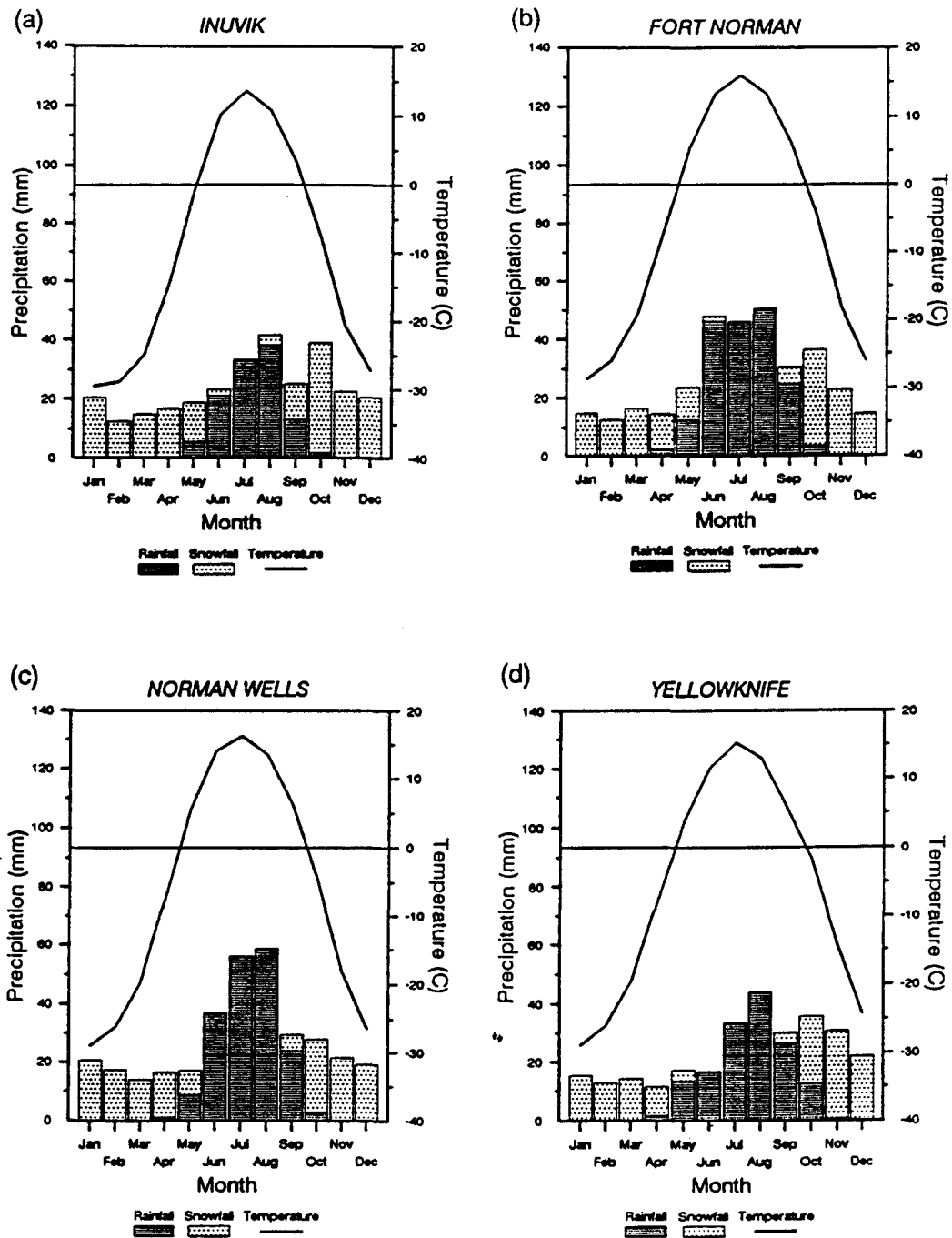


Figure 2.2 Climate normals (from Environment Canada, 1982).



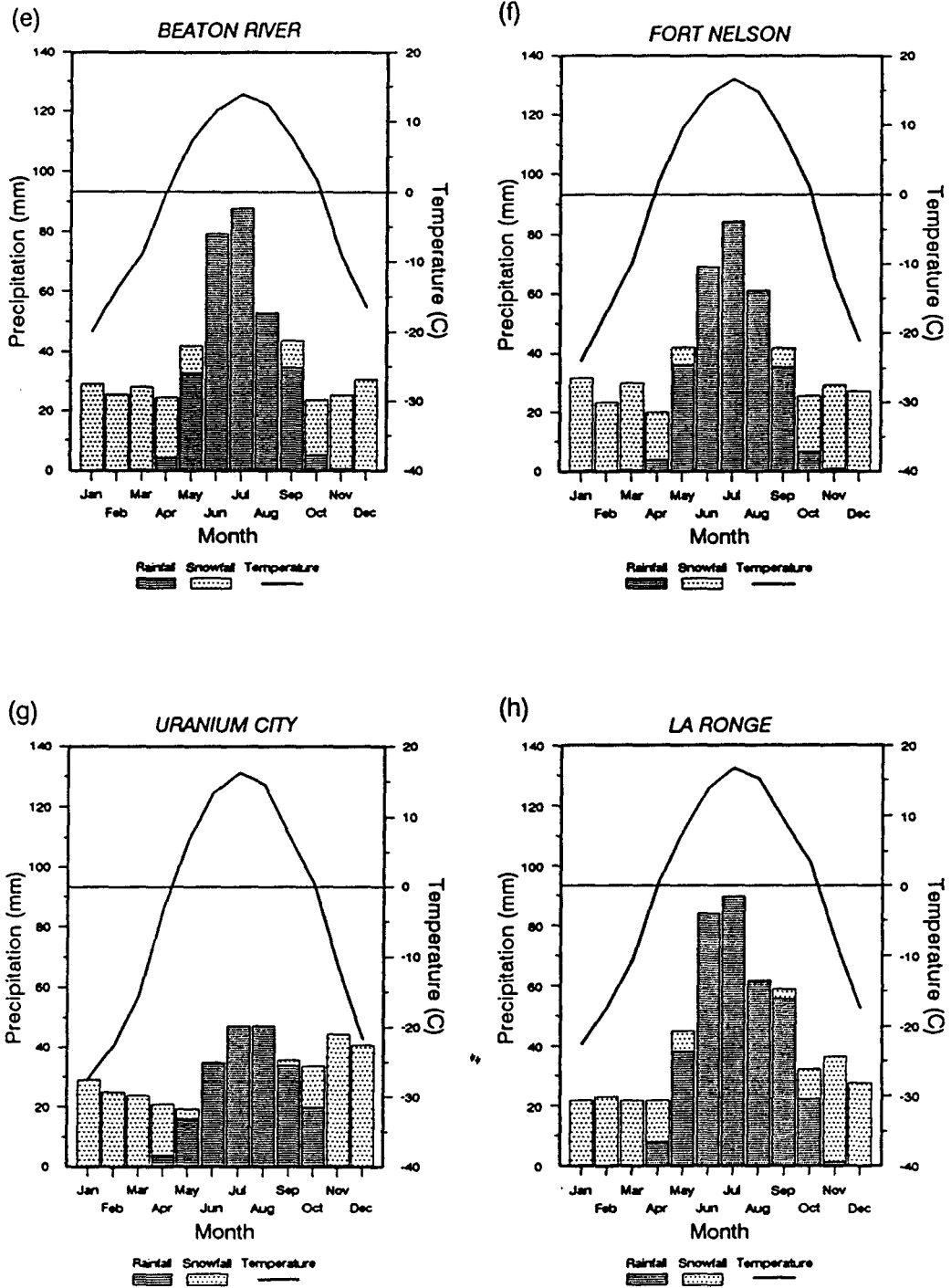


Figure 2.2 Climate normals (from Environment Canada, 1982).

The sites are some distance apart which is reflected in small variances in typical climatic conditions: site 4 and 5 are near the Fort Norman climate station (Figure 2.2c); site 6 in the Horn Plateau and site 8 in the Caribou Mountains may be typified by Yellowknife (Figure 2.2d); site 11 is near Uranium City (Figure 2.2e).

### **Subhumid Mid-Boreal**

The summers in this region are relatively warm and moist with a growing season longer than five months. Mean annual temperature is approximately  $-0.6^{\circ}\text{C}$ . Annual precipitation is higher, ranging from 400 to 460 mm. Sites 7, 12, and 13 are found in this zone though they are located in different areas of western Canada; site 7 is located in northeast British Columbia near Fort Nelson (Figure 2.2f), and sites 12 and 13 are within northern Saskatchewan near Lac La Ronge (Figure 2.2g).

### **Boreal Southern Cordilleran**

This is a transition zone between the Boreal and Cordilleran ecoclimatic zones. Temperatures are slightly cooler in the summer compared to the Mid-Boreal zone, with higher annual precipitation ranging from 400 to 600 mm. Winters are also cold here but are often moderated by chinook winds with a mean annual temperature of approximately  $2.6^{\circ}\text{C}$ . Sites 9 and 10 are located in this area as is the Beaton River climate station (Figure 2.2h).

### **2.3 Soils and Surface Conditions**

Sites 1 and 2 are located within the zone of continuous permafrost, while sites 3 to 6 are in the zone of widespread permafrost and sites 7 through 13 are found within the zone of sporadic permafrost (Harris, 1986; Heigenbottom, 1984). Soils, in general, are highly diverse and within the area of each site soil types vary. Broad classifications of the area around the sites are available from Clayton *et al* (1977) that indicate the general differences (Table 2.1).

#### **Cryic Regosol**

In the area of sites 1 and 2 these soils dominate. These shallow soils are well to imperfectly drained and may have a weakly developed organic-rich mineral horizon. They are characterized by considerable cryoturbation in the active layer. Soil textures are variable reflecting the diverse glacial and fluvial parent materials. Approximately 1 to 4% of the surface area around these sites are wetland.

#### **Cryic Fibrisol**

These soils are generally described as muskeg and are prominent in the area of sites 7 and 8, and of secondary around sites 1, 2, 6, 9 and 10. Because of their high porosity and high water holding capacities, these soils are prone to contain ice lenses which may persist late into the growing season. Soil texture is commonly clayey or loamy and surface horizons are not calcareous. Approximately 78% and 28% of the area around site 7 and 8, respectively, is wetland.

### **Eutric Brunisol**

These soils are also classified as Brown Wooded soils and are dominant in the area of sites 3 and 6. These mainly well-drained soils developed in a Subarctic environment with both tundra and forest vegetation and have a thin organic-rich mineral layer overlying a prominent brown B horizon. In this area the soils are often sandy and moderately calcareous due to the occurrence of glaciofluvial deposits and alluvium. Areas of rockland are also present. The surface area of wetland is approximately 3-4% for site 3 and 23% around site 6.

### **Cumulic Regosol**

Soils along the Mackenzie and Peace Rivers, in the area of sites 4, 5 and 11, are mainly Cumulic Regosols. These soils typically occur within alluvial floodplains and often have buried humus layers. Soils are loamy and moderately calcareous on parent materials of glacial diamict, glaciofluvial sediments and alluvium. The soils are well-drained although significant poorly-drained sites are present. Surface conditions differ slightly around site 11 as significant bare rock outcrops and sandy glaciofluvial deposits occur. The area around site 5 is up to 23% wetland, for site 4 only 1% and for site 11, 15% of the area is wetland.

### **Orthic Gray Luvisol**

These soils are important in the area of sites 9 and 10 and are of secondary importance in the areas of sites 7 and 8. These soils form under boreal forest vegetation, are weakly acidic and have surface layers of slowly decomposing leaf litter

with only thin organic-rich mineral horizons. Around sites 9 and 10 wetland composes between 14 and 20% of the surface area.

### **Orthic Humo-Ferric Podzol**

These soils, common around sites 12 and 13 and are a minor component around site 11, are characterized by their podzolic B horizon which is normally enriched in iron and organic material and perhaps aluminium. These soils are primarily well-drained and coarse textured, largely developed on stony and sandy glaciofluvial deposits. Bedrock outcrops are also prominent. In the area of sites 12 and 13, up to 6-8% is wetland.

### **Fibrisol Rockland**

Soils of secondary importance in the vicinity of sites 11, 12, and 13, this type is defined as Fibrisols overlying bedrock which is usually not more than 10 cm below the surface.

## **2.4 Modern Vegetation**

All of the sites in this study occur within the western Canadian Boreal Forest (Figure 2.3). Sites 1, 2, 3, and 6 are located in the Forest and Barren zone (Rowe, 1972) with the dominant trees being *Picea glauca* (white spruce), *Picea mariana* (black spruce), and *Larix laricina* (tamarack). The remaining sites are found within the Predominantly Forest zone (Rowe, 1972) which includes *Picea glauca*, *Picea mariana*, *Abies balsamea* (balsam fir), *Pinus banksiana* (jack pine), *Pinus contorta*

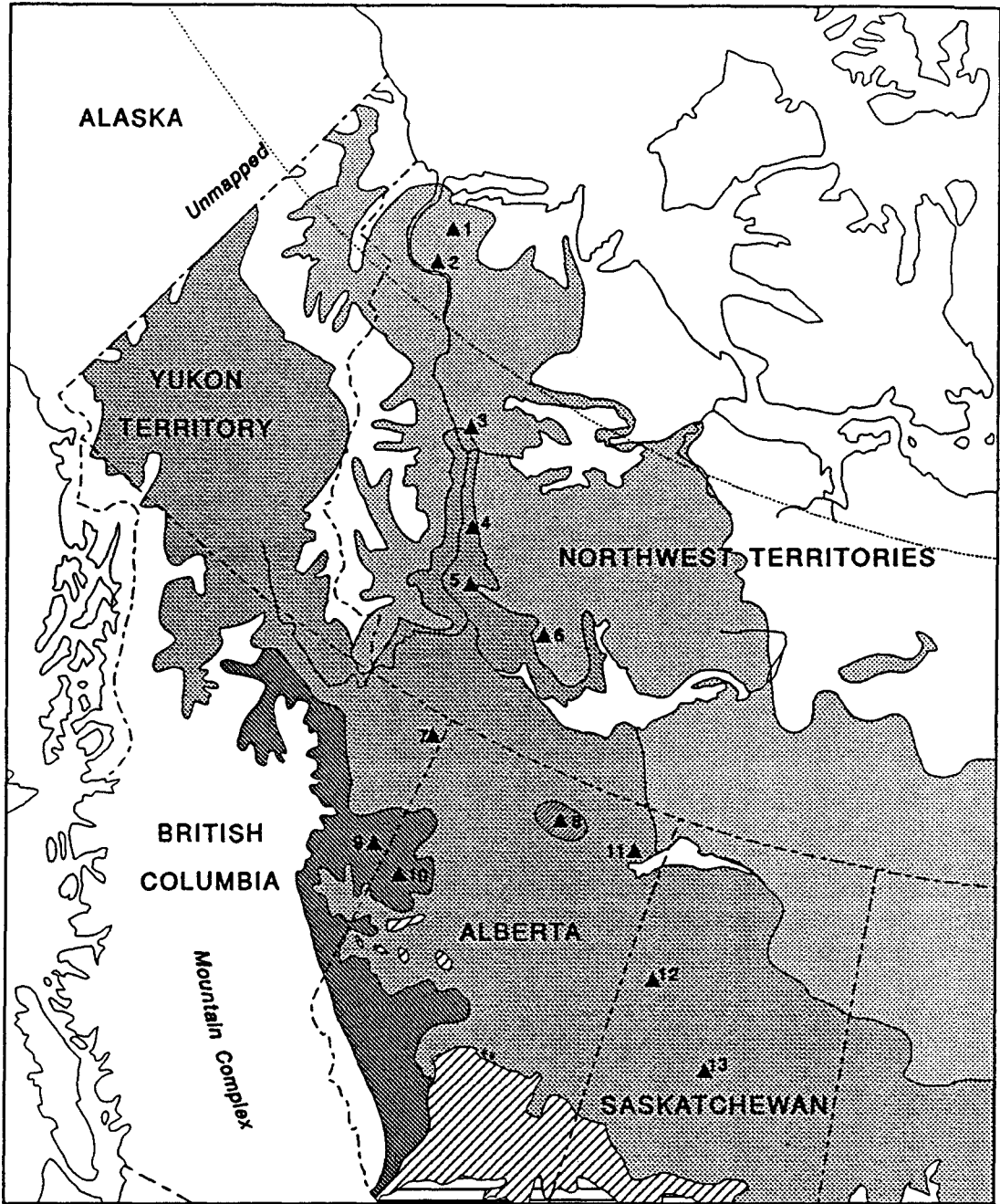
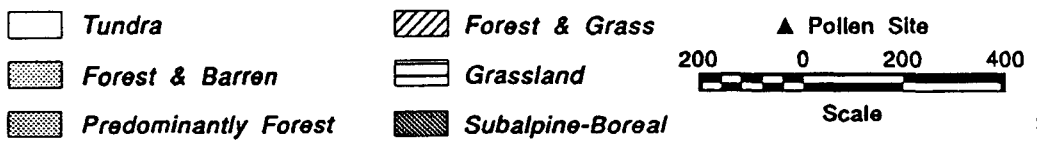


Figure 2.3. Vegetation Zones (from Rowe, 1972)



(lodgepole pine), *Betula papyrifera* (paper birch), and *Populus tremuloides* (trembling aspen). In the north, site 1 is quite close to the Tundra zone while to the southwest of sites 9 and 10, disjunct grasslands and parklands are present (Figure 2.4).

Further subdivisions are needed to classify the variations in the botanical composition that exist within the boreal forest. The two northern sites (sites 1 and 2) are located within an area of transition between the boreal forest and the tundra, termed the Forest-Tundra (Rowe, 1972). Here the vegetation has characteristics of both zones; opens stands of small and occasionally stunted trees, and treeless areas of herbs, sedges, moss and lichen. Dry sites are dominated by open stands of white spruce particularly where the active layer is thick (Rowe, 1972), with ground cover of *Vaccinium vitis-idaea* (bog cranberry), *Arctostaphylos alpina* (alpine bearberry), *Betula glandulosa* (dwarf birch), moss and lichen. *Carex* spp. (sedges), *Eriophorum* spp. (cottongrass) and *Sphagnum* spp. (sphagnum, peat moss) occur on poorly drained sites with open stands of black spruce and tamarack. Along the rivers, *Populus balsamifera* (balsam poplar), white spruce, and paper birch are common (Ecoregions Working Group, 1989). In the northwest boreal forest, spruce may comprise of up to 99% of the arboreal vegetation, primarily because few tree species are able to survive in the area (Halliday and Brown, 1943). Work on black spruce in the vicinity of these two sites shows a decrease in tree volume and height northward from the area of site 2 (zone iv, Table 2.2) to site 1 (zone ii, Table 2.2; Black and Bliss, 1980).

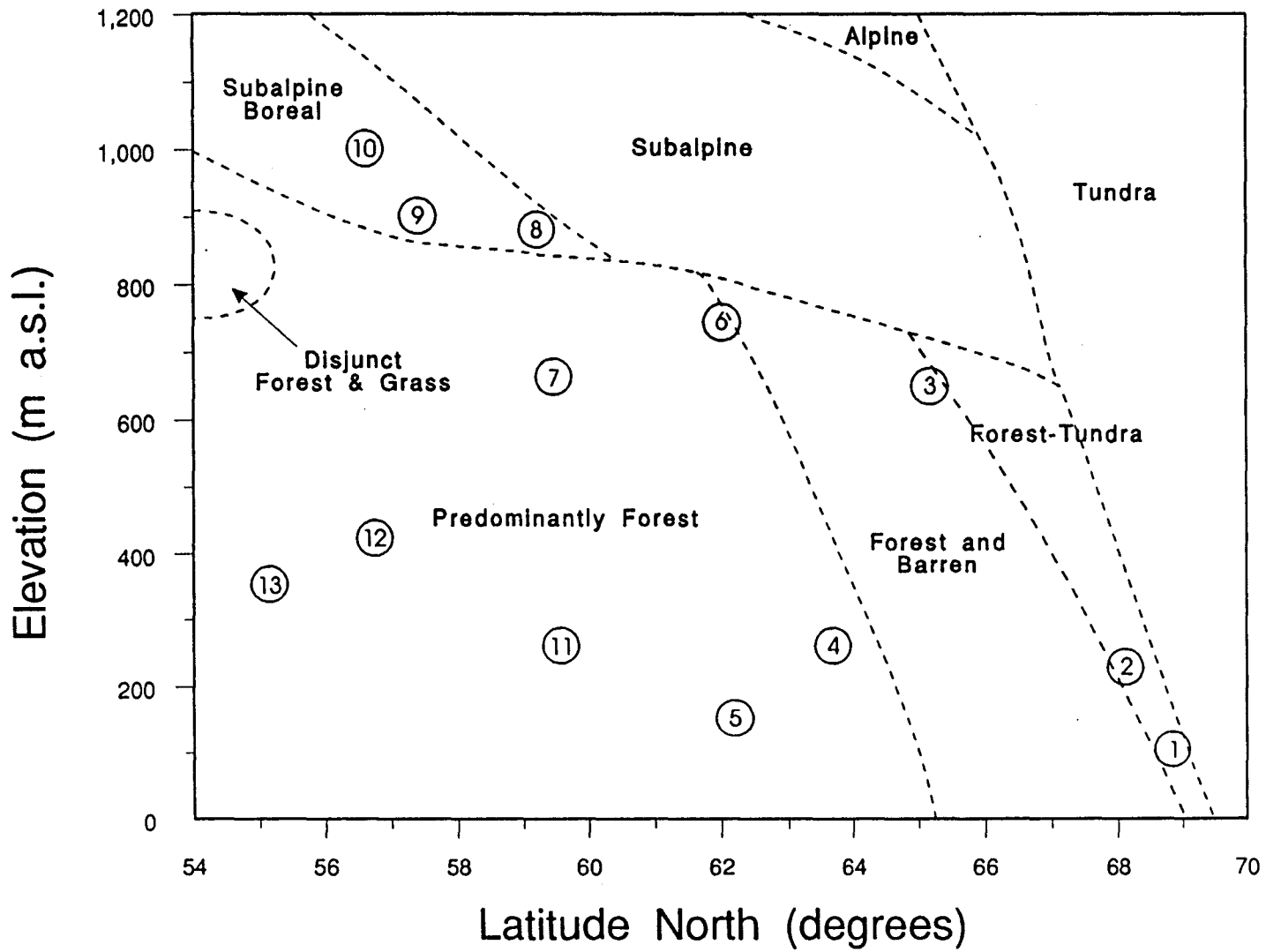


Figure 2.4. Elevational and latitudinal vegetation zones. Numbered circles are site locations (from Rowe, 1972; Ecoregions Working Group, 1989).



**Table 2.2.** Stand volumes and dominant tree heights for *Picea mariana* sites across the eastern Mackenzie Delta area (Black and Bliss, 1980). Site 1 is located within Region II, and site 2 is found within Region IV.

Location	Age (yr)	Volume (m <sup>3</sup> /ha)	Height (m)
Region I Northeast Mackenzie Delta	50	.21	0.8
	100	2.18	2.7
	150	3.94	4.2
Region II Southeast of Inuvik	50	.47	1.5
	100	4.81	3.4
	150	8.69	4.9
Region III South of region II, east of Mackenzie Delta	50	1.47	2.5
	100	15.07	4.4
	150	27.25	5.9
Region IV Southeast area of Mackenzie Delta	50	3.36	3.2
	100	34.32	5.1
	150	62.07	6.6

Site 3 occurs within the Northwestern Transition (Rowe, 1972), where trees are larger and grow more densely, though open stands of trees are still found. In poorly drained locations black spruce, *Ledum groenlandicum* (Labrador tea), *Vaccinium* spp. (blueberry), *Andromeda polifolia* (bog rosemary), and *Rubus chamaemorus* (cloudberry) dominate. On recently burned sites paper birch and/or black spruce are found. White spruce and paper birch, with a discontinuous understorey of bearberry, bog cranberry, dwarf birch, lichen and moss, are common.

Trembling aspen is also found in protected sites (Ecoregion Working Group, 1989). Towards the southern part of this area, jack pine can be found on sandy, upland soils (Rowe, 1972). More than 60% of the arboreal vegetation in the area is spruce (Halliday and Brown, 1943).

Sites 4, 5, and 11 occur within the Upper Mackenzie subdivision (Rowe, 1972). Floodplain alluvium along the Mackenzie and Slave Rivers support white spruce and balsam poplar. Balsam fir grows on well-drained sites. Jack pine and trembling aspen occur on sandy soils in the upland areas above the floodplains. In poorly-drained sites black spruce and tamarack dominate with muskeg often bordering the floodplains (Ecoregions Working Group, 1989; Rowe, 1972). In the area of sites 4 and 5 spruce abundance is greater than 60% and in the area of site 11 spruce abundance ranges from 31 to 60%. Pine in this subdivision ranges from as little as 1% to 20% (Halliday and Brown, 1943).

Site 7 occurs within the Hay River subdivision (Rowe, 1972). Black spruce is the dominant tree on the numerous boggy, poorly-drained areas with Labrador tea, blueberry, bog rosemary, and cloudberry ground cover. White spruce and trembling aspen are less common in this area (Ecoregions Working Group, 1989). Jack pine decreases in abundance to the west of the area where lodgepole pine becomes more common (Rowe, 1972). Spruce abundance in the area is greater than 60% with pine ranging from 1 to 20% (Halliday and Brown, 1943).

Sites 8, 9, and 10 are located within the Lower Foothills subdivision (Rowe,

1972) which is an area of transition between the Subalpine and the Boreal Forest zones. In areas affected by fire, lodgepole pine dominates with trembling aspen and balsam poplar and diverse herb and shrub understories. In older stands white spruce is prominent with some black spruce and scattered tamarack in poorly-drained sites. Paper birch has a scattered occurrence in well-drained sites. Balsam fir and *Abies lasiocarpa* (alpine fir) are common in high elevation sites near the Subalpine zone. Jack pine, black spruce, and occasionally paper birch are found on drier, fire-prone sites (Rowe, 1972). In this subdivision spruce abundance is greater than 60% and pine varies from 21 to 40% of the arboreal vegetation (Halliday and Brown, 1943).

