

COMPARATIVE ANALYSIS OF GROWTH-CLIMATE RELATIONSHIPS,  
GROWTH PERFORMANCE, AND MICROENVIRONMENTS OF  
WHITE SPRUCE (*PICEA GLAUCA*) WITHIN THREE HABITATS IN  
SPRUCE WOODS PROVINCIAL PARK, MANITOBA

By

Sophan Chhin

A Thesis

Submitted to the Faculty of Graduate Studies

in Partial Fulfillment of the Requirements

of the Degree of

MASTER OF SCIENCE

Department of Botany

University of Manitoba

Winnipeg, Manitoba

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THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

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## ABSTRACT

Growth – climate relationships, growth performance, and microenvironments of a disjunct population of white spruce [*Picea glauca* (Moench) Voss] were examined within three contrasting habitats (i.e., white spruce tree islands, open prairie, and aspen groves) at its southern limit of distribution in the prairie-forest boundary. The study was conducted within four mixed-grass prairie preserves in the Spruce Woods Provincial Park (SWPP) of southwestern Manitoba. Light and temperature conditions within the open prairie and island periphery accentuated the effects of the dry regional climate of the aspen parkland and mixed-grass prairie region. In contrast, light and temperature conditions under tree canopy of islands and aspen groves moderated the effect of the dry regional climate. The light-limited environments of the aspen groves and spruce islands outweighed the effect of moderated microclimatic conditions as low light conditions limited diameter growth and height growth of white spruce seedlings and saplings. Moisture deficiency exacerbated by temperature induced drought stress were factors that limited the growth of white spruce trees from spruce islands. The response of white spruce trees to the regional climate was moderated by the microclimatic conditions of the aspen groves since growth was restricted mainly by temperature induced drought stress.



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## CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

### 1.1 Introduction

The ecosystem complexity and large temporal and spatial scales of forest communities have precluded any direct examination of their past response to global change (Brubaker, 1986). Consequently, studies which have examined past climate-vegetation interactions make use of surrogate measures of that relationship without examining directly such factors as species composition or biomass changes. Surrogate measures include the use of tree pollen in paleoecology, age structure in demographic studies, the use of tree rings in dendrochronology, and the use of instrumental data.

General circulation models (GCMs) are mathematical models of the climate system and express the interrelationships amongst abiotic climatic factors over the land-sea-atmosphere interface (Breymeyer et al., 1996; IPCC, 2001). Current GCMs forced with a doubling of atmospheric CO<sub>2</sub> forecast future climate warming of 1.5°C - 4.5°C by 2070 - 2100 (IPCC, 2001). The projected increase in temperature is in addition to the 0.5°C increase over the last 140 years in the northern hemisphere (Jones and Briffa, 1992; Jones, 1994; IPCC, 2001). The rate of the projected warming is unparalleled in the twentieth century, and even during the last 10,000 years of the Holocene. Dendroclimatic reconstruction of proxy climate data also indicate that the current rate of warming is anomalous in comparison to past climatic changes (Jacoby and D'Arrigo, 1997). The prediction of precipitation changes is more variable due to regional differences in precipitation patterns. Overall, precipitation is expected to increase.

Although other greenhouse gases such as methane (CH<sub>4</sub>) and nitrous oxide (N<sub>2</sub>O) contribute to the greenhouse effect, CO<sub>2</sub> is the dominant greenhouse gas accounting for

60% of the total amount of greenhouse gases. The CO<sub>2</sub> concentration in 1750 measured at 280 ppm increased to 367 ppm by 1999, representing an increase of 31% (IPCC, 2001). Even if CO<sub>2</sub> levels were curtailed through mitigation efforts the effect of CO<sub>2</sub> would still persist due to its long residence time. The role of CO<sub>2</sub> as a causal factor of the past warming has been confirmed unequivocally by IPCC (2001), such that the warming is not part of natural climatic variation but is due to human industrial activity based on the use of fossil fuels.

Vegetation is expected to respond to climatic warming through changes in vegetation structure and function, as changes in precipitation and temperature patterns will affect growth, reproduction, survival and species migrations (Davis, 1989; Roberts, 1989; Long and Hutchin, 1991; Kirschbaum and Fischlin, 1995). The impact of climate on vegetation is expected to differ on a regional, seasonal, and a diurnal basis. Regionally, the effects of climate change are expected to be most apparent at mid to high latitudes. Therefore, the boreal forest ecosystem is expected to be sensitive to climatic change. Seasonally, the effects of climate change are expected to be most apparent during the winter when most of the warming will occur. Diurnally, temperatures are expected to rise mainly during the night. The increase in temperature is expected to change the seasonal water balance. That is, although precipitation is expected to increase, this will not offset the increased rate of water loss from soil and plant surfaces at higher temperatures. In addition to the change in abiotic components of the climate system (i.e., temperature, precipitation, and CO<sub>2</sub>), tree species must contend with natural and anthropogenic disturbance regimes.



## **1.2 Vegetation Response to Past Global Change**

### **1.2.1 Tree Pollen: Paleoecology**

Pollen analysis is a subdiscipline of paleoecology and involves the measurement of pollen abundance and composition in the strata of lake beds (Davis, 1989; Innes, 1991; Overpeck et al., 1991). The composition within a strata is considered a reflection of the actual species composition during a historical time period. The differential concentration of pollen between the different strata of lake sediments is therefore considered a reflection of changing vegetation composition with time. The pollen record indicates that since the last glaciation, tree species in North America began to migrate north during the Holocene. Trees migrated at a rate of approximately 10-45 km a century. Migration was affected by the dispersal method (e.g., wind versus animal dispersed seeds) and natural barriers (e.g., bodies of water and mountain ranges). Although the magnitude of future climate change is similar to that of the past, the projected rate is faster than the rate of warming during the Holocene. The migration rate of previous plants during the Holocene was possible due to the slow rate of warming.

### **1.2.2 Age Structure: Demography**

Demographic studies of tree species have been utilized to examine tree responses to past climatic change (Brubaker, 1986). Following tree cohorts from birth to death is impractical considering the longevity of trees. Therefore, studies of forest ecosystems relies on the examination of static age structures of trees in order to deduce the relationship between survivorship and past climatic variations. Since the effect of climatic changes are expected to be most apparent at mid to high latitudes and for tree species at their edge of distribution, most demographic studies have focused on tree populations within the boreal forest-tundra ecotone (Payette and Filion, 1985; Brubaker,

1986; Scott et al., 1987b; Szeicz and MacDonald, 1995a). These studies have indicated that tree establishment of conifer populations at the tree-line have responded to climatic warming. The altitudinal tree line has expanded and the density of conifers has increased within their current range of distribution. However, a latitudinal expansion has not been observed, and has been attributed to unsuitable microclimatic and edaphic conditions past the northern limit.

### **1.2.3 Tree Rings: Dendrochronology**

Dendrochronology is the science that deals with the dating of tree rings and the study of tree ring characteristics (Fritts, 1976; Schweingruber, 1988). Such tree ring characteristics include ring width and density. Dendroclimatology is a subdiscipline specializing in using tree rings to study past and present climate and therefore is pertinent in highlighting tree growth-climate interactions (Fritts, 1976; Hughes et al., 1982; Schweingruber, 1988). Studies in dendrochronology have highlighted the importance of selecting a suitable site and tree species which have the potential to be sensitive to environmental change. The extraction of relevant information from tree rings while removing the effects of confounding factors is a goal within the discipline of dendrochronology.

#### **1.2.3.1 Effect of Increased CO<sub>2</sub> on Radial Growth**

Under increased concentrations of CO<sub>2</sub>, stomatal conductance will decrease since a smaller stomatal pore will be required for CO<sub>2</sub> diffusion (Eamus and Jarvis, 1989; Mooney et al., 1991; Bazzaz and Fajer, 1992). The decrease in stomatal conductance is expected to lead to a decreased rate of evapotranspiration and therefore a decrease in the amount of water lost. This translates into a greater water use efficiency (WUE) which is defined as the amount of water respired per amount of CO<sub>2</sub> utilised. Consequently, well

drained, xeric site locations represent an ideal site location to detect the CO<sub>2</sub> fertilization effect, which is the hypothesis that increasing atmospheric CO<sub>2</sub> will enhance the growth of natural vegetation. Dendrochronological studies have attempted to demonstrate a CO<sub>2</sub> fertilization effect on tree radial growth but have generally resulted in mixed and confounding results (Kienast and Luxmoore, 1988; Graumlich, 1991; Innes, 1991; Luxmoore et al., 1993; Jacoby and D'Arrigo, 1997). These studies underscore the role of interacting factors such as climatic warming and nitrogen fertilization which have confounded the effect of CO<sub>2</sub>. LaMarche et al. (1984) reported increased radial growth of bristlecone pine (*Pinus longaeva* D.K. Bailey and *Pinus aristata* Engelm.) within a high-altitude environment and attributed it to increasing levels of CO<sub>2</sub>. Bristlecone pine showed a strip bark morphology which is postulated to lead to primary allocation of CO<sub>2</sub> into the active cambial region. This strip bark morphology was not observed in the study of Graumlich (1991) and therefore could explain her inconclusive results. LaMarche et al. (1984) reason that the low concentration of CO<sub>2</sub> at high altitudes would predispose plants to benefit from increasing CO<sub>2</sub> in the atmosphere. However, the results of LaMarche et al. (1984) may be confounded as they did not account for the possible effect of climatic change concomitant with the change in CO<sub>2</sub>.

### **1.2.3.2 Effect of Climatic Warming on Radial Growth**

Dendroclimatic studies have shown that temperature has influenced tree radial growth (Innes, 1991; Jacoby and D'Arrigo, 1997; Barber et al., 2000). Innes (1991) showed that climatic warming between 1850-1940 coincided with the onset of increased radial growth for trees growing at high northern latitudes. However, Innes (1991) demonstrated that the extraction of climatic information from tree rings can be confounded with the effects of other factors such as CO<sub>2</sub> and nitrogen fertilization. In

contrast to the expected increase in radial growth at high latitudes, Barber et al. (2000) demonstrated that the radial growth of white spruce [*Picea glauca* (Moench) Voss] within the boreal forest of Alaska showed reduced growth during the twentieth century. They attributed the decline in radial growth to temperature induced drought stress. The effect of drought stress in turn may impair the ability of boreal forests to act as a CO<sub>2</sub> sink.

Latewood density is considered an indicator of summer temperature, the period during which latewood is formed (Briffa et al., 1998). Briffa et al. (1998) examined the relationship between tree ring density and temperature and found that over the twentieth century density increased as climate became warmer. Barber et al. (2000) also showed a positive correlation between maximum latewood density and summer temperature. In a study of tree ring density of white spruce in western Canada's boreal forest, Jozsa and Powell (1987) demonstrated that white spruce showed increased biomass productivity coinciding with increased warming ever since the end of the Little Ice Age (ca. 1850).

Plants contain less of the carbon isotope (<sup>13</sup>C) compared to the surrounding atmosphere due to two photosynthetic fractionating processes (Brooks et al., 1998). First, fractionation occurs as a result of the property that <sup>12</sup>CO<sub>2</sub> diffuses into the leaf at a faster rate than <sup>13</sup>CO<sub>2</sub>. Second, fractionation occurs since Rubisco (Ribulose-1-5-bisphosphate carboxylase/oxygenase) is more reactive to <sup>12</sup>CO<sub>2</sub> than <sup>13</sup>CO<sub>2</sub>. Tree rings thus provide a record of carbon fractionation and in turn represent a record of photosynthesis and stomatal conductance. The effect of growing season drought through its effect on gas exchange will in turn affect isotope ratios. Generally, the amount of <sup>13</sup>C increases in plant tissues as drought stress increases. Brooks et al. (1998) studied the relationship between ring width and carbon isotope in relation to past climatic fluctuations within the

boreal forest in central Canada. They established that potential evapotranspiration (PET) was strongly related to  $^{13}\text{C}$  concentration at sites in the southern boreal forest thus indicating that growth in that region is restricted by low soil moisture supplies. Barber et al. (2000) also showed that the carbon isotope concentration was positively correlated with summer temperature.

#### **1.2.4 Instrumental Data**

Responses of forest vegetation to global change in the recent past have also been ascertained from satellite remote sensing measurements (Solomon and Shugart, 1993; Myneni et al., 1997). Satellite imagery data was obtained from Advanced Very High Resolution Radiometers (AVHRRs) on board the National Oceanic and Atmospheric Administration (NOAA) meteorological satellites. The satellites are capable of remotely sensing the visible red and infrared spectral bands of the light spectrum. The satellite imagery was used to delineate a vegetation index which is a surrogate measure of the photosynthetic activity of vegetation. They showed increased levels of plant growth in northern high latitudes from 1981 to 1991 and showed that it corresponded with increased surface air temperature. Keeling et al. (1996) documented a seasonal cycle of  $\text{CO}_2$  which rises during the fall and winter and declines in the spring and summer due to increased  $\text{CO}_2$  uptake by land vegetation. The amplitude of the seasonal cycle of  $\text{CO}_2$  has increased in recent decades and has been explained in terms of increased  $\text{CO}_2$  utilization by high latitude boreal forest ecosystems under a longer growing season. Therefore, the instrumental analysis of the seasonal cycle of  $\text{CO}_2$  levels can be used to infer past responses of boreal forests to  $\text{CO}_2$  induced climate change.

### 1.3 Vegetation Response to Future Global Change

#### 1.3.1 Global Climate Change

##### 1.3.1.1 Effect of Increased CO<sub>2</sub>

Physiology experiments in field and laboratory conditions have examined the response of juvenile plants to abiotic environmental changes in general, and the effect of CO<sub>2</sub> in particular (Eamus and Jarvis, 1989; Mooney et al., 1991; Bazzaz and Fajer, 1992; Diaz et al., 1993). Studies are conducted predominately in greenhouses where such studies are economically and logistically feasible. Field studies are more limited and usually do not extend for more than three growing seasons. Because of their focus on short term effects of CO<sub>2</sub>, these studies can not accurately be extrapolated to longer term temporal scales. Nevertheless, these studies have shown that in the short term young plants have responded favourably to an increase in CO<sub>2</sub>. The effect of CO<sub>2</sub> over larger time scales has been shown to dissipate due to plant acclimation to increased levels of CO<sub>2</sub>, a process which is also referred to as down regulation (Eamus and Jarvis, 1989). Such negative feedback mechanisms include an accumulation of starches in leaves, decrease in translocation of starches to tissue sinks, or a saturation in the activity of Rubisco. The level of CO<sub>2</sub> may lead to competitive displacement of one plant species over another. For instance, under current climatic conditions C<sub>4</sub> plants outcompete C<sub>3</sub> plants in xeric environments due to the higher WUE of the C<sub>4</sub> photosynthetic pathway. However, with increasing CO<sub>2</sub>, C<sub>4</sub> plants lose this competitive edge which may translate into changes in species diversity and plant community composition.

The increased concentration of CO<sub>2</sub> is expected to lead to an increase in the carbon to nitrogen (C:N) ratio of plant tissue and consequently lead to a decrease in litter quality (Paster and Post, 1988; Eamus and Jarvis, 1989; Mooney et al., 1991; Bazzaz and

Fajer, 1992; Breymeyer et al., 1996). This reduction in litter quality may affect nutrient cycling and decomposition processes mediated by microbial activity. The decrease in the mineralization rate may in turn affect plant growth. An increase in temperature due to climatic warming may result in higher mineralization rates which may reverse the effect of poor litter quality. However, increased temperature may also result in an increase in CO<sub>2</sub> released from soil organic matter decomposition and soil respiration and therefore cause a positive feedback mechanism which will in turn nullify any effect of an increased amount of mineralized nutrients. The C:N ratio of plant tissue may also influence plant relationships with insect herbivores which are expected to consume greater quantities of plant tissue in order to acquire enough nitrogen for insect development. An increase in the amount of CO<sub>2</sub> will decrease the rate of photorespiration, contribute to more photosynthate allocated to the roots, and increase the amount of carbon released to the soil as root exudates (Long and Hutchin, 1991). Microbial degradation of root exudates will sequester soil nutrients which in turn will limit plant growth (Diaz et al., 1993). Overall, the utilisation of CO<sub>2</sub> by plants may have the potential to ameliorate the effect of climatic stress, and highlights the role of plants as future potential CO<sub>2</sub> sinks which can offset the magnitude and rate of CO<sub>2</sub> induced climate change.

### **1.3.1.2 Effect of Increased Temperature**

Vegetation is expected to respond to future climatic warming through ecophysiological responses of tree species, changes in tree species distribution and composition, changes in the range of forest extant, and changes in the adaptive response of tree species (Kirschbaum and Fischlin, 1995; Breymeyer et al., 1996). Future climatic warming is expected to affect physiological processes at the individual tree level such as photosynthetic CO<sub>2</sub> uptake and respiration, processes which underpin the primary

production of forest ecosystems (Long and Hutchin, 1991; Kirschbaum and Fischlin, 1995). Photosynthesis shows a temperature optimum above which photosynthesis rates decline. At high temperature and ambient levels of CO<sub>2</sub>, C<sub>3</sub> plants show decreased rates of photosynthesis as a result of reduced CO<sub>2</sub> uptake due to an increased rate of photorespiration. The photorespiratory cycle is initiated upon the binding of O<sub>2</sub> to Rubisco which is costly to plant physiological function because it results in the waste of CO<sub>2</sub> and cellular energy. C<sub>4</sub> plants in contrast have an alternate photosynthetic system which has a higher affinity for binding CO<sub>2</sub>. Consequently, at higher temperatures C<sub>3</sub> plants show decreased photosynthesis due to increased photorespiration while C<sub>4</sub> plants are not similarly affected. The competitive edge of C<sub>4</sub> plants over C<sub>3</sub> plants is reduced if the level of CO<sub>2</sub> is increased. These results translate into competitive interactions between C<sub>3</sub> and C<sub>4</sub> plants in field conditions during climate change.

Respiration of plants can be divided into maintenance and growth respiration (Long and Hutchin, 1991; Kirschbaum and Fischlin, 1995). Growth respiration occurs during the construction of new plant material. Maintenance respiration is that portion of photosynthate which is utilized to maintain plant parts. At high temperatures, maintenance respiration is expected to increase. Although an increased concentration of CO<sub>2</sub> may increase tree and therefore forest growth, tree growth potential can not be entirely realised due to higher rates of maintenance respiration. The increased maintenance respiration may also contribute to a positive feedback effect by contributing further to climate change as more CO<sub>2</sub> is lost. This will also offset the role of the forests as potential carbon sinks during climate change.

In addition to these physiological responses, forests will also respond to climate warming at larger temporal and spatial scales. Forest and species distributions will



change with an overall trend towards a poleward advance of species distributions (Kirschbaum and Fischlin, 1995). Furthermore, species composition may also change in favour of early versus late successional species and species adapted to a warmer climate. Changes in species distribution and composition are expected to take place mainly at ecotonal regions which are expected to be the most sensitive to climate change (Rizzo and Wiken, 1992; Neilson, 1993; Noble, 1993; Lenihan and Neilson, 1995; Loehle, 2000). For example, in western Canada, the southern limit of the boreal forest is expected to be invaded by deciduous and grass species from the aspen parkland and great plains region respectively (Hogg, 1994; Hogg and Hurdle, 1995). The expansion will be at the expense of reduced productivity of the boreal forest due to dieback and fragmentation. At the northern limit of the boreal forest, boreal forest tree species are expected to dominate the southern tundra region. However, the northward expansion of the boreal forest may be halted by natural barriers (e.g., lakes, rivers, mountain ranges) or unsuitable edaphic conditions which can not change as fast as the rate of the projected warming.

Inherent to the adaptive success of tree species in the face of future climatic warming are migration rates of tree species. Tree species would have to migrate at rates 10 times faster than previously achieved during the more gradual climatic changes during the Holocene era to keep pace with the repositioning of climatic zones (Davis, 1989). Tree species unable to cope with the unprecedented rate of climate warming will face the prospect of extinction. Therefore, climatic change has the potential to contribute to the decrease in biological diversity. The loss of biological diversity is the main detrimental impact of global warming since once biological diversity is reduced, extinct species can not be reclaimed (Peters and Lovejoy, 1992). The migration rates will depend on the lag

in vegetation response since mature trees will still grow in areas beginning to be unsuitable for its continued survival. This ecological inertia may be removed through climate induced changes in disturbance regimes which will decrease the lag in vegetation response and accelerate the process of vegetation change due to species migration (Overpeck et al., 1990).

### **1.3.1.3 Effect of Variable Precipitation Patterns**

Forest response to precipitation patterns will depend on the regional pattern of precipitation (Kirschbaum and Fischlin, 1995; IPCC, 2001). In general, precipitation is expected to decline in continental areas which will become more prone to drought and fire. Such areas will show similar responses as in the subsequent section on drought and fire disturbance. In regions experiencing greater amounts of precipitation, the additional moisture may offset the effect of increased evapotranspiration under a warmer climate. A warmer climate will probably not have drastic consequences in wet, mesic regions. However, in areas already prone to drought during the growing season, increased precipitation will not likely offset the increased rate of transpirational water loss under a warmer climate. Overall, the amount of precipitation in a region, although variable in its geographical distribution, will nonetheless help to mitigate the effects of future climatic warming.

### **1.3.2 Disturbances**

The rate of vegetation change may be accelerated through the impact of disturbances (Overpeck et al., 1990; Kirschbaum and Fischlin, 1995). Forested ecosystems are expected to show a degree of ecological inertia to climate change (Brubaker, 1986; Davis, 1989). The constitution of a forest may belie the effects of climate change. Although regeneration of trees depends on favourable microclimatic,

edaphic, and regional climatic conditions, once established, trees can live through harsh climates (Brubaker, 1986). Upon the return of ameliorating conditions, new tree cohorts can reestablish. The degree of ecological inertia can be removed by climate induced changes in disturbance regimes. Disturbances can be divided into two categories: natural and anthropogenic disturbances. Natural disturbances include the effect of fire, drought and insect outbreaks while anthropogenic stresses and disturbances include land use (e.g., logging, agriculture) and pollution. These disturbance factors will likely exacerbate the effect of global warming.

### **1.3.2.1 Natural Disturbances**

Of the natural disturbances, fire will likely have the greatest impact on forest structure and function (Overpeck et al., 1990). A warmer climate is expected to lead to a higher frequency of fire in forest ecosystems such as the boreal forest of Canada (Flannigan and van Wagner, 1991; Li et al., 2000). The increase in fire frequency will likely change the composition of forests by favouring early successional species at the expense of climax species. For instance, in the western Canadian boreal forest, species such as trembling aspen (*Populus tremuloides* Michx.) are expected to dominate in a warmer climate while coniferous species such as white spruce are expected to decline (Hogg, 1994; Hogg and Hurdle, 1995). Fire will accelerate the rate of vegetation change and lead to the decreased rate of carbon storage. The combustion of forest biomass and the release of soil carbon will result in a positive feedback between fire activity and global warming.

Since increased temperature is expected to increase the amount of water lost from soil and plant surfaces, this will result in an increased risk of drought stress. The integration of drought stress in future projections of forest responses to climate change

indicate catastrophic forest dieback at the southern boundary of tree species range limits. Dieback will occur as species composition shifts towards tree species more adapted to a dryer climate. The early successional tree species will again dominate. Drought conditions are usually accompanied with the concomitant increase in fire frequency.

Insect pathogens too may cause forest dieback (Kirschbaum and Fischlin, 1995). As plant vegetation migrates northwards under a warmer climate so will the northern range limits of insect species. In addition to the extension of their geographical ranges, a warmer climate is expected to increase the magnitude and rate of insect reproductive development. This will allow insect species to complete more reproductive life cycles particularly given a larger growing season under a warmer climate. Since climate change is expected to lead to mild winters, this will improve the probability of insect survival into hitherto uncharted geographical areas. This in turn will pose a risk to tree species previously unexposed to certain groups of insect pathogens. In response to increased insect pathogen pressure under a warmer climate, trees may protect themselves through acclimation and the production of secondary metabolites to ward off insect attack.

#### **1.3.2.2 Anthropogenic Stresses and Disturbances**

The principal source of anthropogenic stress is pollution from industrial activities (IPCC, 2001). Part of the pollution contributes to the greenhouse gases which contributes to CO<sub>2</sub> induced climate change. In addition to acting as greenhouse gases, pollutants such as sulfur dioxide (SO<sub>2</sub>), ozone (O<sub>3</sub>), and oxides of nitrogen (NO<sub>x</sub>) cause stress on forest growth and ecosystem functioning (i.e., nutrient cycles), although at low concentrations NO<sub>x</sub> can also act as a nutrient source. Pollution will exacerbate the effect of climatic stress and lead to forest decline. The increase in CO<sub>2</sub> may have the potential

to ameliorate the effect of air pollution; however, this may be offset by the effect of increased temperature.

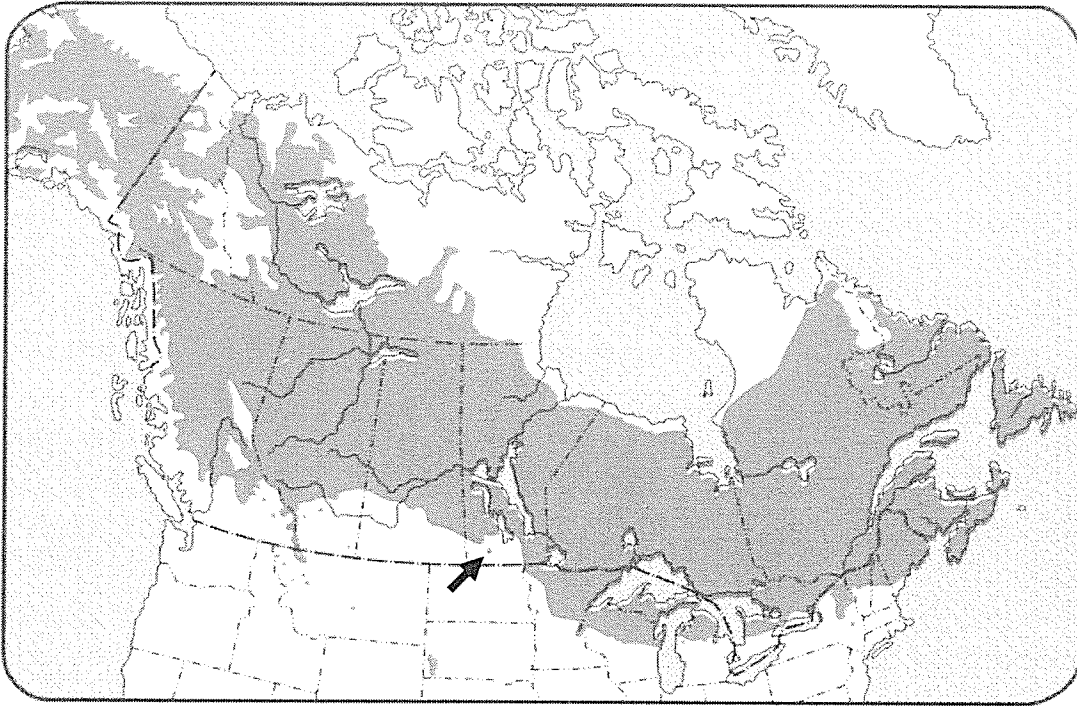
Tree species will attempt to migrate north in order to track climate change and therefore remain in their optimal climatic zone; however, anthropogenic barriers may prevent their migration efforts (Davis, 1989; Roberts, 1989; Kirschbaum and Fischlin, 1995). Human industrial activity and land use policies have created a network of modified agricultural and logged land as well as a grid of roads and cities, all of which serve as obstacles to tree seed dispersal. Habitat destruction due to agriculture and logging have also reduced the area occupied by trees and has effectively reduced the amount of seed source to improve the prospects of successful migration (Davis, 1989). On such a highly modified and dissected landscape, some researchers have proposed human intervention to assist the northward progression of species ranges (Davis, 1989; Roberts, 1989). Such attempts may be difficult however, due to the astronomical logistic and economic costs of such a large scale undertaking. Furthermore, transplantation may upset symbiotic relationships between roots and mycorrhizae and may not guarantee that the transplanted plant species will adapt to the new edaphic and microenvironmental conditions (Davis, 1989; Roberts, 1989).