Sites 12 and 13 occur within the Northern Coniferous subdivision (Rowe, 1972). Poorly drained depressions within areas of hummocky moraine support black spruce and muskeg vegetation with some tamarack. Drier upland sites and river valleys are dominated by white spruce, trembling aspen, and balsam poplar. Jack pine dominates areas disturbed by fire (Ecoregion Working Group, 1989; Rowe, 1972) and the abundant coarse-grained, sandy substrates that are characteristic of the outer edges of the Canadian Shield (Richards and Fung, 1969). Understories include blueberry, *Arctostaphylos* spp. (bearberry), Labrador tea, feather mosses, lichens, *Alnus* spp. (alder) and *Salix* spp. (shrub willow; Ecoregions Working Group, 1989). The spruce component of the tree vegetation ranges from 31 to 60% and pine reaches 21 to 40% (Halliday and Brown, 1943).

## **2.5 Postglacial Physical Environmental Change**

The Wisconsin ice sheets reached their maximum extent in the study region around 18,000 BP (Dyke and Prest, 1987; Trenhaile, 1990). Strong anticyclonic circulation occurred around the Laurentide ice sheet resulting in strong, dry easterly winds along the southern edge of the ice. Temperatures were very cold near the ice but sharply increased away from the glaciers (COHMAP, 1988). Between 15,000 BP and 9,000 BP the earth-sun distance decreased in the northern summer, while the axial tilt of the earth increased resulting in an increase in summer solar radiation in the northern hemisphere, an increase in seasonality and an increase in land surface summer temperatures (COHMAP, 1988; Ritchie, 1987; Trenhaile, 1990). Glacial retreat began between 14,000 and 13,000 BP separating the Cordilleran and Laurentide ice sheets. After 13,000 BP retreat was much more rapid and by 12,000 BP there was a decrease in the anticyclonic circulation and an increase in westerlies. Between 11,000 and 10,000 BP warm, arid conditions existed in southern Alberta, though the period between 10,000 and 9,000 BP was relatively moist (MacDonald, 1989). By 10,000 BP the Cordilleran glaciers were not much larger than exists today (Trenhaile, 1990).

Associated with glacial retreat was the formation of proglacial lakes. Glacial Lake Agassiz began to form approximately 11,700 years ago due to the trapping of meltwater between the Laurentide ice and the Manitoba Escarpment. Over time it varied in size and disappeared between 8,000 and 7,800 BP when the Laurentide ice

sheet had retreated to the northeast allowing the proglacial waters to drain into Hudson Bay (Trenhaile, 1990) Lake McConnell extended from Great Bear Lake, through the Great Slave Lake Basin and into the Athabasca and Peace River Valleys. It existed between approximately 11,000 and 9,500 BP (Fulton, 1989).

By 9,000 BP summer temperatures were approximately 2° to 4°C higher than present (COHMAP, 1988). Solar radiation over the Northern Hemisphere was approximately 8% higher in the summer and 8% lower in the winter than at present (COHMAP, 1988). Easterly winds were replaced by westerlies due to the retreat of the Laurentide ice sheet. From 9,000 until 6,000 BP conditions were warm and arid and the ratio of precipitation to evaporation was low (COHMAP, 1988; Kutzbach and Guetter, 1986). Maximum summer aridity and temperatures occurred between approximately 8,000 and 7,000 BP (MacDonald, 1987a,b; Ritchie, 1987). After 6,000 BP summer insolation decreased to present (COHMAP, 1988), and by approximately 4,000 BP cooler and moister conditions similar to modern conditions began (Ritchie, 1987).

During the Holocene, soils have developed from the mineral deposits left by the receding glaciers. Changes in water-holding capacities and organic components were important. Increases in humus content occurred particularly between 8,000 and 4,000 BP with the regional development of muskeg (MacDonald, 1987a,b; Ritchie, 1987). Changes in fire frequency and intensity have also occurred in the postglacial. Fire occurrence may have peaked in the mid-Holocene between 8,000, and 6,000 BP,

a time of high aridity and when full boreal forest conditions existed providing sufficient fuel (MacDonald, 1987a,b; Ritchie, 1987).

## 2.6 Postglacial Vegetation Development

Synthetic reconstructions of postglacial regional vegetation in the western interior of Canada have been presented by MacDonald (1987a,b) and Ritchie (1987). Based on these sources, this section reviews changes in vegetation. A general succession sequence of herb tundra - shrub tundra (shrub birch) - poplar - spruce, occurs throughout the region. However, the spatial and temporal patterns of vegetation change were not uniform across the region due to the form of deglaciation and latitudinal range covered.

The earliest pollen levels in most sequences are characterized by high nonarboreal pollen including *Artemesia* (wormwood), Gramineae (grass family), Cyperaceae (sedge family), diverse herbs and *Salix* (willow). The density of the initial vegetation was likely very low as evident from the low levels of pollen influx and low organic content of the lake sediments suggesting open mineral soils. This pollen zone is followed by an increase in *Betula* pollen suggesting that shrub birch dominated the vegetation in the northern Mackenzie basin by 10,000 BP. At this time there were decreases in *Artemesia*, Gramineae, and many herbs, with increases in Cyperaceae and *Salix* pollen influx. It is suggested that shrub birch dominated the upland areas while sedges and willow grew in wet, low-lying areas. The vegetation was different

from any modern assemblages since the pollen influx is higher than that for modern tundra and lower than modern grassland. There is some evidence that various herbs and shrub birch had persisted in the ice-free areas in Beringia and may have spread into the study area from both the north and the south.

*Populus* (poplar) pollen increases following the shrub tundra zone. The rise in poplar occurred prior to, or in conjunction with, spruce pollen increases depending on the area. Spruce pollen abundance increased between 10,000 and 8,500 BP. Spruce spread very quickly throughout the basin and this was accompanied by a decrease in the abundance of shrub birch and poplar. They may have been restricted to dwindling open sites as closed spruce forests developed. After approximately 8,000 BP, *Sphagnum* (sphagnum), *Myrica* (tupelo), and *Ericales* (heath) increased and reached modern levels by 4,000 BP indicating increased muskeg development.

Between 9,000 and 7,000 BP tree birch, pine, balsam fir and tamarack pollen appear. *Pinus contorta* (lodgepole pine) reached the southwest part of the region possibly as early as 10,000 BP and reached southwest N.W.T. by 5,600 BP. *Pinus banksiana* (jack pine) increased in the southeast part of the region around 7,000 BP and reached the central Mackenzie River Basin by 2,400 BP. *Alnus* (alder) pollen occurred at low levels throughout the area in the early Holocene though did not reach modern levels until approximately 6,500 BP. All tree taxa appear to originate from populations to the south of the region and by the middle Holocene (~ 6,000 to 5,000 BP) all of the modern boreal taxa had arrived.

## CHAPTER III

### AUTECOLOGY

#### 3.0 *Picea glauca*

*Picea glauca* (white spruce) has a range covering much of Canada and the northern part of the United States (Figure 3.1). Its southern limits reach into northeastern New York and Maine, central Ontario, Minnesota and Wisconsin. In the Prairie provinces white spruce is found just south of Lake Winnipeg in Manitoba, and through central Saskatchewan and Alberta. White spruce extends into the grassland regions along river valleys. It occurs in the Rocky Mountains as far south as Idaho with outlying populations in South Dakota, Montana, and Wyoming. In British Columbia it reaches just east of the main range of the coastal mountains. In the north, white spruce extends throughout the central part of Alaska, the Yukon, and the Districts of Mackenzie and Keewatin, N.W.T. In these areas, white spruce extends into the forest-tundra along river valleys. The northern limit dips south from the Mackenzie Delta along the northern shores of Great Bear and Great Slave Lakes reaching Hudson Bay near the Churchill River. The limit then cuts northeast across Quebec to the eastern shores of Ungava Bay and then east into Labrador where it forms the treeline with *Picea mariana* (black spruce) and *Larix laricina* (tamarack) (Fowells, 1965; Hosie, 1979; Ritchie, 1987; Payette, 1983). Generally, white spruce



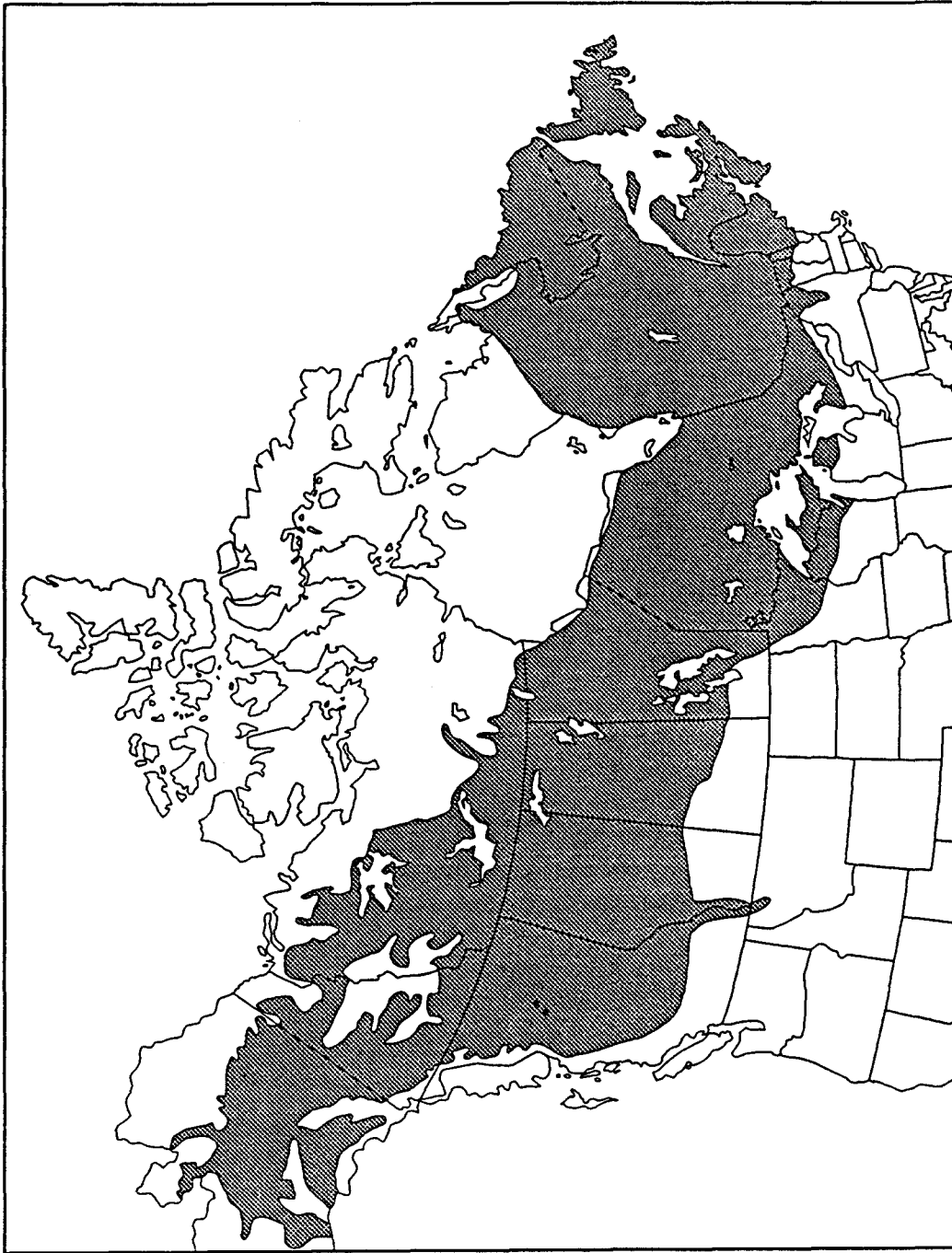


Figure 3.1. The range of white spruce (Fowells, 1965).

increases in importance from the east to the west (Rowe, 1970).

Corresponding to its wide distribution, white spruce grows in climatic conditions ranging from wet insular in eastern Canada, to semi-arid continental in the west and northwest (Fowells, 1965). Precipitation within its range varies from 1225 mm in Nova Scotia and Newfoundland to 245 mm in the N.W.T., Yukon, and Alaska. However, conditions are most severe in the southern parts of its range in Alberta, Saskatchewan, and Manitoba where the combination of low precipitation (370 to 490 mm) and high temperatures (average July maximum temperature 24° C) produce high levels of evapotranspiration (Fowells, 1965). Mean daily July temperatures range from 21° C in the southeast to 13° C in the central and northern areas. Mean January temperatures in the northwest fall to -30° C. The growing season decreases from 160 days in the south to 20-25 days in the north; on a broad scale white spruce generally grows south of the 60 day growing season line (Fowells, 1965)

White spruce grows on a variety of substrates, occupying glacial, lacustrine, marine, alluvial, fluvial, or aeolian deposits. White spruce exists on upland sites, slopes and river plains, preferring moderate to well-drained sites. It occurs on grey wooded soils, brown forest soils, and podzolized soils and is more exacting in its nutrient requirements than other spruce taxa or pine (Fowells, 1965; Rowe, 1970). White spruce is less tolerant of highly acidic soils than black spruce (Ritchie, 1987). It is well adapted to growing in the cold soils within the permafrost zones. Roots are often shallow, particularly if the water table is high, but are able to grow deeper in

warmer, light-textured soils (Spurr and Barnes, 1979)

White spruce on average reaches 25 m to 37 m in height and 0.6 m to 1.2 m in diameter (Hosie, 1979). However, average heights of 56 m have been measured in the Peace River plains (Fowells, 1965). Many trees have been recorded older than 300 years and 350 years, with individuals reaching 400-500 years in Alaska and the Mackenzie Delta (Critchfield, 1985). White spruce can outlive both black spruce and jack pine (Ritchie, 1987).

White spruce is shade tolerant (Hosie, 1979), but it can act as either: an early invader, as on recent fluvial deposits (Rowe, 1970) or; as a late successional species replacing *Pinus* (pine), *Populus tremuloides* (trembling aspen) and, at times, black spruce (Fowells, 1965; Rowe, 1970). In southern and central areas, faced with competition from hardwoods, white spruce experiences decreased growth, but can remain as an understorey tree until released by the death of the hardwoods (Fowells, 1965). In northern areas white spruce may grow in pure stands, but it is more often associated with trees such as *Betula* (birch), black spruce, *Populus* (poplar), and trembling aspen. It occurs with *Pinus contorta* (lodgepole pine), less often with *Pinus banksiana* (jack pine), and rarely with tamarack (Fowells, 1965).

Reproductive maturity occurs around 45-60 years of age, with peak seed production at approximately 60 years. In more northern locations seed and pollen production may be delayed and infrequent. Under favourable conditions, good seed crops occur every 2-6 years with moderate crops in the intervening years (Fowells,

1965). Seed is scattered by wind in autumn, but some may be held in the cone until the following spring and summer (Rowe, 1970). Seed dispersal measurements estimate an average dispersal distance of 100 m, but with high winds dispersal distances can be greater than 300 m (Fowells, 1965). Vegetative reproduction by layering does occur in northern regions but is rare (Ritchie, 1987).

The moisture condition of the seedbed is the most important factor affecting germination and early seedling survival (Fowells, 1965; Rowe, 1970), though experiments have indicated that white spruce seedlings are more drought resistant than either black spruce or jack pine (Ritchie, 1987). Seedbeds of thick humus, leaf litter and moss can easily dry out to below seedling root depths particularly in dry years. Best survival and growth occurs on surfaces with a <sup>high</sup> nutrient content, such as on mineral soils and on decayed wood of old tree trunks and stumps (Fowells, 1965; Rowe, 1970). White spruce does well after fires have removed litter and perennials, which compete against the seedlings for light and moisture and which produce leaf litter that may crush the seedlings (Rowe, 1970; Fowells, 1965).

### 3.1 *Picea mariana*

The range of *Picea mariana* (black spruce) is similar to that of white spruce, though it does not extend so far to the southwest in mountainous regions and it extends as far north in the west (Figure 3.2). Black spruce forms the latitudinal treeline in northern and central Canada and is joined by white spruce and tamarack



Figure 3.2. The range of black spruce (Fowells, 1965).

at the treeline in Labrador (Payette, 1983; Fowells, 1965). It occurs beyond treeline in krummholtz form (Payette, 1983) and is one of the most abundant conifers in Canada (Fowells, 1965).

Climate across the range of black spruce varies from dry continental in the northwest to the wet maritime conditions of Newfoundland (Ritchie, 1987; Fowells, 1965). Maximum daily July temperatures range from 21<sup>o</sup>-24<sup>o</sup> C in the central part of its range, to 27<sup>o</sup> C in the southeast and decrease to 16<sup>o</sup> C in the north. Mean January temperatures can dip to -30<sup>o</sup> C in the far northwest (Fowells, 1965). Annual precipitation varies from 1150-1400 mm in eastern Quebec and Labrador to less than 250 mm in the northwest. In the latter areas low temperatures, reduced evapotranspiration, snowmelt and thawing soil ice combine to produce a moisture supply that supports spruce forests (Fowells, 1965).

Black spruce is able to grow in the cold soils of permafrost zones (Spurr and Barnes, 1973) and tolerates areas where the active layer is less than 0.25 m deep (Ritchie, 1987). In the south, black spruce most often limited to peat bogs and organic soils in lowlands, but in the central and northern parts of its range it also grows on clayey diamicts and glacio-lacustrine clay plains (Ritchie, 1987; Fowells, 1965). In these areas, black spruce often grows in pure stands but on sandy loams, loams, and gravelly soils it grows in mixed stands (Fowells, 1965). Black spruce can tolerate acidic soil conditions which occur where sphagnum predominates. As black spruce is abundant in poorly-drained and boggy areas, local relief becomes important

in determining abundance, as relief affects drainage conditions and bog formation (Fowells, 1965). Compared to white spruce, black spruce is more tolerant of low nutrient levels; decaying mosses provide suitable nutrients for black spruce growth, particularly nitrogen (Robinson, 1974). In boggy areas or sites with thin soils, its roots are shallow and branch out in pockets of nutrients or moisture. In sites with a sandy soils the roots are deeper (Robinson, 1974).

The average height of black spruce is 10 to 15 m and 15 to 25 cm in diameter, and it is generally smaller than white spruce (Hosie, 1979; Rowe, 1970). In favourable areas, it can reach a height of 30 m; in northern areas there is often a decrease in size, with black spruce forming krummholtz in the shrub tundra (Hosie, 1979; Payette, 1983; Black and Bliss, 1980). Commonly it reaches ages between 100 and 200 years though there are records of trees > 250 years of age (Fowells, 1965).

Black spruce becomes sexually mature at an earlier age than white spruce (Rowe, 1970), producing seed by 20 years of age (Robinson, 1974). However, in northern areas seed production is often delayed; at Inuvik seed production is delayed 15-20 years (Black and Bliss, 1980). Heavy crops of seed are produced on average every 4 years (Fowells, 1965). The semi-serotinous cones partially open in the fall releasing some seed, but most of the seed is retained within the cone and released gradually. Most of the seed is released within 4 years, but some viable seed has been found in 15 year old cones (Fowells, 1965; Hosie, 1979). High temperatures, such as those encountered with fire, promote cone opening and seed release. Cones are

grown in dense clusters and the seed is usually uninjured by fire unless directly burned. The result is a heavy postfire seedfall. Studies have shown that seedfall is greatest near the trunk and is sharply reduced with distance. Levels of seedfall at 15 and 30 metres from the main stem are only 30 and 6%, respectively, of the maximum. Very little seed is transported up to 90 m from the stand (Fowells, 1965).

Fires also prepare suitable seedbeds for seed germination. Black spruce seeds germinate well on mineral soil and burned duff, with decreased germination and survival on unburned duff. Seedlings have short roots; in its first year the root is no longer than 5 cm and are susceptible to damage during drought conditions. Deep litter often dries out and limits the ability of the seedling to reach the soil layer and a reliable water supply (Fowells, 1965). Fire also removes competitors and opens the canopy. Black spruce is shade intolerant; less tolerant of shade than white spruce but more tolerant than jack pine (Robinson, 1974). Light burns may not be favourable for black spruce regeneration as the humus layer may not be fully removed. Certain forest plants, such as aspen, may be able to regenerate from parts in the organic horizon undisturbed by light burns. Spruce trees produce deep accumulations of material at their bases which become fuel for intense fires, thereby promoting conditions for regeneration (Rowe, 1970).

Because of its semi-serotinous cones, shade intolerance, short reproductive cycles, and need for the removal of the organic layer for germination and growth, black spruce is classified as moderately fire-dependant or fire-tolerant. In fire-prone



sites black spruce often replaces white spruce (Rowe, 1970). Black spruce will also succeed jack and lodgepole pines if the fire cycle is sufficiently long (Fowells, 1965). In bog and fen, tamarack is the first tree to invade, but is often succeeded by black spruce (Black and Bliss, 1980; Fowells, 1965).

In addition to sexual reproduction, black spruce is able to reproduce vegetatively by layering. Lower branches may be covered by mosses or litter, develop adventitious roots, and grow to form new trees (Hosie, 1979). This form of reproduction is more common in poor sites such as in swamps and bogs and in far northern regions where seed production and germination are limited (Fowells, 1965; Black and Bliss, 1980).

### **3.3 *Pinus banksiana***

The modern range of *Pinus banksiana* (jack pine) is more restricted than that of spruce (Figure 3.3). Its southern limit runs from Nova Scotia through central Maine, Michigan, Wisconsin, and Minnesota, then swings into Manitoba south of Lake Winnipeg, and into central Saskatchewan and Alberta. Its northern limit reaches up in the Mackenzie valley as far as Great Bear Lake, swings southeastward north of Great Slave Lake, down into northern Manitoba and Ontario. It reaches northward again on the eastern side of James Bay and crosses Quebec to the mouth of the St. Lawrence River (Fowells, 1965; Hosie, 1979). Its northwest limit may be controlled limited by the length of the growing season and mean annual degree-days

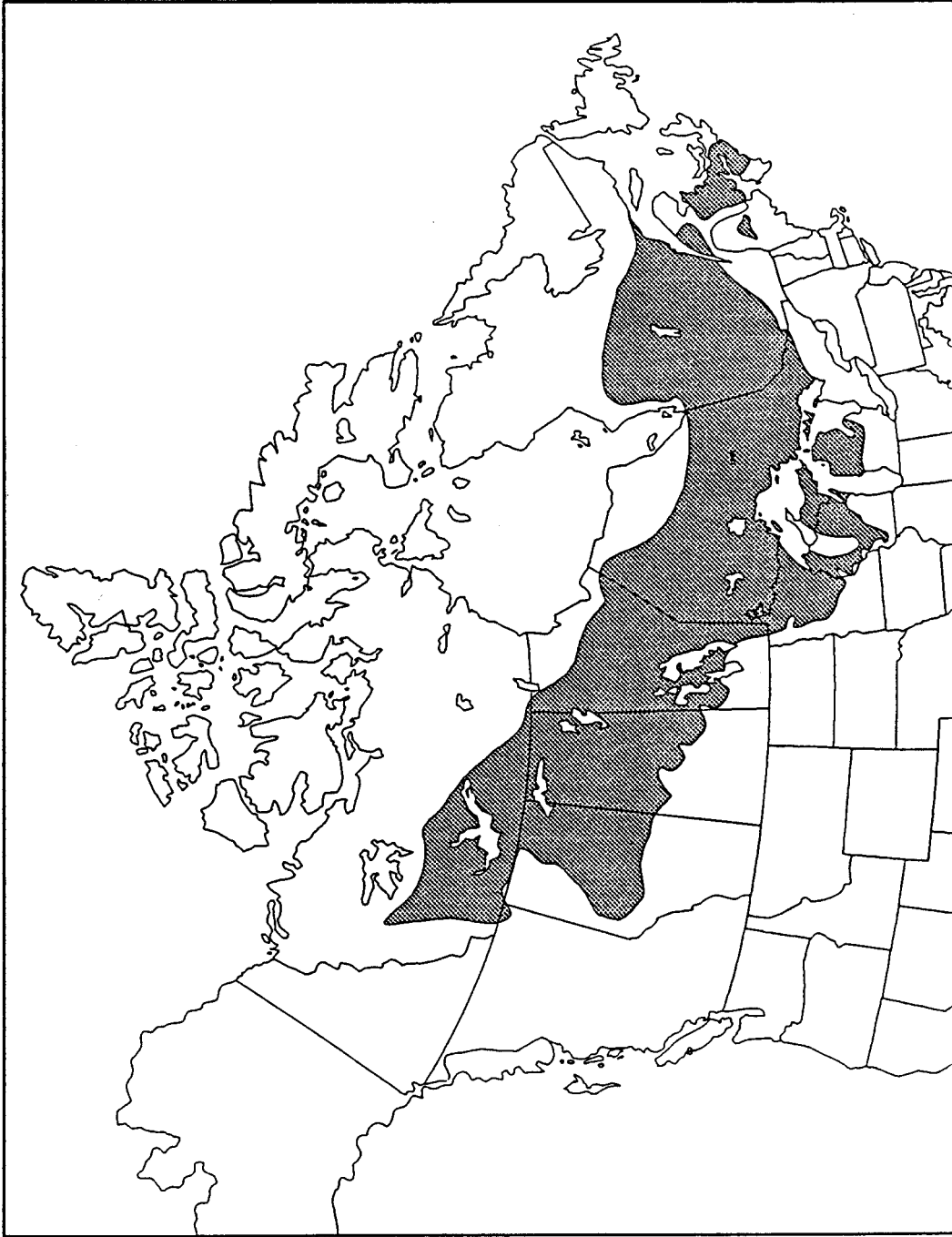


Figure 3.3. The range of jack pine (Fowells, 1965).

above 5°C. In Saskatchewan and Manitoba jack pine may be limited in the north by growing season temperatures but in the east it appears to be limited by its intolerance of deep snowfall. Its southern limits appear to be set by soil moisture and summer temperatures in the west, and in the east by the added stress of competition (Ritchie, 1987). It is commonly associated with trembling aspen, *Betula papyrifera* (paper birch), and black spruce, and sometimes with white spruce and *Populus balsamifera* (balsam poplar). In Alberta its range overlaps with lodgepole pine and there is some hybridization between the two species (Fowells, 1965; Hosie, 1979).

Jack pine grows mainly within zones of continental climate with cool summers, cold winters and variable precipitation. Mean annual temperatures vary from -5°C to 9.5°C, average January temperatures are as low as -28° C to -32° C in the northern part of the range, and average July temperatures range from 13° C to 22°C. The frost free period averages 50 to 180 days. Mean annual precipitation varies from 250 to 1400 mm, decreasing from the southeast to the northwest (Fowells, 1965).

Jack pine occurs mainly on level to rolling topography, on light sandy or gravelly soils with very good drainage and aeration. It can grow on loamy and clayey soils but it is usually outcompeted on these sites and becomes restricted to nutrient poor rocky upland sites and outcrops with thin soils. It can grow on calcareous soils but occurs more often on acidic soils. Jack pine does well on sites less favourable to other species (Fowells, 1965; Rudolph and Yeatman, 1982). It commonly grows on sands of glacial, fluvial or lacustrine origin (Fowells, 1965).

Jack pine averages 25 m in height and 20 to 30 cm in diameter (Hosie, 1979). It grows rapidly in the early stages; in the first 20 years it is one of the fastest growing conifers (Fowells, 1965). Seed production can begin as early as 5 to 10 years of age, though it peaks at 40 to 50 years of age. Good seed crops are produced every 3-4 years (Fowells, 1965). Jack pine has serotinous cones and the seeds are not released until high temperatures, such as those associated with fire, force open the cones. The degree of serotiny tends to vary with age and with latitude. Open cones are more common on trees 7 to 10 years old and in the southern parts of the range towards the Great Lakes region (Critchfield, 1985). The seeds are small and light and are easily dispersed. Transport can also occur over snow and ice and by water transport of the closed cones (Critchfield, 1985).

Jack pine is highly fire-dependant. Along with fire releasing its seeds, fire prepares a suitable seedbed by burning off the organic layer and leaving light duff or mineral soil which is favoured for seed germination (Rudolph and Yeatman, 1982; Fowells, 1965). Fire also eliminates competitors and opens the canopy for the shade intolerant jack pine to grow. Jack pine is more intolerant of shade than either white or black spruce (Fowells, 1965; Critchfield, 1985). In sites where the frequency of fire is high, jack pine dominates. Its storage of seed in cones, rapid growth, and early seed production combine to produce the potential for rapid population increase. With decreasing rates of fire, jack pine is replaced by other species including black and white spruce, paper birch and *Abies balsamea* (balsam fir). Jack pine will be

replaced by more competitive species on all sites except on the poorest and driest sites where it may form an edaphic climax (Fowells, 1965).

## CHAPTER IV

### METHODS

#### 4.0 Site Selection

The source area of pollen deposited in a lake may be described as local if the pollen originates from plants within approximately 20 m of the lake edge, extralocal if the pollen comes from plants located between approximately 20 to several hundred metres from the lake, and regional if the pollen is derived from plants at greater distances (Jacobson and Bradshaw, 1981). To study variations in the development of vegetation within the western interior of Canada, a series of sites with extra-local pollen records are needed. The characteristics of lakes that affect the measured pollen influx and in part determine the areal extent of the source pollen are: (i) the size of the lake, (ii) inflowing streams, (iii) the shape of the lake bottom, and (iv) water depth. Lake size influences the proportion of pollen derived from local, extra-local, and regional sources (Jacobson and Bradshaw, 1981). In the case of small to medium sized lakes (<20 ha, Bennett, 1985) most of the pollen within the sediments originates from local and extra-local sources (Jacobson and Bradshaw, 1981). Inflowing streams increase the regional component by transporting pollen long distances.

The morphometry of the lake affects the relationship between plant

abundance, pollen deposition, and the pollen accumulation rate (PAR). The pollen accumulation rate is calculated as the number of pollen grains  $\text{cm}^{-2} \text{yr}^{-1}$  and can vary with the sedimentation rate independent of absolute pollen deposition. Lehman (1975) suggests that in steep-sided, hyperboloid or lakes, sediment accumulation rates will vary as the basin is infilled, even though the amount of sediment deposited remains constant over time. This process, called sediment focusing, is due to the increase in depositional area (lake bottom) as the basin fills and results in erroneous PAR values.

Shallow lakes may experience extensive water circulation, producing differential deposition of pollen over the lake bottom. Light, small pollen grains may be carried and deposited more often in the downwind side of the lake. Shallow lakes that freeze to the bottom in winter may be prone to resuspension and redeposition of pollen. As a result, pollen records from sediment cores of shallow lakes may have under and over represented pollen types (Jacobson and Bradshaw, 1981).

Therefore to select sites that reflect the extra-local vegetation, the following characteristics should be satisfied: (i) small lake size (<20 ha), (ii) no inflowing streams, (iii) depth greater than maximum ice thickness, and (iv) gentle concave lake bottom profile.

#### **4.1 Site Characteristics**

The lakes selected were small to intermediate in size ranging from 3.5 to 20

**Table 4.1. Site Characteristics**

Site #	Site Name	Location	Latitude Longitude	Elevation (m a.s.l.)	Surface Area (ha)	Depth (m)	Core Length (m)
1	Twin Tamarack Lake	Campbell-Dolomite Uplands, N.W.T.	68° 18' N 133° 25' W	105	3.7	2.8	3.55
2	Sweet Little Lake	Mackenzie River Lowlands, N.W.T	67° 39' N 132° 01' W	230	6	6.2	3.96
3	Lac Meleze	Franklin Mountains N.W.T.	65° 13' N 126° 07' W	650	4	2.5	4.6
4	Gannet Lake	Mackenzie River Lowlands, N.W.T.	63° 35' N 123° 39' W	305	12	2.75	2.45
5	Rugged Lake	Mackenzie River Lowlands, Alberta	62° 15' N 122° 24' W	152	1	1.65	3.32
6	Lac Demain	Horn Plateau N.W.T.	62° 03' N 118° 42' W	745	5	1.5	2.2
7	Lac Ciel Blanc	Estho Escarpment B.C.	59° 31' N 120° 11' W	660	17	2	4.4
8	Wild Spear Lake	Caribou Mountains Alberta	59° 15' N 114° 09' W	880	16	2.5	3.2
9	Snowshoe Lake	Milligan Hills B.C.	57° 27' N 120° 40' W	900	8	2	4
10	Lone Fox Lake	Clear Hills Alberta	56° 43' N 119° 43' W	1000	5	3	3.6
11	Hobbes Lake	Slave River Lowlands, Alberta	59° 41' N 110° 59' W	260	6.4	3.75	4.65
12	Long Lake	Clearwater Valley Saskatchewan	56° 51' N 108° 59' W	423	20	1.2	7.75
13	Cycloid Lake	La Ronge Lowlands Saskatchewan	55° 16' N 105° 16' W	370	18	2.4	3.4



ha with relatively shallow water depths of 1.2 to 4 m (Table 4.1) without significant inflowing streams. The pollen source area for these lakes should primarily record the extra-local pollen signal, with smaller local and regional pollen inputs (Jacobson and Bradshaw, 1981). Sites 4, 5, and 11 were cored for use in this study while sediment samples from the remaining ten lakes were available for use from other researchers (Table 4.2).

**Table 4.2.** Sources of lake sediment cores used in the study in addition to cores obtained directly by author for use in the study.

Site #	Site Name	Source
1	Twin Tamarack	Ritchie, 1985
2	Sweet Little Lake	Ritchie, 1984
3	Lac Meleze	MacDonald, 1987a
6	Lac Demain	MacDonald, 1987a
7	Lac Ciel Blanc	MacDonald and Cwynar, 1985
8	Wild Spear Lake	MacDonald, 1987a
9	Snowshoe Lake	MacDonald, 1987b
10	Lone Fox Lake	MacDonald, 1987b
12	Long Lake	Anderson (unpublished)
13	Cycloid Lake	Mott, 1973

Twin Tamarack (site 1, Table 4.1) is the northernmost site. The woody vegetation around the lake is sparse. To the west and northwest there are open

forests dominated by *Picea mariana* (black spruce) in large, flat, moist areas. *Alnus crispa* (green alder), *Betula glandulosa* (dwarf birch), *Sphagnum* spp.(peat mosses) and some *Larix laricina* (tamarack) are also present. To the south and east, better drained areas are dominated by open *Picea glauca* (white spruce) woodland with *Betula papyrifera* (paper birch), *Alnus crispa* (green alder), and *Salix glauca* (blue-green willow; Ritchie, 1985). Relief varies up to 100 m with rocky uplands and peaty lowlands.

Sweet Little Lake basin (site 2, Table 4.1) is similar to Twin Tamarack in its vegetation. Large areas of muskeg around the lake are dominated by *Picea mariana* with *Picea glauca* occurring on well drained upland sites. Elevation varies within the area from approximately 165 m to 285 m a.s.l.

Lac Meleze is situated on the western side of the Franklin Mountains at an elevation of 650 m a.s.l. (site 3, Table 4.1). There is greater relief (up to 500 m) surrounding this lake. *Picea glauca* dominates the well drained slopes with occurrences of *Populus tremuloides* (trembling aspen), *Betula papyrifera*, *Betula glandulosa* (dwarf birch), and *Alnus crispa*. *Picea mariana* -- *Sphagnum* muskeg occupy poorly drained depressions.

Gannet Lake (site 4) and Rugged Lake to the south of it (site 5, Table 4.1) are located in lowlands. The terrain around both sites is flat and fully forested, with some large and small areas of muskeg. The vegetation consists of *Picea mariana* and *Picea glauca*, *Betula papyrifera*, *Populus tremuloides* and *Pinus banksiana* (jack pine)

on upland, well drained sites.

Lac Demain is located on Horn Plateau at 745 m a.s.l. (site 6, Table 4.1). The landscape is relatively flat with an elevational range of approximately 150 m. The tree cover is sparse. *Picea mariana* - *Sphagnum* muskeg occur the area around the lake, with *Picea glauca*, *Pinus banksiana*, and *Betula papyrifera* on the areas of minor topographic relief.

Lac Ciel Blanc (site 7, Table 4.1) is situated on the Estho Escarpment , British Columbia, at an elevation of 660 m a.s.l. The area is relatively flat with numerous large peatlands. The area supports mainly *Picea mariana* - *Sphagnum* muskeg with *Picea glauca* and *Pinus contorta* (lodgepole pine) limited to local well-drained areas. *Alnus crispa* and *Betula glandulosa* are abundant along the lake shore.

Wild Spear Lake is located in the Caribou Mountains, Alberta at an elevation of 880 m a.s.l. (Table 4.1). Local relief is more than 200 m in the area. *Pinus banksiana* is found on well-drained sites at lower elevations. *Picea mariana* dominates the boggy areas around the lake with *Picea glauca*, *Pinus contorta*, *Betula papyrifera*, and *Populus* spp. (poplar) occur on well-drained sites.

The two southwest sites are Snowshoe Lake and Lone Fox Lake (sites 9 and 10, Table 4.1) at 900 and 1000 m a.s.l. respectively. Both areas are relatively flat with abundant poorly-drained sites which are dominated by *Picea mariana* - *Sphagnum* muskeg. Fire serial stands of *Pinus contorta*, *Alnus crispa*, and *Betula glandulosa* are found along the lake shores with *Picea glauca* in upland localities.

Hobbes Lake is at an elevation of 260 m a.s.l., located to the northwest of Lake Athabasca (site 11, Table 4.1). The topography is characteristic of the Canadian Shield with gently rolling granitic outcrops and numerous depressions. *Pinus banksiana* dominates the uplands with *Betula papyrifera* mixed in, and scattered *Picea glauca*. *Picea mariana* is found in low-lying areas with some *Larix laricina*.

Two of the sites are located in northern Saskatchewan; Long Lake is in the northeast at 423 m a.s.l. and Cycloid Lake is to the south at 375 m a.s.l. (sites 12 and 13, Table 4.1). Both sites have relatively flat topography with small to large areas of marsh. *Picea mariana* - *Sphagnum* muskeg are supported on wet sites. On outcrops and well-drained upland sites *Pinus banksiana* dominates along with some *Betula papyrifera* and scattered *Picea glauca*, *Alnus* spp. (alder) and *Populus tremuloides*.

### 4.3 Field Methods

Coring of lakes occurred during the early spring when lake ice provided a stable platform from which to work. Holes were drilled through the ice at the centre of the lakes and the lake sediments were cored using a 5 cm diameter modified Livingstone piston sampler (Wright *et al*, 1964). Core segments were removed in one metre lengths. The stable ice surface ensured that all core segments were obtained from the same hole, minimizing error in matching the segments. Each core segment was extruded from the sampler at the site, the length recorded and the sediment was

wrapped in plastic and aluminium foil. Up to the first 20 cm of the core were liquidy; for these segments samples were removed in the field and placed in plastic sample bags. The remainder of the liquid material was removed to avoid contamination of the rest of the (solid) core. Coring continued until bedrock or impenetrable sediment was reached. The core segments were packed in wooden boxes for transportation back to the laboratory where they were stored at 5° C. The cores ranged from 2.2 m to 7.75 m in length (Table 4.1). Descriptions of the surrounding vegetation and topography were recorded in the field.

#### 4.4 Laboratory Analyses

Radiocarbon dating provided stratigraphic control (Table 4.3 and 4.4) and allowed calculation of sediment accumulation rates. Bulk lake sediments were used for dating at all sites with the exception of one level at site 8, 255-268 cm, in which *Drepanocladus* was used. Many of the samples for dating came from the lower levels of the core in order to bracket as closely as possible the increase in spruce and pine pollen. To avoid using contaminated sediment, the surface layers were removed before sampling the sediment for either <sup>14</sup>C dating or pollen analysis. At 5 to 10 cm intervals 1 ml sediment samples were removed from the cores for pollen analysis. Calibrated *Lycopodium* or *Eucalyptus* tablets were added as 'exotic' pollen to permit calculation of pollen influx (Stochmarr, 1971). The sediments were chemically processed following the established methods of Faegri and Iverson (1975): 10% HCl

removed carbonates; 10% KOH in a hot water bath removed humic acids; 50% HF

**Table 4.3.** Radiocarbon dating of organic lake sediment from collected cores.

Site	Laboratory #	Depth (cm)	<sup>13</sup> C Corrected Radiocarbon Date (years BP)
4	WAT-20352	33-39	1560 +/- 90
	WAT-20353	111-117	3710 +/- 90
	WAT-20354	176-182	5000 +/- 120
5	WAT-20348	61-68	2660 +/- 80
	WAT-20349	137-145	5050 +/- 90
	WAT-20350	197-205	7720 +/- 110
	WAT-20351	240-247	9050 +/- 110
11	WAT-20357	51-57	1590 +/- 90
	WAT-20358	151-157	3750 +/- 90
	WAT-20359	261-267	4830 +/- 80
	WAT-20360	321-327	6700 +/- 100
	WAT-20361	365-371	8500 +/- 110
	WAT-20362	381-387	8920 +/- 120
12	Beta-36253	394.5-405.5	5670 +/- 50
	Beta-36254	494.5-505.5	7360 +/- 90
	Beta-36255	595-605	8800 +/- 150
	Beta-36256	645-655	9910 +/- 130
13	WAT-20333	142-148	3180 +/- 90
	WAT-20335	296-304	7530 +/- 90
	WAT-20336	317-322	8130 +/- 100

in a hot water bath removed silica; an acetolysis treatment (9 parts  $(\text{CH}_3\text{CO})_2\text{O}$  to 1 part  $\text{H}_2\text{SO}_4$ ) in a hot water bath removed cellulose; dehydration using  $(\text{CH}_3)_3\text{COH}$ ; staining with safranin; and silicone oil 2000 cs viscosity for storage of the material and as a slide mounting medium. Micro-sieving (Cwynar *et al*, 1979) was used at times to remove clay particles which were common in some cores near the base.

**Table 4.4** Previously published radiocarbon dates made available for use from sources listed in Table 4.2.

\* Radiocarbon dating of *Drepanocladus* for site 8, laboratory # GSC-3313.

For all other dates lake sediments were used.

Site	Laboratory #	Depth (cm)	<sup>13</sup> C Corrected Radiocarbon Date (years BP)
1	GSC-3394	5-10	440 +/- 60
	GSC-3377	60-65	3640 +/- 90
	GSC-3384	120-125	5830 +/- 90
	GSC-3347	170-175	7810 +/- 100
2	GSC-3346	300-305	11600 +/- 140
	GSC-3443	123-127	3350 +/- 100
	GSC-3439	239-245	5620 +/- 80
	GSC-3436	305-310	8550 +/- 80
	GSC-3430	344-351	9600 +/- 100
3	GSC-3437	90-95	2220 +/- 90
	GSC-3667	190-195	3360 +/- 150
	GSC-3651	260-265	4390 +/- 160
	GSC-3624	345-350	5970 +/- 160
	GSC-3496	384-389	9240 +/- 120

Site	Laboratory #	Depth (cm)	<sup>13</sup> C Corrected Radiocarbon Date (years BP)
3 (con't)	GSC-3536	434-439	11000 +/- 340
6	GSC-3639	45-50	2570 +/- 70
	GSC-3673	70-75	3380 +/- 70
	GSC-3628	100-105	6450 +/- 90
	GSC-3487	121-126	7620 +/- 180
	GSC-3524	192-197	10500 +/- 200
7	GSC-3791	96-100	4090 +/- 100
	GSC-3786	248-252	7400 +/- 120
	GSC-3778	298-302	8750 +/- 120
	GSC-3755	346-350	9350 +/- 150
	GSC-3749	370-375	9910 +/- 120
8	GSC-3619	18-25	1850 +/- 60
	GSC-3612	66-70	5630 +/- 70
	GSC-3358	93-95	7870 +/- 90
	GSC-3313*	255-268	10200 +/- 490
9	GSC-3762	95-100	3460 +/- 70
	GSC-3724	206-210	6130 +/- 90
	GSC-3718	280-284	8150 +/- 100
	GSC-3708	347-352	9550 +/- 100
	GSC-3704	373-377	10400 +/- 140
10	GSC-3643	50-55	1960 +/- 60
	GSC-3669	100-105	3960 +/- 90
	GSC-3630	200-205	6890 +/- 90
	GSC-3675	300-305	8810 +/- 110
	GSC-3482	342-348	9990 +/- 100
	GSC-3520	355-360	10700 +/- 140



The pollen grains of *Picea mariana* and *P. glauca* were distinguished using grain size and four morphological characteristics described by Hansen and Engstrom (1985): (1) the attachment of the two bladders to the main body of the grain, (2) the shape of the bladder, (3) the density and arrangement of the internal reticulate in the bladders, (4) the size of the bladders compared to the main body. The pollen of *Pinus banksiana* (jack pine) is morphologically indistinguishable from that of *Pinus contorta* (lodgepole pine). Pine pollen grains were counted only from sites east of the current range of lodgepole pine. Outliers of lodgepole pine occur in the Caribou Mountains of Alberta so site 8 (Wild Spear Lake) was not used for the pine pollen counts. Jack pine pollen records were obtained from sites 4, 5, 6, 11, 12, and 13, all to the east of lodgepole pine.

Pollen identification (using reference pollen collections) and previously counted levels were used until accuracy and consistency were attained. For each sampling level 50 to 100 *Picea* grains were counted and identified to species and 100 to 200 grains of *Pinus* were counted. Samples which had low levels of pollen influx were counted until the exotic pollen counts reached the average counts of normal levels. Sample levels counted per site ranged from 15 (site 1) to 42 (site 12). Recounts of 3 to 5 levels per lake were made to verify consistency of the counts.

#### 4.5. Statistical Analyses

At each level, pollen accumulation rates were calculated by multiplying the pollen concentration (grains  $\text{cm}^{-3}$ ) by the sediment accumulation rate ( $\text{cm yr}^{-1}$ ) (Bennett, 1983). These PAR values were then plotted against time for each species and site. For each species, the record of PAR is divisible into three phases (Figure 4.1). The first phase is the beginning of the expansion when fossil pollen is first detected (Phase I, Figure 4.1). The start of this interval is interpreted as the point at which there was continuous influx of pollen grains (Bennett, 1983, 1985, 1986; Birks, 1989). Jack pine pollen is very aerodynamic and is transported long distances. Spruce pollen grains are larger and heavier than jack pine pollen grains ( $\sim 84$  and  $100 \mu\text{m}$  for black and white spruce, respectively, and  $\sim 58 \mu\text{m}$  for pine; Bassett *et al*, 1978) and not dispersed as far. Prentice (1985, 1988) calculated that the source area for the majority of pine pollen in the sediments of a lake with a radius of 300 m, to be approximately 59 km with approximately 10 to 20% of the pollen from regional sources (greater than several hundred kilometres). In contrast, the majority of spruce pollen originated from sources within approximately 2 km. Though only approximate measures, the large source area for pine pollen indicates that it will normally be registered before the tree is locally present (MacDonald, 1988; Prentice, 1985). Therefore, for much of the first phase of the PAR record, pine is probably present regionally, but not extra-locally. The start of pine pollen expansion is interpreted as the earliest continuous increase in the influx to sustained high values (Birks, 1989).

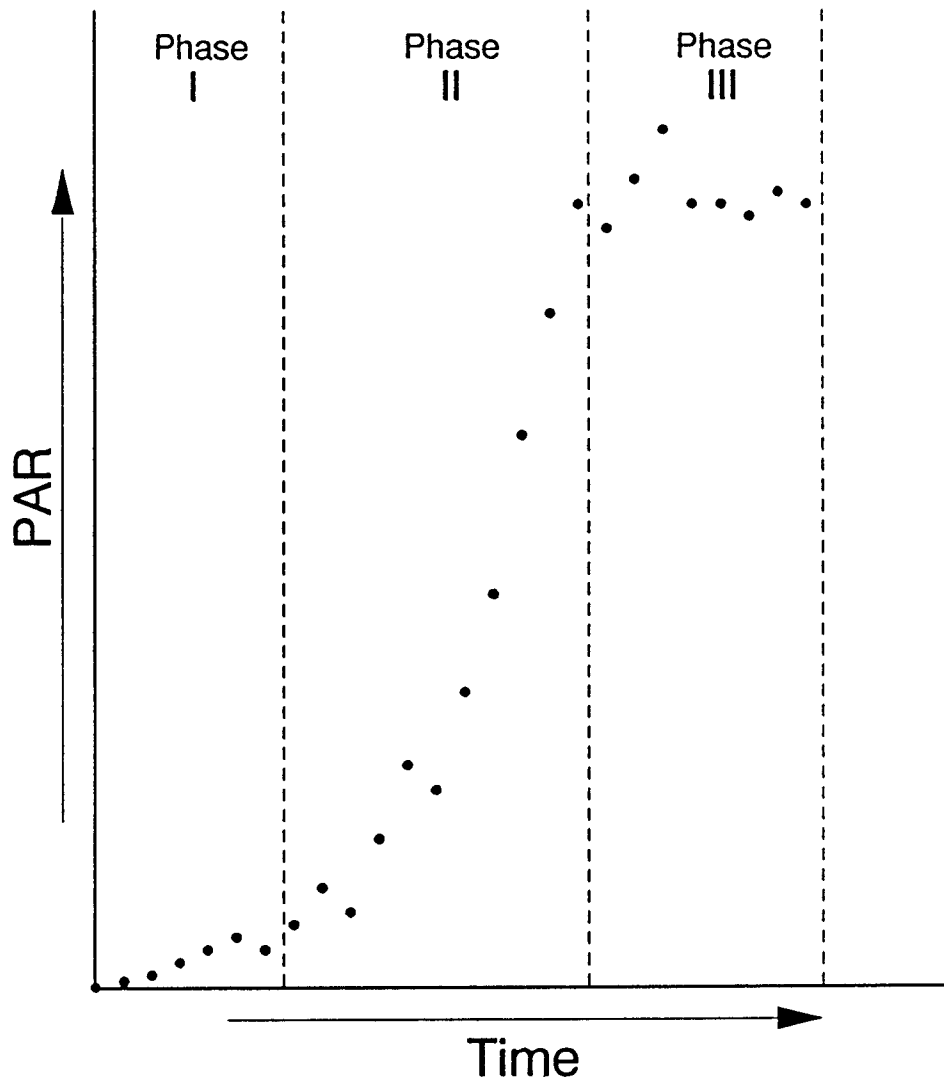


Figure 4.1. Theoretical rise in pollen influx.

Phase I- initial expansion

Phase II- rapid rise in influx

Phase III- fluctuation around average or modern influx

In the second phase of the record, there is usually a rapid rise in PAR (Phase II, Figure 4.1). The end of the second phase is the point at which the influx equals or exceeds the average influx value of the remaining levels. In the final phase (Phase III, Figure 4.1) PAR values fluctuate about a mean value which represents an environmentally controlled carrying capacity. The focus of this thesis is the initial expansion of the trees and any subsequent increases or declines were not examined.

To describe the nature of the expansions (Phases I and II), exponential equations were calculated, along with logistic and linear equations. All calculations were performed using Lotus 123, version 2.20 and Freelance Plus, version 2.01.

Exponential increase may be written as:

$$dN/dt = rN$$

where  $r$ = the unrestricted rate of increase per individual  
 $N$ = the number of individuals  
 $t$ = the time period

In order to calculate the rate of increase ( $r$ ), the equation may be integrated to give:

$$\ln N = rt + a$$

where,  $r$  and  $N$  are defined above and  $a$ = the constant of integration. In this study:

$N$ = the pollen influx level (PAR) at time  $t$  (estimated from the radiocarbon dates)  
 $r$ = the slope of the least squares regression line  
 $a$ = the constant of integration

Logistic increase may be calculated as:

$$dN/dt = rN(K-N)/K$$

where  $r$ = the slope of the least squares regression line  
 $N$ = the population size (approximated by PAR) at time  $t$  (estimated from radiocarbon dates).  
 $K$ = the carrying capacity of the taxon at the site (approximated by the average PAR value after the end of expansion).