## 1.4 Silvics of White Spruce

### 1.4.1 Distribution and Habitat

White spruce is a transcontinental species and is present in every forest region in Canada except the Pacific coast (Sutton, 1969; Nienstaedt and Zasada, 1990; Sims et al., 1990; Farrar, 1995) (Fig. 1.1). During the late Wisconsin glaciation (18,000 years B.P.), white spruce existed as a full glacial refugial population in the southern United States, between 35° to 40° N latitude (Ritchie and MacDonald, 1986; Ritchie, 1987; McLeod and MacDonald, 1997). According to fossil pollen records the post-glacial spread of white spruce following the glacial retreat differed between different regions of Canada. The spread of white spruce in eastern and central Canada was slow and continuous whereas the spread of spruce in the western Canadian interior was initially slow but increased rapidly as white spruce progressed further north. The strong southerly winds along the receding Laurentide ice sheet is postulated to have increased the rate of dispersal of white spruce in western Canada. The flat and gently rolling terrain of the western interior further assisted in seed dispersal.

White spruce occurs in a wide range of climatic regions (Sutton, 1969; Hosie, 1979; Nienstaedt and Zasada, 1990; Sims et al., 1990; Farrar, 1995). Its preferred climatic range is the cold, moist climate of the boreal forest (Sims et al., 1990). The northern limit of white spruce and the position of the tree line has been correlated with the 10°C isoline of mean July temperature, heat-sum (growing degree days), and low light intensities. Other biotic and abiotic factors which limit growth at its northern limit and altitudinal tree line include lack of soil, low fertility, low soil temperature, fire, insects, and disease. Nonetheless, white spruce is one of the hardiest conifers at the tree line (Sutton, 1969). The southern limit of white spruce has been related to the 18°C July



**Figure 1.1** Distribution of white spruce in North America. The arrow indicates the location of the disjunct population of white spruce at its southern limit in Spruce Woods Provincial Park of southwestern Manitoba. Source: Farrar (1995).

isotherm. Conditions are most severe at its southern limit in the Prairie Provinces of Canada due to low precipitation levels. White spruce also occurs on a wide range of soil substrates of glacial, lacustrine, marine and alluvial origin. Podzolic soils occur over most of the range of white spruce; however, spruce is also able to grow on brunisolic, luvisolic, gleysolic, and regosolic soils (Nienstaedt and Zasada, 1990). White spruce is capable of growing on both acidic and alkaline soils while growth is optimal in the pH range of 4.7 to 7.0 (Nienstaedt and Zasada, 1990). In addition, white spruce is able to tolerate a range of fertility levels. Growth of white spruce is optimal on well aerated, well drained soil although spruce is capable of growing on a range of soil moisture conditions (Sutton, 1969; Nienstaedt and Zasada, 1990). However, trees show a stunted and scrubby growth form where there is stagnant ground water, or in dry sites. Pure stands of white spruce occur on wet, dry and upland fire sites in the Prairie Provinces (Sutton, 1969); however, pure stands of white spruce are rare as spruce generally occurs in association with other tree species. Commonly associated tree species in the boreal mixed-woods region include black spruce (*Picea mariana* (Mill.) B.S.P., balsam fir (*Abies balsamea* (L.) Mill., paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.) (Sutton, 1969; Nienstaedt and Zasada, 1990).

#### **1.4.2 Reproduction and Early Growth**

White spruce is monoecious with male and female reproductive organs on different branches of the same tree (Sutton, 1969; Hosie, 1979; Nienstaedt and Zasada, 1990; Sims et al., 1990; Farrar, 1995). In late summer, the reproductive buds develop before the year of cone production. These buds overwinter in the mother cell stage (Sutton, 1969). Meiosis occurs in the following spring. In May and June, pollination,



which is temperature dependent, takes place. Fertilization is followed by embryo growth and seed maturation. Cones open in August and seeds are dispersed in September. In southern areas, seeds are dispersed earlier. White spruce reaches a seed bearing age by 30 years. The seeds are winged and are subsequently dispersed by wind. Good seed crops are produced about every 10 to 12 years (Sims et al., 1990). After winter has broken the dormancy of the seeds, seed germination and development occurs in the year after seed dispersal. Before manual seeding, seeds must be stratified to break their dormancy. Germination of seeds occurs from mid-June to late-July, and seeds which are dispersed in the fall show 75-100% germination by early July (Nienstaedt and Zasada, 1990). Adverse conditions such as a large litter and fermentative layer can delay germination (Sims et al., 1990). These layers restrict regeneration due to their poor water holding capacity. Furthermore, deciduous litter is known to smother and crush white spruce seedlings. In contrast to litter, exposed mineral soil represents the best seed beds for white spruce establishment. Seedling survival and growth is negatively affected by frost heaving. Natural regeneration of white spruce is poor in central and western Canada due to dry climatic conditions (Sutton, 1969).

Free continuous growth, which is a juvenile characteristic, is maintained in the absence of environmental stresses (e.g., water stress) (Sutton, 1969; Nienstaedt and Zasada, 1990; Sims et al., 1990). White spruce seedlings generally require 10-20 years to reach breast height. Growth is greatest at full light intensity although growth is still favourable at 45% sunlight for young seedlings up to 5 years of age. Full light intensity is preferred by seedlings older than 10 years (Sims et al., 1990). Reduction of light intensity reduces both shoot and root growth as well as diameter growth. Furthermore, height growth usually depends on carbohydrate reserves manufactured during the

previous year (Sutton, 1969). Deficiency of rainfall, suppression of rooting depth, and competition are detrimental to spruce growth. White spruce can withstand open conditions although winter browning can occur on exposed leaders above the snow surface. Vegetative reproduction is rare in white spruce although at its northern limit white spruce does reproduce vegetatively by the process of layering in which branches become buried in moss and produce roots prior to the establishment of new individuals (Nienstaedt and Zasada, 1990).

### **1.4.3 Sapling and Tree Growth**

Flushing of white spruce saplings and trees is controlled by temperature, whereas cessation of growth is determined by photoperiod (Nienstaedt and Zasada, 1990). Maximal ages of white spruce are attained on stressed sites and can reach 250-300 years. In contrast, the largest individuals are obtained on better sites. The rooting habit of white spruce is characterized as being shallow rooted since white spruce has wide-spreading lateral roots. White spruce is considered shade tolerant and thus can grow in the understory of other tree species and can regenerate in its own shade. White spruce is a late successional species and in the absence of disturbance will eventually over-top early successional species such as trembling aspen. Due to the prevalence of disturbances such as fire in the boreal forest, white spruce rarely occurs in pure stands but instead in association with other tree species.

White spruce is affected by damaging agents such as fire, floods, windthrow, snow, ice, frost damage, and insect and fungal attack (Sutton, 1969; Nienstaedt and Zasada, 1990; Sims et al., 1990). Although fire may consume seeds, fires nonetheless expose the mineral soil thereby providing suitable seed bed conditions for surviving spruce or spruce seed blown in from an unburned area. Since white spruce has a shallow

root system, it is not considered windfirm. Snow and ice cause stem lesions and leader mortality; there is no regrowth of a damaged leader (Sims et al., 1990). White spruce vegetative and reproductive growth is susceptible to frost damage during flushing in spring, whereas damage by fall frost is less common. Densely stocked stands of white spruce are prone to disease and trees older than 200 years are usually affected by rot. White spruce is damaged by a number of bark beetle species although trees which are of low vigour and dying or damaged by windthrow are the most susceptible. Bark beetles bore into the phloem or inner bark and consequently girdle the tree. White spruce is susceptible to the spruce budworm (*Choristoneura fumiferana* Clem.) although balsam fir is the principal host. Spruce budworm larvae develop and feed on reproductive and vegetative buds, and in new foliage of the expanding shoot. Severe defoliation leads to reduced growth and mortality.

The genotypic and phenotypic plasticity of white spruce allows for its wide distribution pattern although populations of spruce at its northern limit have more genetic diversity than their southern counterparts (Sutton, 1969; Nienstaedt and Zasada, 1990; Sims et al., 1990). Four varieties of white spruce are recognized and include *Picea glauca glauca*, *Picea glauca* var. *albertiana*, *Picea glauca* var. *densata*, and *Picea glauca* var. *porsildii* (Nienstaedt and Zasada, 1990). Hybrids between white spruce and Engelmann spruce occur in British Columbia and are similar to *Picea glauca* var. *albertiana*. A Sitka and white spruce hybrid (*Picea x lutzi*) occurs in northwestern British Columbia and in Alaska. Hybrids between black and white spruce are rare although the occurrence increases from south to north. Inbreeding leads to reduced vigor and lowered survival and occurs in isolated stands of white spruce.

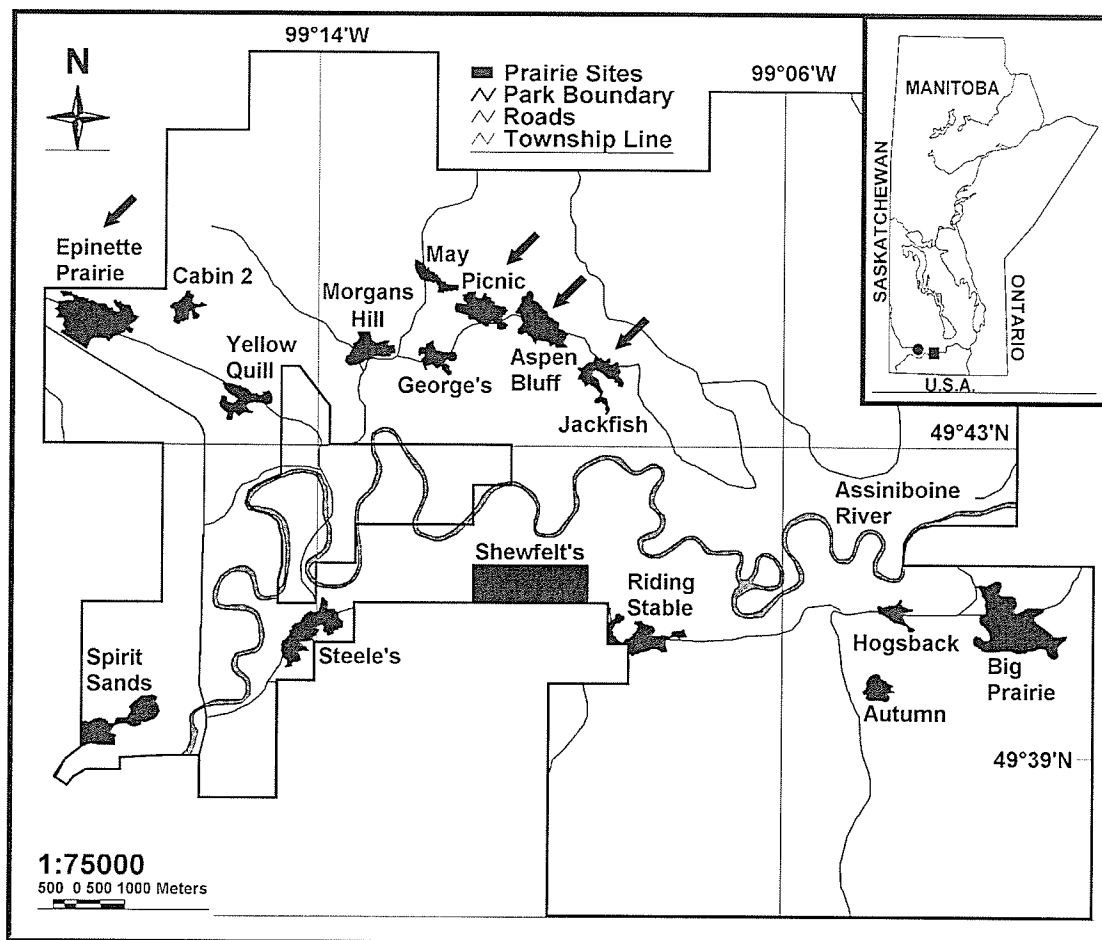
## **1.5 Study Area**

### **1.5.1 Climate**

The study was conducted in the Spruce Woods Provincial Park (SWPP) which is located in southwestern Manitoba (49° 40' N, 99° 15' W) (Fig. 1.2). The climate is subhumid and continental with hot summers and cold winters (ESWG, 1996) which is characteristic of the climate of much of southern Manitoba (Blair, 1996). The nearest meteorological station is the Brandon Agriculture Station (Brandon CDA; 49° 52' N, 99° 59' W) which is located about 88.5 km northwest of the SWPP (Fig. 1.2). For the reference period of 1971-2000, the area experienced an average annual temperature of 2.4°C (Environment Canada, 2002). Average annual precipitation amounts to 474.0 mm, with 78.3% as rainfall and the remainder as snowfall. In the mixed-grass prairie region, soil moisture is depleted by late July when temperature is at its highest (Coupland, 1950), reaching a daily mean maximum of 25.9°C (Environment Canada, 2002).

### **1.5.2 Glacial and Post-Glacial History**

At the height of the late Wisconsin glaciation (18,000 years B.P.) the study area was covered by the Laurentide Ice Sheet (Ritchie, 1987). The ice sheets receded with climate warming and glacial melt water accumulated in southern Manitoba because the usual northward drainage into the Hudson Bay was blocked by ice. The melt water formed glacial Lake Agassiz over southern Manitoba. The SWPP currently resides over a great belt of deltaic sands with an area of about 6,500 km<sup>2</sup> created 12,000 years B.P. when a predecessor of the Assiniboine river flowed into glacial Lake Agassiz (Schykulski and Moore, 1997). The SWPP is located on this delta, and this area has been designated as the Assiniboine Delta Natural Region (Schykulski and Moore, 1997). Once the ice receded and the glacial lakes drained leaving behind the current lakes (i.e., Lake



**Figure 1.2** Regional setting of the Spruce Woods Provincial Park (SWPP) (■) and the Brandon Agriculture Station (●) in southwestern Manitoba and a map of the SWPP. Source: Schykulski and Moore (1997).

Winnipeg, Lake Manitoba), revegetation of the Western Interior plains was from full-glacial refugia to the south of the ice sheets from the mid-latitude United States (Wells, 1970; Ritchie, 1987; Pielou, 1991). Tree species such as white spruce were able to recolonise the plains region since they were able to establish on the poorly developed soils consisting of the glacial deposits (Ritchie, 1987; Pielou, 1991). Fossil pollen records indicate that woody vegetation generally dominated the area during cool periods (i.e., Little Ice Age), while herbaceous species dominated during warmer periods (i.e., Hypsithermal Period, Little Climatic Optimum) (Ritchie, 1987; Pielou, 1991).

### **1.5.3 Hydrology**

The Assiniboine River transects the study area from west to east (Fig. 1.2), and drains water from west to east into the Saskatchewan-Nelson drainage basin which eventually empties out into the Hudson Bay via the Nelson River (Welsted, 1996). The SWPP also resides on top of a sand and gravel aquifer known as the Assiniboine Delta Aquifer which has an area of about 3885 km<sup>2</sup> and an average thickness of about 18 m (Halstead, 1959; Kulshreshtha, 1994; Betcher et al., 1995; Welsted, 1996). The Assiniboine Delta Aquifer is the largest underground aquifer in Manitoba. The aquifer ranges in depth from over 21 m in areas of large sand dunes and hills to approximately ground surface in areas close to streams (Kulshreshtha, 1994). While part of the aquifer discharges into the Assiniboine River, the aquifer is used primarily in agriculture as irrigation water (Halstead, 1959; Kulshreshtha, 1994; Betcher et al., 1995). Groundwater resources are important in this arid and semi-arid climate in which surface water is scarce. The aquifer is a renewable resource that is recharged by precipitation and snow melt.

#### **1.5.4 Geology and Topography**

The SWPP is located on the Upper Assiniboine Delta which in turn resides on the Second Prairie Steppe west of the Manitoba Escarpment (Corkery, 1996). The SWPP is bounded to the south by the Tiger Hills and Pembina Mountain. The bedrock geology of the study area consists of sedimentary rocks of the Upper Cretaceous shales and sandstones of the Vermillion River Formation as well as the Riding Mountain Formation (Corkery, 1996). The surficial deposits are characterized mainly by the glacial deltaic deposits of the Pleistocene glaciations (Rogosin, 1996). Other surficial deposits include the wind blown aeolian deposits that form sand dunes. Along the Assiniboine River valley, the terraces are covered by old alluvial deposits whereas the river bottom is covered by young alluvial deposits. Topography of the SWPP is characterized by sand dunes which are up to 70 m thick. The sand dunes are a result of wind action which has carved out the ancestral Assiniboine delta deposits. The park in turn is surrounded by more level, gentler rolling topography (Rogosin, 1996).

#### **1.5.5 Soils**

The soils of the mixed-grass prairie region are predominantly classified in the Black Chernozems and are characterized by a dark Ah horizon as a result of the accumulation of organic matter from the decomposition of xerophytic and mesophytic grasses and forbs (SCWG, 1998). In areas influenced by forest vegetation (i.e., aspen parkland) the forest litter slightly lowers the soil pH such that leaching and eluviation of organic matter leads to the production of Dark Gray Chernozems. However, within the SWPP itself, the deltaic wind blown sands have had little time to develop a pronounced Ah horizon and are classified as Regosols and Humic Regosols (SCWG, 1998).

### 1.5.6 Vegetation

Vegetation in the park is characterized as the Aspen-oak Grove of the Boreal Forest Region (Rowe, 1972) or Aspen Parkland of the Prairie Ecozone (ESWG, 1996). In its native state, park vegetation consists of aspen parkland dominated by trembling aspen (*Populus tremuloides* Michx.) which exists as continuous forest or as groves intermixed with prairie (Bird, 1961; Chapman, 1980; Scott, 1995; Scott, 1996; Higgs and Holland, 1999). A sandhill prairie community unique to the aspen parkland is located in the SWPP and consists of trembling aspen intermixed with a disjunct population of white spruce at its southern limit of distribution (Fig. 1.1). In this environment, white spruce is considered a pioneer species since it can establish in the open prairie environment (Bird, 1961). Its pioneer role is assisted by its common association with the shrub creeping juniper (*Juniperus horizontalis* Moench) which is also a pioneer species commonly distributed on dry, sandy and rocky sites (Tirmenstein, 1988). Creeping juniper is believed to assist white spruce establishment by reducing mortality of white spruce seedlings during prairie ground fires (Bird, 1961; Chhin and Wang, 2002). The progressive recruitment and establishment of white spruce in the open prairie results in the development of white spruce tree islands which are surrounded by mixed-grass prairie. The islands have an asymmetric spatial structure as white spruce recruitment is concentrated on the northern aspect of the tree islands (Chhin and Wang, 2002). In addition to its pioneer role, white spruce is also the climax species since white spruce in the trembling aspen understory will eventually replace aspen to form white spruce forests in the absence of disturbances.



### 1.5.7 Natural and Anthropogenic Disturbances

Natural and anthropogenic disturbances have contributed to the landscape mosaic of the aspen parkland (Bird, 1961). In presettlement times, disturbances included fire which occurred naturally or started by Aboriginals in order to maintain the prairie environment for the buffalo (*Bison bison* L.). Grazing by herbivores such as buffalo and elk (*Cervus canadensis* Erxl.) prevented the encroachment of the forest onto the prairie. European settlement contributed to the decline of the buffalo population due to hunting, livestock grazing, intensive agriculture, and the policy of fire suppression (Bird, 1961). The reduction of grazing and fire pressure has resulted in the encroachment of the forest onto the prairie. A policy of fire suppression continues within the SWPP, with intermittent prescribed burning permitted within the mixed-grass prairie sites protected under the mandate of the Prairie Management Plan of Manitoba Conservation (Schykulski and Moore, 1997). Agriculture continues on privately owned land within the centre of the park, and livestock grazing has been relegated to Shewfelt's grazing lease (Schykulski and Moore, 1997) (Fig. 1.2).

## 1.6 Overall Research Objectives and Hypotheses

The main objective of the present study was to examine the growth-climate relationships of a disjunct population of white spruce at its southern limit of distribution in south-western Manitoba within the forest-prairie transitional zone. The study was conducted within the Spruce Woods Provincial Park (SWPP). The response of white spruce was examined primarily in relation to the macro-scale regional climate. The role of microclimate of three contrasting habitats (i.e., white spruce tree islands, open prairie, and aspen groves) within the study area in moderating or accentuating the effects of the regional climate were examined. The growth performance of juvenile white spruce (i.e., seedlings and saplings) was also examined within the three habitats.

Within the forest-prairie boundary climatic moisture deficiency leads to an increased risk of drought and fire (Bird, 1961; Zoltai, 1975; Hildebrand and Scott, 1987; Hogg, 1994; Hogg and Hurdle, 1995; Hogg and Schwarz, 1997). These factors in turn affect the vegetation dynamics within this transitional zone by favouring prairie over forest during dry periods and an invasion of forest onto prairie during wet periods. Therefore, it is predicted that the growth characteristics of a disjunct population of white spruce at its southern limit within the forest-prairie boundary is sensitive to climatic change, and that microenvironmental conditions which offset the dry regional climate in turn improves white spruce growth.

## CHAPTER 2: COMPARATIVE ANALYSIS OF MICROENVIRONMENTS AND JUVENILE GROWTH PERFORMANCE OF WHITE SPRUCE WITHIN SPRUCE ISLANDS, OPEN PRAIRIE, AND ASPEN GROVES

### 2.1 Introduction

In the absence of fire and severe grazing, succession in the parkland proceeds from prairie to aspen forest and then climaxes into a white spruce forest (Bird, 1961). A critical step in that successional sequence is the successful establishment of trees in grasslands (Yarranton and Morrison, 1974; De Steven, 1991a; De Steven, 1991b; Kellman and Kading, 1992; Magee and Antos, 1992; Li and Wilson, 1998). This process of establishment is influenced by abiotic and biotic factors.

The prevailing regional climate of the aspen parkland and mixed-grass prairie in southwestern Manitoba is characterized by low precipitation, high summer temperatures, and dry winds, any of which may be limiting factors to plant growth (Coupland, 1950). Within this dry climate, tree invasion into grasslands can be assisted by favorable microenvironments or 'safe sites' (Harper, 1977; Johnstone, 1986; De Steven 1991a; Kellman and Kading, 1992; Kelly and Canham, 1992; Wilson and Agnew, 1992). Shrubs are known to facilitate tree seedling establishment (Bertness and Callaway, 1994; Callaway, 1995; Chambers, 2001) by crowding out grass competition (Bird, 1961; Werner and Harbeck, 1982), and by providing protective conditions from abiotic forces such as fire (Coupland, 1950; Scoggan, 1957; Bird, 1961). The presence of previously established trees in open prairie not only reduces evaporative water loss from plants (Scoggan, 1957; Kellman and Kading, 1992) but also increases soil moisture and nutrients (Parker and Muller, 1982; Inouye et al., 1987; Wilson and Kleb, 1996; Li and

Wilson, 1998; Wilson, 1998; Kleb and Wilson, 1997; Kleb and Wilson, 1999).

Furthermore, woody canopies modify the understory microclimate through shading, interception of precipitation, and litter fall (Vetaas, 1992; Breshears et al., 1997b).

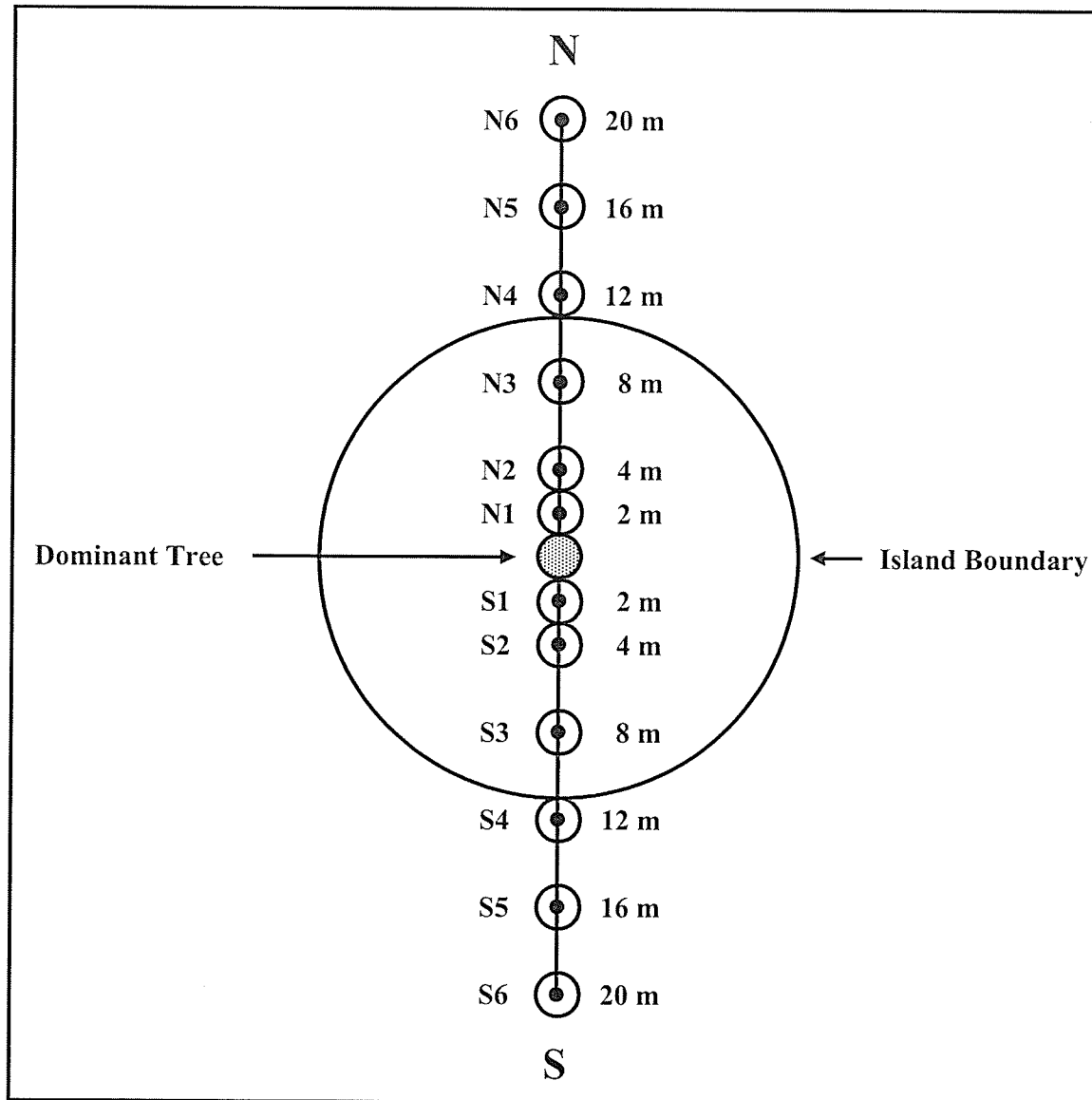
The first objective of this study was to compare the microenvironment of forest and grassland habitats within the aspen parkland of the Spruce Woods Provincial Park (SWPP). The habitats included white spruce tree islands, adjacent open prairie, and aspen groves. White spruce establishment occurred almost exclusively in the northern aspect of tree islands and on juniper mats (Chhin and Wang, 2002). Field observations suggested more successful establishment under trembling aspen groves. Therefore, the second objective was to examine which microenvironmental parameters may have contributed to or impeded successful white spruce establishment. The third objective of the study was to compare white spruce seedling and sapling growth among the three environments and relate growth patterns to the microenvironmental patterns.