This equation may be integrated to give:

$$\ln(K-N)/N = a-rt$$

where,  $a$ = the constant of integration and the other symbols are as above.

Linear increase may be calculated as:

$$N = rt + b$$

where,  $b$ = a constant and the other symbols are as above.

Coefficients of determination were calculated from least squares linear regression, and along with the number of data points used in the equation, were used to determine the equation that best approximated the pollen increase.

As an estimate of the rate of increase, pollen influx doubling times (DT) were calculated as (symbols as above):

$$DT = \ln 2 / r$$

The 95% confidence intervals ( $Z = 1.96$ ) were calculated by:

$$\text{upper and lower limits} = r \pm [Z \times (\text{standard error in } r)]$$

The range in the doubling times are calculated by (Bennett, 1983):

$$\ln 2 / (\text{upper limit}), \quad \ln 2 / (\text{lower limit})$$

When pollen accumulation values are used instead of pollen percentages it is not possible to directly compare PAR's from different sites. This is due to the variation in the catchment of the lakes. Along with differences in the size and shape of the lake, various environmental factors (wind direction and speed, vegetation structure, topography) affect the pollen influx recorded in the sediments (Prentice, 1988; Davis *et al*, 1981; Jacobson and Bradshaw, 1981). In order to compare the degree of expansion between sites, a non-dimensional pollen index was used:

$$N/K \times 100$$

where N= PAR at time t

K= the average PAR level after the end of expansion

This index essentially allows the comparison of the timing and rates at which the taxa at different sites reached their modern abundance. Using PLOT88 Software Library Reference Manual, Third Edition (Young and Van Woert, 1989), three-dimensional (time, space, and pollen index) models of spread were produced.

## CHAPTER V

### RESULTS

#### 5.0 Fossil Pollen Increase

Pollen records in which the initial phases of population growth were present for black and white spruce were available from sites 1, 2, 3, 5, 6, 7, 8, 9, 10, and 12 (Figures 5.1, 5.2, 5.3, 5.5, 5.6, 5.7, 5.8, 5.9, 5.10, and 5.12); at the remaining sites, sedimentation began after initial spruce expansion. Complete pollen records of jack pine population growth were produced from sites 4, 5, 6, 11, 12, and 13 (Figures 5.4, 5.5, 5.6, 5.11, 5.12 and 5.13). For both spruces Phase I (Figure 4.1) is relatively short, lasting at most a few hundred years. Spruce expansion is determined to begin at the start of continuous pollen deposition. Phase I for jack pine is an extended period of very low pollen influx, possibly derived from distant sources. Therefore, jack pine expansion within the area of each site is assumed to begin in the latter part of Phase I at the point at which pollen accumulation rates increase continuously (Figure 4.1).

For black and white spruce increases all sites, either (i) the coefficient of determination ( $r^2$ ) was greater using the exponential equation, or (ii) in cases where the  $r^2$  values for two equations were similar, the exponential equations were used as they were calculated using a higher number of data points (Table 5.1 and 5.2). For jack pine, the initial increases at sites 11 and 13, were best approximated by linear

equations, and at sites 4, 5, 6, and 12 by exponential equations (Table 5.3). However, in order to compare the rates of increase, exponential equations were used for all species at all sites (Figures 5.14, 5.15, and 5.16).

Pollen accumulation rates for all species first began to increase in the southern sites (Figures 5.9, 5.10, 5.12, 5.13) with initial expansion occurring at later times with increasing latitude and altitude (Figures 5.1 through 5.8 and 5.11). At sites 9, 10, and 12 (Figures 5.9, 5.10, and 5.12) in the southern part of the study region, black and white spruce pollen began to increase around 10,000 BP. Jack pine pollen at sites 12 and 13 (Figures 5.12 and 5.13) begins to expand at approximately 6,800 and 7,200

**Table 5.1.** Coefficients of determination for logistic, linear, and exponential equations calculated for black spruce PAR data.

Site	Exponential $r^2$	n	Logistic $r^2$	n	Linear $r^2$	n
1	0.94	5	0.75	3	0.63	5
2	0.94	8	0.96	5	0.66	8
3	0.78	9	0.37	9	0.40	9
5	0.91	5	0.55	4	0.66	5
6	0.76	8	0.72	6	0.72	8
7	0.95	7	0.68	5	0.71	7
8	0.76	18	0.63	16	0.71	18
9	0.82	9	0.54	7	0.77	9
10	0.84	10	0.64	9	0.77	10
12	0.90	14	0.78	13	0.48	14

$r^2$ = Coefficient of Determination calculated from least squares regression.  
n= Number of data points used in regression.



BP respectively. Jack pine PAR values increased at site 12 before increasing in the southern site (site 13). In central areas both spruce species begin to expand around 9,800 BP (Figures 5.5 through 5.8) and jack pine showed initial expansion around 6,500 BP (Figure 5.11). The northern sites record the latest initial expansions, beginning between approximately 9,500 to 8,500 BP for spruce (Figures 5.1 and 5.2) and at approximately 3,800 BP for jack pine (Figure 5.4).

**Table 5.2.** Coefficients of determination for exponential, linear, and logistic equations approximating white spruce PAR data.

Site	Exponential $r^2$	n	Logistic $r^2$	n	Linear $r^2$	n
1	0.95	5	0.90	3	0.77	5
2	0.80	7	0.66	5	0.46	7
3	0.68	10	0.38	7	0.60	10
5	0.91	5	0.55	4	0.82	5
6	0.84	5	0.44	3	0.83	5
7	0.81	6	0.88	3	0.80	6
8	0.73	16	0.51	12	0.40	16
9	0.59	5	0.43	3	0.59	5
10	0.90	5	0.89	4	0.80	5
12	0.68	15	0.25	13	0.40	15

$r^2$  = Coefficient of determination calculated from least squares regression.  
n = Number of data points used in the regression.

**Table 5.3.** Coefficients of determination for equations approximating jack pine PAR data.

Site	Exponential $r^2$	n	Logistic $r^2$	n	Linear $r^2$	n
4	0.82	9	0.81	8	0.74	9
5	0.83	10	0.49	7	0.83	10
6	0.98	4	0.65	4	0.92	4
11	0.75	8	0.28	7	0.92	8
12	0.92	9	0.78	8	0.83	9
13	0.83	7	0.50	5	0.89	7

$r^2$  = Coefficient of Determination calculated from the least squares regression.  
 n = Number of data points used in the regression.

### 5.1 Black Spruce Increase

The earliest expansion of black spruce populations is recorded at site 12 (Table 5.4) at 11,000 BP and the most recent is at site 1 at 8,550 BP. Black spruce pollen is recorded throughout the region within 2,450 years of the first increase in the southern sites. The expansion period for black spruce varied between sites. Complete expansion, from initial pollen increase to modern pollen levels, ranged from 1,150 to 2,200 at the three southern sites (sites 9, 10, and 12). The periods of increase were longer at sites located in areas of combined high latitude and high elevation (sites 3, 6, and 8) where expansion to modern levels of abundance took 2,300 to 3,300 years. The central sites (sites 5 and 7) completed expansion within approximately 700 years and the two northern sites (sites 1 and 2) expanded quite

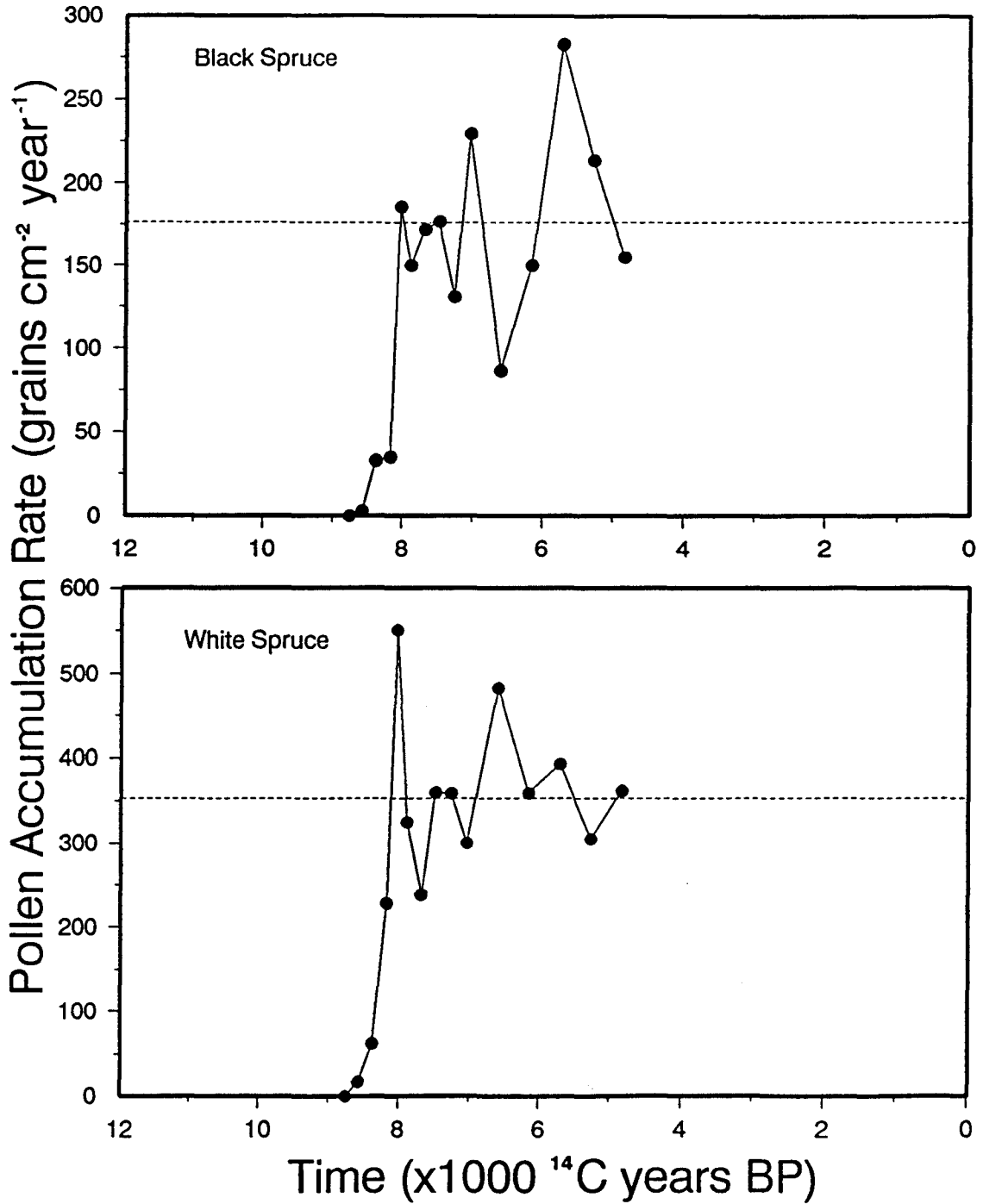


Figure 5.1. Pollen accumulation rates for black and white spruce at site 1, Twin Tamarack Lake. Dashed line represents the average PAR level after the initial increase.

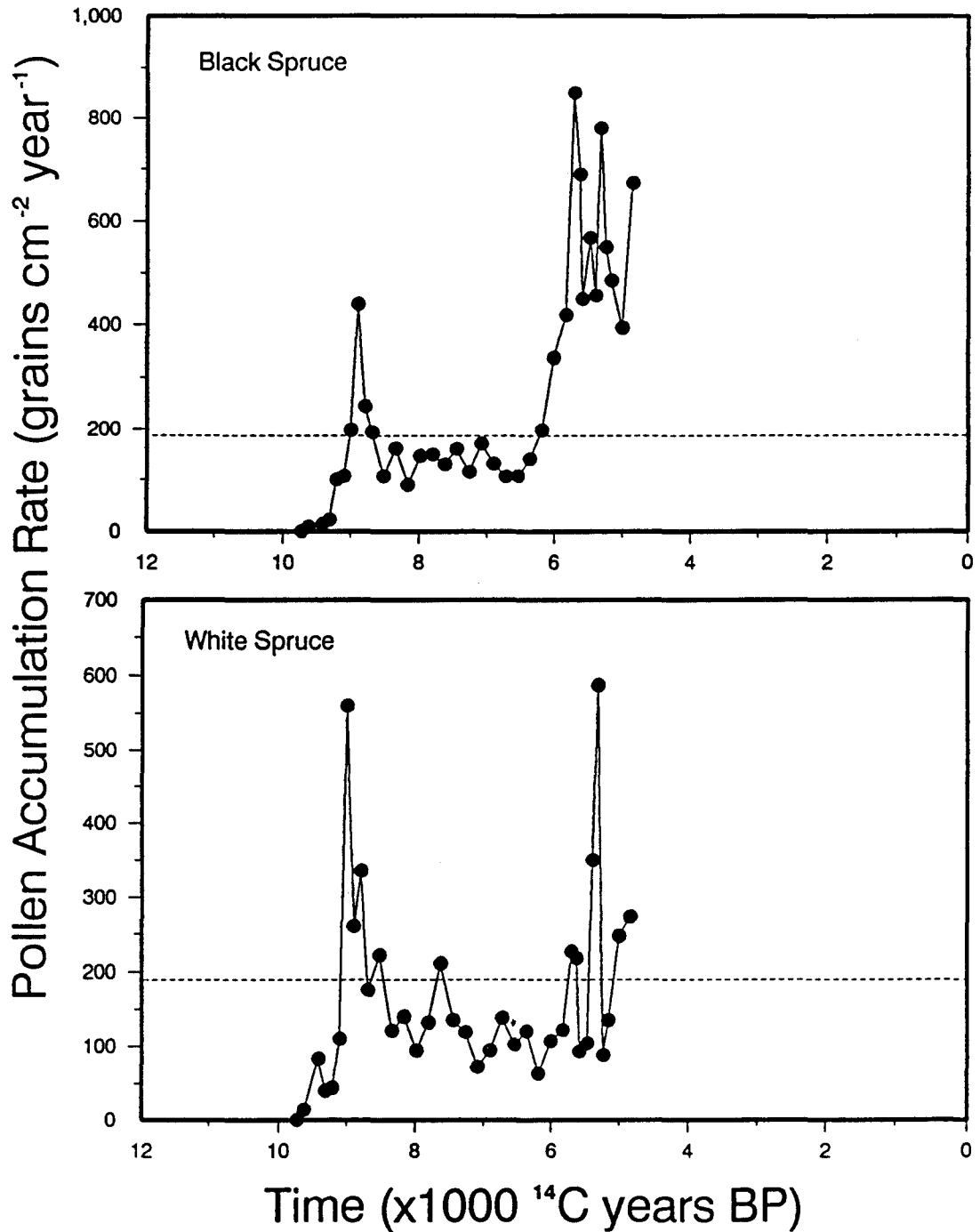


Figure 5.2. Pollen accumulation rates for black and white spruce at site 2, Sweet Little Lake. Dashed line represents the average PAR level after the initial increase.

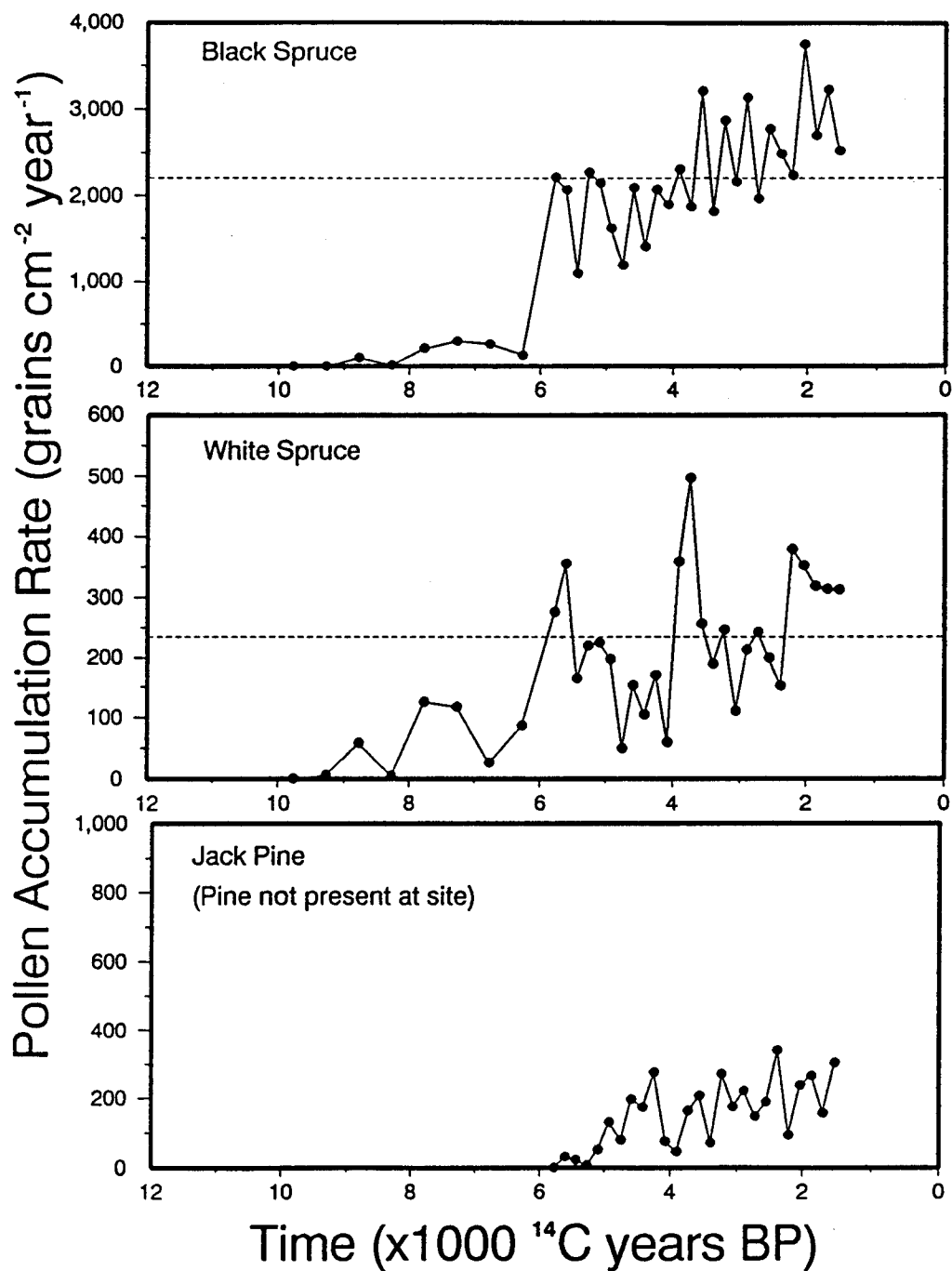


Figure 5.3. Pollen accumulation rates for black and white spruce at site 3, Lac Meleze. Jack pine is not locally present. Dashed line represents the average PAR level after the initial increase.

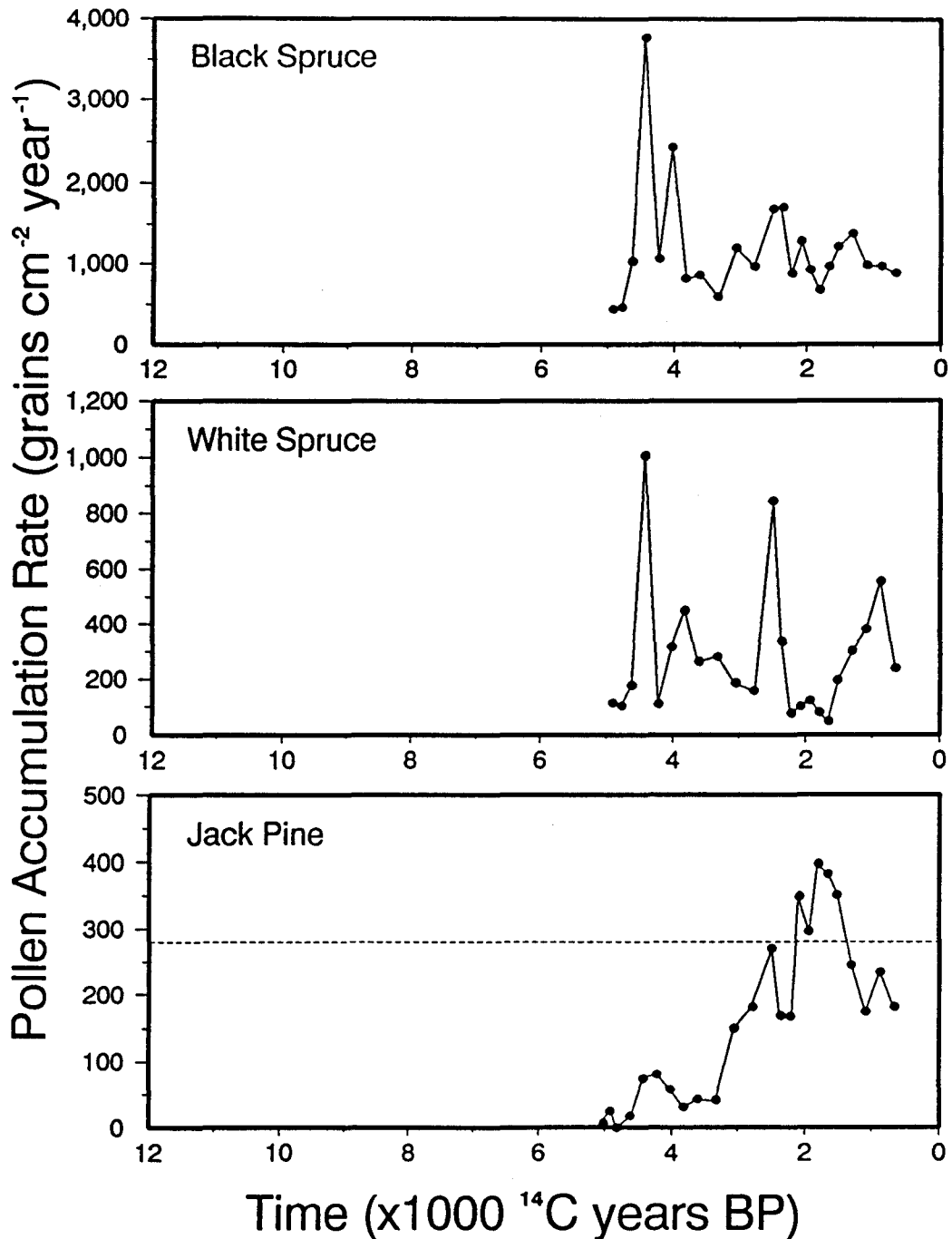


Figure 5.4. Pollen accumulation rates for jack pine at site 4, Gannet Lake. The pollen records for black and white spruce were incomplete as their increases began before lake sedimentation. Dashed line represents the average PAR level after initial increase.

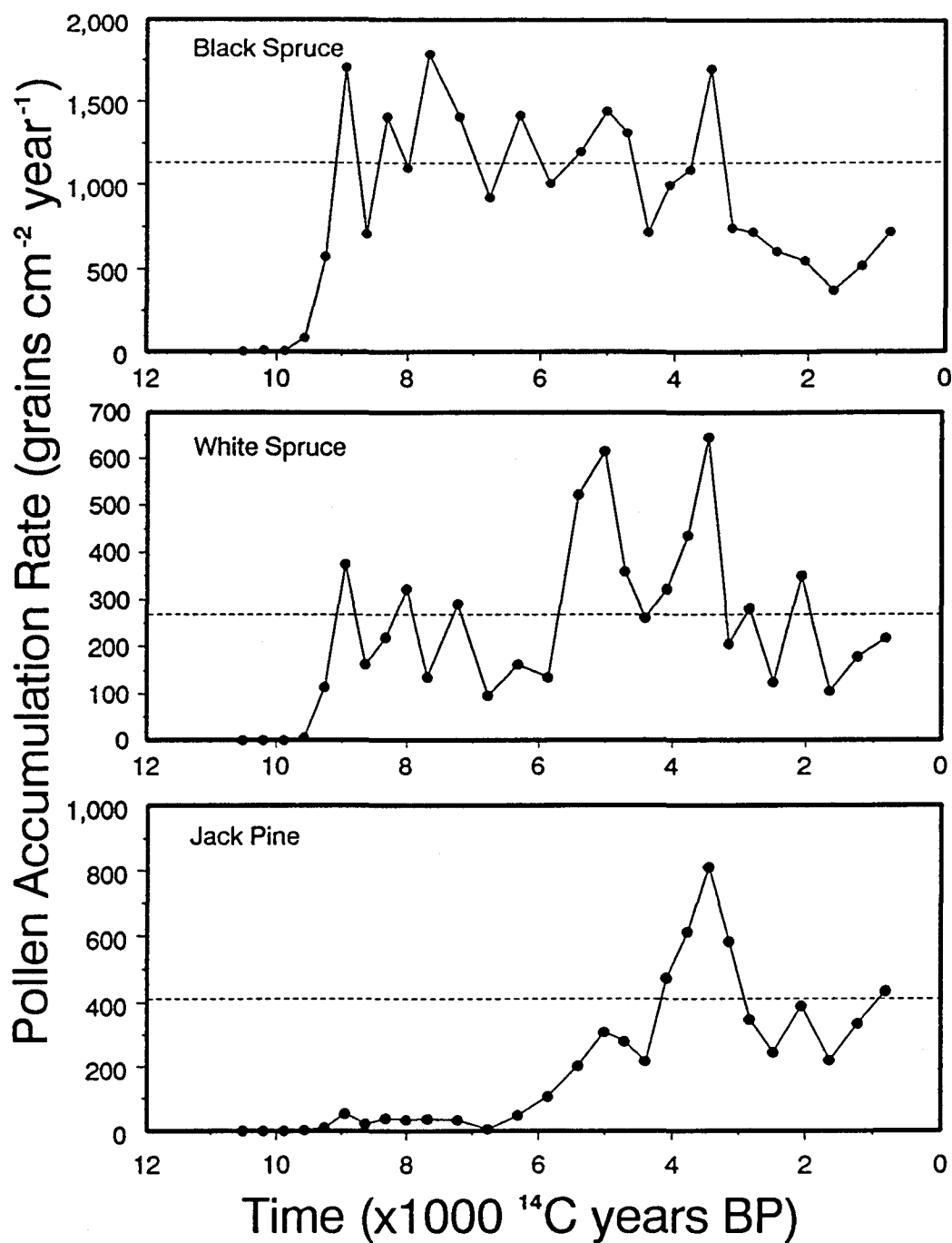


Figure 5.5. Pollen accumulation rates for black spruce, white spruce, and jack pine at site 5, Rugged Lake. Dashed line represents the average PAR level after initial increase.

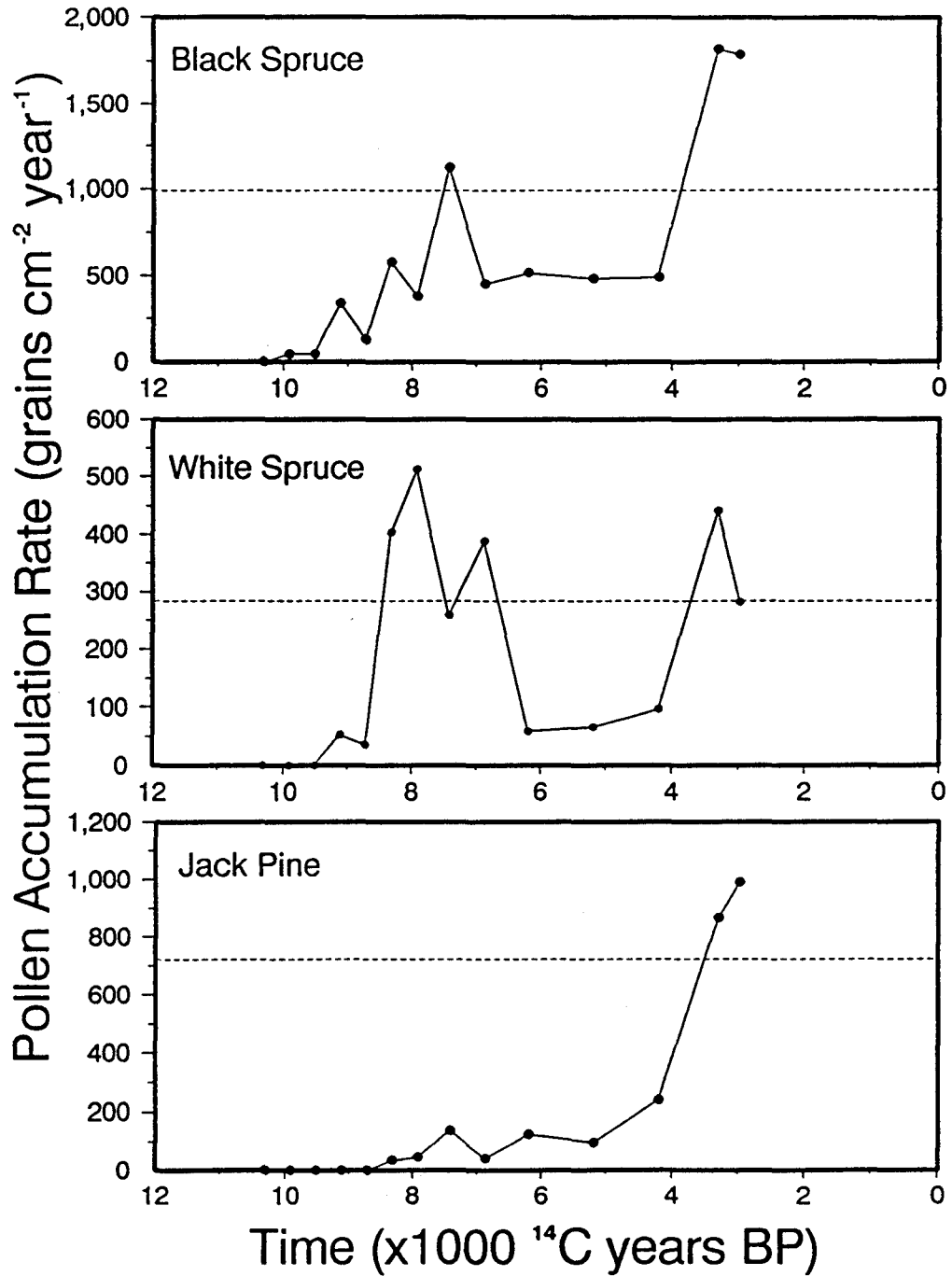


Figure 5.6. Pollen accumulation rates for black spruce, white spruce, and jack pine at site 6, Lac Demain. Dashed line represents the average PAR level after initial increase.



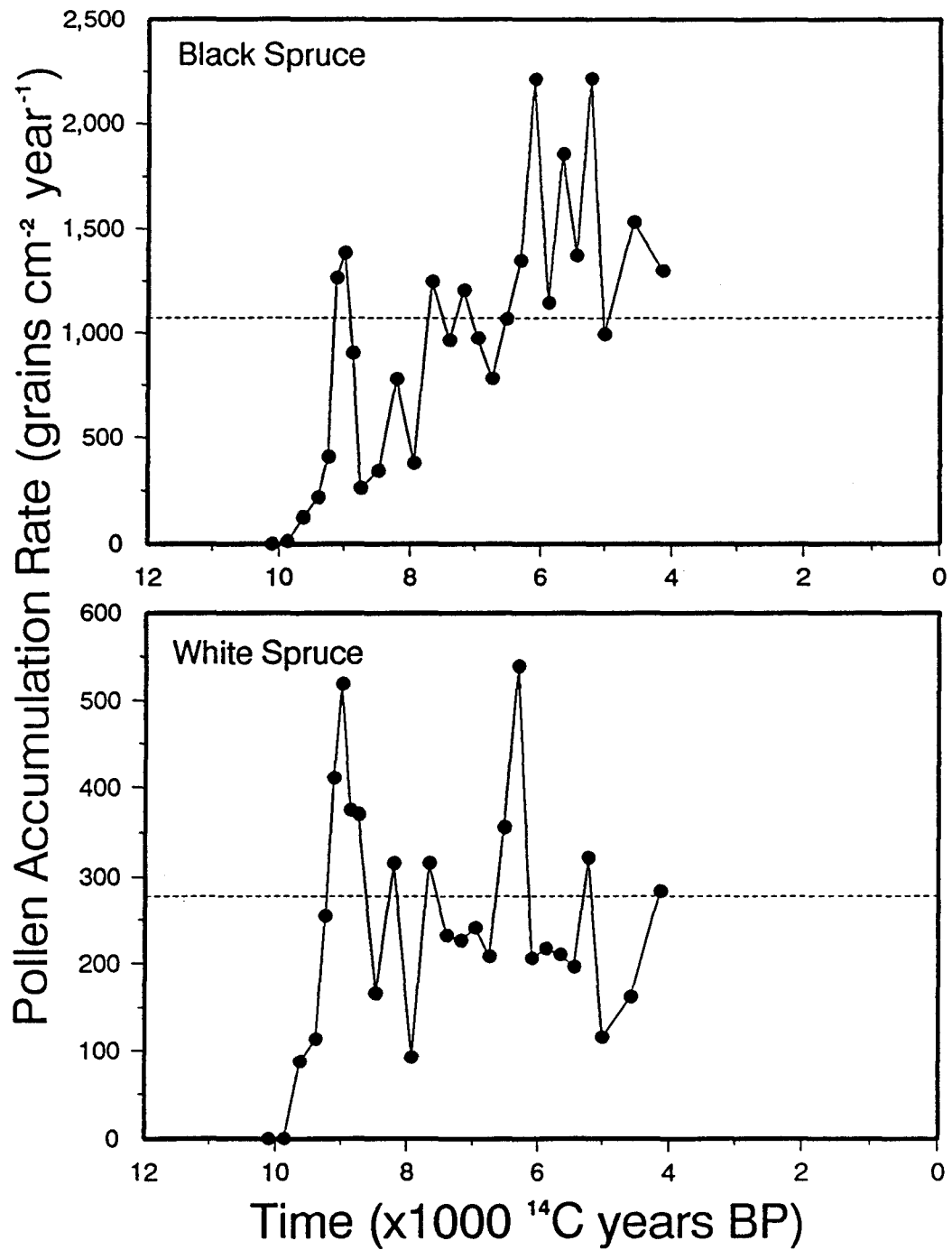


Figure 5.7. Pollen accumulation rates for black and white spruce at site 7, Lac Ciel Blanc. Dashed line represents the average PAR level after initial increase.

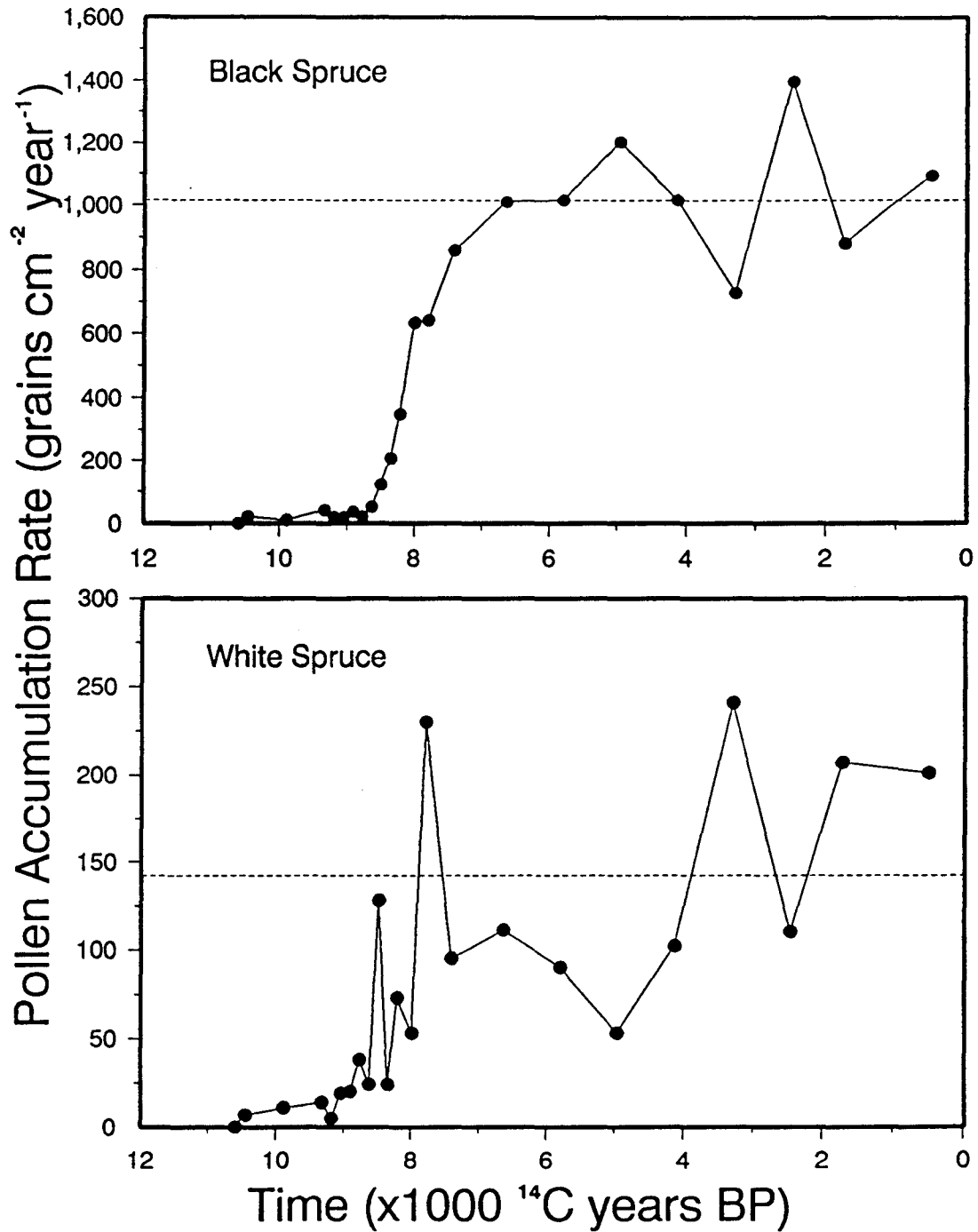


Figure 5.8. Pollen accumulation rates for black and white spruce at site 8, Wild Spear Lake. Dashed line represents the average PAR level after initial increase.

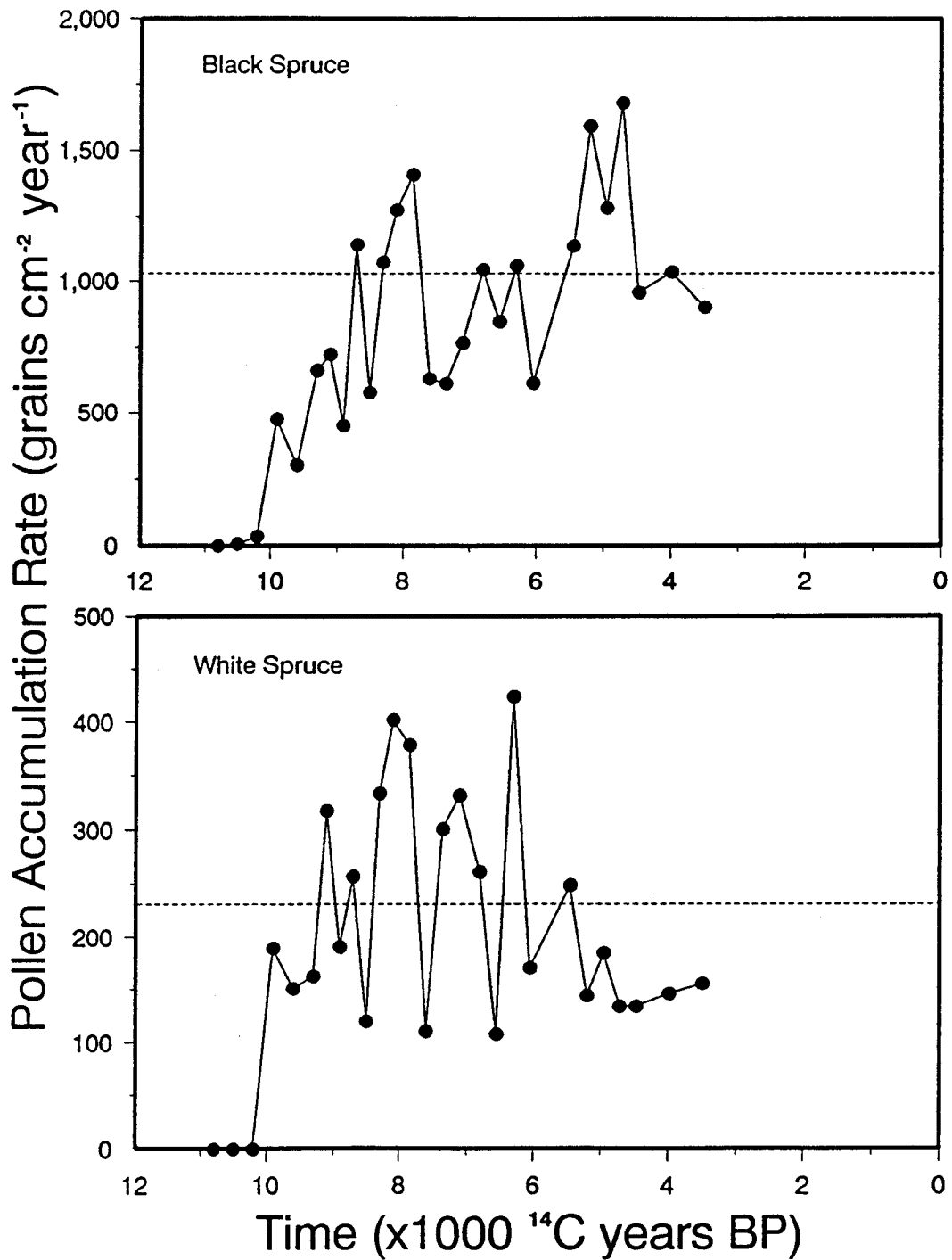


Figure 5.9. Pollen accumulation rates for black and white spruce at site 9, Snowshoe Lake. Dashed line represents the average PAR level after initial increase.

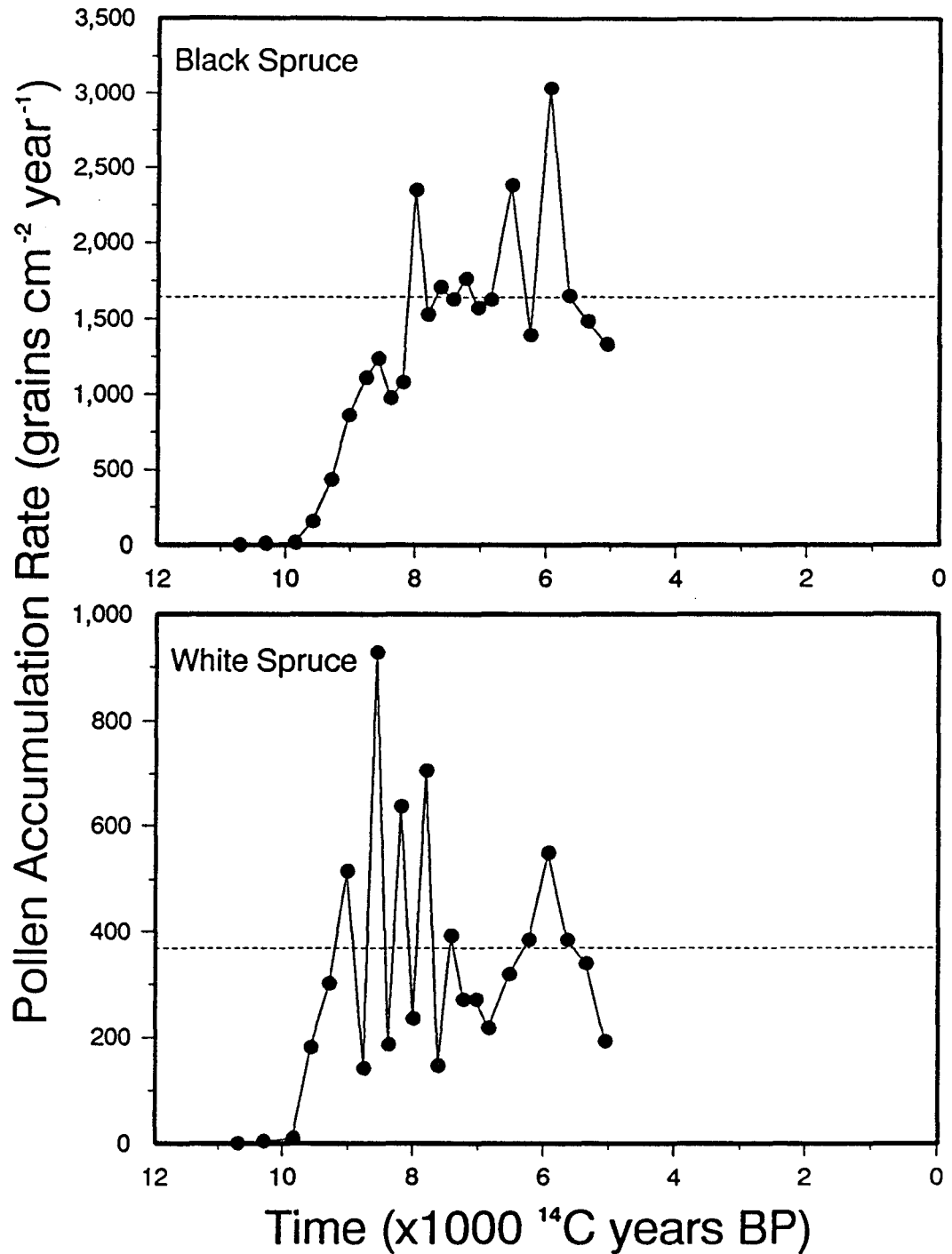


Figure 5.10. Pollen accumulation rates for black and white spruce at site 10, Lone Fox Lake. Dashed line represents the average PAR level after initial increase.

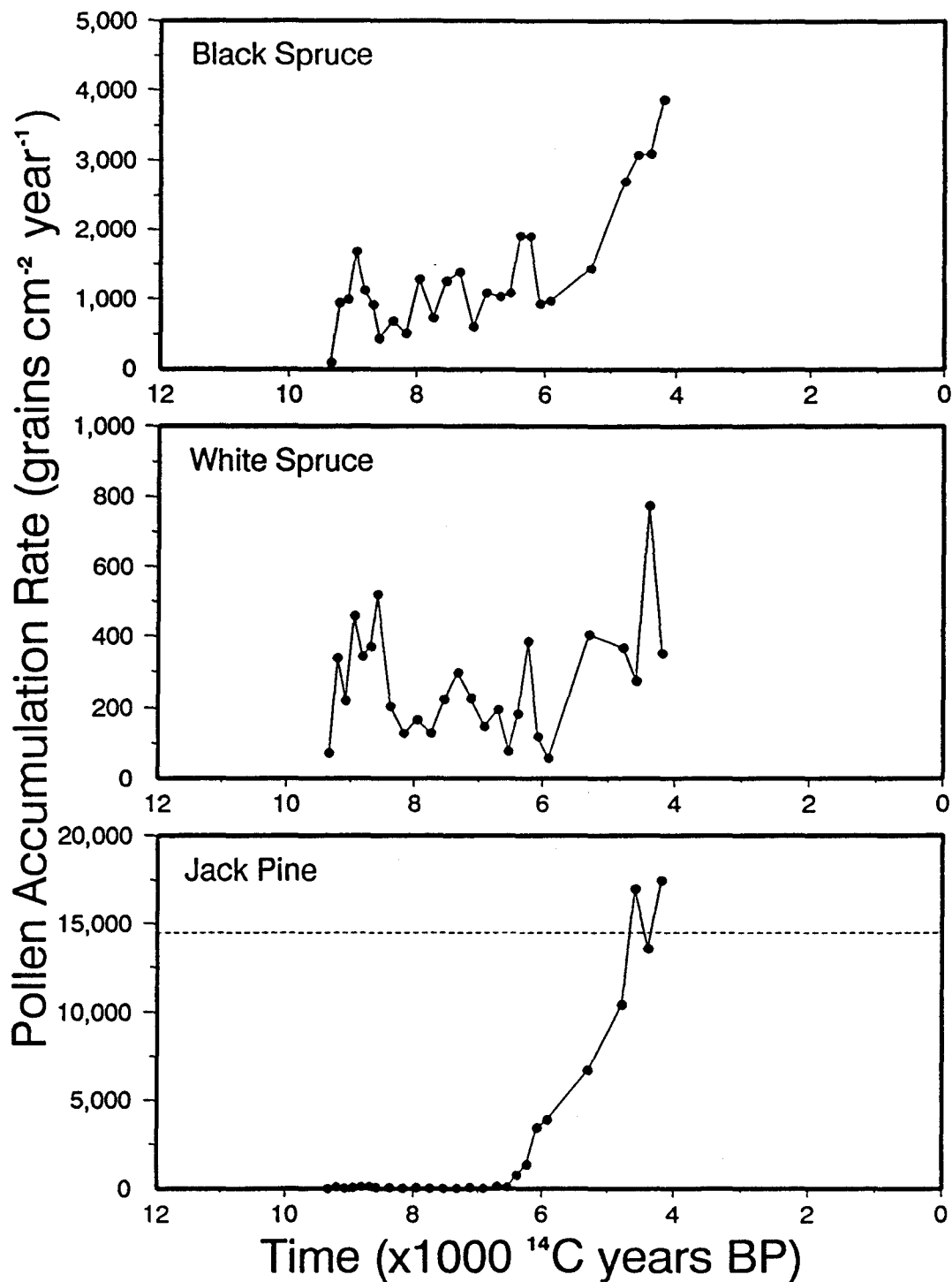


Figure 5.11. Pollen accumulation rates for jack pine at site 11, Hobbes Lake. The pollen records for black and white spruce were incomplete as their increases began before lake sedimentation. Dashed line represents the average PAR level after initial increase.