## 2.2 Methods

### 2.2.1 Sampling Design

The study was located in three mixed-grass prairie preserves north of the Assiniboine river: Picnic, Aspen Bluff, and Jackfish prairie (Fig. 1.2). Ten white spruce islands, ten open prairie sites with creeping juniper mats, and ten aspen stands were selected using aerial photographs and field reconnaissance. The criteria for island selection were that islands be at least 20 m apart from each other or from the forest edge and that the sampled islands occurred on similar topography. Open prairie sites containing patches of grass and juniper were selected adjacent to but at least 20 m away from a spruce island or forest edge. Aspen groves containing understory development of juvenile white spruce were selected.

The sampling design in a white spruce island consisted of a north-south (N-S) transect line 20 m on each side of the largest dominant tree (Fig. 2.1). Twelve microenvironmental sites were selected along the transect line within each spruce island; the microenvironments differed in terms of aspect and distance from the largest dominant tree. Six of the microenvironmental sites were selected on the north side (N1, N2, N3, N4, N5, and N6) and six on the south side (S1, S2, S3, S4, S5, and S6) in each spruce island. Each microenvironmental site was delimited by a one-meter radius circular plot. On each side of an island, the centre of the single plot of each microenvironmental site was placed 2, 4, 8, 12, 16, and 20 m from the island center (Fig. 2.1). Two microenvironmental sites were selected in each open prairie site and included a grass microenvironment (OG) and a juniper microenvironment (OJ). Each grass microenvironment of each open prairie site was represented by three circular plots. Similarly, each juniper microenvironment of each open prairie site was represented by



**Figure 2.1** Diagrammatic representation of the methodology for sampling microclimatic parameters within tree islands. A 20 m transect line was extended on the north (N) and south (S) side of the largest dominant tree. Circular plots (1 m radius) were placed along the transect lines. The distance of the centre of each quadrat from the island centre is indicated.

three circular plots. One microenvironment was selected in the interior of each aspen grove (AG) such that there was at least a ten meter buffer zone to the aspen stand edge. The aspen grove interior microenvironment was represented by six circular plots.

## **2.2.2 Microenvironment**

### **2.2.2.1 Field Measurements**

Solar radiation was measured with an AccuPAR Ceptometer (Decagon Devices Inc., 1994; Wang, 1994). Solar radiation was measured in the morning (10:00 a.m. – 12:00 p.m.) and afternoon (2:00 p.m. – 4:00 p.m.). Measurements for these two periods were averaged. Light was not measured at midday (12:00 p.m. – 2:00 p.m.) to avoid measurements when the sun was at its zenith. Light measurements were taken at a height of 1.3 m from the north, east, south, and west sides of each plot of each microenvironment within each habitat. Light intensity of each plot was expressed as an average of these four measurements. Light intensities in tree islands and aspen groves were expressed as percentages of the average light intensity of the open prairie.

Air temperature and relative air humidity (15 cm above ground) were measured using digital thermohygrometers; soil (15 cm below the surface) and surface temperatures were measured with thermocouples (Barnant Co., 1997). These measurements were taken in the centre of each plot and were measured once between 10:00 a.m. – 4:00 p.m.

Surface soil moisture was measured at the centre of each plot with a digital Theta probe soil moisture sensor (Delta-T Devices Ltd., 1999). A profile probe was used to measure soil moisture at the depths of 10, 20, 30, and 40 cm below the soil surface (Delta-T Devices Ltd., 2001). The profile measurements were taken in an augured hole near the centre of each plot. In spruce islands, profile measurements were taken in the single plot of each of the following four microenvironments: N3, N6, S3, and S6 (Fig.

2.1). One plot of each juniper microenvironment and one plot of each grass microenvironment were randomly selected for measurements in each open prairie site. Two plots of the aspen grove interior microenvironment were randomly selected from each of aspen groves. Three profile readings were taken at each plot by rotating the profile probe 120° after each individual reading (Delta-T Devices Ltd., 2001). The profile measurements of each plot was expressed as an average of these three measurements. The Theta probe and profile probe recorded soil moisture in units of DC voltage ( $V$ ).

Absolute values of percent coverage was determined for the following ground cover types in each plot of each habitat: shrubs, creeping juniper, broadleaf herbaceous, grass, forest floor litter, and bare ground (i.e., mineral soil).

The schedule for sampling the microenvironmental conditions in the summer of 2002 is shown in Table 2.1. The microenvironmental parameters were measured on sunny clear days at least 24 hours after any rainfall. These conditions ensured that the three habitats were contrasted as much as possible. Percent cover of ground cover types and light intensity were measured once during the first week of July. Soil moisture (surface and profile), relative humidity, and temperature were measured during the first week of the months of June, July, August and September. In July however, some parameters could not be measured in aspen groves to limit over-exposure to poison ivy (*Rhus radicans* L. var. *rydbergii* (Small) Rehd.). Furthermore, in August most of the parameters could not be measured due to the lack of suitable weather for measurements (i.e., rainfall and thunderstorms).



**Table 2.1** Microenvironmental sampling schedule of tree islands (TI), open prairie (OP), and aspen groves (AG). Parameters were measured on sunny clear days at least 24 hours after any rainfall during the first week of each month.

| Parameter         | June     | July <sup>1</sup> | August <sup>2</sup> | September             |
|-------------------|----------|-------------------|---------------------|-----------------------|
| Light Intensity   | -        | TI-OP-AG          | -                   | -                     |
| Percent Cover     | -        | TI-OP-AG          | -                   | -                     |
| Soil Moisture     |          |                   |                     |                       |
| Surface           | TI-OP-AG | TI-OP             | -                   | TI-OP-AG              |
| Profile           | TI-OP-AG | TI-OP             | TI-OP-AG            | TI-OP-AG              |
| Relative Humidity | TI-OP-AG | TI-OP             | -                   | TI-OP-AG <sup>3</sup> |
| Temperature       | TI-OP-AG | TI-OP             | -                   | TI-OP-AG              |

<sup>1</sup> Some parameters could not be measured in aspen groves in order to limit over-exposure to poison ivy.

<sup>2</sup> Most of the parameters could not be measured due to lack of suitable weather for measurements (i.e., rainfall and thunderstorms).

<sup>3</sup> Relative humidity was measured on the ground surface in addition to the air.

### 2.2.2.2 Data Analysis

The Theta probe and profile probe measures the volumetric soil moisture content ( $\theta$ ) which is the ratio between the volume of water present and the total volume of the soil sample. Units of soil moisture in  $V$  is proportional to volumetric moisture content via the following linear relationship (Delta-T Devices Ltd., 1999):

$$\theta = \frac{[1.1 + 4.44V] - a_0}{a_1} \quad (2.1)$$

where  $a_0$  and  $a_1$  represent constants which characterize different soil types. Based on a large number of soil samples, generalized values of the parameters are  $a_0 = 1.6$  and  $a_1 = 8.4$  for mineral soils, and  $a_0 = 1.3$  and  $a_1 = 7.7$  for organic soils (Delta-T Devices Ltd., 1999). Volumetric moisture content is a dimensionless parameter expressed as a percentage (%vol) or as a ratio ( $\text{m}^3 \text{m}^{-3}$ ). Equation 2.1 is suitable to convert moisture readings in  $V$  to %vol for soils of low moisture content ( $\theta < 50$  %vol). For soils of higher moisture content a polynomial conversion equation is recommended (Delta-T Devices Ltd., 1999).

For the subsequent statistical analyses, the parameters measured in microenvironmental sites represented by more than one plot were averaged. Consequently, the value of each microenvironmental parameter (except profile moisture) from the three plots of the grass microenvironment within each open prairie site were averaged. Similarly, the value of each parameter from the three plots of the juniper microenvironment within each open prairie site were averaged. Furthermore, the value of each parameter for the six plots within the aspen grove interior microenvironment within each aspen grove were averaged. Thus, the value of each microenvironmental parameter of the single plot of each of the 12 microenvironments within each spruce island (N6, N5,

N4, N3, N2, N1, S1, S2, S3, S4, S5, S6); as well as the average value of each parameter for the grass microenvironment (OG) and juniper microenvironment (OJ) within each open prairie site; and the average value of each parameter of the aspen grove interior microenvironment (AG) within each aspen grove were inputted into the subsequent statistical analyses. For the analysis of the profile moisture data, the moisture values of the two plots of the aspen grove interior microenvironment within each aspen grove were averaged. Thus, the profile moisture of the single plot of each of the 4 microenvironments within each spruce island (N6, N3, S3, S6); as well as the single plot of the grass microenvironment (OG) and the single plot of the juniper microenvironment (OJ) within each open prairie site; and the average value of each aspen grove interior microenvironment (AG) within each aspen grove were inputted into the subsequent statistical analyses.

Except for the temperature data, all microenvironmental parameters with percentage data were log-transformed ( $\text{LOG } X+1$ ). Analysis of variance (ANOVA) followed by Tukey's multiple comparisons was conducted on the light data to compare light conditions between the environmental plots (15 levels) (Wilkinson, 1990). Repeated measures ANOVA (Wilkinson, 1990) was conducted on the temperature data to examine the effects of microenvironment (15 levels), height (3 levels) and date of sampling (3 levels). Repeated measures ANOVA was performed on relative air humidity to examine the effects of microenvironment (15 levels) and date of sampling (3 levels). In September, repeated measures ANOVA was conducted to examine the effects of microenvironment (15 levels) and height of sampling (2 levels). Repeated measures ANOVA was performed on surface soil moisture to examine the effects of microenvironment (15 levels) and date of sampling (3 levels). For profile moisture,

repeated measures ANOVA was conducted to examine the effects of microenvironment (7 levels), profile depth (4 levels), and date of sampling (3 levels). ANOVA was performed on each of the ground cover classes to examine the relative differences between microenvironments (15 levels). The mean values of the microenvironmental variables for each microenvironmental site and the lower and upper limits of a 95% confidence interval were back-transformed by taking antilogs ( $10^X - 1$ ) so that all means could be reported on their original scale of measurements.

Hierarchical classification was performed on the 15 microenvironmental sites (N6, N5, N4, N3, N2, N1, S1, S2, S3, S4, S5, S6, OG, OJ, AG) from the three habitats with respect to the mean ( $n = 10$ ) of each of the microenvironmental variables (except profile moisture). Microenvironmental variables with percentage data were normalized (except temperature data). All microenvironmental variables were then standardized to unit variance before the multivariate analysis to ensure that the variables were commensurable (Legendre and Legendre, 1998). Surface soil moisture, relative humidity, and temperature were selected for the months of June and September in which measurements were taken from all three environments. The hierarchical agglomerative clustering was determined using an unweighted arithmetic average (UPGMA) of a chord distance matrix (Legendre and Legendre, 1998; Podani, 2001) using the program SYNTAX (version 2000) (Podani, 2001). The chord distance, in contrast to the Euclidean distance, was selected as it minimizes the distortion of the relationship amongst the microenvironmental sites within the multidimensional data space (Legendre and Legendre, 1998).

## 2.2.3 Seedling and Sapling Growth

### 2.2.3.1 Field and Laboratory Measurements

Three seedlings (< 0.5 m tall) and three saplings (0.5 – 2 m tall) were destructively sampled from each of the same 10 spruce islands and 10 aspen groves used to collect the microenvironmental data. Within spruce islands, the seedlings and saplings were selected on the northern aspect 4-12 m from the island centre where recruitment was concentrated (Chhin and Wang, 2002). As the open prairie sites did not contain any recruitment of white spruce, each of the three prairie preserves were surveyed and a total of 30 seedlings and 30 saplings were selected which were at least 20 m from the forest edge, tree islands or aspen groves. Within the prairie preserves, at each sampling location no more than three seedlings and three saplings were selected. The ground cover type of each seedling and sapling collected in the open prairie was also recorded. Seedlings and saplings were collected in the summer of 2000 from spruce islands, and in the summer of 2001 from the open prairie and aspen groves.

Height and root collar diameter (RCD) were recorded for each seedling and sapling. A section taken from the root collar of each destructively sampled seedling and sapling was prepared following standard dendrochronological techniques (Stokes and Smiley, 1968; Yamaguchi, 1991). That is, all wood samples were sanded with progressively finer grades of sandpaper to highlight ring-width patterns. The young age of the samples precluded the possibility of effective crossdating due to the lack of sufficient pointer years. Consequently, dating of samples was mainly conducted by simply counting rings.

### **2.2.3.2 Data Analysis**

The RCD/age ratio, height/age ratio, and RCD/height ratio of white spruce seedlings, saplings, and both seedlings and saplings were compared between the three environments via ANOVA.

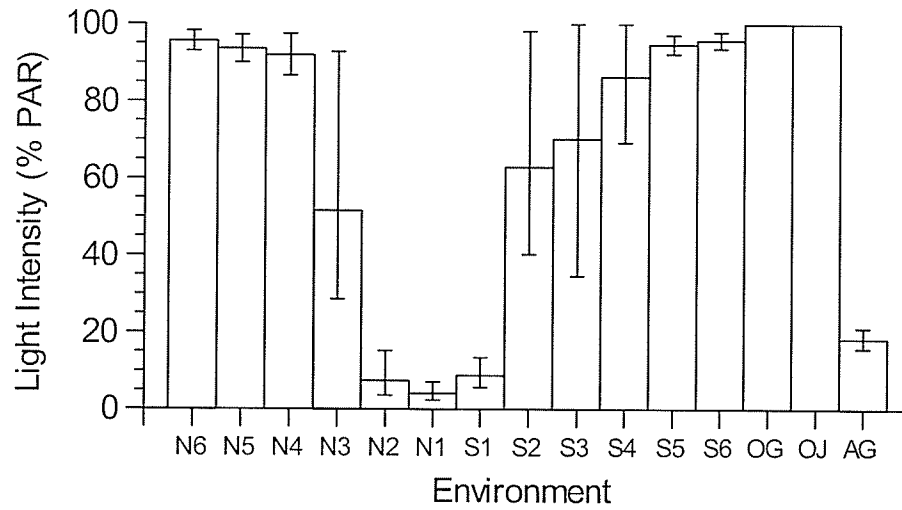
## 2.3 Results

### 2.3.1 Microenvironment

Relative to the open prairie conditions, light intensity in spruce islands was greatest at the periphery but declined towards the island centre (Fig. 2.2). Light intensity of microenvironmental sites at the island periphery (N6, N5, S5, S6) and island intermediary zone (N4, N3, S2, S3, S4) were not significantly different than that of open prairie conditions (OG, OJ) (all  $p > 0.05$ ). Light intensity in aspen groves (AG) was slightly higher than microenvironmental sites at the island centre (N2, N1, S1) (all  $p < 0.05$ ); these microenvironmental sites (AG, N2, N1, S1) in turn were significantly less than the other microenvironmental sites (all  $p < 0.05$ ).

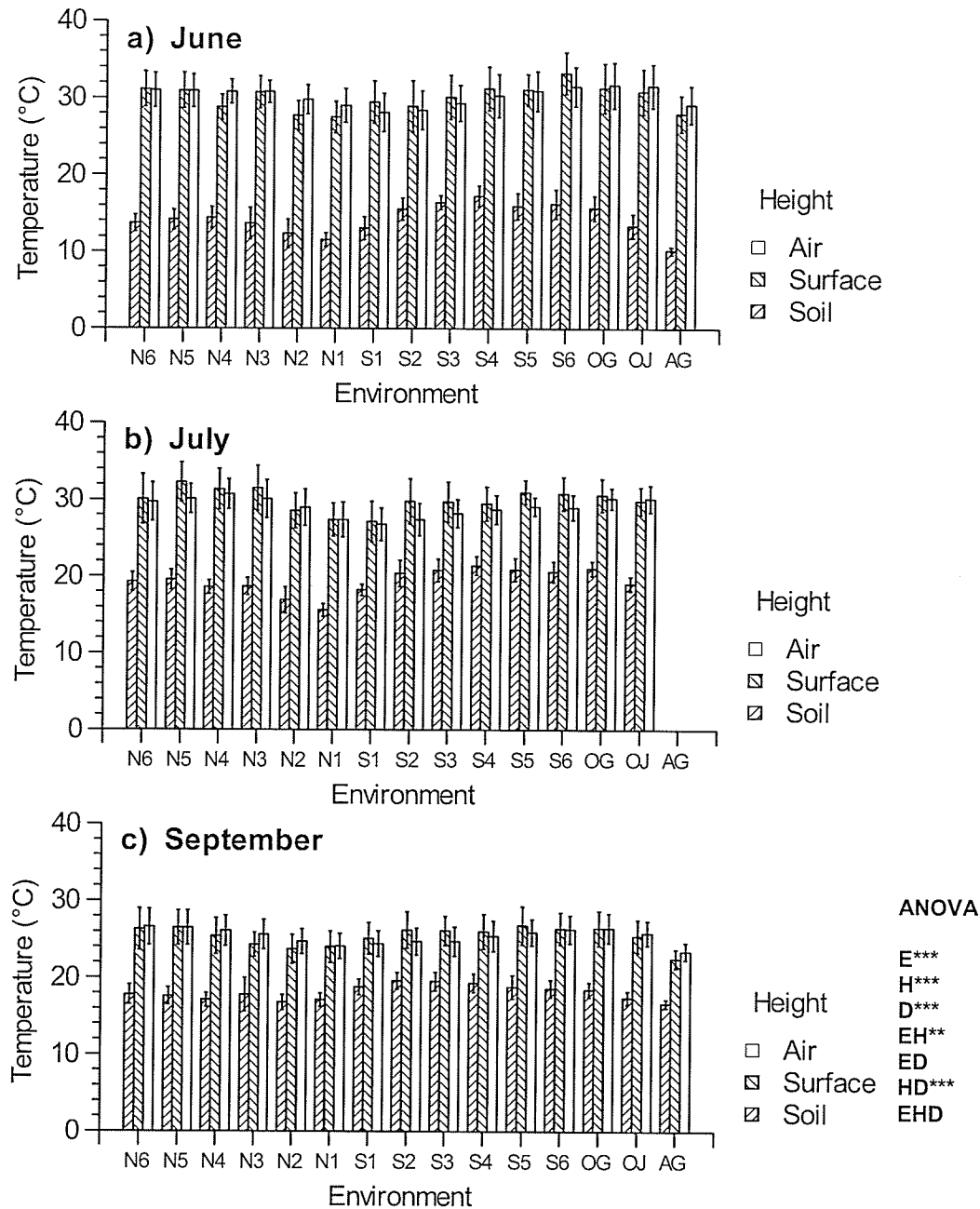
Temperature conditions differed among the microenvironmental sites (microenvironment effect,  $p < 0.001$ ) (Fig. 2.3). That is, the north side close to the island centre (N1, N2) as well as the aspen stand (AG) were generally the coolest. Soil temperature was always lower than surface and air temperature (height effect,  $p < 0.001$ ). Temperature differed significantly between measuring dates in that temperature in July (Fig. 2.3b) was slightly higher than in June (Fig. 2.3a), while conditions were coolest in September (Fig. 2.3c) (date effect,  $p < 0.001$ ). There was significant interaction between environment and sampling height ( $p < 0.01$ ). The difference among microenvironmental sites did not change with date ( $p > 0.05$ ). There was significant interaction between sampling height and date ( $p < 0.001$ ). There was no significant interaction between microenvironment, height of measurement and date ( $p > 0.05$ ).

There were no significant differences in relative air humidity between microenvironmental sites (microenvironment effect,  $p > 0.05$ ) (Fig. 2.4). Relative air humidity differed significantly between sampling date as July was the driest month (Fig.

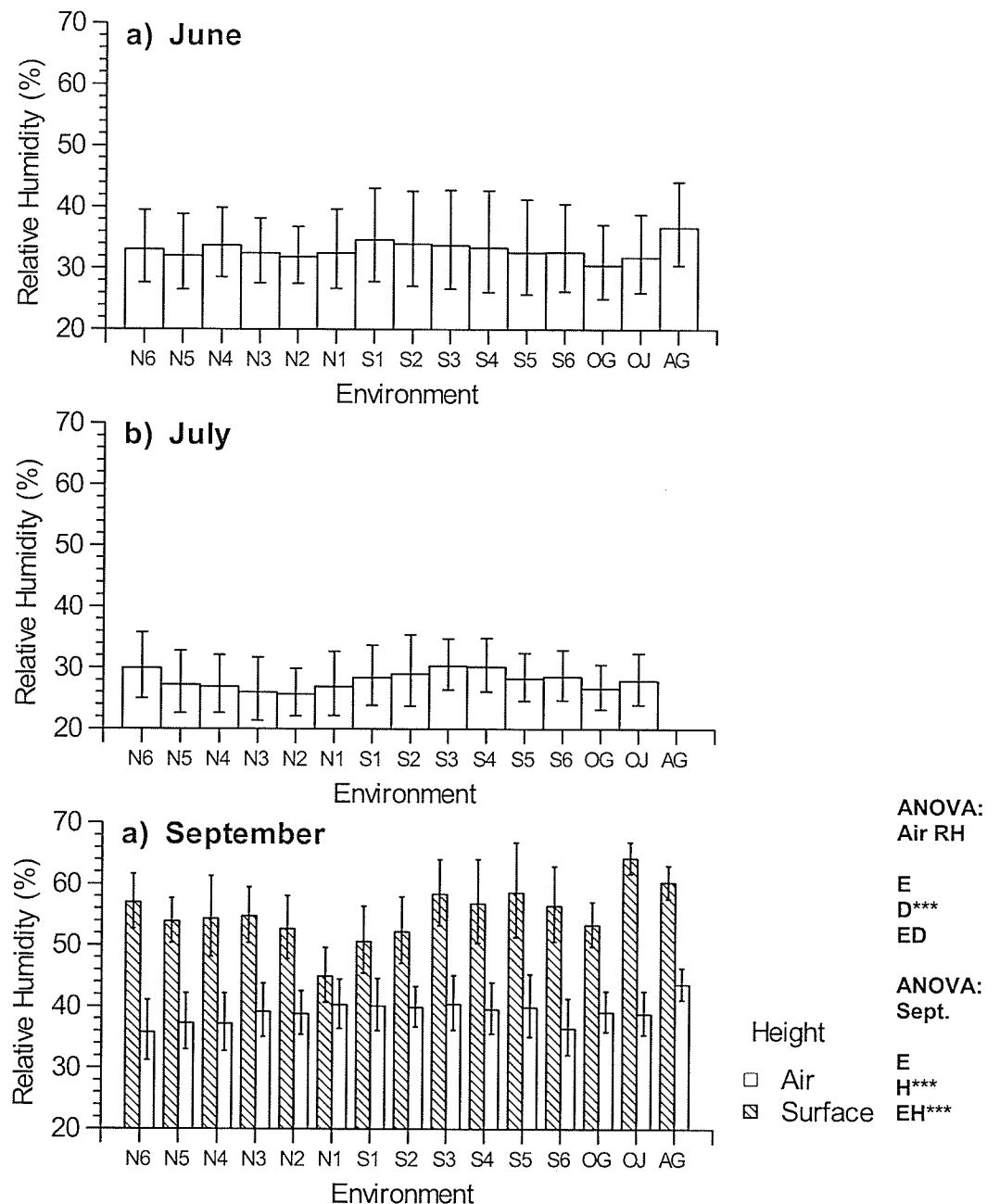


**Figure 2.2** Light intensity of tree islands [north (N) and south (S)] and aspen groves (AG) expressed as a percentage of the open prairie [grass (OG), juniper (OJ)]. Light intensity was measured on a sunny clear day during the first week of July. Mean values ( $n = 10$ ) are bounded by the lower and upper limits of a 95% confidence interval.





**Figure 2.3** Temperature of tree islands [north (N) and south (S)], open prairie [grass (OG) and juniper (OJ)], and aspen groves (AG), measured in the first week of the months of June (a), July (b), and September (c). For each month, temperature was measured in the soil (15 cm below soil surface), on the soil surface, and in the air (15 cm above soil surface). Measurements were not taken in aspen groves in July to prevent over-exposure to poison ivy. Mean values ( $n = 10$ ) are bounded by the lower and upper limits of a 95% confidence interval. ANOVA results for effects; E: microenvironment; H: height; D: date; combinations of letters refers to interactions; \*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ .

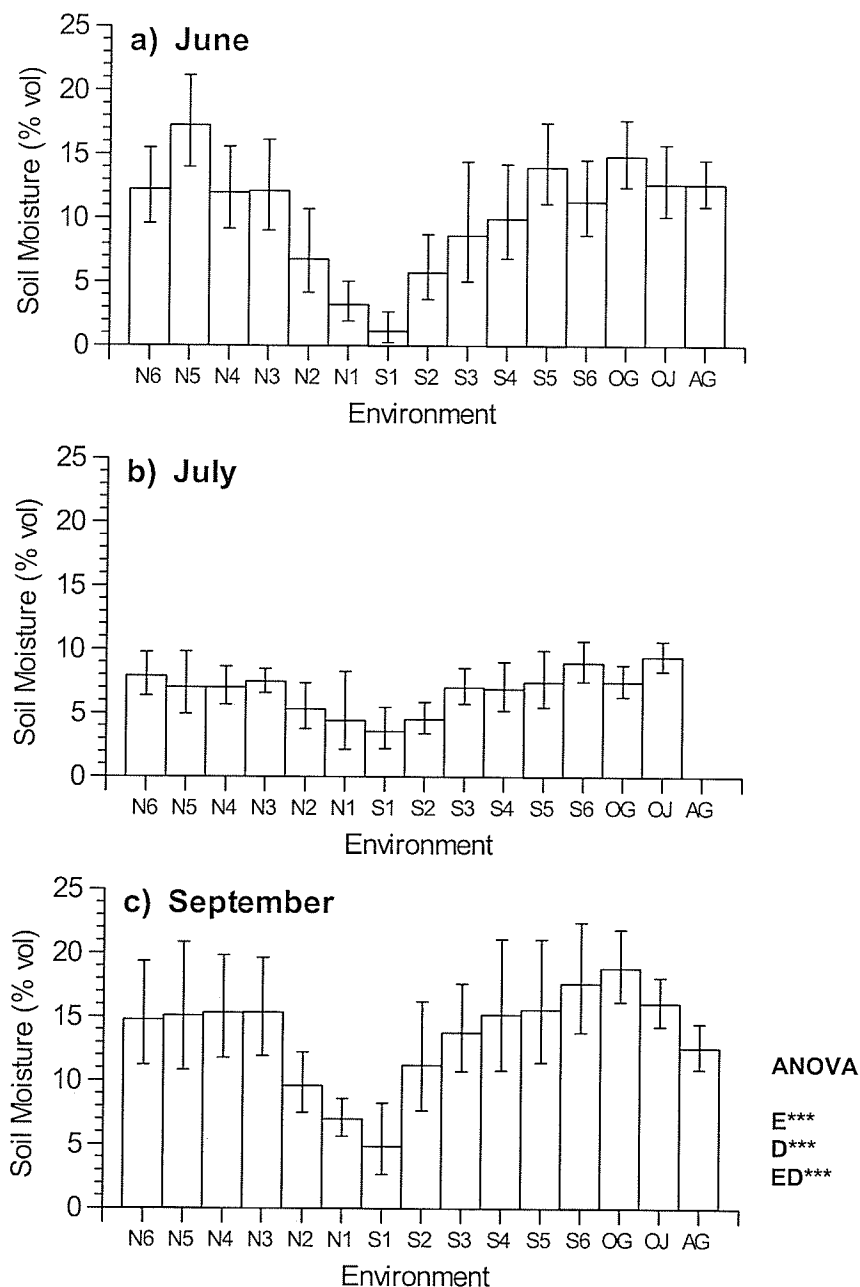


**Figure 2.4** Relative humidity (RH) of tree islands [north (N) and south (S)], open prairie [grass (OG) and juniper (OJ)], and aspen groves (AG), measured in the first week of the months of June (a), July (b), and September (c). RH was measured in the air (15 cm above soil surface) in June and July, while RH was measured on the ground surface in addition to the air in September. Measurements were not taken in aspen groves in July to prevent over-exposure to poison ivy. Mean values ( $n = 10$ ) are bounded by the lower and upper limits of a 95% confidence interval. ANOVA results for effects; E: microenvironment; H: height; D: date; combinations of letters refers to interactions; \*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ .

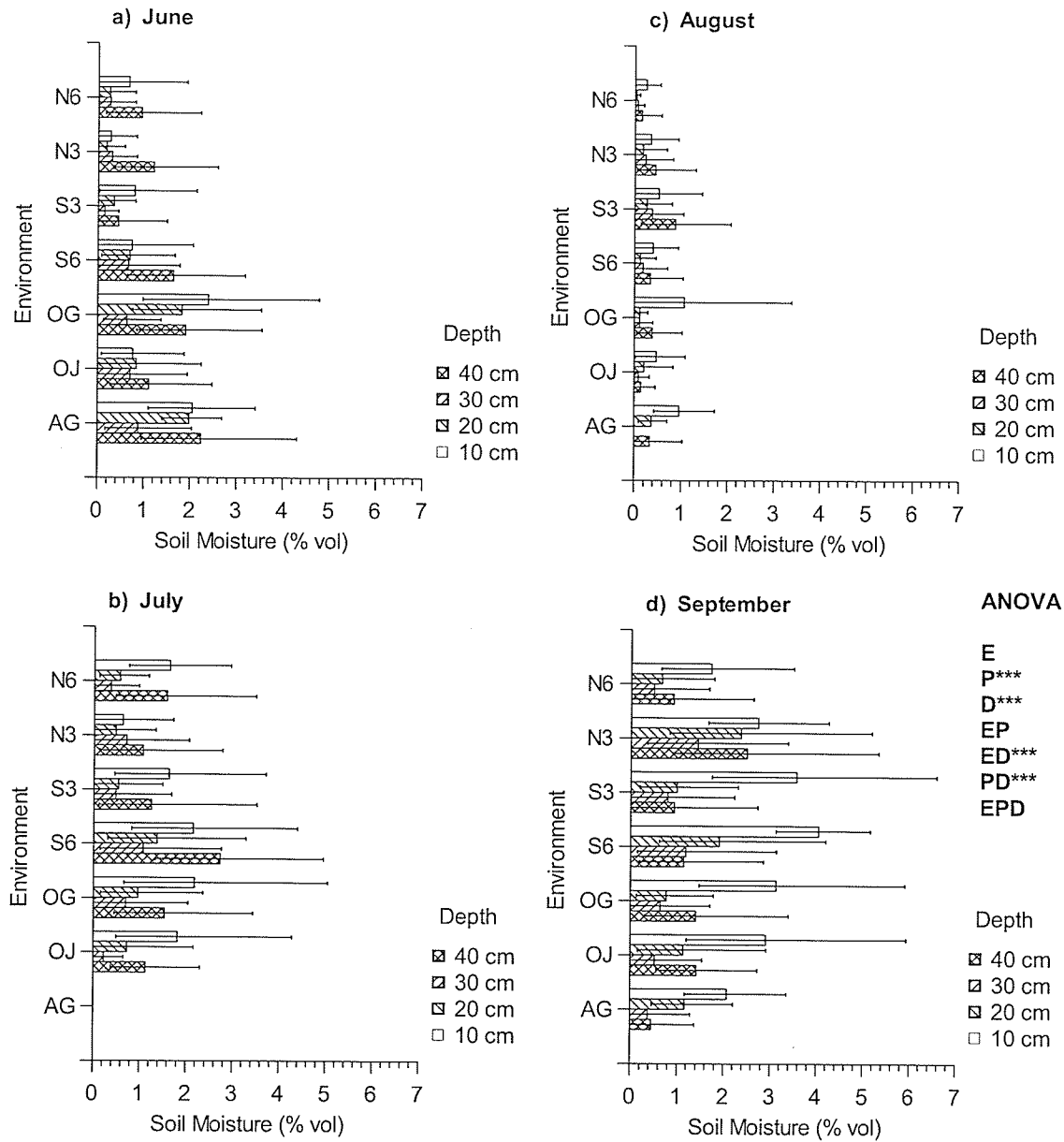
2.4b), followed by June (Fig. 2.4a), while September was the most humid (Fig. 2.4c) (date effect,  $p < 0.001$ ). The relative patterns of air humidity between the microenvironmental sites did not change with sampling date ( $p > 0.05$ ). In September, relative humidity did not differ significantly between microenvironmental sites (environment effect,  $p > 0.05$ ). Surface humidity was greater than air humidity (height effect,  $p < 0.001$ ). There was significant interaction between microenvironment and height of measurement ( $p < 0.001$ ) as plots near the island centre (N1, S1) had similar humidity levels between surface and the air.

Surface soil moisture differed significantly between the microenvironmental sites as moisture was generally greater at the island periphery, in open prairie sites, and in aspen stands versus the island centre (microenvironment effect,  $p < 0.001$ ) (Fig. 2.5). Surface moisture differed between sampling date as moisture was greatest in September (Fig. 2.5c), followed by June (Fig. 2.5a), and then July (Fig. 2.5b) (date effect,  $p < 0.001$ ). There was significant interaction between microenvironment and measurement date ( $p < 0.001$ ).

Compared to surface moisture levels, profile soil moisture levels were appreciably lower. There were no significant differences in moisture between the microenvironmental sites (microenvironment effect,  $p > 0.05$ ) (Fig. 2.6). Moisture differed significantly along the profile depths as moisture was greatest at the depths of 10 and 40 cm versus 20 and 30 cm (profile depth effect,  $p < 0.001$ ). Profile moisture differed significantly between sampling date, as moisture levels in June (Fig. 2.6a) were generally similar to July (Fig. 2.6b), while moisture levels were lowest in August (Fig. 2.6c) and highest in September (Fig. 2.6d) (date effect,  $p < 0.001$ ). No significant interactions occurred between microenvironment and profile depth ( $p > 0.05$ ). An



**Figure 2.5** Soil moisture of the soil surface of tree islands [north (N) and south (S)], open prairie [grass (OG) and juniper (OJ)], and aspen groves (AG), measured in the first week of the months of June (a), July (b), and September (c). Measurements were not taken in aspen groves in July to prevent over-exposure to poison ivy. Mean values ( $n = 10$ ) are bounded by the lower and upper limits of a 95% confidence interval. ANOVA results for effects; E: microenvironment; D: date; combinations of letters refers to interactions; \*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ .

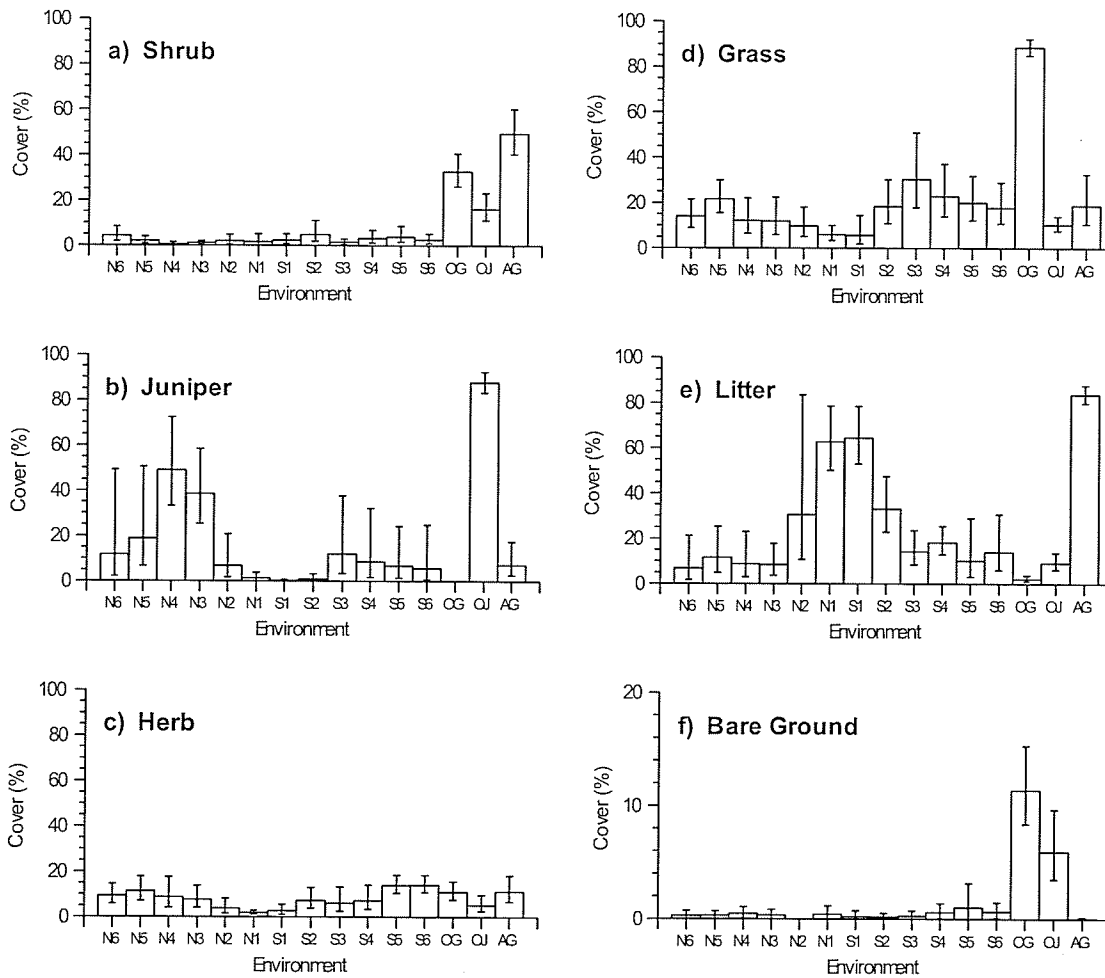


**Figure 2.6** Soil moisture of the soil profile (i.e., depths of 10, 20, 30, and 40 cm below the soil surface) of tree islands [north (N) and south (S)], open prairie [grass (OG) and juniper (OJ)], and aspen groves (AG), measured in the first week of the months of June (a), July (b), August (c) and September (d). Measurements were not taken in aspen groves in July to prevent over-exposure to poison ivy. Mean values ( $n = 10$ ) are bounded by the lower and upper limits of a 95% confidence interval. ANOVA results for effects; E: microenvironment; P: profile depth; D: date; combinations of letters refers to interactions; \*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ .

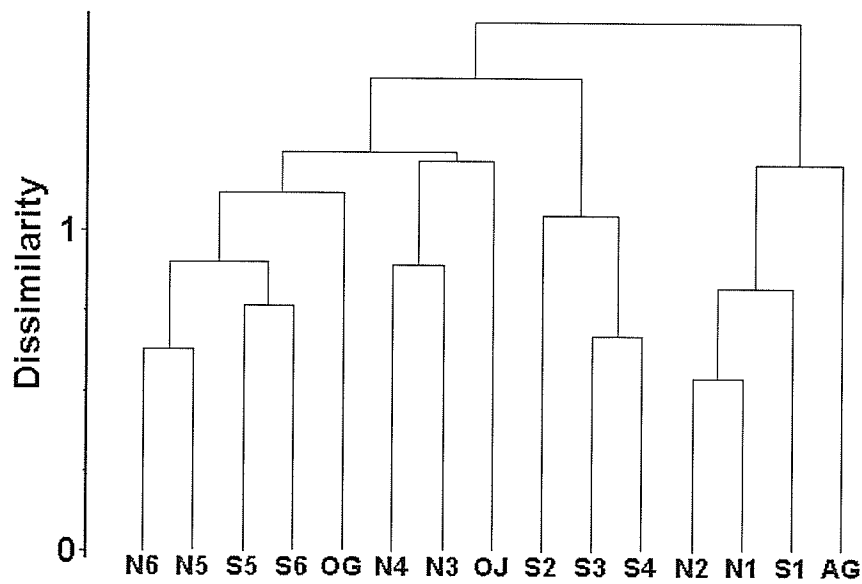
interaction did exist between microenvironment and sampling date ( $p < 0.001$ ). There were also differences in profile depth with sampling date ( $p < 0.001$ ). There was no interaction between microenvironment, profile depth, and sampling date ( $p > 0.05$ ).

Shrub cover was similar in the aspen groves and open prairie grass ( $p > 0.05$ ); these microenvironmental sites in turn were significantly greater than in the remaining microenvironments (all  $p < 0.05$ ) except for the open prairie juniper (all  $p > 0.05$ ) (Fig. 2.7a). Juniper cover was greatest in the open prairie juniper than in the remaining microenvironmental sites (all  $p < 0.05$ ) (Fig. 2.7b). The amount of juniper cover in microenvironments on the north side of the tree islands (N3, N4) was significantly greater than microenvironments at the island interior (N2, N1, S1, S2) (all  $p < 0.05$ ). Herb cover did not differ significantly among the microenvironmental sites (all  $p > 0.05$ ) (Fig. 2.7c). Grass cover was significantly greatest in the open prairie grass than in the remaining microenvironmental sites (all  $p < 0.05$ ) (Fig. 2.7d). Forest floor litter was similar at the island centre (N1, S1) and in the aspen groves (all  $p > 0.05$ ) (Fig. 2.7e); these plots in turn had higher litter cover than the remaining microenvironments (all  $p < 0.05$ ) except plot N2 (all  $p > 0.05$ ). Bare ground was similar in the open prairie grass and juniper microenvironments ( $p > 0.05$ ); these microenvironments in turn had more bare ground than in the other remaining microenvironmental sites (all  $p < 0.05$ ) (Fig. 2.7f).

Hierarchical agglomerative clustering of the microenvironmental sites with respect to microenvironmental variables except profile moisture indicated that microenvironments at the island periphery (N6, N5, S5, S6) had similar microenvironmental conditions; these microenvironmental sites in turn were similar to conditions in the open prairie grass microenvironment (Fig. 2.8). Plots in the northern island intermediary (N3, N4) had similar microenvironmental conditions to open prairie



**Figure 2.7** Percent cover of ground cover types [shrub (a), juniper (b), herb (c), grass (d), litter (e), and bare ground (f)] of tree islands [north (N) and south (S)], open prairie [grass (OG) and juniper (OJ)], and aspen groves (AG). Percent cover was recorded in the first week of July. Mean values ( $n = 10$ ) are bounded by the lower and upper limits of a 95% confidence interval.



**Figure 2.8** Hierarchical classification of microenvironmental sites in tree islands [north (N) and south (S)], open prairie [grass (OG) and juniper (OJ)], and aspen groves (AG) with respect to the mean of each of the microenvironmental variables except profile moisture. Environmental variables were normalized and standardized before the cluster analysis. The hierarchical agglomerative clustering was determined using an unweighted arithmetic average (UPGMA) of a chord distance matrix.



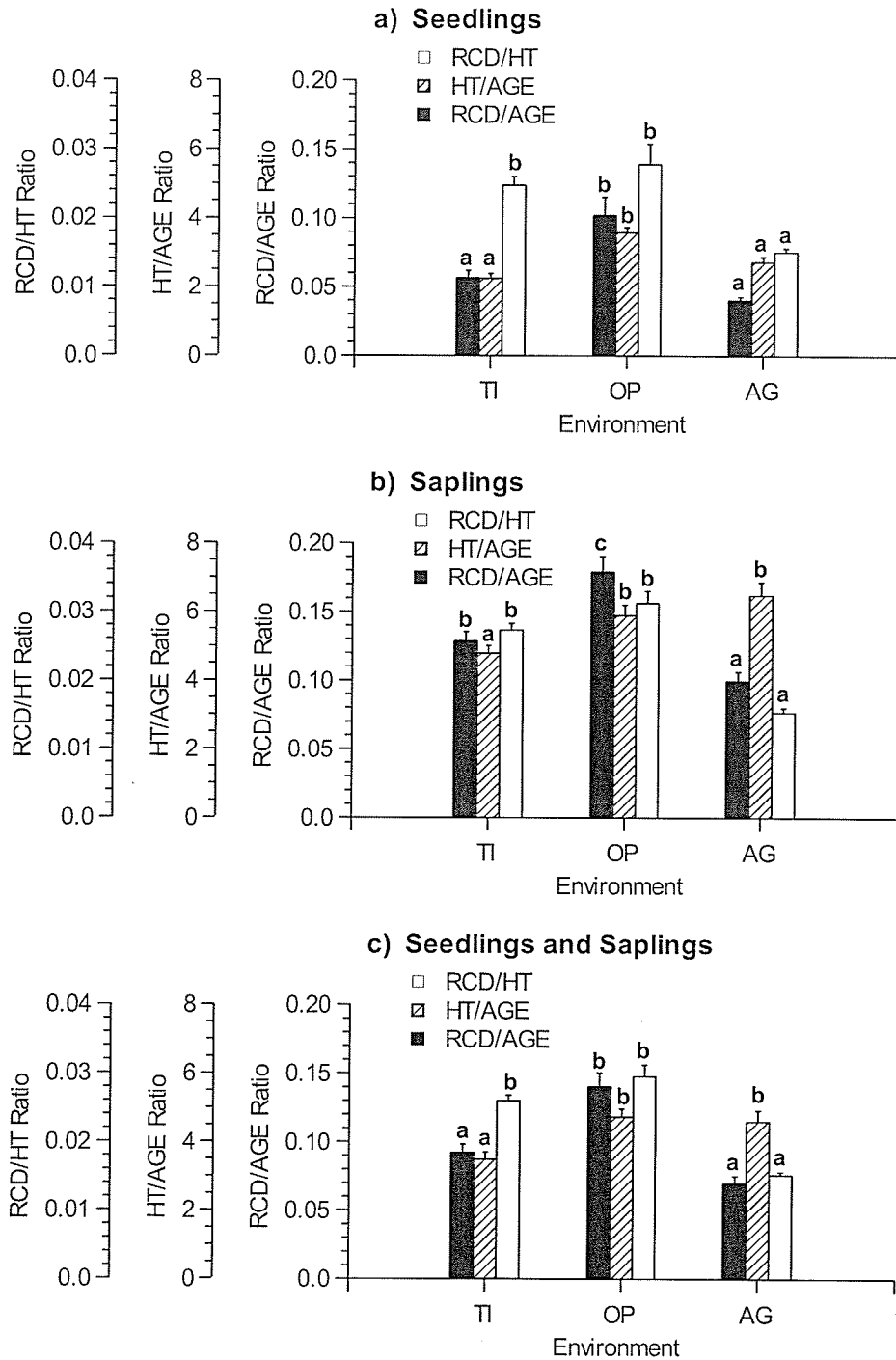
juniper microenvironment. Microenvironmental sites in the southern island intermediary (S2, S3, S4) had similar microenvironmental conditions to each other. Plots at the island centre (N1, N2, S1) had similar microenvironmental conditions to the aspen groves; these microenvironments in turn were distinctly different from the other microenvironmental sites.

### **2.3.2 Seedling and Sapling Growth**

Seedlings and saplings in the open prairie established exclusively on creeping juniper. General seedling and sapling growth attributes are shown in Table 2.2. Regardless of whether seedlings or saplings were considered separately (Figs. 2.9a, 2.9b) or combined (Fig. 2.9c) the general relative patterns of the RCD/age ratio between the three habitats were similar. Seedlings and saplings from the open prairie generally had the greatest RCD/age ratio compared to tree islands and aspen groves. The relative pattern of the height/age ratio differed between seedlings and saplings. The seedling height/age ratio was greater in the open prairie than in tree islands and aspen groves. In contrast, the sapling height/age ratio was similar in the open prairie and aspen groves while this ratio was lowest in the tree islands. Seedlings and saplings showed similar relative patterns in the RCD/height ratio which was greatest in the open prairie compared to tree islands and aspen groves.

**Table 2.2** Attributes [height, root collar diameter (RCD), and age] of seedlings and saplings separately and pooled together from tree islands, open prairie, and aspen groves. Standard error of the mean in parentheses. The minimum and maximum of age are indicated.

| Attribute                     | Tree Island | Open Prairie | Aspen Grove |
|-------------------------------|-------------|--------------|-------------|
| <b>Seedlings</b>              |             |              |             |
| Sample Size (n)               | 30          | 30           | 30          |
| Height (cm)                   | 19.9 (2.0)  | 33.9 (1.6)   | 32.0 (2.1)  |
| RCD (cm)                      | 0.50 (0.06) | 0.96 (0.11)  | 0.48 (0.04) |
| Age (year)                    | 8.6 (0.5)   | 9.5 (0.3)    | 11.8 (0.6)  |
| Minimum                       | 6           | 6            | 7           |
| Maximum                       | 17          | 12           | 18          |
| <b>Saplings</b>               |             |              |             |
| Sample Size (n)               | 29          | 30           | 30          |
| Height (cm)                   | 80.6 (4.7)  | 90.1 (7.7)   | 126.8 (7.6) |
| RCD (cm)                      | 2.19 (0.15) | 2.94 (0.37)  | 1.97 (0.15) |
| Age (year)                    | 17.0 (0.7)  | 15.2 (0.9)   | 20.3 (1.1)  |
| Minimum                       | 13          | 8            | 14          |
| Maximum                       | 25          | 29           | 32          |
| <b>Seedlings and Saplings</b> |             |              |             |
| Sample Size (n)               | 59          | 60           | 60          |
| Height (cm)                   | 49.7 (4.7)  | 62.0 (5.3)   | 79.4 (7.3)  |
| RCD (cm)                      | 1.33 (0.14) | 1.95 (0.23)  | 1.23 (0.12) |
| Age (year)                    | 12.7 (0.7)  | 12.4 (0.6)   | 16.1 (0.8)  |
| Minimum                       | 6           | 6            | 7           |
| Maximum                       | 25          | 29           | 32          |



**Figure 2.9** Comparison of the root collar diameter (RCD)/age ratio, height (HT)/age ratio, and RCD/HT ratio of white spruce seedlings (a), saplings (b), and both seedlings and saplings (c) from tree island (TI), open prairie (OP), and aspen grove (AG). Error bars represent the standard error of the mean. For each parameter, habitats with different letters are significantly different ( $p < 0.05$ ).

## 2.4 Discussion

### 2.4.1 Ecophysiological Implications of Microenvironment

#### 2.4.1.1 Light

The dominant white spruce trees cast shade onto the understory near the island centre. The amount of shade decreased further away from the island centre although the extent of shade was more on the north versus south aspect. Shade was also produced under aspen canopy at levels similar to other studies of aspen (Archibold et al., 1996; Carlson and Groot, 1997; Ripley and Archibold, 1999) and other deciduous stands (Morecroft et al., 1998). The importance of shade in moderating the microclimate in forest/grassland ecosystems has been examined by previous studies (Belsky, 1994; Breshears et al., 1997b; Gass and Barnes, 1998; Martens et al., 2000). For instance, Chhin and Wang (2002) demonstrated the modifying effect of older white spruce trees in providing shade to reduce evapotranspiration rates of seedlings, saplings, and younger trees. This led to the improved germination capacity of white spruce such that recruitment was concentrated on the north side versus the south side of tree islands, and seedling, sapling, and tree density were greater closer to the center than at the island periphery. Similarly, Kellman and Kading (1992) confirmed the importance of shade as a favourable microenvironment for tree seedling establishment during sand dune succession. They observed a nucleated pattern of establishment of pine seedlings (*Pinus strobus* L. and *P. resinosa* Ait.) in the shade cast by oak trees (*Quercus rubra* L.) versus treeless areas, and that seedling density was greater on the north than the south side of the trees. Others have observed growth of white spruce in the aspen parkland region on favourable microenvironments such as the north side of river valleys (Zoltai, 1975; Hogg, 1994). Furthermore, in grassland environments, Hogg and Schwartz (1997) reported

almost exclusive establishment of white spruce seedlings on the north side of trees and on north-facing slopes and micro-sites where shade resulted in cool, moist conditions for seedling establishment.

Although both white spruce islands and aspen groves have a shady understory, the degree of shade produced and its seasonality in distribution differs between a coniferous versus deciduous canopy (Man and Lieffers, 1997). That is, a coniferous canopy intercepts light to a larger degree than deciduous canopies due to the denser canopy and greater leaf area density of white spruce canopies (Landhausser et al., 2001). This may explain the greater reduction of light levels in the island interior compared to the higher light levels observed under aspen canopy. Coniferous canopies remain intact despite changes in season whereas in a deciduous stand more light penetrates to the forest floor in spring before leaf-out and in the fall after leaf fall (Archibold et al., 1996; Ripley and Archibold, 1999). The degree that aspen stands can moderate the understory microclimate via shade is thus interrupted in the spring and fall.

#### **2.4.1.2 Temperature**

The pattern in soil, surface, and air temperature between the microenvironmental sites were similar to the relative patterns of light intensity as areas with increased shade were also cooler. This was expected since temperature is generally a function of solar insolation (Archibold et al., 1996; Ripley and Archibold, 1999). Decreased temperature may lead to decreased evapotranspirative demands in the aforementioned shaded areas. Other studies have also reported reduced soil and air temperature of aspen (Archibold et al., 1996; Carlson and Groot, 1997; Ripley and Archibold, 1999) and other deciduous stands (Morecroft et al., 1998). Landhausser et al. (2001) determined that white spruce was not affected by soil temperatures in the range of 5°C to 25°C. As such, in the present

study, soil temperature may not directly affect white spruce growth, and stress due to temperature may mainly exert itself via ground surface and air temperature and its affect on evapotranspirative water loss. Soil temperature may influence growth performance indirectly by controlling the degree of evaporative water loss from the soil column. Overall, temperature conditions varied seasonally as it was moderate in June, increased in July, and decreased back to cooler conditions in September. These seasonal changes are consistent with the climatic normals from the Brandon Agriculture Station for the reference period of 1971-2000 (Environment Canada, 2002).