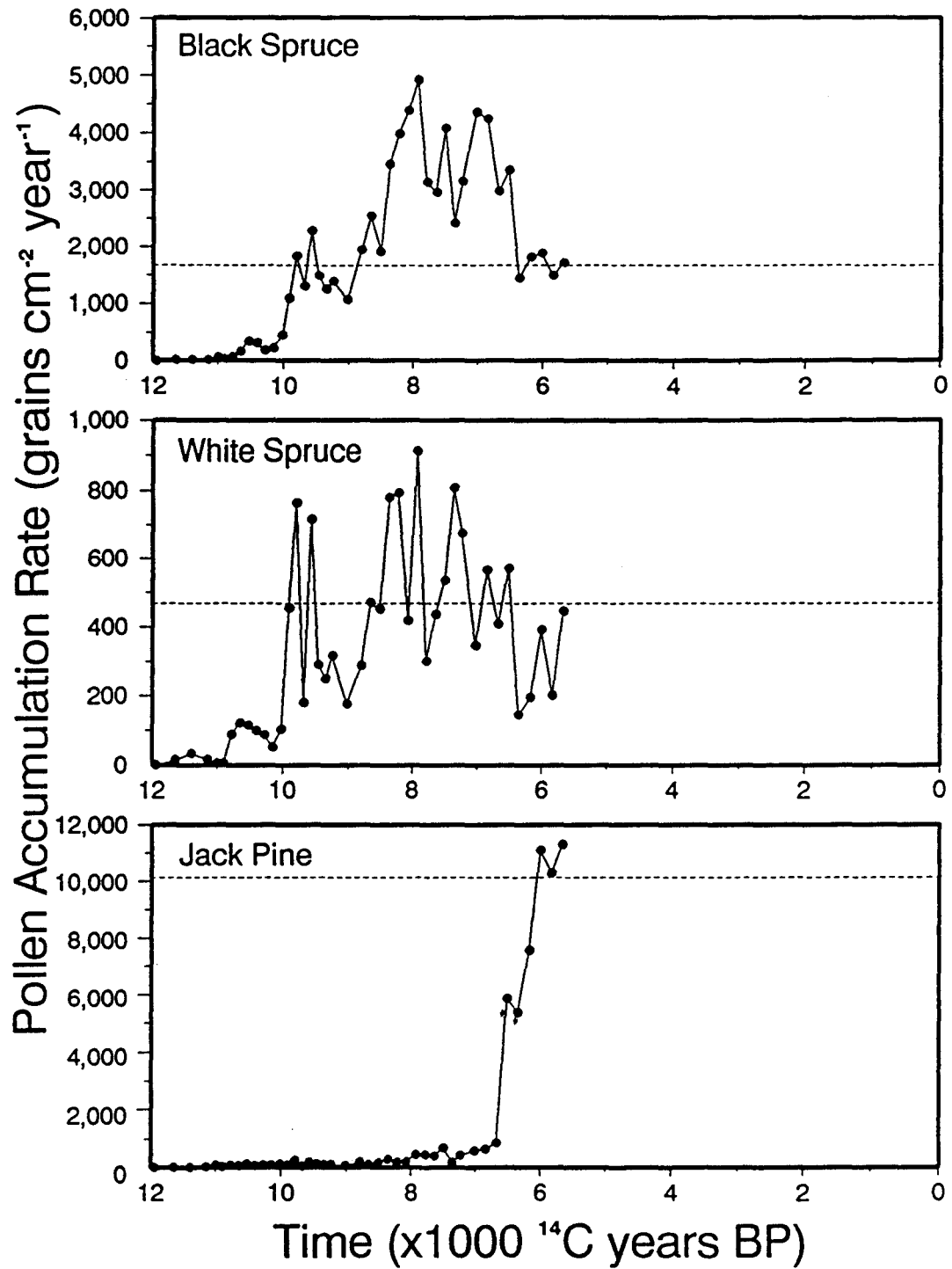


Figure 5.12. Pollen accumulation rates for black spruce, white spruce, and jack pine at site 12, Long Lake. Dashed line represents the average PAR level after initial increase.

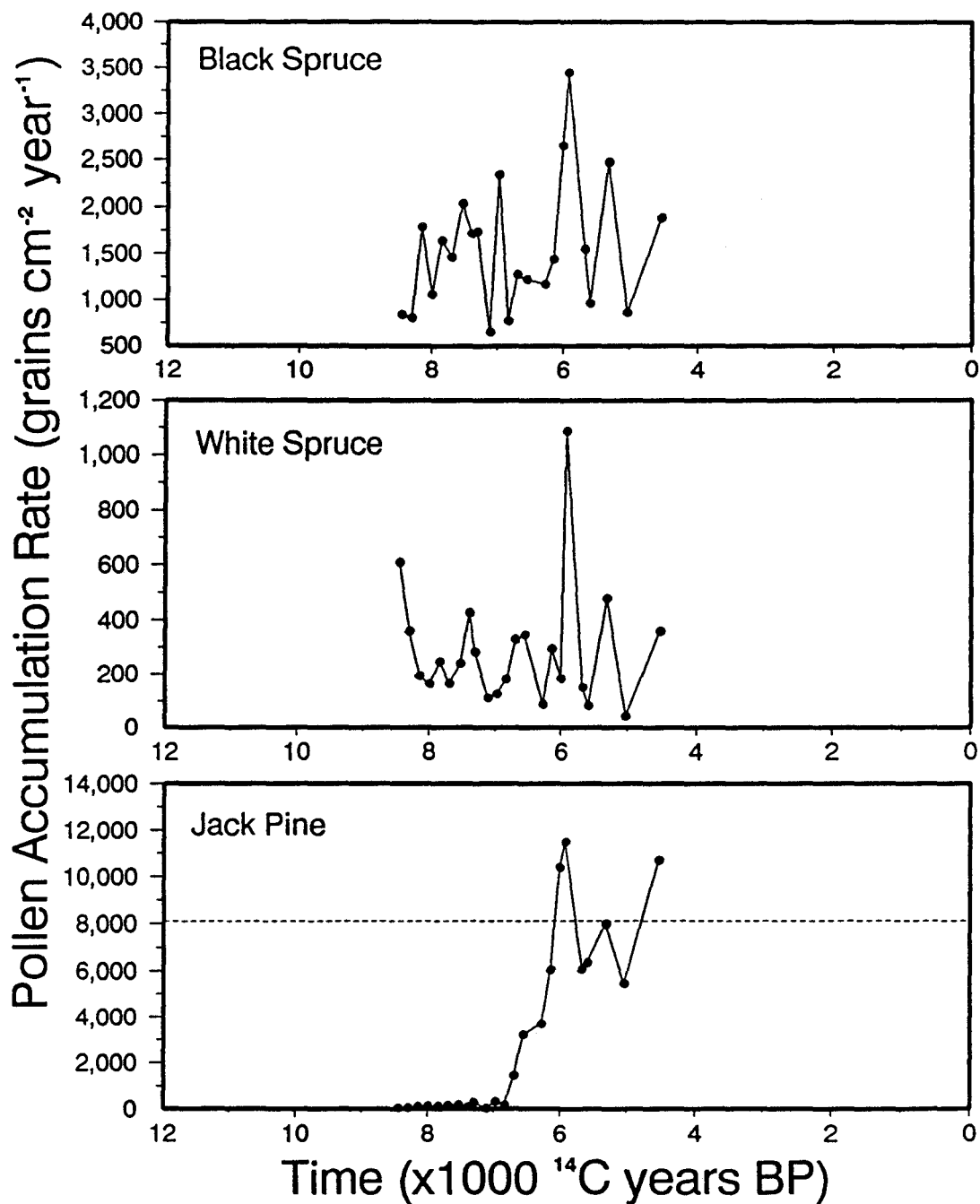


Figure 5.13. Pollen accumulation rates for jack pine at site 13, Cycloid Lake. The pollen records for black and white spruce were incomplete as their increases began before lake sedimentation. Dashed line represents the average PAR level after initial increase.

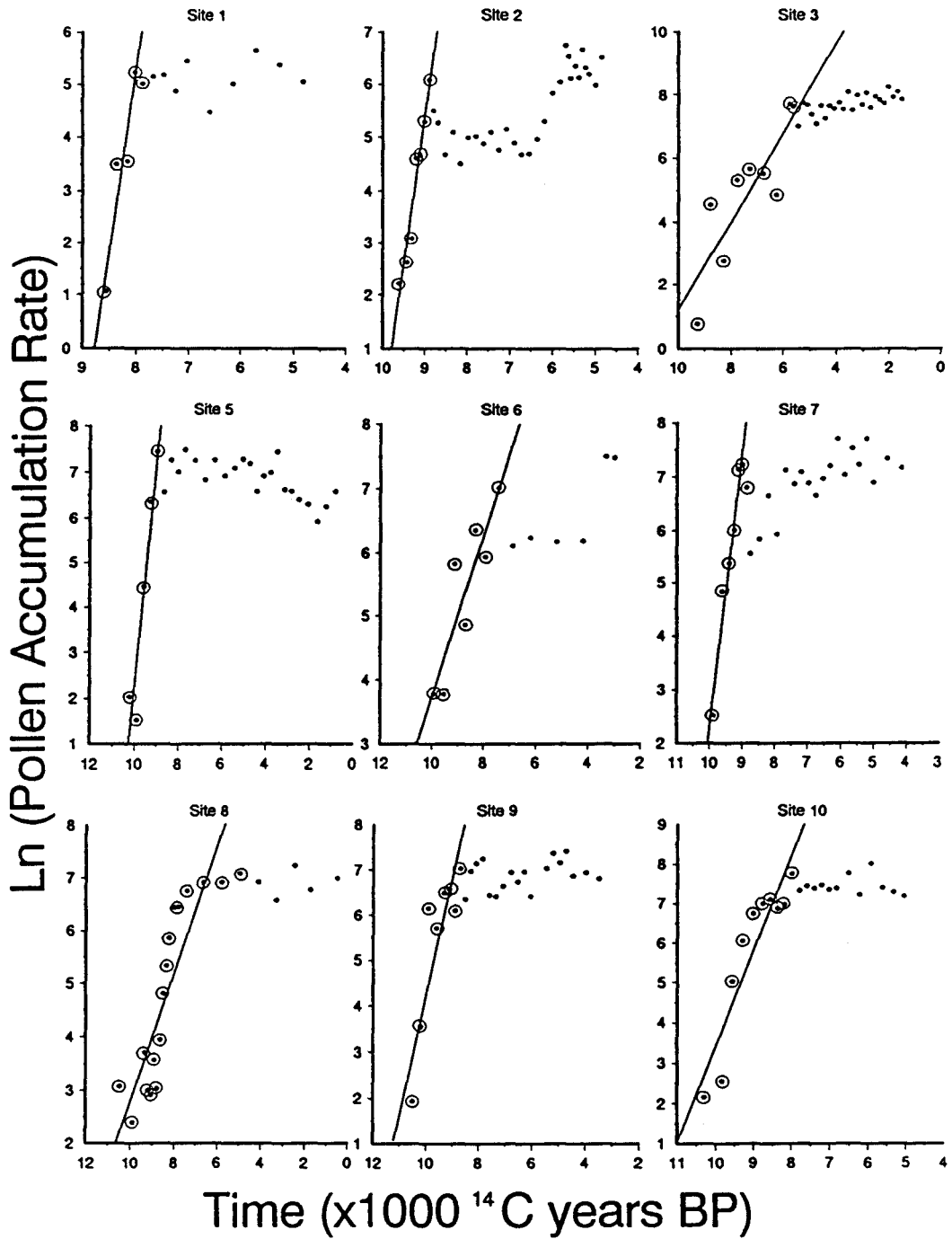


Figure 5.14. Exponential equations approximating the increases in black spruce pollen. Circled data points represent data used in the equations.



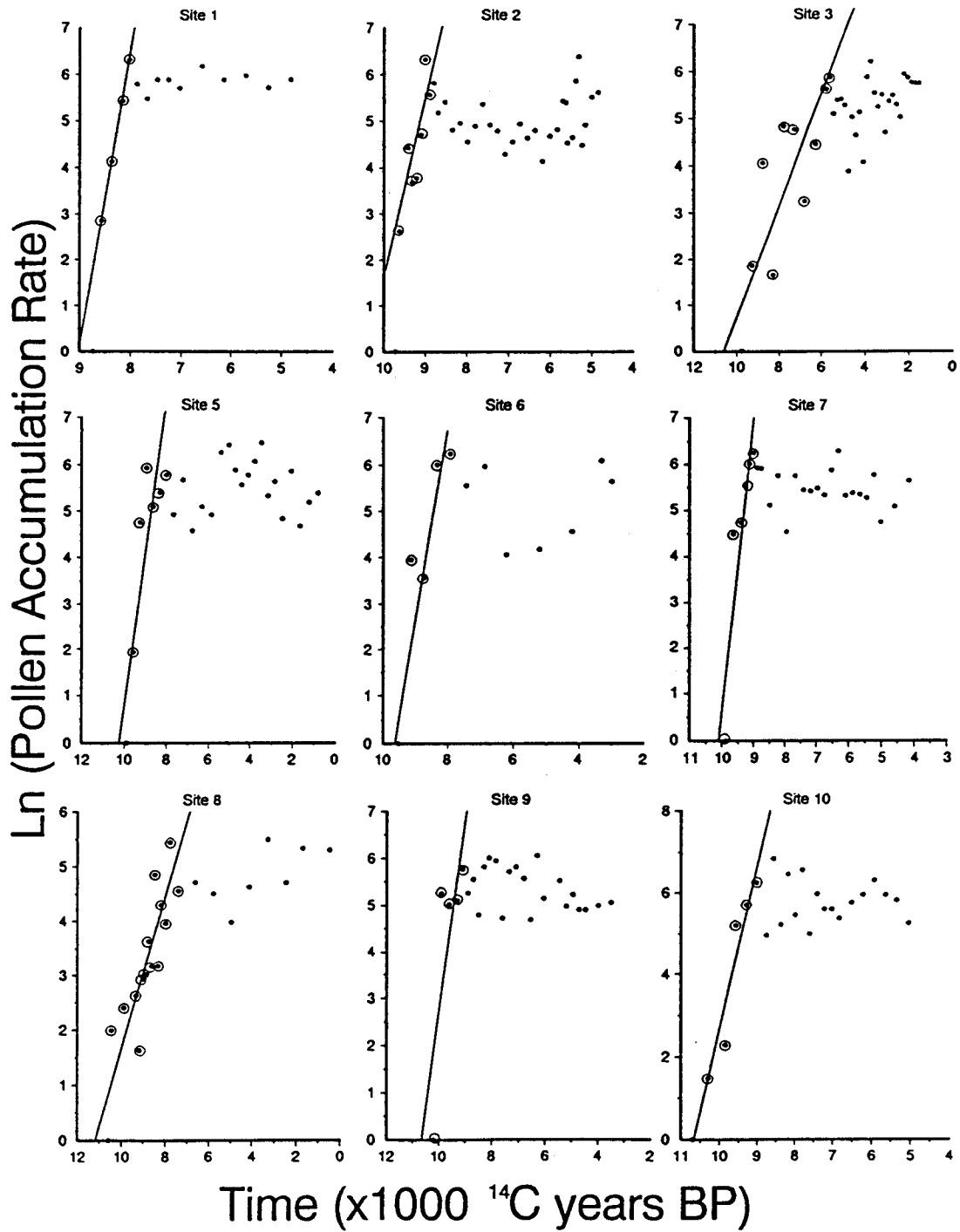


Figure 5.15. Exponential equations approximating the increases in white spruce pollen. Circled data points represent data used in the equations.

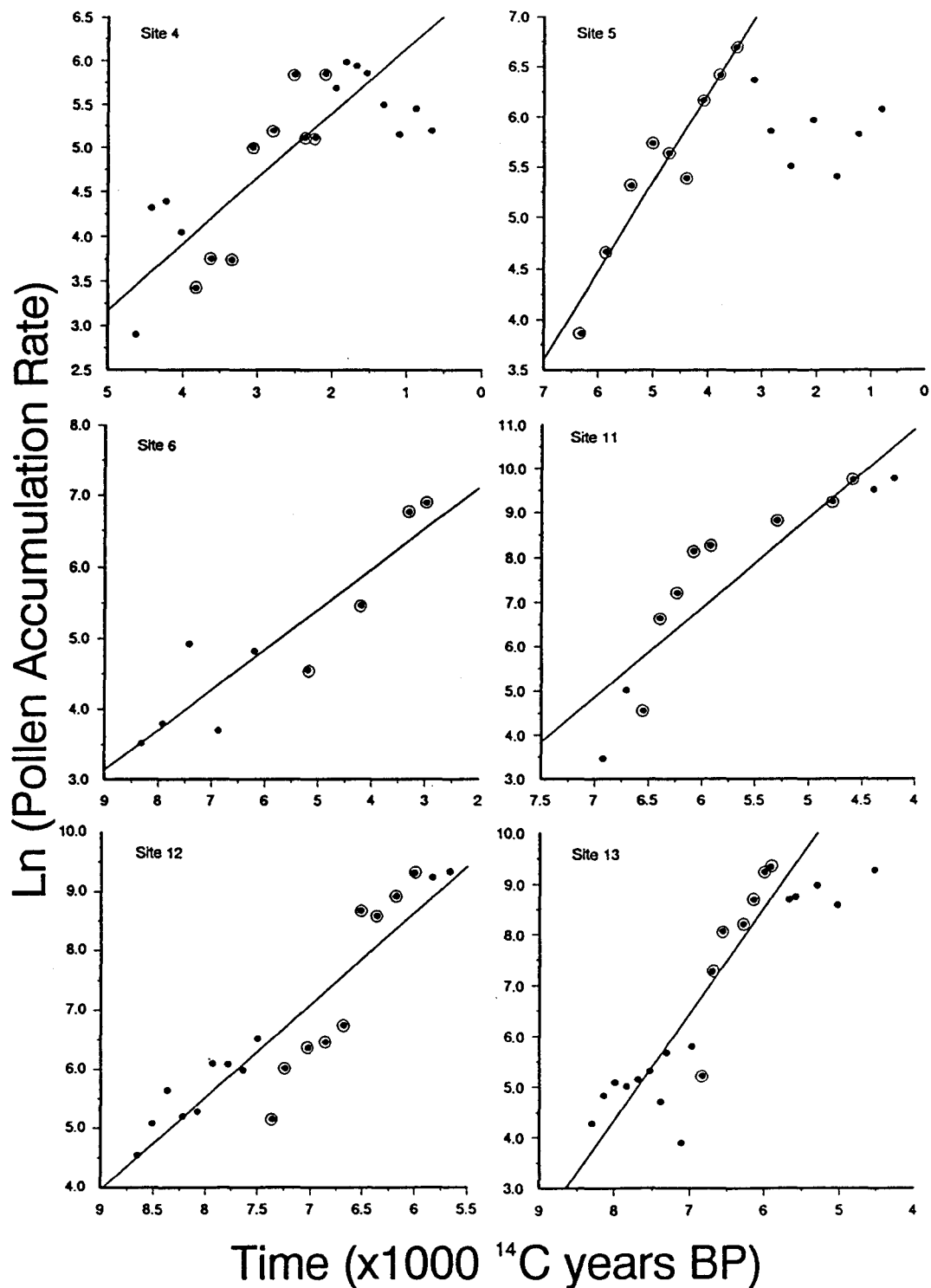


Figure 5.16. Exponential equations approximating the increases in jack pine pollen. Circled data points represent data used in the equations.

rapidly, reaching modern levels of abundance within approximately 500 years of the initial pollen rise.

The rate of fossil pollen expansion at each site is reflected in the doubling times (Table 5.4). The slowest doubling times occur in the southern sites (sites 9, 10, and 12) with times of 242 to 290 years and at the high latitude/high elevation sites (sites 3, 6, and 8) with times of 357 to 582 years. The central and northern sites (sites 1, 2, 5, and 7) have low doubling times (100 to 143 years). Expansion at high elevation northern sites was slower than for low elevation northern sites. High elevation sites in the south did not experience the same slow rate of PAR increase.

To display spruce expansion in the dimensions of space, time, and pollen abundance (pollen index: N/K), sites 1, 2, 3, 5, 6, 7, 8, 9, and 10 along a transect south to north were used. The combination of rapid expansion northward across the region and the rapid rise in PAR to modern levels at each site, produces a distinctive form of expansion (Figures 5.17 and 5.18). The slow expansion of black spruce at high latitude/high elevation sites is clearly indicated by the large trough between 62° and 65°N latitude (influence of sites 3 and 6) and the smaller trough around 59°N latitude (site 8; Figure 5.17). Excluding these sites (Figure 5.18) it can be seen that black spruce spread very quickly northward across the region at low PAR levels. South of the initial wave of spread, black spruce rose to modern PAR levels.

**Table 5.4.** Black spruce fossil pollen increase (shading indicates a high latitude high elevation site).

Site	$r^2$ *	Doubling Time (years)	Doubling Time Range (years)**	n	Expansion		
					Start (yr BP)	End (yr BP)	Duration (years)
1	0.94	100	78, 139	5	8550	8050	500
2	0.94	106	88, 133	8	9500	8950	550
3	0.77	443	309, 722	9	9000	5800	3200
5	0.94	143	115, 189	6	9800	9100	700
6	0.76	357	246, 654	8	9900	7600	2300
7	0.95	110	91, 139	7	9900	9200	700
8	0.76	582	456, 805	18	9900	6600	3300
9	0.75	280	197, 484	9	10300	8800	1500
10	0.84	290	223, 414	10	10300	8100	2200
12	0.92	242	207, 289	15	11000	9850	1150

\* $r^2$  = coefficient of determination for  $\ln(\text{PAR})$  vs Time

\*\* Range = 95% confidence intervals for Doubling Times

n = number of data points used in the equation

## 5.2 White Spruce Increase

White spruce pollen was first detected in the southeast site (site 12, Table 5.5) at approximately 10,800 BP and in the southwestern sites (sites 9 and 10, Table 5.5) at approximately 10,000 years BP. The pollen is continuously recorded in the northernmost site by 8,550 BP. White spruce pollen is recorded throughout the region within 2,250 years, slightly faster than for black spruce.

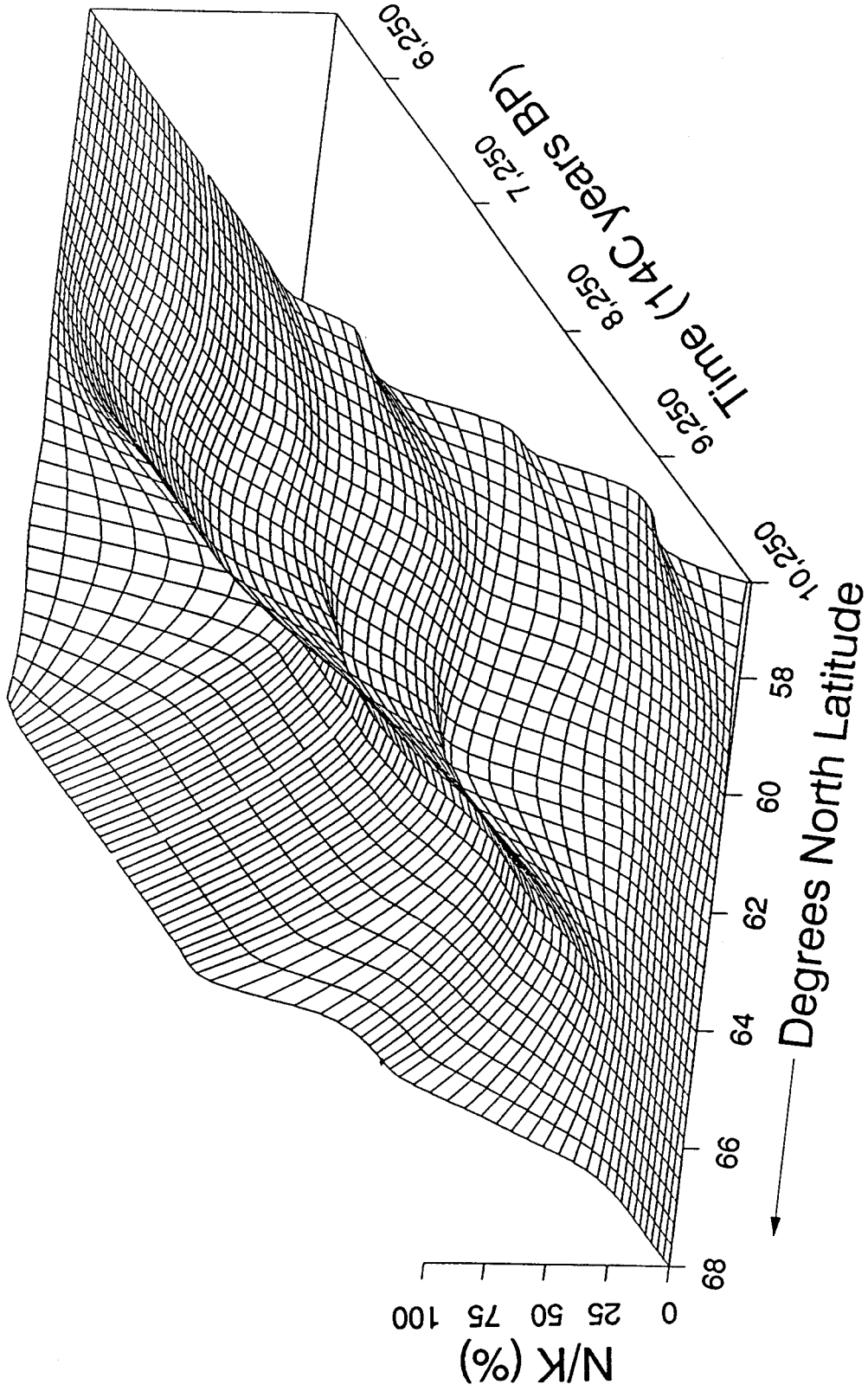


Figure 5.17. The postglacial spread of black spruce across the western interior of Canada (includes all high elevation and low elevation sites 1, 2, 3, 5, 6, 7, 8, 9, and 10). 9

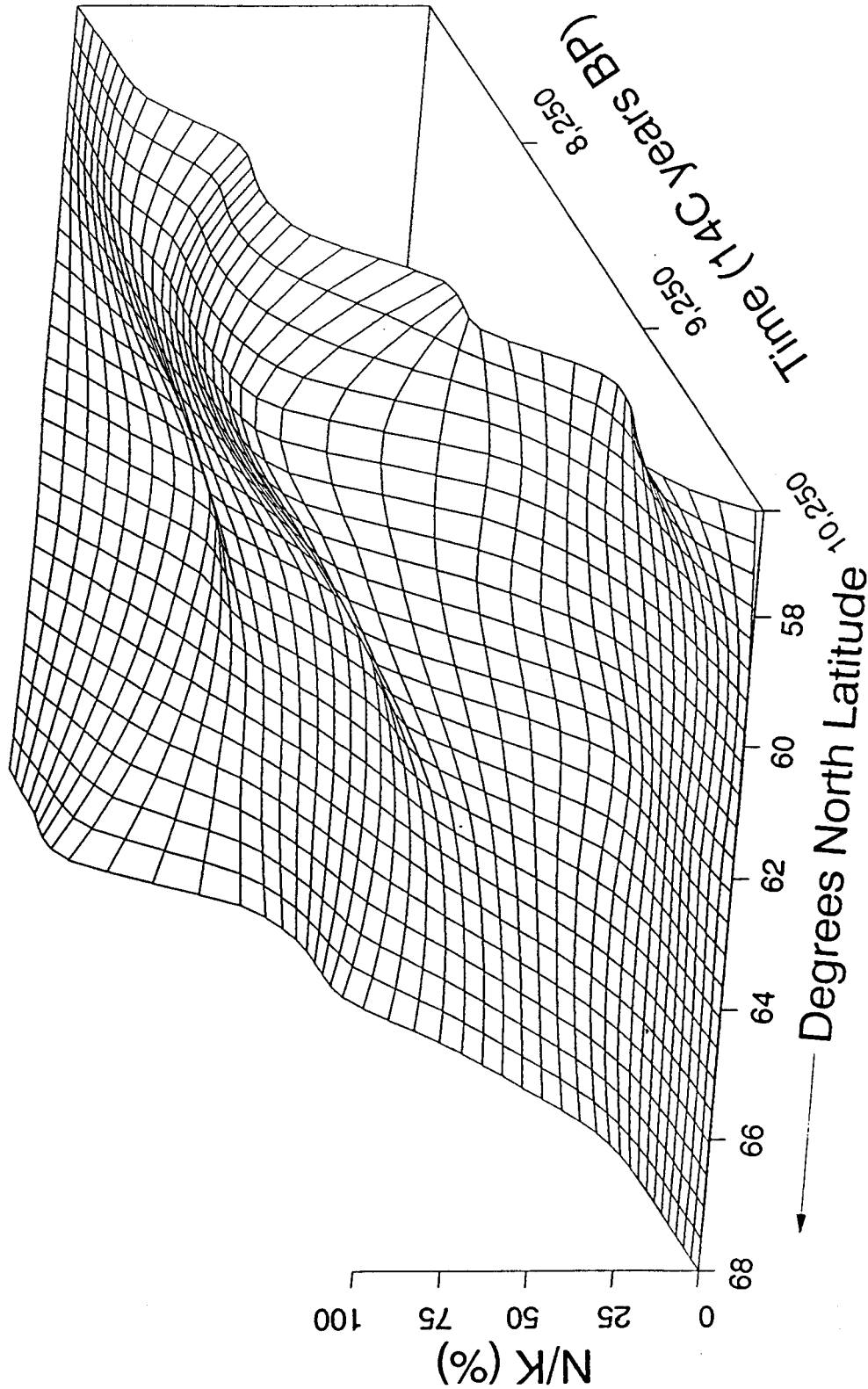


Figure 5.18. The postglacial spread of black spruce across the western interior of Canada (includes only the low elevation, low latitude sites 1, 2, 5, 7, 9, and 10).