#### **2.4.1.3 Relative Humidity**

The pattern of relative air humidity did not differ among the microenvironmental sites regardless of month. Relative humidity did however change seasonally and was similar to the seasonal changes in temperature. This relationship was expected since relative humidity is partly a function of temperature (Roberts and Zwiazek, 2001). In September, relative humidity was greater at the ground surface versus the air above. However, the difference in sampling height varied between the microenvironmental sites as the difference between surface and air humidity diminished at the island interior and may be due to the sparse amount of vegetation cover which led to increased air circulation which in turn lowered humidity levels. The microenvironment which showed the highest surface humidity was the juniper mats in the open prairie habitat. Fire ecology studies of juniper have shown that its large, mat-like growth form (Looman and Best, 1987) reduces its flammability by creating conditions of poor air circulation, limited fuels, and higher relative humidity (Tirmenstein, 1988). Consequently, ground fires are limited to the periphery of large juniper mats and do not consume the center. The increased humidity and fire protection would assist in white spruce recruitment. This was

hypothesised by Chhin and Wang (2002) who observed a close association of white spruce seedlings with creeping juniper. Furthermore, Roberts and Zwiazek (2001) showed that low humidity conditions negatively affected the growth of white spruce seedlings in a growth chamber experiment.

The slightly higher air humidity of the aspen groves may be due to the reduced influence of edge effects such as high wind speeds (Archibold et al., 1996; Ripley and Archibold, 1999). That is, the aspen understory has reduced edge effects because of an extensive buffer whereas this buffer is limited in spruce islands and entirely absent in the open prairie. Thus, the open prairie conditions would be more greatly affected by high winds, followed by the spruce islands and then the aspen understory. For instance, in an aspen grove in Saskatchewan, wind speed was reduced to 7% of that in adjacent prairie (Archibold et al., 1996; Ripley and Archibold, 1999).

#### **2.4.1.4 Soil Moisture**

Surface soil moisture was lowest at the island interior and increased towards the periphery where moisture levels were similar in both the open prairie and in the aspen groves. The decreased amount of surface moisture at the island interior may be due to the interception of rainfall and snowfall by the tree canopy and thus limiting the amount of throughfall (Vetaas, 1992). Although water also enters the island via stemflow it has been shown that such water is more likely to infiltrate to deep soil layers to be used by tree species (Parker, 1983; Vetaas, 1992; Breshears et al., 1997b). Moisture levels may also be low due to the greater loss of moisture through evapotranspiration. The greater amount of moisture at the island periphery may be due to canopy drip (Vetaas, 1992; Breshears et al., 1997b). The pattern of surface soil moisture varied seasonally as moisture levels were moderate in June relative to the lowest amounts in July and highest

amounts in September. This seasonal trend however does not conform with the climatic normals of the Brandon climate station which instead showed the highest precipitation in June (75.7mm), followed by July (72.5mm) and September (48.3mm) (Environment Canada, 2002). It could simply mean that this September was wetter than usual. Another possible explanation of the increased surface moisture in September is that surface moisture is moderated by cooler surface temperatures in September. This would suggest that surface soil moisture may not reflect precipitation levels particularly on sandy substrates of poor water holding capacity.

Moisture levels of the soil profile were less than their corresponding levels at the soil surface. This underscores the extreme sandy texture of the soils which have poor water holding capacity, whereas the more organic surface layer had better water holding capacity. Profile soil moisture did not vary significantly between microenvironments. The drop in soil moisture at the depth of 30 cm suggests that soils at this depth may contain less organic matter than soil at the other depths. Consequently, soils at the depth of 30 cm would have poor water holding capacity. The seasonal pattern of profile moisture was similar to that of surface moisture in that moisture was greatest in September. This again contradicts the precipitation record and may be due to the same reasons given for the patterns of soil moisture.

#### **2.4.1.5 Ground Cover**

Shrub cover was greatest under the aspen canopy followed by the open prairie microenvironments. The presence of other woody species may increase the degree of below and above ground competition for white spruce growing under aspen stands. Shrubs have the potential to overtop young white spruce seedlings in addition to the aspen overstory thereby increasing the degree of shade. Studies in the aspen parkland



have confirmed that tree species thrived after neighbors were removed and thus limited the degree of competition for above-ground and below-ground resources (Peltzer and Wilson, 2001; Partel and Wilson, 2002).

Juniper was concentrated on the north versus south side of spruce islands. Chhin and Wang (2002) demonstrated that white spruce seedlings, saplings and younger trees were concentrated on the north versus south aspect and within 4-12 m from the island centre. Therefore, the recruitment patterns of white spruce correspond with the patterns of juniper cover. Furthermore, Chhin and Wang (2002) observed that white spruce seedlings were also in close association with creeping juniper. They concluded that juniper facilitates white spruce establishment by providing favourable microclimatic site conditions. The important role of fire in the drought prone ecosystem of the aspen parkland may suggest that juniper has reduced mortality of white spruce seedlings from prairie fires. Chhin and Wang (2002) observed that patches of juniper which were exposed to prescribed fire were not completely burnt, and that white spruce seedlings growing in the middle of juniper patches had survived the fire. Other researchers (Coupland, 1950; Scoggan, 1957; Bird, 1961) who have observed the close association between creeping juniper and white spruce in the Spruce Woods Forest Reserve have also attributed it to juniper providing white spruce protection from prairie ground fires. The concentration of juniper on the north side of an island in addition to the decrease in grass cover on the north side may suggest that juniper has reduced competition between grasses and white spruce seedlings. The role of juniper would be similar to that of western snowberry (*Symphoricarpos occidentalis* Hook) and wolf willow (*Elaeagnus commutata* Bernh.) in crowding out grass competition for the successful establishment of trembling aspen (Bird, 1961).

In contrast to juniper, grass was more concentrated on the south versus north aspect of tree islands. Competition between grasses and woody plants is known to suppress germination and growth of tree seedlings (Li and Wilson, 1998; Wilson, 1998). Chhin and Wang (2002) observed a reduction in seedling and sapling numbers at the periphery of the spruce islands and at the southern island aspect and attributed it to direct competition with grasses.

The amount of forest floor litter was greatest at the island centre and decreased towards the periphery. Litter cover was also great in the aspen groves. Decomposition of litter beneath tree canopies can contribute to the addition of nutrients to the soil (Belsky, 1994; Kochy and Wilson, 1997). Litter also acts as a barrier to infiltration and therefore slows down the leaching of nutrients into the soil (Breshears et al., 1997b). However, the infiltration barrier of litter may also limit movement of moisture to the soil. This in turn may suppress germination of tree seedlings and may explain why Chhin and Wang (2002) observed no establishment of white spruce at the island centre. In the aspen stands coniferous tree seedlings are particularly susceptible to being smothered by deciduous litter (DeLong et al., 1997).

The amount of bare ground was greatest in the open prairie microenvironments. Exposed mineral soil is considered an ideal substrate for white spruce seedling establishment (Nienstaedt and Zasada, 1990). Although the open prairie grass microenvironment contained more bare ground than the juniper microenvironment, the higher degree of mineral soil exposure may not offset the negative effects of a harsher microenvironment and the influence of tree-grass competition. The favourable microclimate of juniper mats combined with the exposed mineral soil may serve as future

locations for white spruce establishment when white spruce seed is distributed by wind to these adjacent open prairie locations.

#### **2.4.1.6 Influence Zones in Tree Islands and their Relation to the Open Prairie and Aspen Groves**

Hierarchical classification provided the analysis of higher order relationships among the sampling sites. Microenvironmental conditions within a spruce island and its relation to conditions in the open prairie and under aspen groves depended on distance from the island centre and can be categorized into three distinct influence zones. The first zone included microenvironments at the island centre immediately north and south of the dominant tree which were similar to conditions under aspen canopy. The second zone included microenvironments under the island canopy (intermediate to the island centre and the periphery) which showed distinct differences in terms of aspect. Conditions at the northern island canopy had a similar microenvironment to the open prairie juniper conditions. The spatial recruitment patterns of white spruce described by Chhin and Wang (2002) correspond to this influence zone (i.e., northern island canopy) and thus represents an ideal microenvironment for white spruce establishment. The microenvironments at the southern canopy were unique and were most different to conditions under the aspen canopy. The third zone consisted of microenvironments immediately at the island periphery outside the influence of the island canopy which, regardless of aspect, were more similar to conditions in the open prairie grass microenvironment.

#### **2.4.2 Seedling and Sapling Growth**

The diameter/age ratio of seedlings and saplings were generally similar when each was considered separately or when they were pooled together. The diameter/age

ratio was greatest within the open prairie than in either the tree islands and aspen groves. These results were not expected given the harsher microenvironment of the open prairie. Surveying white spruce seedlings and saplings in the open prairie spruce was difficult given the rarity of finding open prairie spruce. Furthermore, those white spruce individuals which were found grew exclusively in association with creeping juniper. Therefore, in addition to unlimited light, the better than expected growth in the open prairie may be due to the moderating influence of a creeping juniper substrate.

The lower than expected growth within spruce islands and aspen groves suggests that the light-limited conditions of these environments may outweigh the benefits of a moderated microclimate. In other words, these results suggest that while shade is an important moderating microclimatic factor that is conducive to successful white spruce establishment, shade is detrimental to subsequent seedling and sapling growth. Furthermore, Groot (1999) reported that diameter growth of young planted white spruce was influenced primarily by light. White spruce attains maximal photosynthesis at 40% full sunlight (Lieffers and Stadt, 1994). Higher light levels do not result in net photosynthetic gain since it increases the likelihood of photoinhibition at high light intensity. Light levels below 8% results in mortality of white spruce (Groot, 1999). Therefore conditions at the island centre are not conducive to white spruce survival due to extremely low light levels below 10%. The amount of light increases from the island centre towards the intermediary zone (N2, N3, N4) where the seedlings and saplings were selected from. This area is characterized by light levels ranging from about 10% (N2) to 90% (N4). On average these light conditions are greater than under aspen canopy, but not as great as at the island periphery and in the open prairie. However, conditions at the island periphery and open prairie conditions are prone to excess sunlight and thus the

increased likelihood of reduced carbon gain due to photoinhibition (Man and Lieffers, 1997). Although symptoms of photoinhibition were confirmed by field observations which included discolouration of the needles of seedlings and saplings from the open prairie, photoinhibition did not adversely affect net diameter growth. While conditions under the aspen canopy were greater than the minimal light level, they are well below that required for effective photosynthetic uptake. Man and Lieffers (1997) also confirmed that light intensity under an aspen canopy was not sufficient to reach the saturation point although light levels were above the compensation point. This in turn curtails carbon gain and thus decreases diameter growth for seedlings and saplings grown under aspen canopy.

The patterns in the height/age ratio between habitats differed with respect to seedlings and saplings. Seedlings showed a higher height/age ratio in the open prairie compared to the other habitats. In contrast, the height/age ratio of saplings was similar in the open prairie or aspen groves. The better than expected height growth of seedlings, and the comparable height growth of saplings in the open prairie compared to aspen groves may be due to the same reasons stated for the diameter/age ratio relationships.

The relative pattern in the diameter/height ratios between environments conform with morphological observations in the field which indicated that white spruce from aspen groves were generally tall and narrow, while spruce from the open prairie were short and thick. Spruce from tree islands were intermediate along this morphological continuum. The morphology of white spruce under aspen canopy is thus suited for quickly gaining a suitable stature in the vegetation strata in order to prevent being overtopped by other vegetation (Lieffers et al., 1996). The morphology of white spruce in the open prairie is suited for a more robust stature which is not tailored towards

increasing height growth since light is amply available. Instead, the robust stature is required to withstand high winds during summer (Archibold et al., 1996; Ripley and Archibold, 1999). In the winter, open prairie spruce must contend with high winds and blowing snow which results in wind and snow abrasion. Damage to open grown spruce were confirmed by field observations which included damage to the leader of previous years that temporally removed apical dominance and consequently lead to a more branching, krummholz growth form. Wind and snow abrasion have also influenced open grown spruce at its northern limit of distribution at the tree-line in Churchill, Manitoba (Scott et al., 1987a; Scott et al., 1993).

#### **2.4.3 Future Research**

Further research should be conducted within the Spruce Woods Provincial Park to elucidate other components of the microenvironment which may affect tree establishment and growth patterns. Microclimatic measures include wind speed (Morecroft et al., 1998) and snow depth (Archibold et al., 1996; Ripley and Archibold, 1999). Microclimatic measurements also need to be taken diurnally to provide a sense of the day-to-day fluctuations of the microclimatic variables (Morecroft et al., 1998). Although the present study focused on measuring the microclimate on sunny clear days to provide as much contrast as possible between the three environments, measurements should also be taken during cloudy days for comparison (Morecroft et al., 1998). To provide a sense of annual changes in the microclimate, measurements should be taken during the fall, winter, and spring to complement the present analysis of microclimate in the summer (Archibold et al., 1996; Ripley and Archibold, 1999). Vegetation cover should be examined down to the level of species particularly for herbs and shrubs (Parker and Muller, 1982; Thorhallsdottir, 1990; Ko and Reich, 1993; Peltzer and Wilson, 2001). This is important

given the role of competition (Wilson, 1993; Belsky, 1994) and facilitation (Werner and Harbeck, 1982; Wilson and Agnew, 1992; Bertness and Callaway, 1994; Callaway, 1995; Gass and Barnes, 1998; Li and Wilson, 1998; Chambers, 2001) that occur between herbs, shrubs, and tree species within forest/grassland ecosystems. Within the aspen stand further studies should examine microclimatic variation along a transect from the grove interior to periphery onwards towards adjacent mixed-grass prairie.

Chhin and Wang (2002) examined the spatial recruitment patterns of white spruce. The present study focused on growth parameters. Further studies should examine other parameters of white spruce performance within the three environments. These parameters include biomass measurements of needles, branches and stems (Ko and Reich, 1993) particularly in light of current global change studies on carbon budgets (Jackson et al., 2002). Further parameters include ecophysiological measurements such as leaf area ratio, foliar nutrients, transpiration, internal water relations, and photosynthetic rates (Burton and Bazzaz, 1995; Breshears et al., 1997a; Man and Lieffers, 1997). The reproductive ecology of white spruce should be examined in terms of whether a disjunct population at its southern limit shows different patterns of reproduction than white spruce near the centre of its range. To meet this goal, cone (e.g., size, mass) and seed (e.g., mass, germination rate) characteristics should be examined particularly under different temperature and moisture regimes (Burton and Bazzaz, 1991). Field germination studies should also be conducted to examine what factors affect germination and whether these factors differ from those that affect growth patterns (Burton and Bazzaz, 1991; De Steven, 1991a; De Steven, 1991b; Burton and Bazzaz, 1995). The reproductive ecology would thus contribute to a holistic perspective of white spruce performance at different stages of development.

Despite the preponderance of research on above-ground heterogeneity in microclimate as well as above-ground vegetation patterns, there has been relatively less research on below-ground patterns of abiotic and biotic factors (Martens et al., 1997). This is understandable due to logistic and technical difficulties. Other researchers studying forest/grassland ecosystems have also highlighted the importance of filling in this research gap given that competition is mainly for below ground resources (Wilson, 1993; Belsky, 1994; Kleb and Wilson, 1997; Kleb and Wilson, 1999). Below ground measurements of biotic factors include root biomass and should include enumeration of fine roots (Partel and Wilson, 2002). Furthermore, the role of mycorrhizal relationships should be explored as such mutualistic associations would be important in assisting tree species in water and nutrient uptake. The abiotic component of the below ground patterns include a detailed soils analysis in terms of enumerating soil moisture patterns as well as the chemical and physical properties of soils (Severson and Arneman, 1973; Fuller and Anderson, 1993; Ko and Reich, 1993; Tiedemann and Klemmedson, 1973; Tiedemann and Klemmedson, 1977; Wilson and Kleb, 1996; Kleb and Wilson, 1997; Kleb and Wilson, 1999). Soil moisture patterns should be examined at depths greater than 40 cm to better understand the mechanism of water uptake by the tap root of woody species (Ng and Miller, 1980).

In addition to the habitats studied, the park also contains closed white spruce forests some of which usually lines the edge of the mixed-grass prairie preserves. It would be interesting to examine the microclimate, establishment, and growth patterns of young white spruce within this environment.



## **2.5 Conclusions**

### **2.5.1 Microenvironment**

1. In contrast to the open prairie and island periphery, conditions under the tree canopy of islands and aspen groves included increased shade with concomitant decreases in soil, surface, and air temperature.
2. The high relative humidity under juniper mats supports the contention that juniper facilitates white spruce establishment by limiting moisture stress and protecting white spruce seedlings from the effect of prairie ground fires.
3. The decreased amount of surface moisture at the island interior may be due to the interception of rainfall by the tree canopy and evapotranspirative water loss; the island interior is thus not ideal for white spruce establishment.
4. The concentration of juniper and white spruce recruitment at the northern island canopy further supports the contention that juniper facilitates white spruce establishment. The concentration of grass on the southern island aspect may have prevented white spruce establishment on that side. Increased litter at the island centre may have limited infiltration of moisture to the soil; decreased recruitment patterns at the island centre may be related to the negative influence of litter. The bare ground within juniper mats may serve as future locations for white spruce establishment.

### **2.5.2 Seedling and Sapling Growth**

1. While shade is an important moderating microclimatic factor that is conducive to successful white spruce establishment, shade in the aspen groves and spruce islands is detrimental to subsequent seedling and sapling radial and height growth. That is, the light-limited environments of the aspen groves and spruce islands

outweighed the effect of moderated microclimatic conditions. In addition to unlimited light, the better than expected growth in the open prairie may also be due to the moderating influence of a creeping juniper substrate.

2. The tall and narrow morphology of white spruce under the aspen canopy is suited for quickly developing a suitable stature in the vegetation strata in order to prevent being overtopped by other vegetation.
3. The short and thick morphology of white spruce in the open prairie is suited for a more robust stature to withstand high winds during summer, and wind and snow abrasion during winter.

## CHAPTER 3: COMPARATIVE DENDROCLIMATIC ANALYSIS OF WHITE SPRUCE TREES WITHIN SPRUCE ISLANDS VERSUS ASPEN GROVES

### 3.1 Introduction

Most dendroclimatological studies of white spruce trees (*Picea glauca* (Moench) Voss) in Canada have been conducted at its northern limit in sub-arctic regions where low temperature (Szeicz and MacDonald, 1995b) and drought stress limit tree growth (Szeicz and MacDonald, 1996; Barber et al., 2000). In contrast, few dendroclimatological studies of white spruce have been undertaken in the Canadian prairies (Sauchyn and Beaudoin, 1998) where climatic moisture deficiency is postulated to control the southern distribution limit of coniferous tree species (Zoltai, 1975; Hogg, 1994).

Ecotonal regions such as the prairie-forest boundary are expected to be sensitive to climatic change (Rizzo and Wiken, 1992). Furthermore, the environment of the aspen parkland is expected to characterize the future boreal forest under a warmer climate (Hogg, 1994; Hogg and Hurdle, 1995). Therefore, studies on the present interaction between vegetation and climate in the aspen parkland may help us to understand future climate-vegetation interactions in the southern boreal forest (Hogg, 1994; Hogg and Hurdle, 1995). In this respect, dendroclimatic studies may provide insight into how forests may respond to future climatic warming through the indirect examination of climate – growth relationships. Dendroclimatic studies thus have the potential to be parameterized into models of forest growth in response to climate change (e.g., Cook and Cole, 1991).

The objective of the study was to examine the sensitivity of a disjunct population of white spruce trees at its southern limit of distribution within the forest-prairie transitional zone in response to past climatic fluctuations. Specifically, establishment and radial growth patterns of white spruce were examined in two environments and included white spruce tree islands and young white spruce trees within the understory of aspen groves. Within the aspen groves, establishment and growth patterns of aspen were also examined as a reference for comparison with white spruce from the two environments. The patterns of establishment and growth were related to past climate and the effects of the microclimate of spruce islands and aspen groves.

## **3.2 Methods**

### **3.2.1 Establishment Dates**

#### **3.2.1.1 Sampling Design and Sample Processing**

A total of 89 spruce islands were sampled over four mixed grass prairie preserves (Epinette, Picnic, Aspen Bluff, and Jackfish prairie) within the Spruce Woods Provincial Park (SWPP) (Fig. 1.2). These islands included 30 which were sampled by Chhin and Wang (2002) in the summer of 2000. The remaining islands were sampled in the summer of 2001. GPS (global positioning system) coordinates were taken of islands in Picnic, Aspen Bluff, and Jackfish prairie and are shown in the aerial photographs in Figures 3.1, 3.2, and 3.3, respectively. The criteria for selection were that islands be at least 20 meters apart from each other, from aspen groves, and from the forest edge (aspen forest, white spruce forest, or mixed forest) and that the islands have similar topography. A total of 29 islands were selected within the largest prairie (Epinette), 24 in each of the medium sized prairies (Picnic and Aspen Bluff) and 12 islands in the smallest prairie (Jackfish). Epinette prairie experienced severe burning in 1997 (Schykulski and Moore, 1997). A disc was collected at breast height (1.3 m) from the largest dominant tree within each of the burned islands of Epinette prairie. Three dominant trees were cored at breast height (1.3 m) with an increment borer from within the islands of the other prairie sites, and 2 cores were obtained per tree. Dead material was also sampled.

A total of 10 aspen groves were sampled in the summer of 2001 from three mixed-grass prairie preserves (Picnic, Aspen Bluff, and Jackfish prairie) and these corresponded to the same stands from which the microenvironmental, and seedling and sapling growth data were obtained (Chapter 2). The three largest dominant white spruce

and aspen trees were sampled from within each aspen stand and 2 cores were taken per tree.

Cores and discs were prepared and crossdated following standard dendrochronological techniques (Stokes and Smiley, 1968; Yamaguchi, 1991). Cores were mounted and all wood samples were sanded with progressively finer grades of sandpaper to highlight ring-width patterns. Crossdating is the procedure of matching relative ring-width variations and other structural characteristics among trees that have grown in nearby areas to identify the exact year in which each ring was formed (Stokes and Smiley, 1968; Fritts, 1976).

### 3.2.1.2 Data Analysis

For spruce islands, the age correction factor for core height was based on a large sample of seedlings and saplings collected by Chhin and Wang (2002) from a total of 30 spruce islands collected over three mixed-grass prairie preserves (Picnic, Aspen Bluff, and Jackfish prairie). The following was the regression equation relating age to height (cm) in spruce islands [ $y = 2.18 (x^{0.47})$ ]; where  $y$  = age (year),  $x$  = height (cm);  $n = 165$ ; standard error of the estimate (SEE) = 2.22;  $R^2 = 0.82$ ] (Chhin and Wang, 2002).

Therefore, it took seedlings and saplings from spruce islands 21.5 years to reach 1.3 m. The age correction factor for core height for spruce from the aspen groves was based on the pooled data of seedlings and saplings collected from the aspen groves [ $y = 3.07 (x^{0.39})$ ]; where  $y$  = age (year),  $x$  = height (cm);  $n = 60$ ; SEE = 4.11,  $R^2 = 0.59$ ] (Chapter 2). Therefore, it took seedlings and saplings from aspen groves 20.5 years to reach 1.3 m. Since no young aspen suckers were sampled, no age correction factor for coring height could be determined for mature aspen. Therefore, establishment dates of aspen were reported at 1.3 m. One year old aspen suckers generally reach heights ranging from 15 -

30 cm (Perala, 1990) to as high as 1 m (Sims et al., 1990). The age correction factors were added to establishment dates at breast height. If coring missed the pith, the pith radius was estimated graphically (Villalba and Veblen, 1997). The number of rings required to reach the pith was then estimated geometrically (Szeicz and MacDonald, 1995a). After the age corrections were applied, the oldest individual within each spruce island represented the date of establishment of that island. Within each aspen grove, the oldest white spruce and aspen represented the date of establishment of their respective species within that aspen grove.

## **4.2.2 Growth-Climate Relationships**

### **4.2.2.1 Sampling Design and Sample Processing**

A subset of forty-four white spruce tree islands were selected from the 89 islands previously sampled in the determination of establishment dates due to time constraints. The criteria for selecting islands for inclusion in the growth-climate analysis was based on a combination of maintaining adequate spatial coverage of the prairie preserves, and selecting islands which contained old trees. Thus, twenty-four islands were selected from the largest prairie (Epinette), eight islands from each of the medium sized prairies (Picnic and Aspen Bluff) and four islands from the smallest prairie (Jackfish). The total number of trees (radii) selected in Epinette, Picnic, Aspen Bluff, and Jackfish prairie were 24 trees (48 radii), 16 trees (32 radii), 16 trees (32 radii), and 8 trees (16 radii), respectively, for a total of 64 trees (128 radii).

White spruce had established before aspen in two of the aspen groves (one in Picnic and one in Jackfish prairie). The white spruce and aspen within these two groves were not included in the subsequent growth-climate analysis. All white spruce and aspen were used in growth-climate analysis except 2 aspen trees (Picnic prairie) from which

twisted cores with distorted growth patterns were obtained in the remaining eight aspen groves. Therefore, the total number of white spruce trees (radii) selected in Picnic, Aspen Bluff, and Jackfish prairie were 9 trees (18 radii), 12 trees (24 radii), and 3 trees (6 radii), respectively, for a total of 24 trees (48 radii) (Table 4.1). Similarly, the total number of aspen trees (radii) selected in Picnic, Aspen Bluff, and Jackfish prairie were 7 trees (14 radii), 12 trees (24 radii), and 3 trees (6 radii), respectively, for a total of 22 trees (44 radii).

The crossdated samples were measured to the nearest 0.001 mm using a VELMEX measuring system. The quality of the visual crossdating was further verified with the program COFECHA (Holmes, 1983; Holmes, 1992). COFECHA computes cross-correlations between individual ring width series and an average chronology, and identifies tree-ring series which are poorly correlated with the average chronology. COFECHA thus identifies tree-ring series which should be rechecked for any dating and measurement errors.

### **3.2.2.2 Chronology Development**

Each ring-width series was standardized with a 50-year cubic smoothing spline with a 50% frequency response (Cook and Peters, 1981) using the program ARSTAN (Cook, 1985; Holmes, 1992). Each measured series was thus converted into dimensionless ring-width indices through standardization by dividing the observed values by the predicted values. The purpose of standardization was to amplify the climatic signal (high frequency or interannual variation) while removing the effect of non-climatic factors (e.g., age-related trend) (low frequency or long term variation) (Fritts, 1976). Autoregressive (AR) modeling was applied to the standardized ring-width series to remove temporal autocorrelation (Fritts, 1976; Cook and Kairiukstis, 1990). Autoregressive modeling thus



makes observations independent to meet the condition of most statistical analyses (Legendre and Legendre, 1998). The standardized chronologies with temporal autocorrelation removed is referred to as the residual chronology. The residual chronology for white spruce from tree islands, and white spruce and trembling aspen from aspen groves was created using a biweight robust mean.

### **3.2.2.3 Descriptive Chronology Statistics**

Descriptive statistics were determined for the chronologies of each of the two environments for the entire chronology length or the common interval analysis (i.e., a period in which all series span the same time period) (Fritts, 1976; Cook and Kairiukstis, 1990). Statistics of the chronology length included mean sensitivity which measures the mean relative change between adjacent ring widths; its values range from 0-2. The standard deviation of the chronology is determined in the usual statistical manner. The degree of high frequency interannual variation is represented by the mean sensitivity and standard deviation. Statistics for the common interval analysis included the percentage of variation in the first principal component (PC1) shared by the ring-width series that make up a chronology. The expressed population signal (EPS) represents the chronology signal as a fraction of the total chronology variance; i.e., quantifies the degree to which a particular sample chronology portrays a hypothetically perfect chronology; EPS values range from 0-1. Intercore correlation is the mean of all possible linear correlations between the ring-width series that comprise a chronology. Intertree correlation explains the degree of growth similarity between trees, while intratree correlation describes the degree of growth similarity between the different radii from the same tree. The degree of a strong common growth signal is reflected by the percentage of variance in common, EPS, and intercore correlation.

#### **3.2.2.4 Climate Data**

Homogenized minimum, mean and maximum monthly temperature (Vincent and Gullet, 1999) and total monthly precipitation (Mekis and Hogg, 1999) were obtained from the Brandon Agriculture Station (Brandon CDA) for the period of 1895-1999 (Table 3.1). The rehabilitated climate data includes estimates of missing values from neighboring stations, and includes corrections for inhomogeneities related to, for example, slight changes in instrumentation (Mekis and Hogg, 1999; Vincent and Gullet, 1999). Monthly meteorological data from the Brandon CDA station were converted into moisture index values (P-PET) by subtracting monthly values of potential evapotranspiration (PET) from monthly precipitation (P). PET was determined using an empirical formula developed by Thornthwaite (1948). The moisture index was determined for the months of May to September. Mean monthly river discharge was obtained from two hydrological stations located at the Assiniboine River at Brandon and at the Assiniboine River near Brandon (Table 3.1) (Water Survey of Canada, 2002). The two hydrological records were merged into one series for a period of 1906-2000. As the hydrological record contained many missing values between 1906-1912, the hydrological record used in the subsequent analyses was for the period of 1913-2000. Missing values in the climate data represent the proportion of monthly values which could not be estimated due to the lack of neighboring stations with a corresponding period of climate data (Table 3.1). These missing monthly values were interpolated with the mean for that month.

#### **3.2.2.5 Dendroclimatic Analysis**

Radial growth-climate relationships were examined between the residual chronology and the climatic variables (i.e., total monthly precipitation, moisture index, and river discharge, minimum, mean and maximum monthly temperature) extending over two

**Table 3.1** Location and characteristics of climatic and hydrological stations.

| Station                        | Location            | Distance       |                    | Period of Records | <sup>1</sup> Missing Data (%) | <sup>2</sup> Mean Annual Temp. | <sup>2</sup> Mean Annual Precip. |
|--------------------------------|---------------------|----------------|--------------------|-------------------|-------------------------------|--------------------------------|----------------------------------|
|                                |                     | from SWPP (km) | Elevation (m asl)  |                   |                               | (°C)                           | (mm)                             |
| Brandon CDA                    | 48°52'N<br>99°59'N  | 88.5           | 363                | 1895 -<br>1999    | <sup>3</sup> 1.3              | 2.4                            | 474.0                            |
| Assiniboine River at Brandon   | 49°51'N<br>99°56'N  | 81.7           | <sup>4</sup> 93800 | 1906 -<br>1973    | 3.3                           | n.a.                           | n.a.                             |
| Assiniboine River Near Brandon | 49°52'N<br>100°06'N | 100.7          | <sup>4</sup> 93700 | 1974 -<br>2000    | 0                             | n.a.                           | n.a.                             |

<sup>1</sup> Proportion of missing monthly values which could not be estimated due to the lack of neighboring stations with a corresponding period of climate data.

<sup>2</sup> Mean annual temperature and precipitation for the reference period of 1971–2000 (Environment Canada, 2002).

<sup>3</sup> Proportion of missing monthly precipitation values.

<sup>4</sup> Drainage area (km).

growing seasons from May of the previous year (t-1) to August of the current year (t). The dendroclimatic analysis was conducted using Pearson correlation and response function analysis (Cook et al., 1987; Cook and Kairiukstis, 1990). Response function analysis is a form of multiple regression analysis in which the predictor variables are principal components of climatic variables (e.g., monthly mean temperature and total precipitation values). Response function analysis resolves the problem of multicollinearity of predictor variables which arises during normal stepwise multiple regression. Response functions assess the amount of chronology variance explained by climate and the relative importance of the original individual climate variables. These analyses were performed with the program PRECON (version 5.17B) using 999 bootstrap iterations (Fritts et al., 1991). The boot-strap method uses Monte Carlo simulation techniques to estimate the standard errors of the response function weights, and thus provides a significance test. The period of climatic comparison corresponded to length of the chronology period represented by at least 10 radii. Within spruce islands, the period of comparison with the climate data was 1913 – 1999 for river discharge, and 1900 – 1999 for the other climatic variables. Within aspen groves, the period of comparison with the climate data was 1970-1999 for white spruce and 1949-1999 for trembling aspen. Response function analysis was conducted on each set of climate data (i.e., total monthly precipitation, moisture index, and river discharge, minimum, mean and maximum monthly temperature), and with total precipitation in combination with minimum, mean and maximum temperature data. Due to the short length of the chronology of white spruce from aspen groves, response function analysis could not be conducted on precipitation in combination with the temperature data. As the climatic variables may have cumulative effects, the relationship between annualization periods of the climate data (except for the moisture index) and radial growth

were also examined using Pearson correlation analysis (Szeicz and MacDonald, 1996; St. George and Nielsen, 2002).

### **3.3 Results**

#### **3.3.1 Establishment Dates**

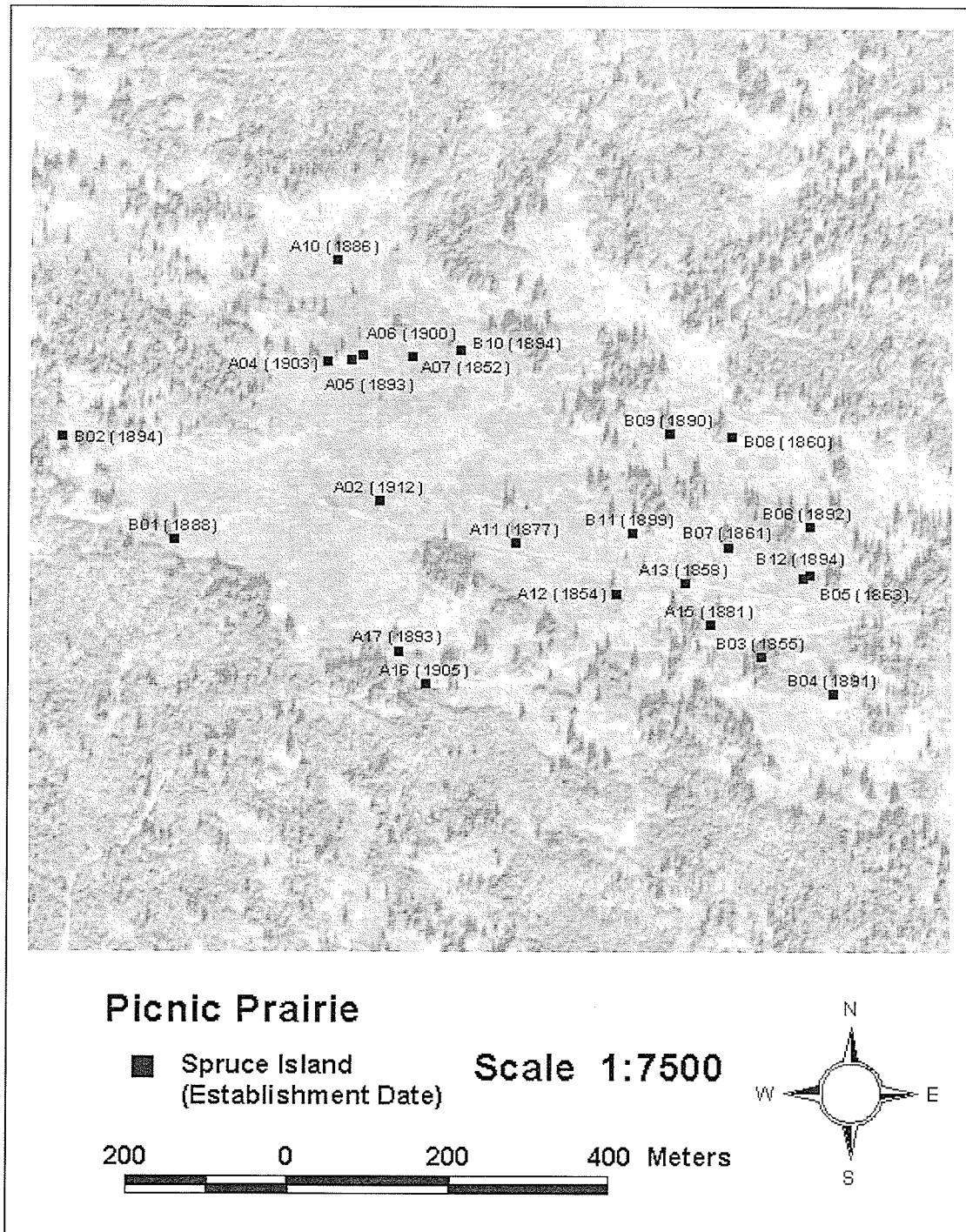
The location of white spruce islands with their respective date of establishment are shown in Figures 3.1, 3.2, and 3.3 for Picnic, Aspen Bluff, and Jackfish prairie, respectively. White spruce islands established between 1850-1925 (Fig. 3.4a). The number of islands establishing increased from 1850 to the early 1860s, followed by a decline in the late 1860s. From the late 1860s, establishment increased and reached the highest amount in the early 1890s. Establishment decreased during the late 1890s. Establishment further decreased from the late 1890s to the early 1920s.

In two of the aspen groves, white spruce established before trembling aspen (Fig. 3.4b). These white spruce established in the early 1890s, and the late 1890s, whereas the corresponding aspen established in the late 1940s and the late 1960s. In the majority of the aspen groves, white spruce established after trembling aspen (Fig. 3.4b). Trembling aspen established predominantly during the late 1930s and declined towards the early 1950s. The corresponding white spruce established minimally in the late 1930s and early 1940s, whereas most established during the late 1940s and early 1950s.

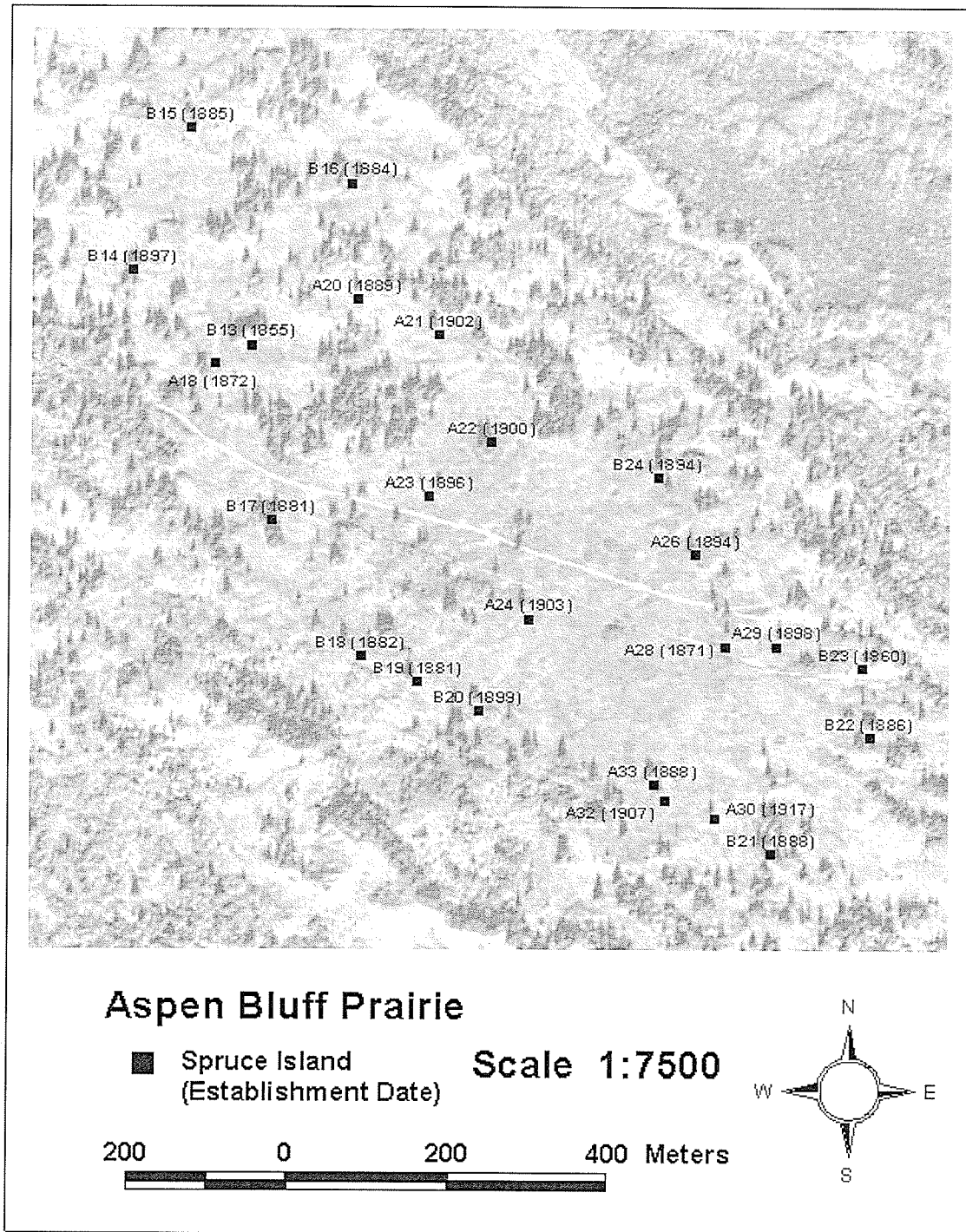
#### **3.3.2 Growth-Climate Relationships**

##### **3.3.2.1 Responses to Climate Within Tree Islands**

The residual chronology (1881-2000) of white spruce tree islands showed reduced radial growth during the 1910s, 1930s, early 1960s, late 1970s, and early 1980s according to the 11-yr running average of the growth indices (Fig. 3.5). Descriptive statistics of the residual chronology of white spruce for the entire chronology length and common interval analysis are shown in Table 3.2. High frequency interannual variation in radial growth was reflected by a high mean sensitivity (0.33) and standard deviation (0.27). A

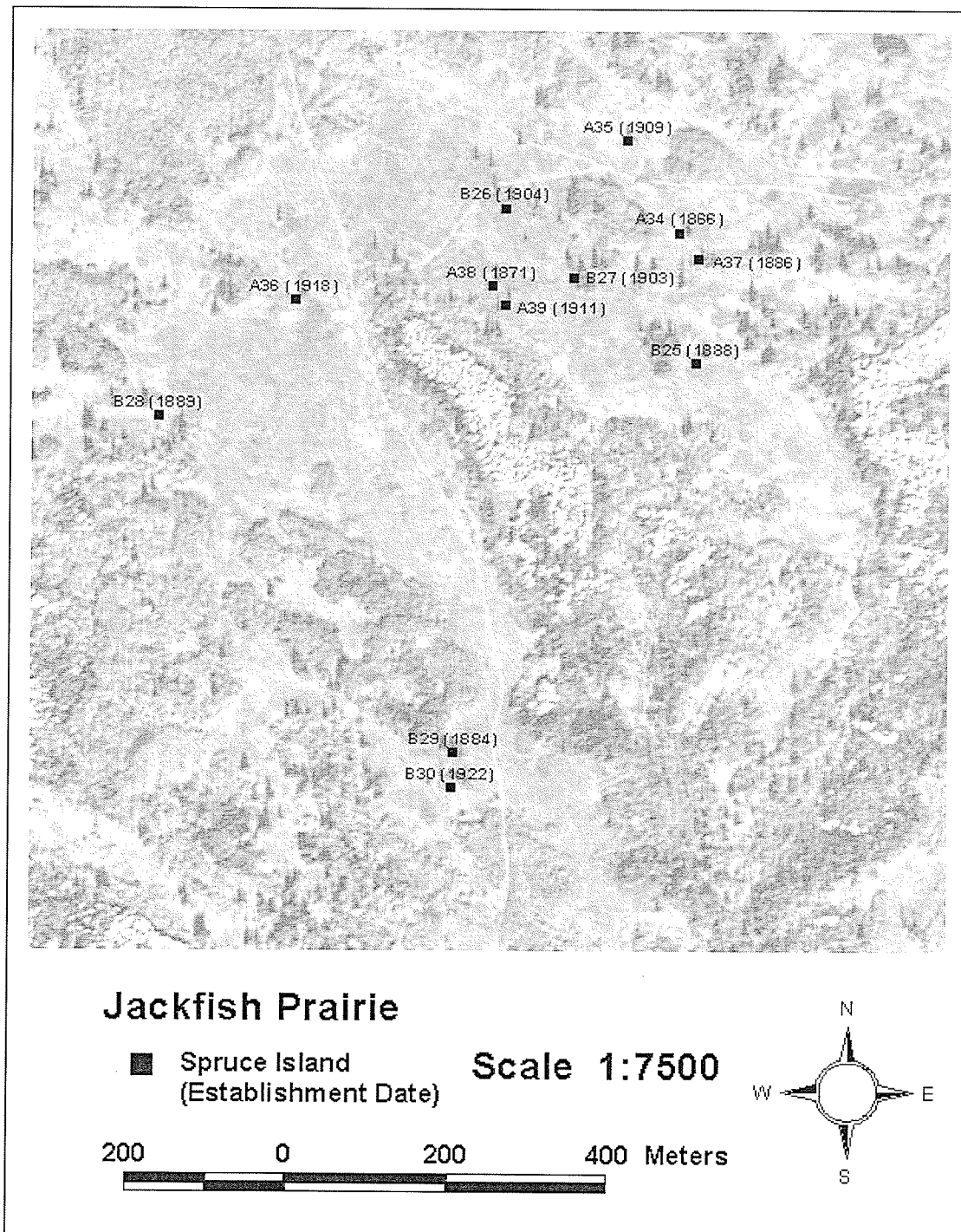


**Figure 3.1** Establishment dates of white spruce islands in Picnic prairie (n = 24).

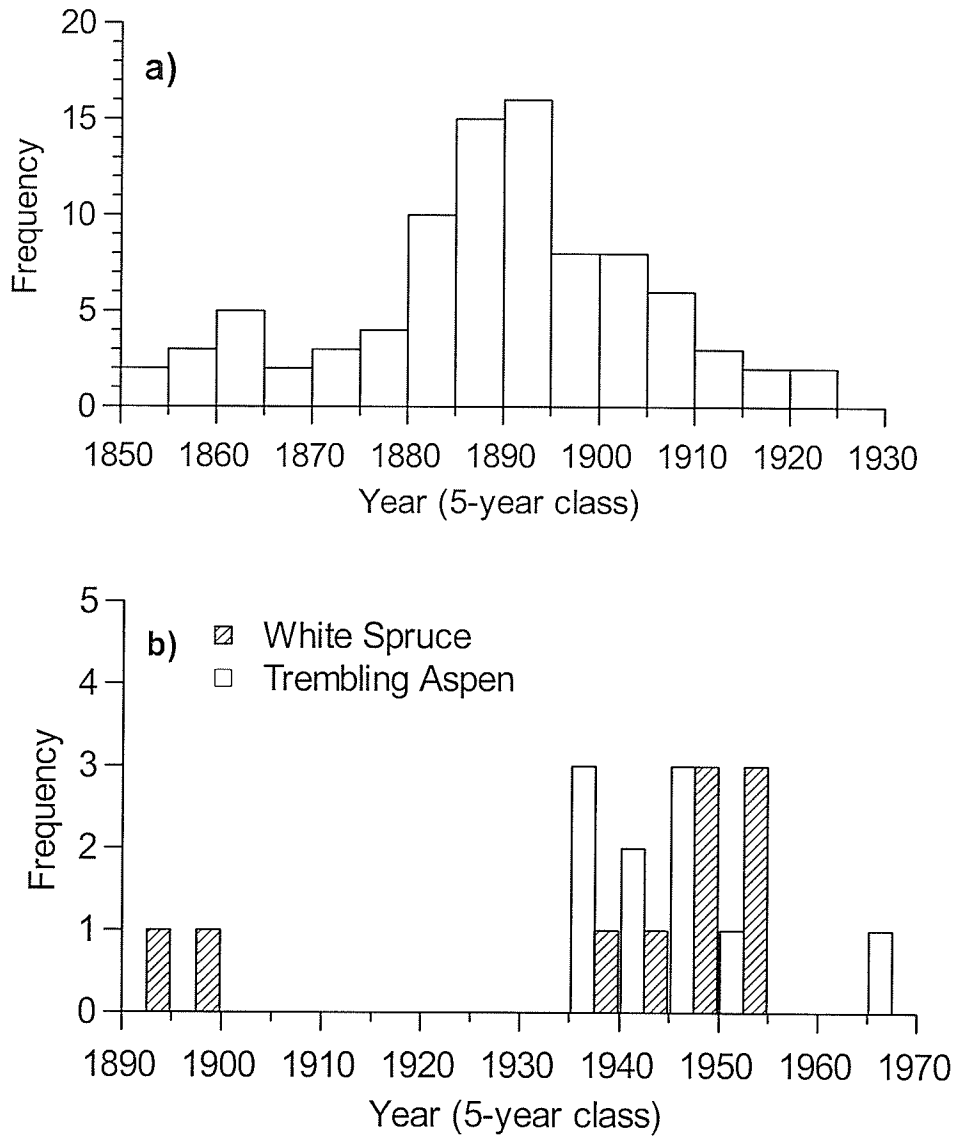


**Figure 3.2** Establishment dates of white spruce islands in Aspen Bluff prairie (n = 24).

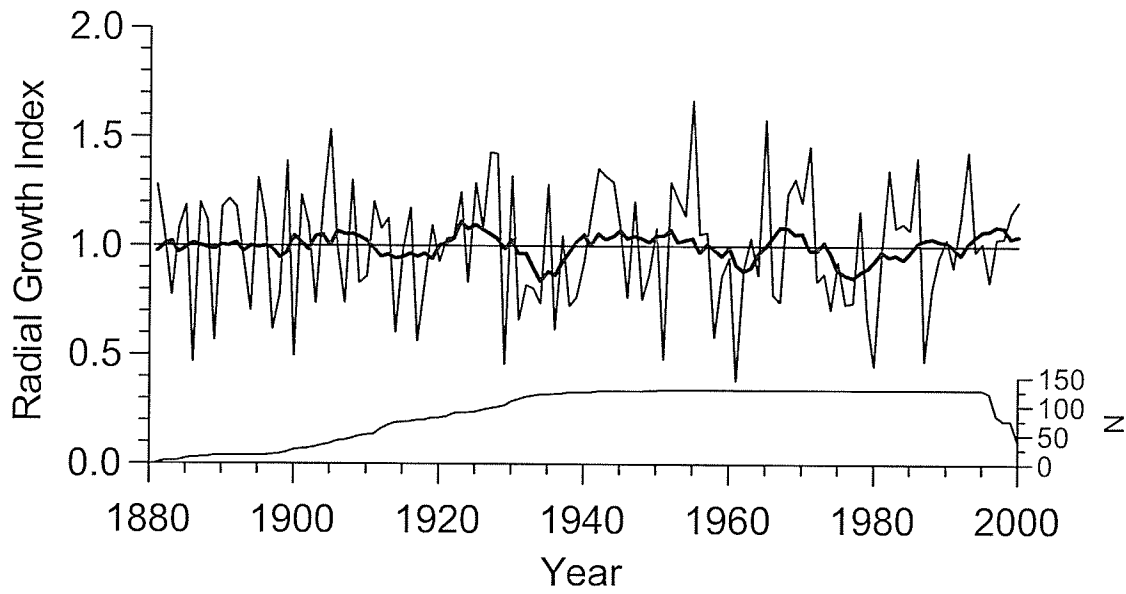




**Figure 3.3** Establishment dates of white spruce islands in Jackfish prairie (n = 12).



**Figure 3.4** Establishment dates of white spruce from tree islands ( $n = 89$ ) (a) and white spruce and trembling aspen from aspen groves ( $n = 10$ ) (b). Aspen establishment dates reported at 1.3 m whereas white spruce establishment dates have been corrected for coring height.



**Figure 3.5** The residual chronology of white spruce (1881-2000) and the corresponding sample size (N, number of tree cores). The bold line indicates a 11-yr running average of the growth indices.

**Table 3.2** General statistics of the residual chronology of white spruce (PGL) from tree islands (TI), and white spruce and trembling aspen (PTR) from aspen groves (AG).