The duration of white spruce PAR increase varied between the sites (Table 5.5). Expansion continued for 800 to 900 years in the south, while in the central and northern sites the increase to modern PAR levels took 450 to 550 years. The durations of expansion were prolonged at the high elevation/high latitude sites (sites 3, 6, and 8), taking 1000 to 3100 years from initial recording to modern PAR levels. At site 2 both black and white spruce took approximately 500 years to reach modern PAR levels, but at all other sites white spruce expansion was faster than black spruce.

**Table 5.5.** White spruce fossil pollen increase (shading indicates a high latitude high elevation site).

Site	$r^2$ *	Doubling Time (years)	Doubling Time Range (years)**	n	Expansion		
					Start (yr BP)	End (yr BP)	Duration (years)
1	0.95	85	68, 113	5	8550	8100	450
2	0.80	105	73, 184	7	9550	9050	500
3	0.68	642	434, 1228	10	9000	5900	3100
5	0.86	105	87, 132	6	9550	9000	550
6	0.84	191	128, 380	5	9400	8400	1000
7	0.81	109	80, 206	6	9800	9250	550
8	0.73	613	466, 899	16	9900	7900	2000
9	0.52	279	145, 420	6	10000	9200	800
10	0.90	168	122, 267	5	10000	9200	800
12	0.64	327	230, 564	14	10800	9900	900

\* $r^2$  = coefficient of determination for ln(PAR) vs Time

\*\*Range = 95% confidence intervals for Doubling Times

n = the number of data points used in the equation

The doubling times for white spruce suggest similar patterns of spatial variation as seen for black spruce. Sites 1 and 2 in the northern part of the region and sites 5 and 6 in the central areas show fast rises in the PAR levels (Table 5.5), with doubling times of 85 to 109 years. Sites 9, 10, and 12 in the southeast and southwest took longer for the PAR levels to double, with doubling times of 168 to 327 years, indicating slower growth. The doubling times at the high latitude/high elevation sites (sites 3, 6, 8) varied. At site 6, the doubling time was 191 years, similar to the doubling times at the southern sites. At sites 3 and 8, the doubling times were 642 and 613 years respectively, far longer than at any other site.

Comparing white spruce to black spruce, the doubling times for one species were not consistently slower or faster than for the other species. At the northernmost site (site 1), at a central site (site 5), at one of the high latitude/high elevation sites (site 6) and at a southern site (site 10), white spruce has more rapid doubling times than black spruce. However, at the southeast site (site 12) and at the other two high latitude/high elevation sites (sites 3 and 8), white spruce has slower doubling times than black spruce. At the other three sites (sites 2, 7, and 9) the doubling times were similar for the two species.

The form of white spruce northward expansion when all sites are included (Figure 5.19) illustrates the delay of expansion in high latitude/high elevation areas by the troughs in the surface between 62° and 65°N latitude and around 59°N latitude (sites 3, 6, and 8). The removal of these sites illustrates the general form of



spread for white spruce (Figure 5.20). As with black spruce, the spread of white spruce takes the form of covering the region at low levels and then expanding to modern levels at each site from the south to the north behind the initial wave.

### **5.3 Jack Pine Increase**

Jack pine pollen is not detected until approximately 7,200 to 6,800 BP at the two southern sites (sites 12 and 13, Table 5.6). By 3,800 BP jack pine pollen is recorded at site 4, the northernmost site in this study where pine is present. At site 3, a continuously low influx of jack pine pollen is registered. However, this site is approximately 50 km north of a jack pine stand recorded by Porsild and Cody (1980) and approximately 200 km north of site 4 where jack pine is present today. Therefore, the pollen influx recorded at site 3 is believed to be derived from distant sources. Jack pine pollen expansion at the northern site (site 4, Table 5.6) occurs approximately 3,400 years after initial pollen rise at the southern sites (site 12 and 13). Thus the period of spread across the region for jack pine is approximately 1,000 years longer than for either spruce species.

Jack pine expansion periods were relatively long at the southern sites (sites 12 and 13, Table 5.6), and longer at the central and northern sites (sites 4, 5, 6, and 11). Jack pine doubling times also show spatial variations in the PAR increases (Table 5.6). Doubling times were quite rapid at the southern sites (224 and 189 years at sites 12 and 13 respectively) and were progressively slower with increasing latitude

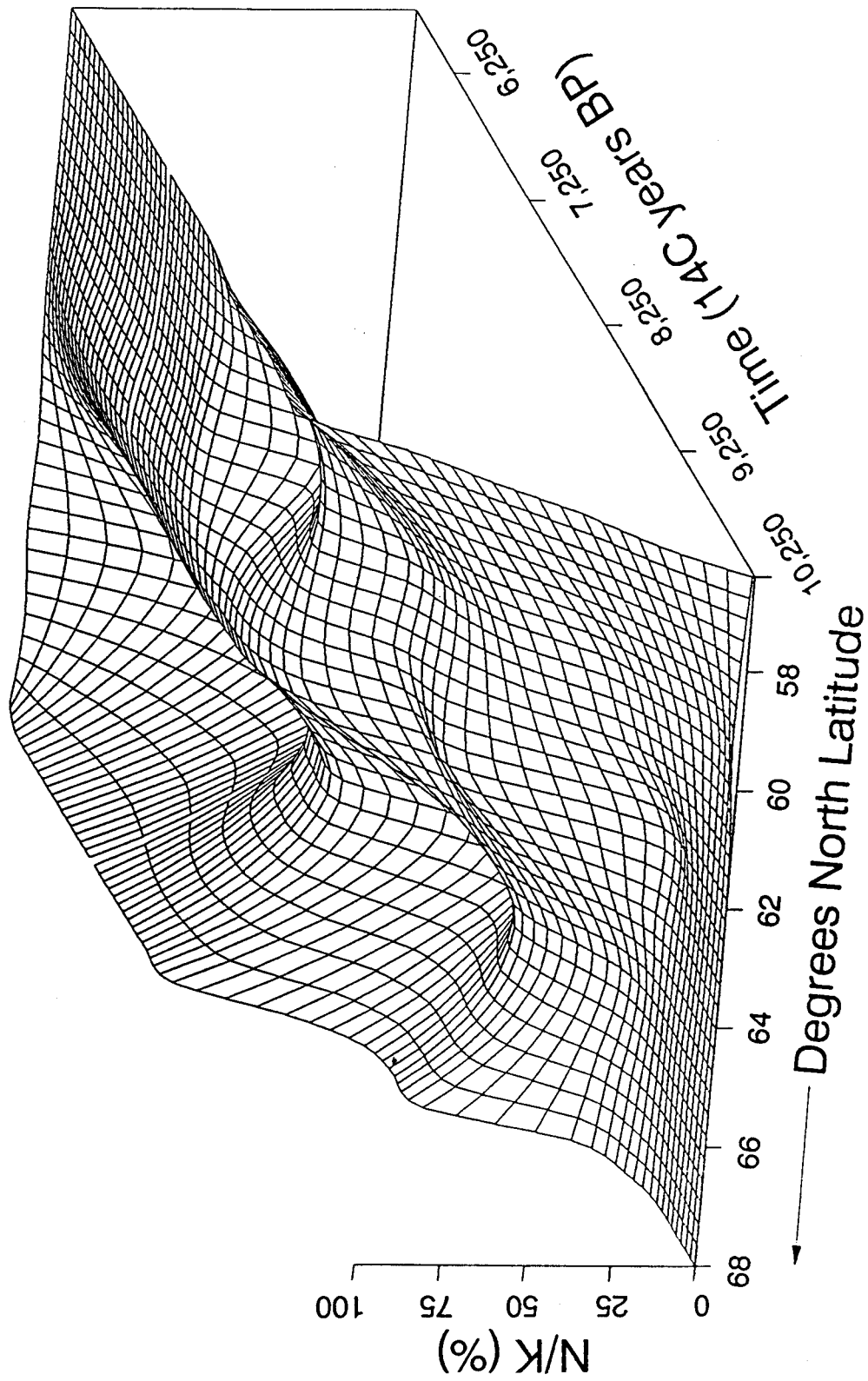


Figure 5.19.

The postglacial spread of white spruce across the western interior of Canada (includes all high elevation and low elevation sites 1, 2, 3, 5, 6, 7, 8, 9, and 10).

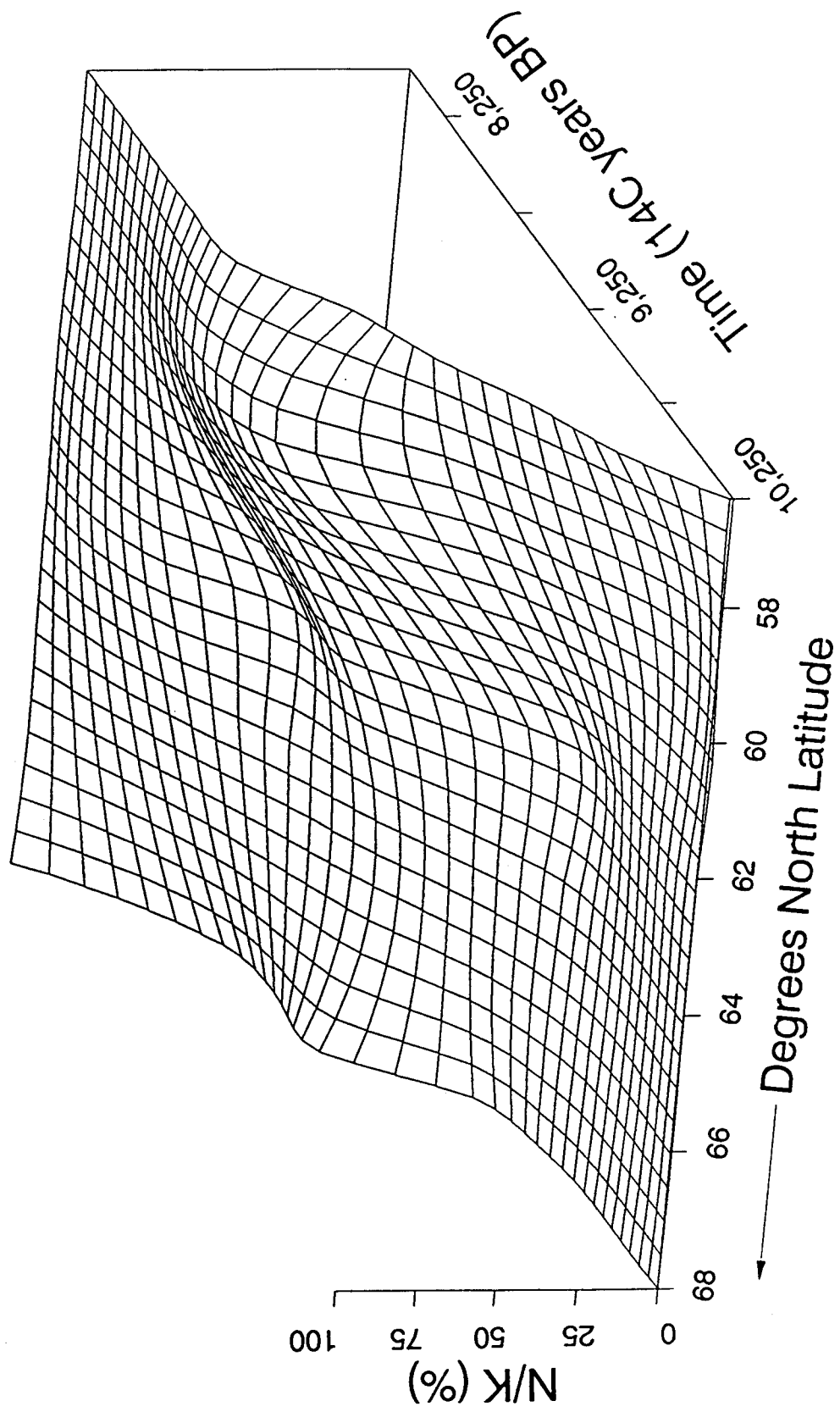


Figure 5.20. The postglacial spread of white spruce across the western interior of Canada (includes only low elevation low latitude sites 1, 2, 5, 7, 9, and 10).

**Table 5.6.** Jack pine fossil pollen increase (shading indicates a high latitude high elevation site).

Site	$r^2$ *	Doubling Time (years)	Doubling Time Range (years)**	n	Expansion		
					Start (yr BP)	End (yr BP)	Duration (years)
4	0.82	525	389, 806	9	3800	2100	1700
5	0.78	564	430, 835	10	6300	4100	2200
6	0.98	624	536, 747	4	5200	3200	2000
11	0.75	359	245, 671	8	6500	4650	1850
12	0.92	224	184, 284	9	7200	6100	1100
13	0.83	189	136, 312	7	6800	6050	750

\* $r^2$  = coefficient of determination for  $\ln(\text{PAR})$  vs Time

\*\*Range = 95% confidence intervals for Doubling Times

n = the number of data points used in the equations.

(359 years at site 11, and 525 and 564 years at sites 4 and 5 respectively). The longest doubling time of 624 years, occurs at the high latitude/high elevation site 6. At the southern sites and the high elevation/high latitude site, the rates of increase are comparable to spruce. However jack pine expansions at the central and northern sites are relatively longer than for spruce.

The pattern of jack pine pollen expansion is considerably different from that seen for spruce. Jack pine expanded northward across the study area at a slow rate. Once established it gradually increased to modern levels suggesting spread in the form of a more compact front (Figure 5.21).

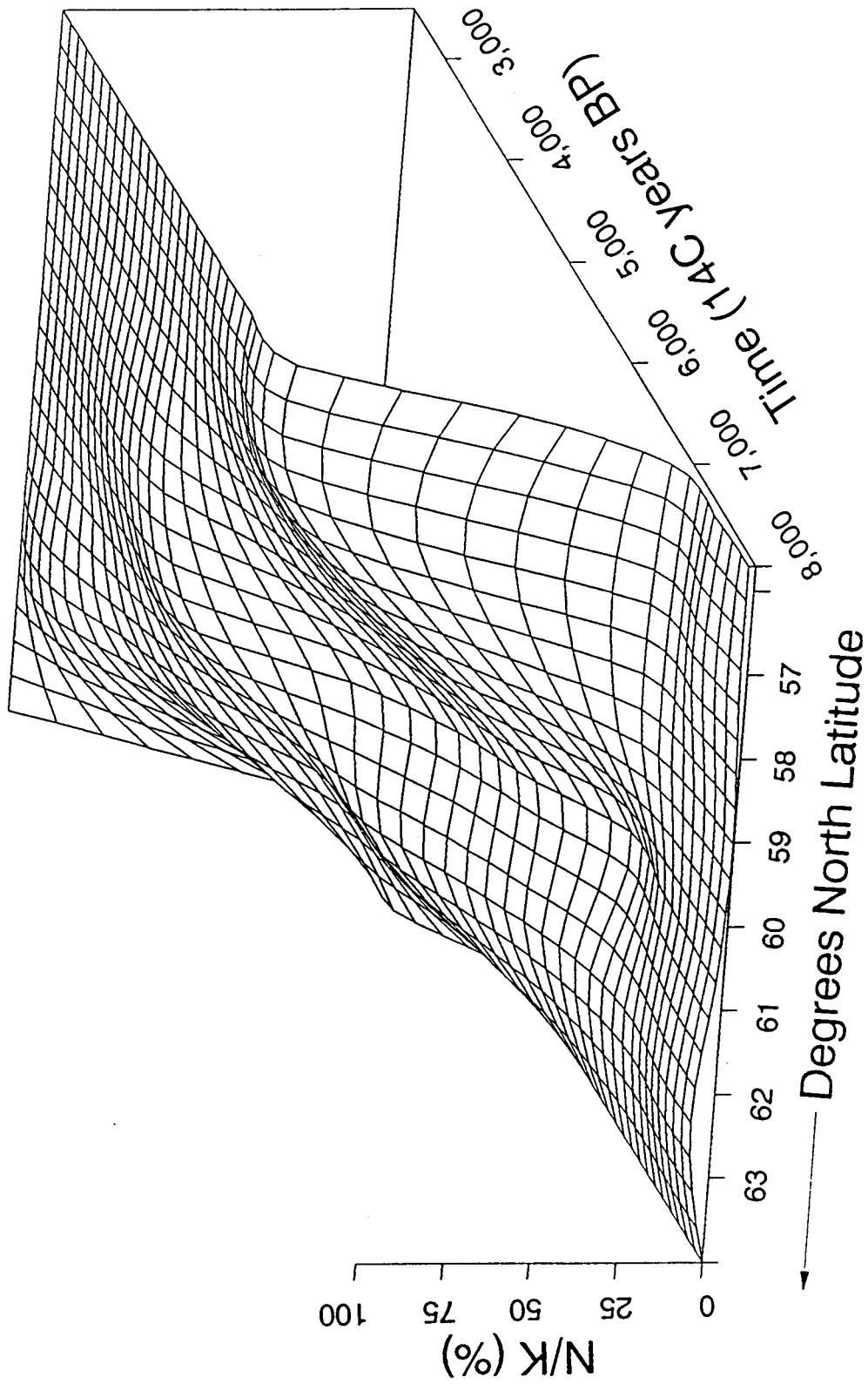


Figure 5.21. The postglacial spread of jack pine across the western interior of Canada (includes sites 4, 5, 6, 11, 12, and 13).

## **CHAPTER VI**

### **DISCUSSION**

#### **6.0 Introduction**

The reconstruction of postglacial expansion of jack pine, black spruce, and white spruce has revealed both intraspecific and interspecific spatial variation in the rates of increase and the spread across western Canada. Black and white spruce experienced slow rates of increase in the southern part of the region and faster rates in the north. In contrast, jack pine increased slowly in the northern sites and more rapidly in the south. At high latitude, high elevation sites all species had slow rates of increase. Interspecific variation in expansion occurred between the two spruce species and jack pine. Relative to spruce, jack pine increased slower, its spread across the region lasted at least 1000 years longer, and the form of the spread was a compact front with a slow expansion northward and slow increase to modern abundance. In contrast, the forms of spread for white and black spruce were low level waves with rapid expansion northward at low abundance levels.

#### **6.1 The Form of Pollen Rise**

Assuming that the pollen record reflects the expansions of past populations of spruce and pine, the population growth at the sites were approximated by

exponential equations, with the populations having increased to environmentally controlled carrying capacities, about which the populations subsequently fluctuated. For the spruce species, and for jack pine at four of the sites (sites 4, 5, 6, and 12), exponential equations approximated the growth better than did the logistic or linear equations. Logistic increase is often considered a more realistic model of population growth as it encompasses the effects of density stress eventually experienced in a resource-limited environment (Kellman, 1980; Pielou, 1970). Wide sampling intervals may not adequately record the period of decreased rates of population growth as the carrying capacity is approached. However, even when temporal resolution is high, the increase in pollen influx has been shown to often be exponential rather than logistic (Bennett, 1983). The prevalence of exponential growth forms in this study and the palynological literature may be primarily due to random fluctuations in the populations and fluctuations in the pollen record unrelated to the population (noise) including variation in pollen production, dispersal, and deposition (MacDonald, 1988). Kellman (1980) produced three growth curves illustrating the effect on logistic growth of randomly fluctuating population levels by  $\pm 30\%$  at each generation (Figure 6.1). The resulting stochastic growth curves (curves b and c, Figure 6.1) may be estimated by either exponential or logistic curves.

For jack pine at sites 11 and 13, population growth may be better modelled by linear equations. Uncommon in population growth models (Pielou, 1977), temporal limitations in the data, and fluctuations in both fossil pollen levels and

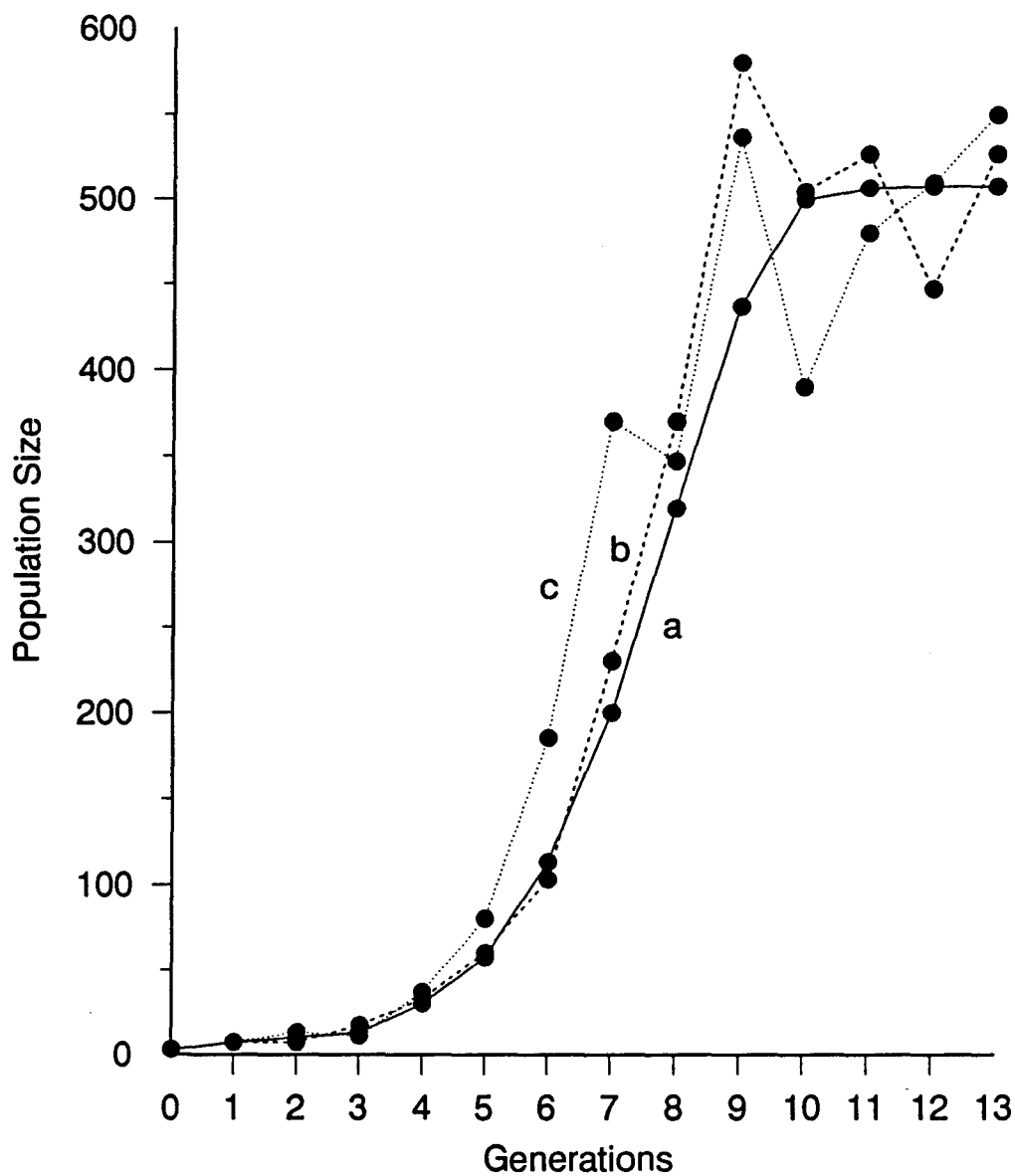


Figure 6.1. Population growth under resource-limited conditions for discrete generations. (a) Deterministic growth curve of logistic form. (b) and (c) Two stochastic growth curves in which populations were allowed to fluctuate randomly by  $\pm 30\%$  at each generation (Kellman, 1980).



actual population levels, may have combined to produce initial expansions that can be modelled by different equations. If, however, jack pine populations did increase linearly at sites 11 and 13, it suggests that the birth rate was independent of population size, and that as the population increased the birth rate per individual decreased. In this case, the reproductive rate and the population growth rate, would have been under tight control of the environmental conditions.