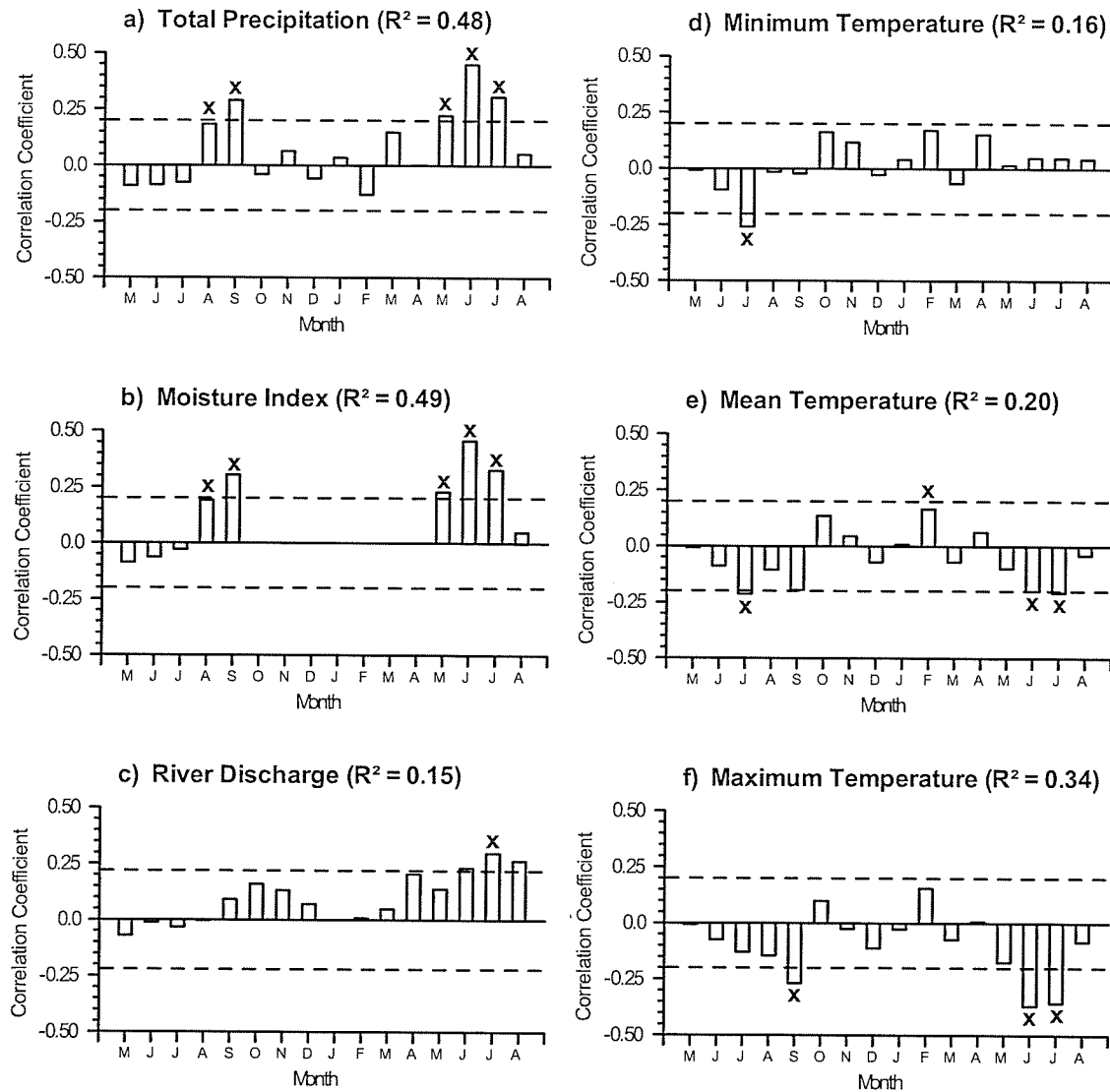
|   | PGL-TI    | PGL-AG    | PTR-AG    |
|---|-----------|-----------|-----------|
| <b>Chronology Length</b>                        | 1881-2000 | 1965-2000 | 1939-2000 |
| No. of trees (radii)                            | 64 (128)  | 24 (48)   | 22 (44)   |
| Mean ring width (mm)                            | 2.07      | 3.11      | 1.27      |
| Mean sensitivity                                | 0.33      | 0.14      | 0.31      |
| Standard deviation                              | 0.27      | 0.13      | 0.27      |
| Variance due to autoregression (%) <sup>1</sup> | 12.30     | 45.00     | 4.2       |
| Autoregressive (AR) model                       | 1         | 2         | 1         |
| <b>Common Interval Analysis</b>                 | 1917-1995 | 1977-2000 | 1964-2000 |
| No. of trees (radii)                            | 39 (79)   | 17 (27)   | 18 (34)   |
| Variance in PC1 (%)                             | 66.21     | 39.28     | 50.69     |
| Expressed population signal                     | 0.99      | 0.89      | 0.94      |
| Intercore correlation                           | 0.66      | 0.33      | 0.48      |
| Intertree correlation                           | 0.66      | 0.32      | 0.47      |
| Intratree correlation                           | 0.84      | 0.58      | 0.67      |

<sup>1</sup> Refers to the standard chronology.

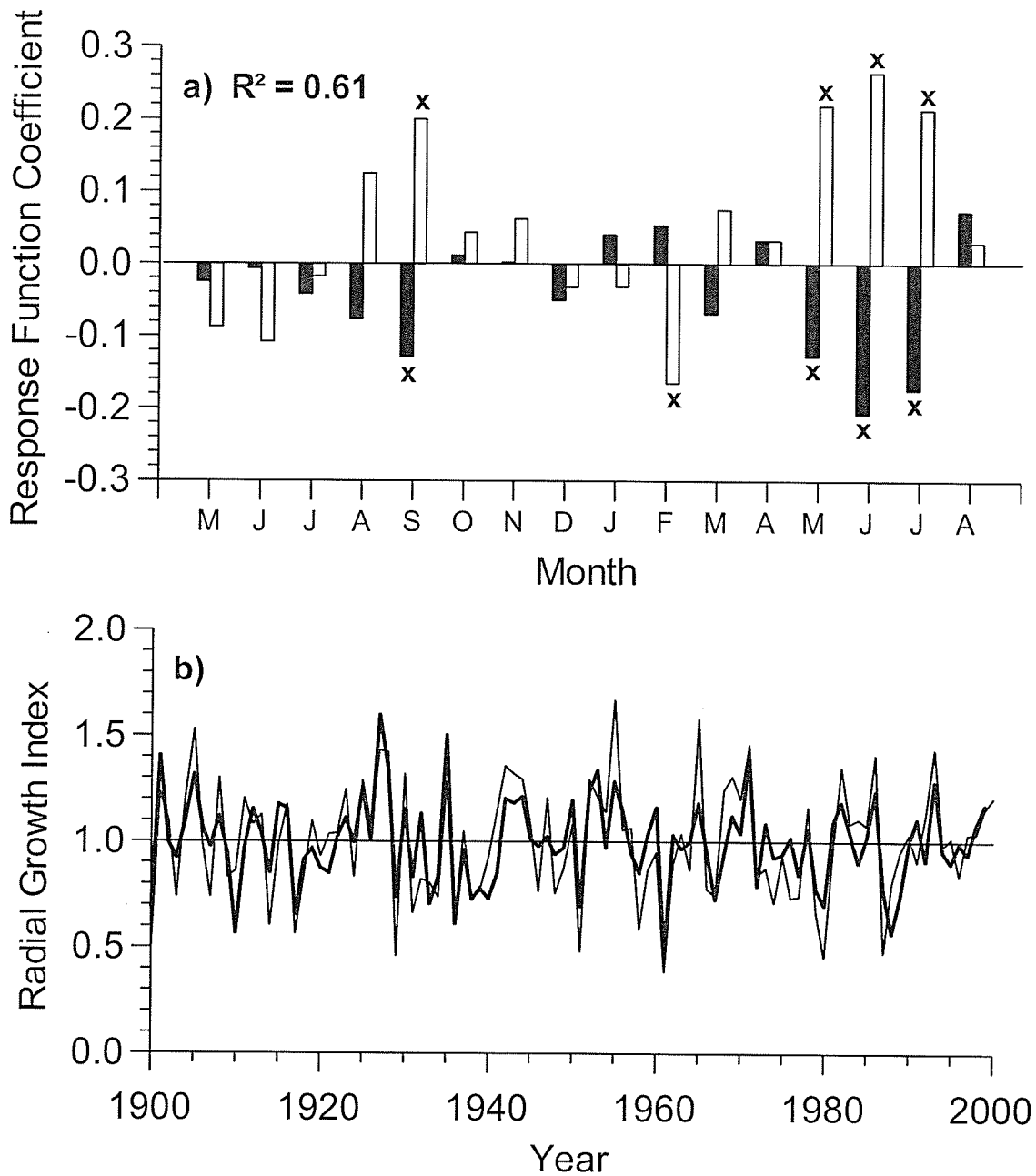
strong common growth signal was reflected by a large percentage of the total variance being explained by the first principal component (PC1) (66.21 %), and high intercore correlation (0.66).

Correlation and response function analysis showed that radial growth of white spruce was positively (+) associated with both total precipitation (Fig. 3.6a) and Thornthwaite's moisture index (Fig. 3.6b) for the month of September of the previous year (t-1), with a stronger correlation with May, June and July of the current year (t). Radial growth was correlated with June (+, t), July (+, t), and August (+, t) river discharge (Fig. 3.6c). Relative to total precipitation ( $R^2 = 0.48$ ) and the moisture index ( $R^2 = 0.49$ ), river discharge explained a small proportion of the variance in radial growth ( $R^2 = 0.15$ ) (Fig. 3.6c). Relationships between radial growth and temperature indicated that the strongest climate response model was with maximum ( $R^2 = 0.34$ ) (Fig. 3.6f), followed by mean ( $R^2 = 0.20$ ) (Fig. 3.6e) and then minimum ( $R^2 = 0.15$ ) (Fig. 3.6d) temperature. Growth was correlated with July (-, t-1) minimum temperature; July (-, t-1), June (-, t), and July (-, t) mean temperature; and September (-, t-1), June (-, t), and July (-, t) maximum temperature.

Response function analysis using combinations of total precipitation and the temperature variables indicated that the combination with maximum temperature explained the most variation in radial growth ( $R^2 = 0.61$ ) (Fig. 3.7a). Significant response function coefficients occurred in September (t-1), May (t), June (t) and July (t) for both total precipitation and maximum temperature. Based on the strong explanation of the variance in radial growth, growth indices were estimated based on the response model of total precipitation and maximum temperature combined (Fig. 3.7b).



**Figure 3.6** Pearson correlation coefficients between the residual chronology of white spruce from tree islands and total precipitation (a), Thornthwaite's (1948) moisture index (b), river discharge (c), minimum temperature (d), mean temperature (e), and maximum temperature (f) for the period of 1913-1999 for river discharge, and 1900-1999 for the remaining climate variables. Significant correlations ( $p < 0.05$ ) determined from correlation analysis extend past dashed lines. Significant climatic variables determined from the response function analysis are denoted with an X. The  $R^2$  value of the response model using each climate variable separately is indicated.



**Figure 3.7** Response function coefficients between the residual chronology of white spruce from tree islands and both total precipitation (open bars) and maximum temperature (solid bars) (a). Significant climatic variables are denoted with an X. Actual growth indices (thin line) compared with a estimation of growth indices (bold line) based on the response function with total precipitation and maximum temperature for the period of 1900-1999 (b).

The relationship between climatic annualization periods and radial growth showed that total precipitation for the period of July (t-1)-June (t), August (t-1)-July (t), and September (t-1)-August (t) all had a significant, positive effect on radial growth (all  $p < 0.001$ ) (Table 3.3). Of these annualization periods, the period of August (t-1)- July (t) had the strongest correlation with growth. Similarly, river discharge showed a positive effect on growth for August (t-1)-July (t) ( $p = 0.054$ ), and September (t-1)-August (t) ( $p < 0.05$ ) (Table 3.3). Of the temperature variables the strongest correlation was a negative response to August (t-1)-July (t) maximum temperature ( $p = 0.052$ ).

### **3.3.2.2 Responses to Climate Within Aspen Groves**

White spruce within aspen groves (1965-2000) showed few periods of reduced radial growth according to the 11-yr running average of the growth indices (Fig. 3.8a). The most prominent yearly growth reductions occurred in 1967, 1974, 1976, and 1979. In contrast, trembling aspen showed many years and periods of reduced growth (Fig. 3.8b). The most prominent year of growth reduction was in 1983. Other years of reduced growth included 1942, 1961, 1986, 1988 and 1991. A period of reduced growth extended from the early 1980s to the early 1990s; growth was most reduced during the late 1980s. The relative year to year radial growth patterns of white spruce and aspen within aspen groves were positively correlated ( $r = 0.42$ ,  $p < 0.05$ ) (Table 3.5). Furthermore, growth of white spruce from aspen groves showed a stronger correlation with the white spruce tree islands ( $r = 0.57$ ,  $p < 0.001$ ). Trembling aspen and white spruce tree islands showed a weak positive correlation ( $r = 0.23$ ,  $p > 0.05$ ).

Within the aspen groves, white spruce had a greater mean ring width (3.11 mm) than trembling aspen (1.27 mm) while mean ring width of white spruce islands was intermediate (Table 3.2). Spruce had a lower mean sensitivity and standard deviation

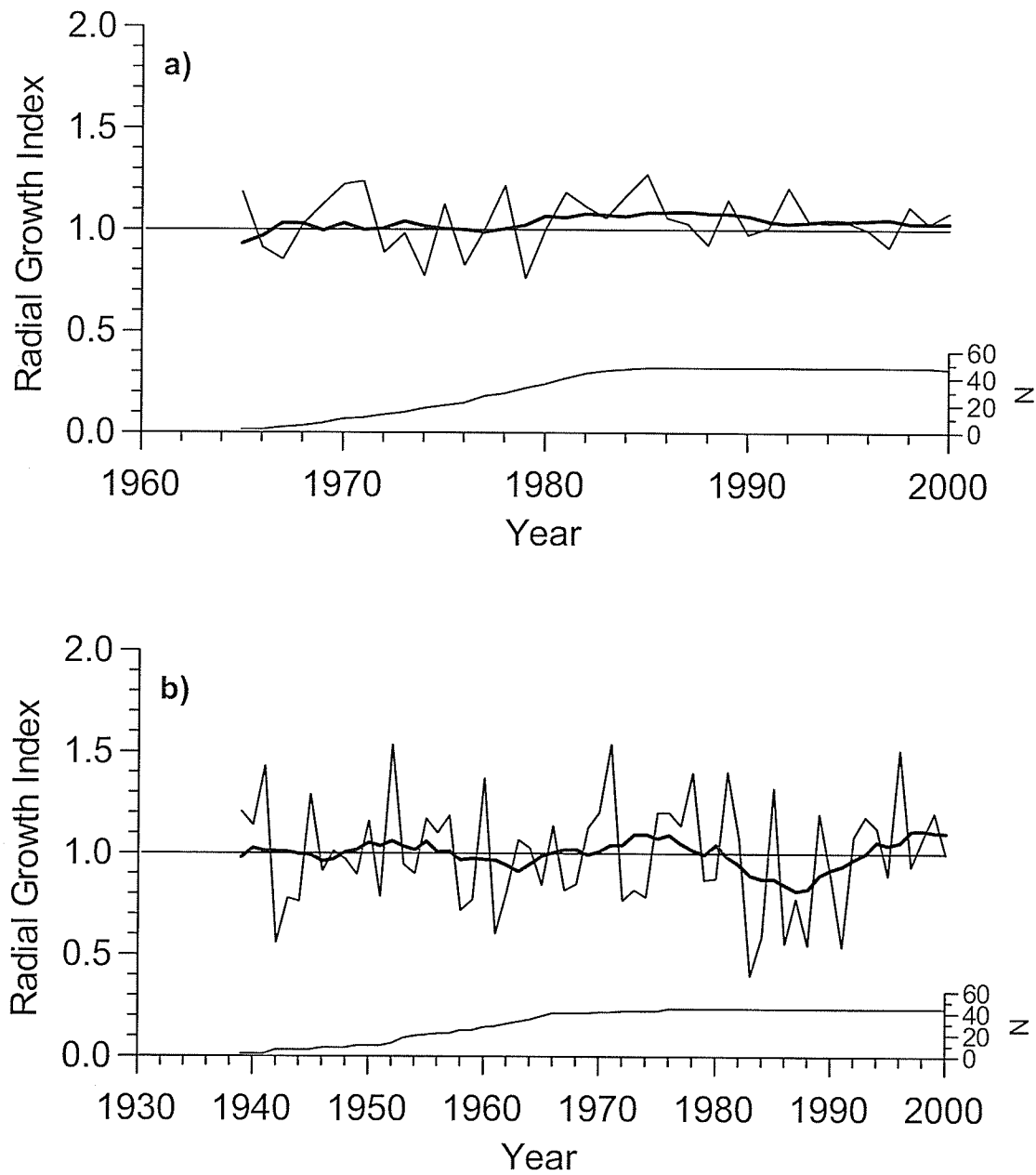


**Table 3.3** Pearson correlation coefficients between the residual chronology of white spruce (PGL) from tree islands (TI), and white spruce and trembling aspen (PTR) from aspen groves (AG) with the annualization periods of climatic variables. The period of analysis for PGL-TI was 1913-1999 for river discharge and 1900-1999 for the remaining climate variables. The period of analysis for PGL-AG and PTR-AG was 1970-1999 and 1949-1999, respectively, for all the climate variables.

| Annualization Period              | Total Precip. | River Discharge | Min. Temp. | Mean Temp. | Max. Temp. |
|-----------------------------------|---------------|-----------------|------------|------------|------------|
| <b>PGL-TI</b>                     |               |                 |            |            |            |
| May (t-1) <sup>1</sup> -April (t) | 0.09          | 0.03            | 0.07       | -0.01      | -0.09      |
| June (t-1)-May (t)                | 0.19          | 0.11            | 0.08       | -0.02      | -0.12      |
| July (t-1)-June (t)               | 0.41***       | 0.16            | 0.09       | -0.04      | -0.16      |
| August (t-1)-July (t)             | 0.54***       | 0.21            | 0.12       | -0.04      | -0.19      |
| September (t-1)-August (t)        | 0.49***       | 0.23*           | 0.13       | -0.03      | -0.18      |
| <b>PGL-AG</b>                     |               |                 |            |            |            |
| May (t-1)-April (t)               | -0.12         | -0.25           | 0.39*      | 0.33       | 0.25       |
| June (t-1)-May (t)                | -0.12         | -0.35           | 0.38*      | 0.34       | 0.29       |
| July (t-1)-June (t)               | -0.01         | -0.39*          | 0.36       | 0.31       | 0.23       |
| August (t-1)-July (t)             | 0.03          | -0.42*          | 0.34       | 0.28       | 0.18       |
| September (t-1)-August (t)        | 0.14          | -0.43*          | 0.34       | 0.25       | 0.15       |
| <b>PTR-AG</b>                     |               |                 |            |            |            |
| May (t-1)-April (t)               | 0.07          | 0.25            | -0.12      | -0.16      | -0.19      |
| June (t-1)-May (t)                | 0.10          | 0.20            | -0.13      | -0.15      | -0.16      |
| July (t-1)-June (t)               | 0.24          | 0.19            | -0.17      | -0.21      | -0.24      |
| August (t-1)-July (t)             | 0.23          | 0.17            | -0.17      | -0.22      | -0.26      |
| September (t-1)-August (t)        | 0.36*         | 0.17            | -0.18      | -0.24      | -0.28      |

<sup>1</sup> t-1 denotes the previous year

\*:  $p < 0.05$ ; \*\*\*:  $p < 0.01$ ; \*\*\*\*:  $p < 0.001$



**Figure 3.8** The residual chronology of white spruce (1965-2000) (a) and trembling aspen (1939-2000) (b) from aspen groves and the corresponding sample size (N, number of tree cores). The bold line indicates a 11-yr running average of the growth indices.

**Table 3.4** Pearson correlation coefficients between the residual chronologies of white spruce (PGL) from tree islands (TI), and white spruce and trembling aspen (PTR) from aspen groves (AG) during the period of 1970-2000.

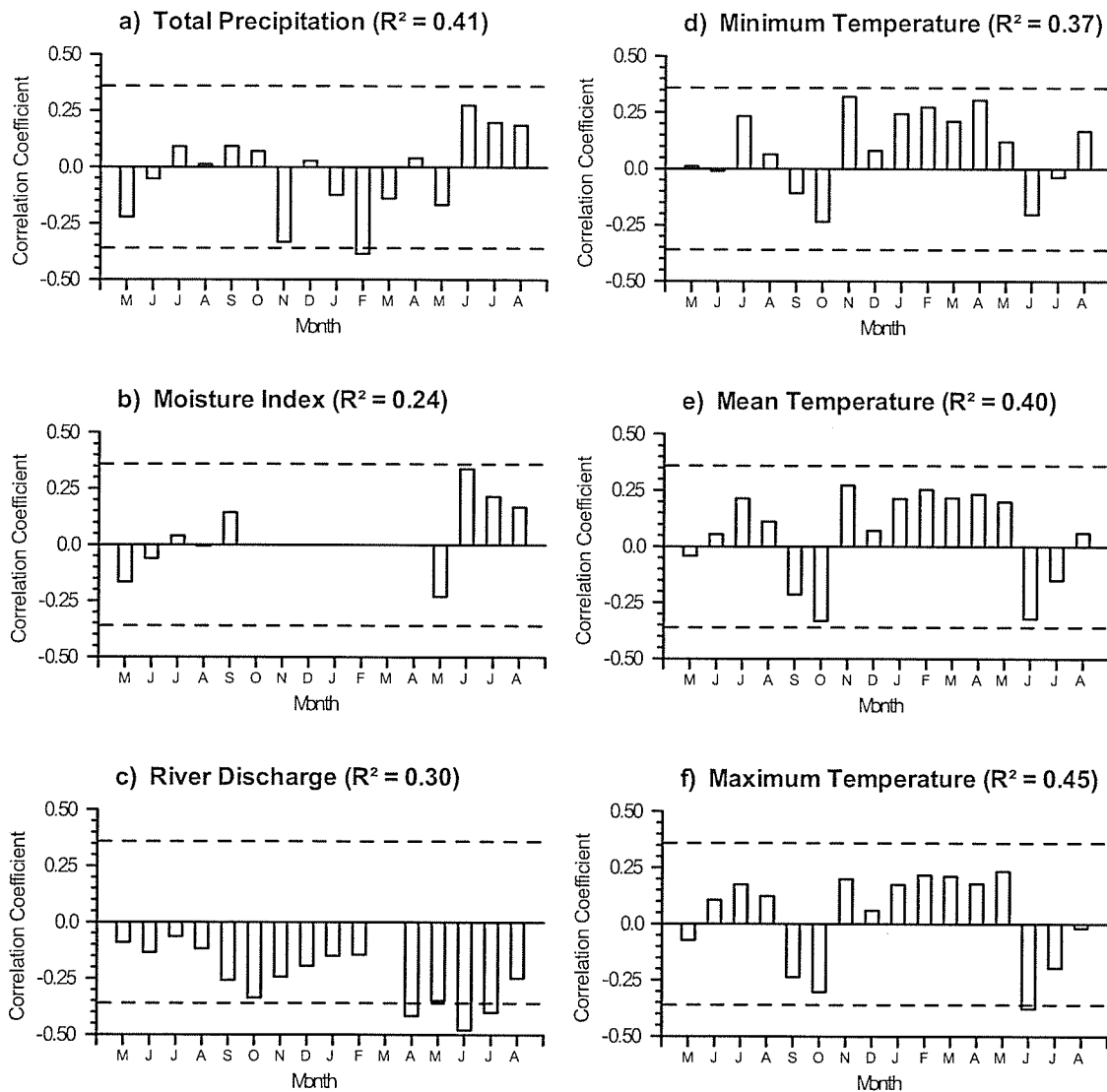
|        | PGL-TI  | PGL-AG | PTR-AG |
|--------|---------|--------|--------|
| PGL-TI | 1.00    | -      | -      |
| PGL-AG | 0.57*** | 1.00   | -      |
| PTR-AG | 0.23    | 0.42*  | 1.00   |

\*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$

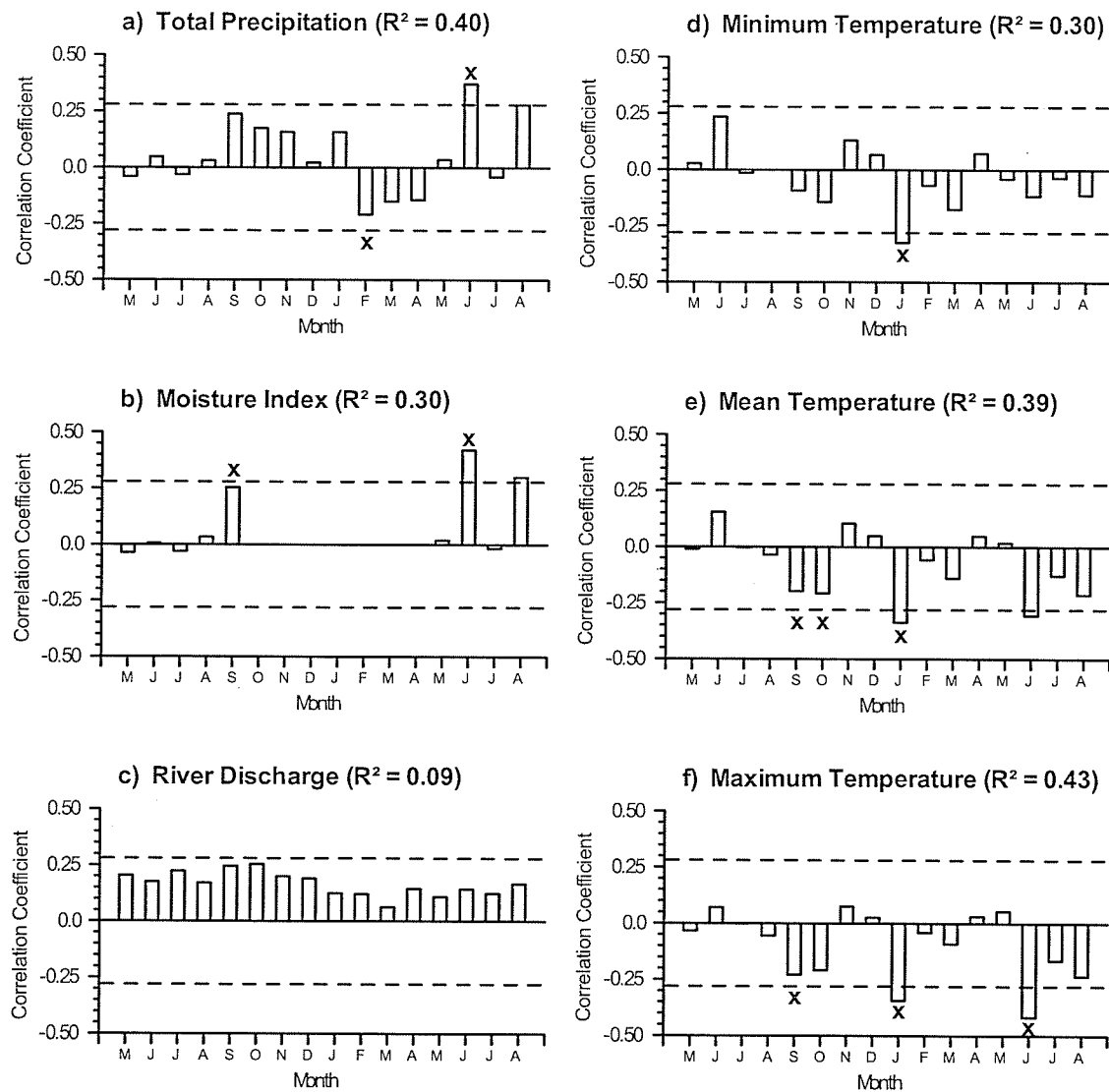
than aspen. In comparison, white spruce islands had the highest mean sensitivity. The variance in PC1, the expressed population signal, intercore, intertree and intratree correlation was lower in spruce than in aspen. White spruce tree islands had greater values of these descriptive statistics during the common interval analysis than spruce and aspen from the aspen groves.

Unlike white spruce islands, white spruce from the aspen groves responded more strongly to maximum temperature ( $R^2 = 0.45$ ) than to total precipitation ( $R^2 = 0.41$ ) and the moisture index ( $R^2 = 0.24$ ) (Fig. 3.9). Growth showed a weak response to river discharge ( $R^2 = 0.30$ ); however, growth was correlated with the months of April (-, t), June (-, t), and July (-, t) (Fig. 3.9c). Of the temperature variables, growth responded more to maximum temperature ( $R^2 = 0.45$ ) (Fig. 3.9f) than to mean ( $R^2 = 0.40$ ) (Fig. 3.9e) and minimum temperature ( $R^2 = 0.37$ ) (Fig. 3.9d). Growth was correlated with June (-, t) maximum temperature.

Similar to associate white spruce, and unlike white spruce islands, trembling aspen responded more to maximum temperature ( $R^2 = 0.43$ ) than to total precipitation ( $R^2 = 0.40$ ) and the moisture index ( $R^2 = 0.30$ ) (Fig. 3.10). Growth was correlated with June (+, t) precipitation (Fig. 3.10a) and moisture index (Fig. 3.10b). Response to river discharge was almost absent in aspen ( $R^2 = 0.09$ ) (Fig. 3.10c). Similar to white spruce from either environment, aspen also responded more to maximum temperature ( $R^2 = 0.43$ ) (Fig. 3.10f) than mean ( $R^2 = 0.39$ ) (Fig. 3.10e) and minimum temperature ( $R^2 = 0.30$ ) (Fig. 3.10d). Growth was correlated with January (-, t) minimum, mean, and maximum temperature. Furthermore, growth was correlated with June (-, t) mean and maximum temperature.



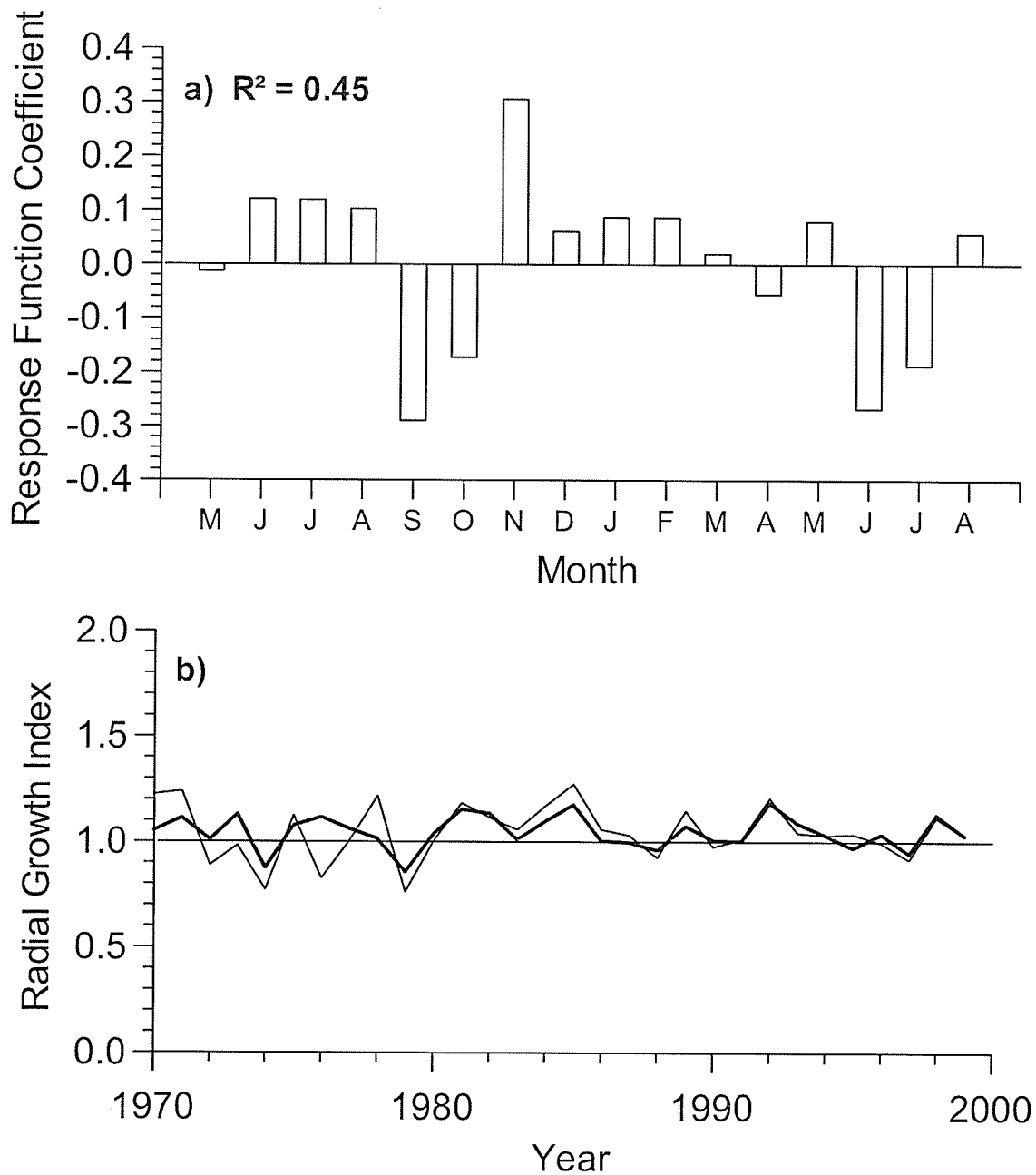
**Figure 3.9** Pearson correlation coefficients between the residual chronology of white spruce from aspen groves and total precipitation (a), Thornthwaite's (1948) moisture index (b), river discharge (c), minimum temperature (d), mean temperature (e), and maximum temperature (f) for the period of 1970-1999. Significant correlations ( $p < 0.05$ ) determined from correlation analysis extend past dashed lines. No climatic variables were deemed significant according to the response function analysis. The  $R^2$  value of the response model using each climate variable separately is indicated.



**Figure 3.10** Pearson correlation coefficients between the residual chronology of trembling aspen from aspen groves and total precipitation (a), Thornthwaite's (1948) moisture index (b), river discharge (c), minimum temperature (d), mean temperature (e), and maximum temperature (f) for the period of 1949-1999. Significant correlations ( $p < 0.05$ ) determined from correlation analysis extend past dashed lines. Significant climatic variables determined from the response function analysis are denoted with an X. The  $R^2$  value of the response model using each climate variable separately is indicated.

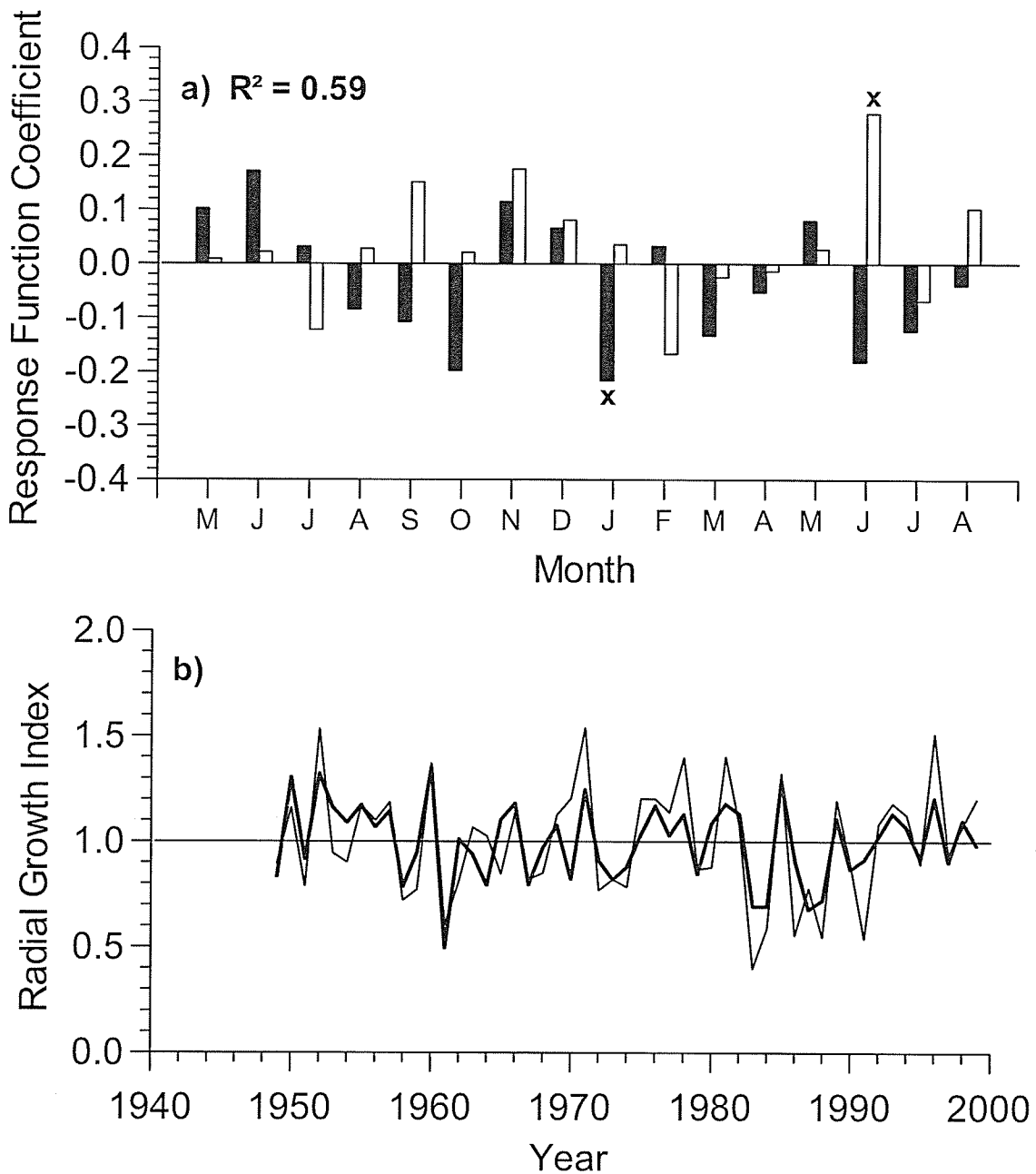
Based on the strong response of white spruce from aspen groves to maximum temperature (Fig. 3.11a), growth indices were estimated and compared to actual indices (Fig. 3.11b). Response function analysis of precipitation in combination with each of the temperature variables indicated that trembling aspen showed the same response to each of the combinations (all  $R^2 = 0.59$ ) (Fig. 3.12a). Since growth mainly responded to maximum temperature (Fig. 3.10f), the climate response model of precipitation and maximum temperature was chosen, and growth indices were estimated and compared to actual indices of trembling aspen (Fig. 3.12b).

Comparison of the chronologies of aspen and associate spruce with the annualization periods of the climatic variables is shown in Table 3.3. Spruce from aspen groves showed no significant correlations with any of the precipitation periods. Instead, growth was inversely related to July (t-1)-June (t), August (t-1)-July (t), and September (t-1)-August (t) river discharge. Furthermore, growth also responded positively to May (t-1)-April (t) and June (t-1)-May (t) minimum temperature. Aspen responded positively to September (t-1)-August precipitation.



**Figure 3.11** Response function coefficients between the residual chronology of white spruce from aspen groves and maximum temperature (solid bars) (a). No climatic variables were deemed significant according to the response function analysis. Actual growth indices (thin line) compared with a estimation of growth indices (bold line) based on the response function with maximum temperature for the period of 1970-1999 (b).





**Figure 3.12** Response function coefficients between the residual chronology of trembling aspen from aspen groves and both total precipitation (open bars) and maximum temperature (solid bars) (a). Significant climatic variables are denoted with an X. Actual growth indices (thin line) compared with a estimation of growth indices (bold line) based on the response function with total precipitation and maximum temperature for the period of 1949-1999 (b).

### 3.4 Discussion

#### 3.4.1 Establishment Dates

In the white spruce islands, no surviving white spruce established before the 1850s. This was unexpected since climatic conditions before the 1850s correspond with the cool conditions of the Little Ice Age (ca. 1350-1870) (Pielou, 1991). The lack of establishment before the 1850s may be due to the mortality of older white spruce individuals. In the aspen parkland of southern Alberta and Saskatchewan, Sauchyn and Beaudoin (1998) also only encountered living white spruce trees less than 200 years old. They attributed the lack of old trees to the short life span of spruce, presettlement fires, and post-settlement demand for wood. Nonetheless, white spruce island establishment did occur over part of the Little Ice Age during the 1850s to the 1870s. The peak in establishment in the early 1890s may be due to a number of reasons. This establishment peak may be due to an establishment lag dependent on the initial establishment of creeping juniper in the open prairie. Another possible explanation is a lag in reproductive potential of the islands which initially established in the 1850s and 1860s since white spruce requires about 30 years to reach a seed bearing stage (Nienstaedt and Zasada, 1990). The decrease in establishment in the late 1890s relative to the peak in establishment in the early 1890s may be due to a number of factors. Drought stress may be a factor as Blasing and Duvick (1984) and Stockton and Meko (1983) have described the 1890s as a dry period. It appears that the dry 1890s manifested itself in the study area more towards the late 1890s. Another likely factor is that the 1890s coincided with the completion of the railways in Western Canada (Bird, 1961). The concomitant increase in settlement may have led to the increased use of trees for fuel and building construction (Bird, 1961; Sauchyn and Beaudoin, 1998). The absence of establishment past the 1920s

corresponds with the onset of conditions in the 1930s which has been described as one of the driest decades on the Canadian Prairies (Wilson, 1998; Nkembirim and Weber 1999) and the Great Plains of the United States (Meko, 1992). Furthermore, the 1930s have also been described as one of the warmest decades in the past 140 years in the Northern Hemisphere (Lamb, 1995; Jones and Briffa, 1992; Jones, 1994). These results suggest that white spruce island establishment may be favoured by cool, moist conditions.

In the aspen groves in which white spruce established before aspen, the period of white spruce establishment in the 1890s corresponded to the period of white spruce island establishment. The white spruce were later invaded by trembling aspen in the late 1940s and late 1960s. Within the aspen groves in which aspen established before spruce, aspen established mainly during the dry 1930s although establishment continued until the early 1950s. Hogg and Schwarz (1999) also reported that aspen in the aspen parkland of Saskatchewan established predominantly during the dry 1930s. Consequently, aspen has established during prominently dry periods. This is supported by the observation of Bailey and Wroe (1974) that aspen root suckering and thus aspen invasion of prairie was related to higher soil temperature conditions. Archibold and Wilson (1978) and Perala (1990) also reported that the process of suckering requires strong light and heat. White spruce established later in the aspen groves predominantly in the late 1940s to early 1950s. These results suggest that aspen establishment may be favoured by high temperatures, whereas spruce establishment may be favoured by cool, moist conditions. However, a larger sample size of aspen groves is required to validate this hypothesis.

### 3.4.2 Growth-Climate Relationships

#### 3.4.2.1 Responses to Climate Within Tree Islands

The periods of growth reduction corresponded to documented periods of drought on the Canadian Prairies (Case and MacDonald, 1995; Sauchyn and Beaudoin, 1998; Nkembirim and Weber, 1999; Case, 2000), and the Great Plains of the United States (Stockton and Meko, 1983; Blasing and Duvick, 1984; Meko, 1992; Cook et al., 1999). Reduced radial growth of white spruce occurred in the dry 1930s and early 1960s. Nkembirim and Weber (1999) also place the decade of the 1910s as comparably dry to the 1930s and 1980s. The dry decade of the 1910s also corresponded to a period of reduced radial growth but to a lesser extent relative to the 1930s and 1980s. In addition to dry periods, white spruce growth also showed a correspondence to dry years such as those in the 1930s (i.e., 1934, 1936), the 1980s (i.e., 1980, 1987 – 1989) (Nkembirim and Weber, 1999; St. George and Nielsen, 2002) and in 1961 (Hogg, 1994; Hogg and Hurdle, 1995). Overall, the correspondence of reduced radial growth to dry years and periods demonstrates the strong role of drought in conditioning tree growth.

The mean sensitivity and standard deviation of white spruce radial growth was comparable to a moisture sensitive limber pine (*Pinus flexilis* James) chronology of Case and MacDonald (1995) from the Canadian Prairies. Furthermore, the amount of variation in radial growth explained by precipitation and maximum temperature (61%) is comparable to dendroclimatic studies in arid site locations where the mean growth variance explained by climate ranges from 60 to 65% (Fritts, 1974; Case and MacDonald, 1995).

Correlation and response function coefficients indicated that precipitation and temperature conditions in the summer and fall of the previous year (t-1), and the summer

of the current year ( $t$ ) strongly influenced white spruce growth. In the year of bud formation ( $t-1$ ), the results suggest that the end of growing season conditions prior to ring formation contributes to photosynthetic reserves for the subsequent growing season (Zahner, 1968; Fritts, 1976; Kozłowski et al., 1991). This preconditioning factor was reflected in the strong positive response to previous August and September precipitation, and a negative correlation to previous September maximum temperature. Other preconditioning effects included a negative association with July mean and maximum temperature of the previous year. High temperatures may increase evotranspirative demands and may lead to an increased rate of respiration and thus deplete food reserves for the following year (Kozłowski et al., 1991).

Dendroclimatic relationships in the year of bud expansion ( $t$ ) also indicate a strong radial growth response to summer drought. The strong effect of drought stress was exemplified by the strong positive relationship between radial growth and May, June and July precipitation and moisture index, and July river discharge, as well as the negative association with June and July mean and maximum temperature. No previous studies have conducted a correlation and response function analysis of white spruce at its southern limit of distribution. Nevertheless, the radial growth-climate relationships are consistent with previous studies of other tree species in the prairie region of Canada (Case and MacDonald, 1995; Case, 2000) and the United States Great Plains (Stockton and Meko, 1983; Blasing and Duvick, 1984; Meko, 1992; Cook et al., 1999).

The importance of previous August to July precipitation period has been reported extensively in dendroclimatic studies in the prairie region of Canada (Case and MacDonald, 1995; Sauchyn and Beaudoin, 1998; Case, 2000; St. George and Nielsen, 2002) and the United States (Blasing and Duvick, 1984; Meko, 1992) in which radial

growth was used to reconstruct August (t-1) to July (t) precipitation. Due to the lack of old material, the short length of the chronology presented here (1881 – 2000) precluded the possibility of reconstructing a long term precipitation record.

### 3.4.2.2 Responses to Climate Within Aspen Groves

White spruce within aspen groves showed few instances of reduced growth. Furthermore, growth did not correspond with the 1980 drought and corresponded very minimally to the 1988 drought. These results indicate that growth of white spruce was moderated by conditions within the aspen groves. In contrast, trembling aspen growth did contain a drought signal, since reduced growth in 1961 and 1988 corresponded to prominent drought years. The drought of 1980 only resulted in minor reduced growth in aspen. Nonetheless, growth reductions did occur during the warm and dry 1980s. Growth of aspen and associate white spruce showed a significant positive correlation. In contrast, Hogg and Schwarz (1999) who examined mixed-wood stands of aspen and spruce within the aspen parkland region showed a poor correlation between the two species. They attributed the poor correlation due to the effects of defoliation of trembling aspen by the forest tent caterpillar (*Malacosoma disstria* Hbn.). Hogg and Schwarz (1999) also concluded that the effect of climate was secondary to the influence of insect infestations on aspen growth. This comparison indicates that within the SWPP growth of aspen and spruce are commonly affected by the dry regional climate.

White spruce from aspen groves showed a higher mean diameter increment than associate aspen and white spruce islands. This may be due to the fact that spruce from the aspen groves were much younger and thus were in their juvenile growth stage of development compared to aspen and white spruce islands. The low mean sensitivity and standard deviation of spruce from aspen groves further underscores the low degree of

interannual variation of spruce in this environment due to the moderated microclimate of the aspen groves. In contrast, white spruce islands and trembling aspen demonstrated higher variability in relative ring-width response from year to year. Furthermore, white spruce from aspen groves showed the lowest common growth signal. These results indicate that white spruce from aspen groves were not responding as much to a strong, external, climate forcing. These results are confirmed by Fritts (1965) who showed that in contrast to trees at the xeric forest border, trees within the mesic forest interior were not sensitive to climate.

Correlation and response function analysis indicated that white spruce from aspen groves responded more to temperature than to precipitation. The weak response to monthly precipitation as well as the lack of correlation with the annualized periods of precipitation suggests that white spruce trees benefited from the moderated microclimate of aspen groves. Of the temperature variables, growth responded most strongly to maximum temperature during the month of June (-, t). Therefore, temperature induced drought stress during the summer of the current year can negatively affect growth. It is unclear why growth was negatively correlated with the spring and early growing season months as well as the annualized periods of river discharge. These results may represent spurious correlations as the overall growth response to river discharge was weak and none of the months were deemed important according to the response function analysis.

Correlation and response function analysis of trembling aspen indicated that growth was limited by moisture deficiency as growth was correlated with both precipitation and moisture index in the month of June (+, t). The influence of moisture deficiency was also reflected in the correlation of growth with the September (t-1) to August (t) precipitation period. The strong response to maximum temperature indicates

that the dry regional climate of the aspen parkland has negatively affected growth. Growth was reduced by temperature induced drought stress during the summer as indicated by the correlation with June (-, t) maximum temperature. Furthermore, aspen growth showed a consistent relationship with the month of January (-, t) for all of the temperature variables. This indicates that mild winters can negatively affect growth as it increases the incidence of thaw-freeze events (Tranquillini, 1979; Havranek and Tranquillini, 1995). In other words, Tranquillini (1979) and Havranek and Tranquillini (1995) reported that while the coldhardiness of trees is elevated during mid-winter, the occurrence of extreme climate anomalies such as warm temperatures in December and January followed by the rapid return to cold temperature results in substantial bud damage. Furthermore, warm temperatures during mid-winter may increase the rate of desiccation and thus deplete water reserves (Tranquillini, 1979; Havranek and Tranquillini, 1995). Thaw-freeze events have also been implicated as having a negative impact on the growth of trembling aspen within the aspen parkland zone of Alberta and Saskatchewan (Hogg and Schwarz, 1999).

### **3.4.3 Determinants of Tree Distribution Limits**

The northern and southern range limits of conifer species are not controlled solely by climate. For instance, at the northern tree-line, a slight altitudinal increase in the tree-line and an increase in density within the current range of white spruce were reported (Scott et al., 1987b; Szeicz and MacDonald, 1995a; Barber et al., 2000). However, a latitudinal increase was not observed even though temperatures have warmed during this century. This lack of a northward expansion has been attributed to unsuitable microclimatic and edaphic conditions for seedling establishment past the northern limit. That is, at its northern limit white spruce is positively associated with moss ground cover



whereas lichen cover is an unsuitable microenvironment for seedling establishment (Scott et al., 1987b). Similarly, at its southern limit white spruce in the SWPP is positively associated with creeping juniper whereas it experiences direct competition with grasses (Chhin and Wang, 2002). Furthermore, northern white-cedar (*Thuja occidentalis* L.) showed a weak response to climate at its north-western limit of distribution in Manitoba (Tardif and Stevenson, 2001). Tardif and Stevenson (2001) postulated that the range limit of *T. occidentalis* may instead be controlled by other factors such as fire and habitat availability. Models based on physiological studies of black spruce (*Picea mariana* (Mill.) B.S.P) have indicated that it is capable of growing beyond its present range limits thus indicating that factors other than climate control its northern and southern limit of distribution (Bonan and Sirois, 1992). Bonan and Sirois (1992) speculated that *P. mariana* is unable to establish on lichen mats at its northern limit while determinants of its southern limit are poorly understood.

Notwithstanding the influence of nonclimatic (e.g., competition, insect outbreaks) and indirect climatic effects (e.g., climate induced changes in disturbance regimes) at tree distribution limits (Loehle and LeBlanc, 1996; Loehle, 1998), climate does contribute directly to the conditioning of tree growth particularly at climatic extremes (Woodward, 1987; Richardson and Bond, 1991). For instance, dendroclimatic studies of white spruce at its northern limit in sub-arctic and alpine environments have documented that low temperature is a limiting factor to radial growth (Szeicz and MacDonald, 1995b), although high temperature may induce moisture stress (Barber et al., 2000), and both temperature and precipitation affect growth on rocky, xeric site locations (Szeicz and MacDonald, 1996). It has been asserted that the southern limit of conifers is controlled by moisture deficiency (Zoltai, 1975; Hogg, 1994; Hogg and Hurdle, 1995). Moreover,

previous studies in the prairie region have demonstrated the influence of temperature on radial growth in addition to the dominant relationship with precipitation (Case and MacDonald, 1995; Case, 2000). The radial growth – climate associations of white spruce in the SWPP further underscores the importance of moisture deficiency intensified by temperature induced drought stress as a major determinant of the southern range limit of white spruce.

#### **3.4.4 Future Research**

Future research should be conducted to examine radial growth-climate relationships of closed white spruce forests. Light rings, false rings, and fire scars were noted in samples of white spruce, and white rings and fire scars were noted in samples of trembling aspen. Therefore further studies are required to examine the underlying cause of these ring anomalies in both these species. Systematic analyses of the fire scars of white spruce islands and of trembling aspen would result in a detailed fire history reconstruction for the study area. In addition, older material of white spruce trees will open the way for drought reconstructions for the study region. Further studies should examine other parameters of tree-rings which may contain climatic information. These parameters include latewood density which has been related to summer temperature (Jozsa and Powell, 1987; Briffa et al., 1998; Barber et al., 2000), and carbon isotope ( $^{13}\text{C}$ ) concentration which has been related to potential evapotranspiration (Brooks et al., 1998).

### 3.5 Conclusions

1. White spruce island establishment occurred predominantly during cool and moist periods.
2. Moisture deficiency exacerbated by temperature induced drought stress limited the growth of white spruce islands.
3. Growth of white spruce was moderated by conditions within the aspen groves as radial growth patterns showed low variability from year to year, a low common growth signal, and a stronger response to temperature than to precipitation. Nonetheless, the dry regional climate still restricted growth during the growing season via temperature induced drought stress.
4. The dry regional climate also restricted aspen growth during the growing season via moisture deficiency and temperature induced drought stress. Mild winters negatively affected growth as it increases the rate of desiccation and increases the incidence of thaw-freeze events which causes substantial bud damage.

## CHAPTER 4: GENERAL SUMMARY AND CONCLUSIONS

In summary, the drought sensitivity of white spruce reinforces the basic principles of undertaking feasible studies of growth-climate relationships in terms of selecting a suitable site and tree species. The study reiterates the sensitivity of ecotonal regions to future climatic change. Furthermore, the study contributes to ameliorating the research gap for conifers at their southern limit of distribution. Given older material, white spruce in the SWPP has a great potential in future drought reconstructions of the Canadian prairies. Moreover, the growth-climate relationships will assist in the parameterization of holistic models of forest growth in response to climatic change.

Results of the study warranted the following general conclusions:

1. Light and temperature conditions within the open prairie and island periphery accentuated the effects of the dry regional climate of the aspen parkland and mixed-grass prairie region. In contrast, conditions under tree canopy of islands and aspen groves moderated the effect of the dry regional climate.
2. Microsite conditions of the creeping juniper mats supported the contention that juniper facilitates white spruce establishment and early growth by limiting moisture stress, protecting white spruce seedlings from the effect of prairie ground fires, providing accessible sites of establishment, and limiting tree-grass competition.
3. The light-limited environments of the aspen groves and spruce islands outweighed the effect of moderated microclimatic conditions since low light conditions limited diameter growth and height growth of white spruce seedlings and saplings.

4. Moisture deficiency exacerbated by temperature induced drought stress were factors that limited the growth of white spruce islands.
5. The response of white spruce trees to the regional climate was moderated by the microclimatic conditions of the aspen groves since growth was restricted mainly by temperature induced drought stress.
6. Aspen growth was negatively affected by moisture deficiency exacerbated by temperature induced drought stress and mild winters that have likely led to bud damage.

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