## **6.2 Factors Controlling Expansion**

Climate change and glacial retreat produced the potential for plant invasion onto deglaciated terrain. However, the differences in the rates of population growth of black spruce, white spruce, and jack pine were likely controlled by a variety of factors present at the time of expansion, including environmental change (particularly climatic) and static environmental conditions (particularly topography and substrate). In addition, ecological characteristics, including the intrinsic reproductive ecology of the individual species, and the botanical conditions encountered, may have had an impact on their expansion and rate of population growth.

## **6.3 Physical Environmental Change**

Postglacial climatic warming and glacial retreat is known to have occurred extremely rapidly in western Canada (COHMAP, 1988; Dyke and Prest, 1987; Ritchie, 1987). However, it is difficult to determine if the spread of tree taxa were

synchronous with climate. Black and white spruce spread quickly across western Canada in the early postglacial and likely occurred throughout region within 2450 years of initial expansion in the south. This short period of expansion suggests that the regional rate of climate change was not limiting to spruce spread and that spruce may not have lagged far behind the environmental changes. Ritchie and MacDonald (1986) proposed that strong anticyclonic winds centred around the Laurentide ice sheet in the late glacial may have promoted rapid seed dispersal over long distances, thereby contributing to the rapid rate of spread of white spruce across western Canada. Both spruce species have small aerodynamic seeds and can be transported long distances (Fowells, 1965) and therefore the spread of both species may have been enhanced by strong surface winds.

At the time of spruce expansion, 11,000 to 8,000 BP, temperatures were increasing and peaked over much of western Canada between 9,000 to 6,000 BP (COHMAP, 1988; Kutzbach and Guetter, 1986). Early initial expansion in the southern sites, occurring in the early postglacial ( $\sim$  10,800 to 10,000 BP), may have experienced slow rates of increase and prolonged the periods of expansion due to the lower temperatures that still existed at that time. In the northern and central sites expansion began later in the postglacial (9,800 to 8,550 BP). Higher temperatures during this period which stimulated the early- to mid-postglacial treeline advance north of the modern treeline position (Ritchie, 1987), may have promoted rapid spruce expansion.

The spread of jack pine throughout the study area occurred over an extended period of time (8,200 to 2,600 BP). Despite the possible onset of favourable climatic conditions in the early Holocene (c. 9,000 BP), jack pine expansion was not initiated until approximately 7,200 BP. The spread of jack pine may have lagged behind climate change. Nonetheless, the spatial patterns in the rates of expansion appeared to be influenced by the climatic conditions during expansion. Pine expansion in the two southern sites occurred during the Hypsithermal. In addition to rising temperatures, an increase in fire frequency due to the warm, dry conditions of the Hypsithermal (Liu, 1980, Ritchie, 1987), may have favoured rapid expansion of jack pine, which is a fire-adapted species (Critchfield, 1985). Expansion in the central and northern areas occurred at the end of the Hypsithermal and/or during the subsequent period of cooling. Less favourable temperatures and possibly an associated decrease in fire frequency may have contributed to the slow rates of increase observed for jack pine at this time.

The development of soils has also been cited as a potential control on the expansion of trees (Pennington, 1986). The increase in black spruce in western Canada has been linked to the increase in *Sphagnum* spores indicative of the development of muskeg (MacDonald, 1987a, b; Ritchie, 1987). The rate of muskeg development may have influenced the rate of expansion and spread of black spruce. However, peak muskeg development is recorded between 8,000 and 4,000 BP (MacDonald, 1987a, b; Ritchie, 1987) which is after black spruce reached modern

pollen levels. Both white and black spruce have the capabilities to establish on a range of substrate conditions including, for black spruce, bare mineral soil and peat deposits and for white spruce, alluvial, fluvial and glacial deposits (Fowells, 1965). Therefore, soil development may not have been the primary influence on the expansion of these species.

#### **6.4 Static Physical Environment Conditions**

Though climate change is an important factor in vegetation development over time, at any point in time the prevailing climatic conditions vary spatially with both latitude and elevation and may have affected expansion. Slower rates of increase for all species at high elevation/high latitude sites may be the result of less favourable climatic conditions at these sites. Daubenmire (1978) has shown that the position of altitudinal treeline within high northern latitudes occurs at lower elevations (Figure 6.2) and suggested that the primary controls are temperature and the length of the growing season. At high elevation and latitude there may be insufficient energy for trees to grow and reproduce, thereby affecting the abundance and stature of trees and ultimately the position of treeline (Payette, 1983; Black and Bliss, 1980).

The high elevation/high latitude sites in this study (sites 3, 6, and 8) are situated within transition zones (Subalpine-Boreal and Forest and Barren zones, Figure 2.4). In these areas, lower temperatures and shorter growing seasons may have resulted in slower growth, delayed sexual maturity, infrequent and reduced seed

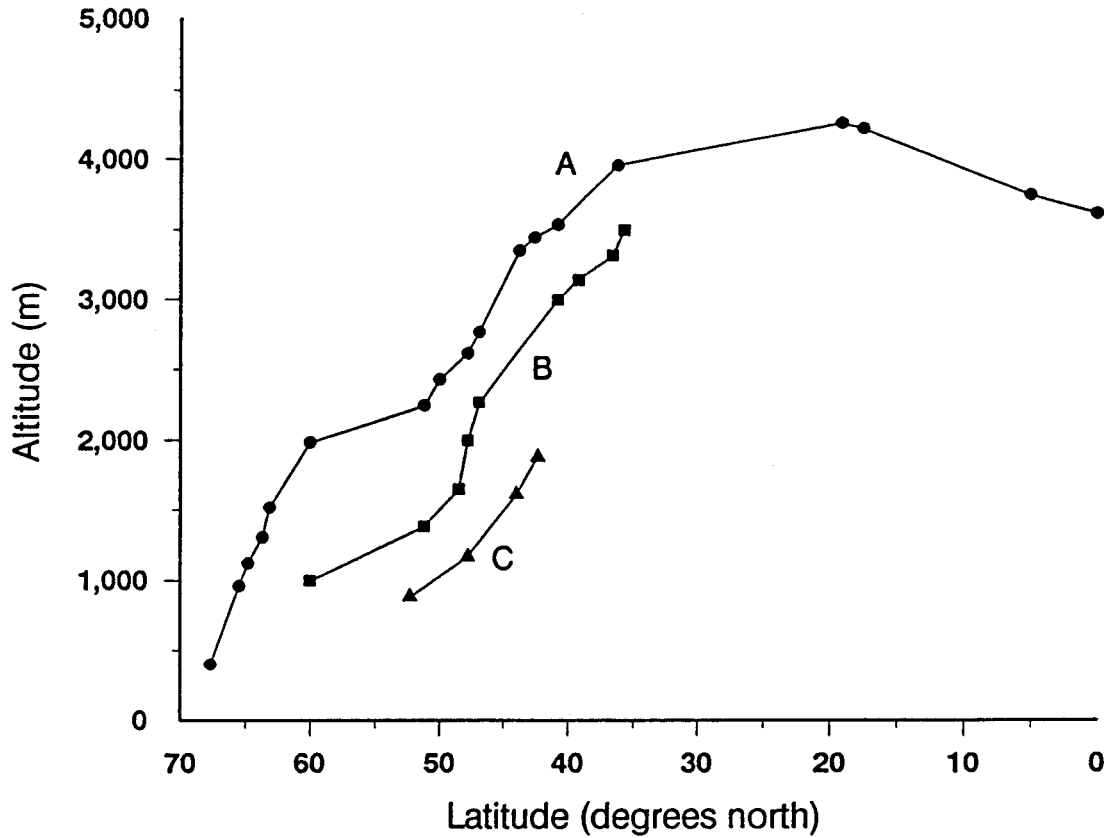


Figure 6.2. Upper altitudinal limits of trees along mountain axes, as related to latitude.  
 A. Cordillera well inland from the Pacific Ocean  
 B. Mountains near the Pacific Ocean from southern Alaska to southern California  
 C. Torngat Mountains to Labrador to northeastern United States (Daubenmire, 1978).

and pollen production, reduced seed viability, and high seedling mortality (Black and Bliss, 1980; Ritchie, 1987; Fowells, 1965). Under stressful climatic conditions, other environmental factors such as topography, exposure, and the presence of bedrock outcrops, become important in the distribution, growth and reproduction of trees (Ritchie, 1987). Suitable habitat may be limited within such environments. These static environmental conditions may have been reflected in the slower rates of population growth recorded at high elevation/high latitude sites.

### **6.5 Ecological Characteristics**

The spread of jack pine across the study region and the rates of increase, particularly in the northern sites, were slower compared to spruce. These variations may have been influenced by the differences in ecological traits between the species and differences in the botanical conditions at the time of expansion. Late glacial pollen records suggest that both spruce species were present just south of the ice limits when climatic warming and glacial retreat began (Jacobson *et al* 1987; Ritchie, 1987; Figure 6.3). Spruce invaded a relatively open herb and shrub dominated landscape with only scattered stands of poplar (MacDonald, 1987a, b). Botanical competition would have been extremely low. In addition, both black and white spruce are able to colonize varying substrates (Fowells, 1965; Rowe, 1970). Plasticity in ecological requirements may augment expansion rates (Brubaker, 1986). With the addition of rapidly ameliorating climatic conditions and long distance dispersal,

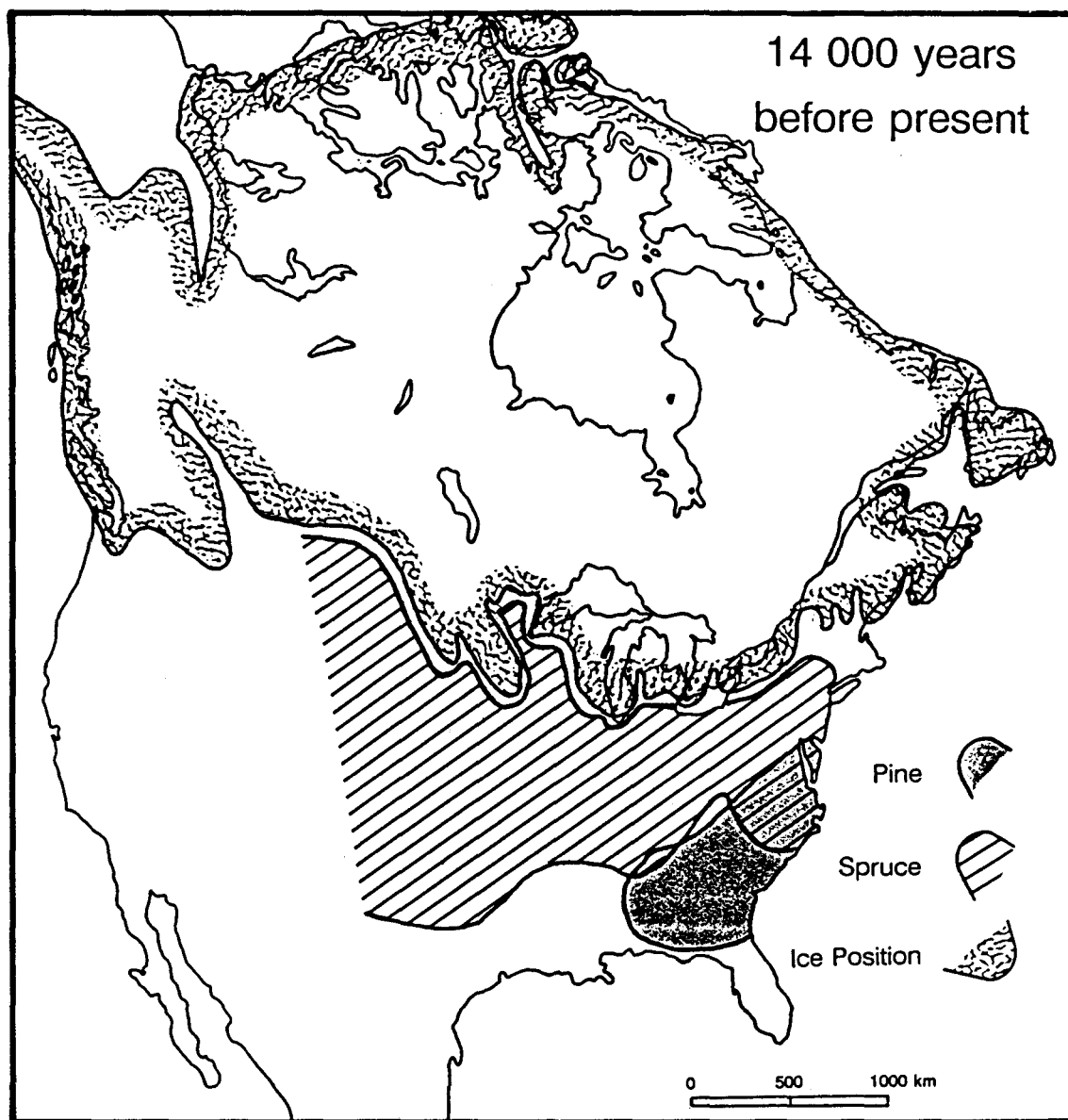


Figure 6.3 Approximate extent of glacial ice and the distribution of lakes recording spruce and pine pollen at 14,000 BP (from Dyke and Prest, 1987; Jacobson *et al*, 1987).

enhanced in the late-glacial by strong southerly surface winds, spruce expansion proceeded quite rapidly. These factors may have promoted expansion via the establishment of small outlying populations with increases in density occurring behind the advancing wave as suggested by the three-dimensional form of expansion presented in this study (Figures 5.18 and 5.20) and by Bennett (1985), Birks (1989), Pennington (1986), Prentice (1986), and Watts (1973). It remains unclear whether the expansion was a continuous low-density spread or whether the spread was patchy with populations later merging (Bennett, 1985). A finer spatial scale and spruce macrofossil studies within western Canada are needed for this determination.

Full glacial and late glacial pollen records suggest that jack pine distribution was restricted to central and eastern United States (Figure 6.3, Jacobson *et al*, 1987). At the onset of climatic warming and glacial retreat, jack pine was far to the south of any open landscape. Pine spread north across eastern United States and then northwest across the Great Lakes Region, at all times having to invade fully forested areas. Jack pine is not a strong competitor; in eastern Canada its southern boundary is set in part by competition from deciduous taxa (Ritchie, 1987) and it is often restricted by competition to poor sites where other taxa cannot grow (Brubaker, 1986). It is dependant on fire to remove vegetation, open areas for invasion and to release its seed stored in serotinous cones (Fowells, 1965). Jack pine did not reach southern Manitoba until approximately 10,000 BP (Jacobson *et al*, 1987) at which point further expansion appeared to be limited by Glacial Lake Agassiz to the west



and glacial ice to the north (Dyke and Prest, 1987; Figure 6.4). At this time spruce had expanded into northern Alberta.

When jack pine reached the southern part of the study region, at approximately 7,200 BP, both spruce species had completed expansion at all low elevation sites. Jack pine had to invade closed spruce forests. Though jack pine seed is light and aerodynamic and can be transported long distances (Harper, 1977), the low competitive ability of pine may have delayed establishment and expansion until the occurrence of fire. Since the source area of jack pine pollen is fairly large (estimated as  $<100 \text{ km}^2$  for small to medium size lakes; Prentice, 1985) numerous fires and a short fire cycle may be needed before jack pine becomes firmly established at all available sites within the pollen source area of a lake. Therefore, the delayed onset and variable rates of jack pine expansion and its slow spread throughout the study region, may have been a result of its fire dependency, the botanical conditions during expansion, and the climatically controlled fire cycle which may have varied throughout the postglacial.

The form of jack pine spread (Figure 5.21) is similar to the *k-migration strategist* model proposed by Delcourt and Delcourt (1987), with slow expansion of jack pine northward and slow rise in population levels. However, the significance of the low levels of pollen influx prior to the rapid increase to modern levels, remains unclear. One alternative to the idea that the pollen originates from distant sources is the possibility of small fugitive populations of pine occurring in sites unfavourable

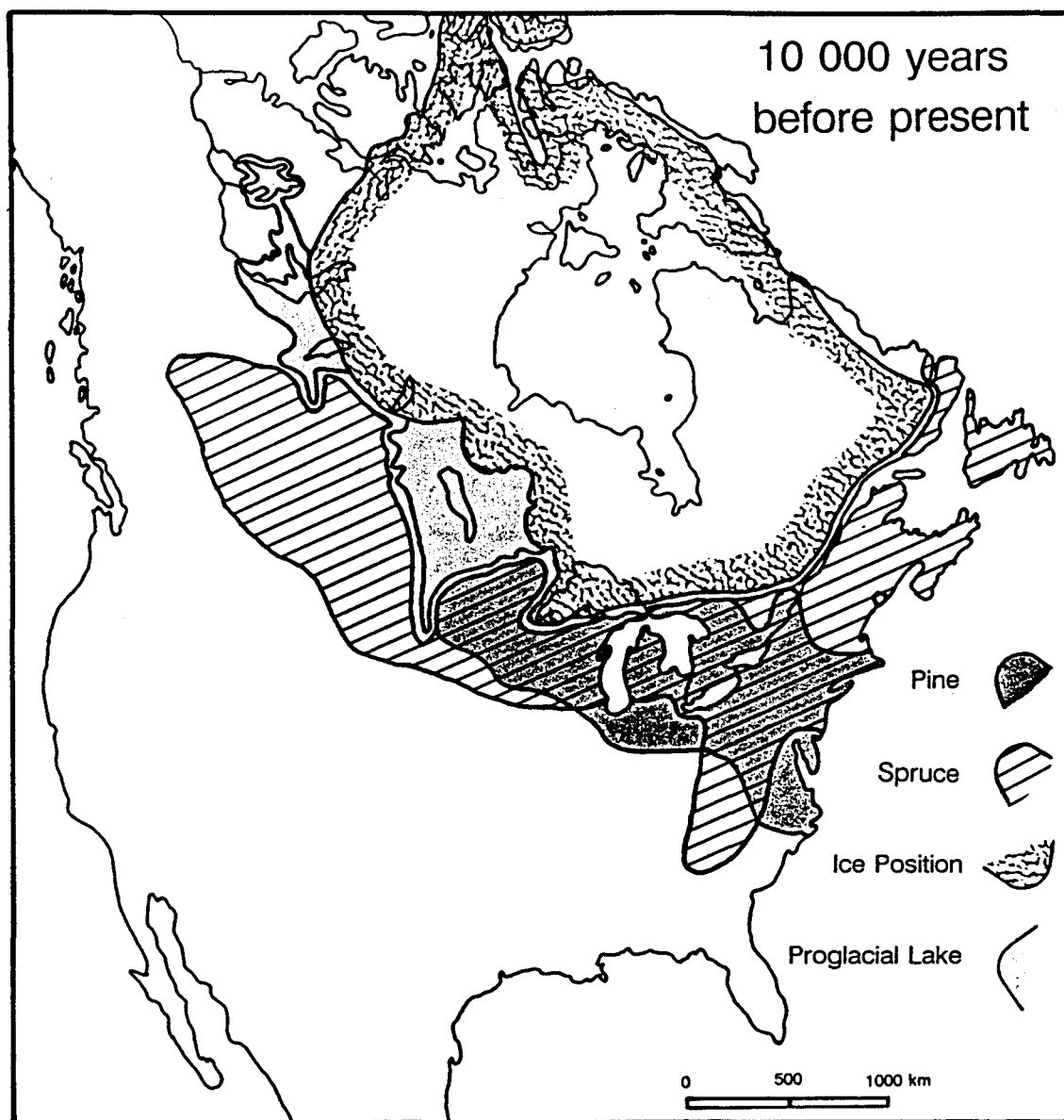


Figure 6.4 Approximate extent of glacial ice and distribution of lake sites recording spruce and pine pollen at 10,000 BP (Dyke and Prest, 1987; Jacobson *et al.*, 1987).

for the growth of other trees. Prominent substrates within the Canadian Shield include thin, dry, sandy, and coarse-grained soils; poor sites on which outlying scattered individuals may be able to invade. This hypothesis may be tested by studying the macrofossil records preserved in the sediments of small lakes within this region.

## **6.6 Conclusions**

With respect to the hypotheses proposed in the introduction, both interspecific and intraspecific variation were shown in the expansion of white spruce, black spruce, and jack pine in western Canada. In particular five points are noteworthy:

- 1) The expansion of white and black spruce began in the late-glacial/early postglacial, and proceeded to rapidly spread northward. The onset of jack pine expansion occurred over 3,000 years later and the spread northward lasted approximately 1,000 years longer than for spruce.
- 2) On average, jack pine had slower rates of increase.
- 3) The doubling times and the expansion periods varied with latitude; rapid spruce expansion was recorded in the central and northern sites, while rapid pine expansion was recorded in the southern sites.
- 4) All species had the slowest expansion at the high elevation sites in the north.
- 5) Spruce rapidly expanded northward at low population levels and increased

to modern levels behind the advancing wave. Jack pine slowly expanded northward and slowly increased to modern population levels, producing a compact front advancing across the landscape.

These observations can be explained in terms of the physical and botanical conditions present at the time of expansion and the ecological traits of each species. Regional climatic change in the early postglacial differentially affected spruce population increase at the various sites, stimulating population growth in the central and northern areas, and slowing the growth in southern sites. Hypsithermal climatic conditions promoted jack pine expansion which occurred at the time in the southern part of the study region. Subsequent cooling may have slowed the expansion in central and northern areas. However, temperatures *per se*, may not have limited or promoted pine expansion. Rather, variance in expansion may have resulted from the effect of climate on fire frequency.

Regional climate change cannot explain all variation in the rates of expansion. Static environmental conditions vary with elevation, latitude, and topography and resulted in reduced rates of population expansion at high elevation/high latitude sites. This has implications concerning the reconstruction of range extension. Care should be exercised in the choice of sites and expansion models should be based on pollen records from sites with similar local and regional environmental conditions. In addition, if a taxon cannot be detected in the pollen record until its population has increased to a particular level, variations in expansion rates may affect the accuracy

of arrival times and therefore the accuracy of migration rates. Macrofossil records and an increase in the number and density of sites in western Canada, are necessary to determine the precise relationship between models of spread based on pollen records and true range extension of a species.

Suitable climatic conditions may not have been the sole factor affecting the expansion of a taxon. Being highly adapted to fire occurrence in the boreal forest and with long distance dispersal capabilities, jack pine is able, in modern times, to quickly colonize and dominate open areas. However, the inability to successfully compete in areas that are undisturbed and densely forested appears to have hindered the spread of jack pine in the postglacial. Dispersal capabilities may not always reflect expansion capabilities. Rather than dispersal-distance curves, data on offspring establishment with distance from the source may be more informative in theories of postglacial expansion.

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## APPENDIX 1

### LIST OF SCIENTIFIC AND COMMON PLANT NAMES

<i>Abies</i>	fir
<i>Abies balsamea</i>	balsam fir
<i>Abies lasiocarpa</i>	alpine fir
<i>Acer</i>	maple
<i>Alnus</i>	alder
<i>Alnus crispa</i>	green alder
<i>Alnus glutinosa</i>	European alder
<i>Andromeda polifolia</i>	bog rosemary
<i>Arctostaphylos</i>	bearberry
<i>Arctostaphylos alpina</i>	alpine bearberry
<i>Artemesia</i>	wormwood
<i>Betula</i>	birch
<i>Betula papyrifera</i>	paper birch
<i>Betula glandulosa</i>	dwarf birch
<i>Carex</i>	sedge
<i>Carya</i>	hickory
<i>Castanea</i>	chestnut
<i>Corylus</i>	hazel
<i>Corylus avellana</i>	hazel, cob-nut
Cupressaceae	cypress family
Cyperaceae	sedge family
<i>Ericales</i>	heath
<i>Eriophorum</i>	cottongrass
<i>Fagus</i>	beech
<i>Fagus grandifolia</i>	American beech
<i>Fraxinus</i>	ash
Gramineae	grass family
<i>Juglans</i>	walnut
<i>Larix</i>	larch
<i>Larix laricina</i>	tamarack
<i>Ledum groenlandicum</i>	Labrador tea
<i>Myrica</i>	bog-myrtle
<i>Nyssa</i>	tupelo

## LIST OF SCIENTIFIC AND COMMON PLANT NAMES

<i>Picea</i>	spruce
<i>Picea abies</i>	Norway spruce
<i>Picea glauca</i>	white spruce
<i>Picea mariana</i>	black spruce
<i>Pinus</i>	pine
<i>Pinus banksiana</i>	jack pine
<i>Pinus contorta</i>	
<i>ssp latifolia</i>	lodgepole pine
<i>ssp contorta</i>	lodgepole pine (coastal form)
<i>Pinus resinosa</i>	red pine
<i>Pinus strobus</i>	white pine
<i>Pinus sylvestris</i>	scotch pine
<i>Populus</i>	poplar
<i>Populus balsamifera</i>	balsam poplar
<i>Populus tremuloides</i>	trembling aspen
<i>Pseudotsuga</i>	Douglas-fir
<i>Quercus</i>	oak
<i>Rubus chamaemorus</i>	cloudberry
<i>Salix</i>	willow
<i>Salix glauca</i>	blue-green willow
<i>Sphagnum</i>	sphagnum, peat moss
<i>Thuja plicata</i>	western redcedar
<i>Tilia</i>	basswood, lime tree
<i>Tilia cordata</i>	small-leafed lime
<i>Tsuga</i>	hemlock
<i>Tsuga mertensiana</i>	mountain hemlock
<i>Ulmus</i>	elm
<i>Vaccinium</i>	blueberry group
<i>Vaccinium myrtilloides</i>	blueberry
<i>Vaccinium vitis-idaea</i>	bog cranberry