# 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

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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.

# ACKNOWLEDGMENTS

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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 $CO_2$ 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 ($CH_4$) and nitrous oxide ($N_2O$) contribute to the greenhouse effect, $CO_2$ is the dominant greenhouse gas accounting for

60% of the total amount of greenhouse gases. The $CO_2$ concentration in 1750 measured at 280 ppm increased to 367 ppm by 1999, representing an increase of 31% (IPCC, 2001). Even if $CO_2$ levels were curtailed through mitigation efforts the effect of $CO_2$ would still persist due to its long residence time. The role of $CO_2$ 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 $CO_2$), 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 $CO_2$ on Radial Growth

Under increased concentrations of $CO_2$, stomatal conductance will decrease since a smaller stomatal pore will be required for $CO_2$ 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 $CO_2$ utilised. Consequently, well

drained, xeric site locations represent an ideal site location to detect the $CO_2$ fertilization effect, which is the hypothesis that increasing atmospheric $CO_2$ will enhance the growth of natural vegetation. Dendrochronological studies have attempted to demonstrate a $CO_2$ 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 $CO_2$. 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 $CO_2$. Bristlecone pine showed a strip bark morphology which is postulated to lead to primary allocation of $CO_2$ 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 $CO_2$ at high altitudes would predispose plants to benefit from increasing $CO_2$ 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 $CO_2$.

## 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 $CO_2$ 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 $CO_2$ 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 ($^{13}$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 $^{12}CO_2$ diffuses into the leaf at a faster rate than $^{13}CO_2$. Second, fractionation occurs since Rubisco (Ribulose-1-5-bisphosphate carboxylase/oxygenase) is more reactive to $^{12}CO_2$ than $^{13}CO_2$. 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 $^{13}$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 $^{13}C$ 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 $CO_2$ which rises during the fall and winter and declines in the spring and summer due to increased $CO_2$ uptake by land vegetation. The amplitude of the seasonal cycle of $CO_2$ has increased in recent decades and has been explained in terms of increased $CO_2$ utilization by high latitude boreal forest ecosystems under a longer growing season. Therefore, the instrumental analysis of the seasonal cycle of $CO_2$ levels can be used to infer past responses of boreal forests to $CO_2$ induced climate change.

## 1.3     Vegetation Response to Future Global Change

## 1.3.1     Global Climate Change

### 1.3.1.1 Effect of Increased $CO_2$

Physiology experiments in field and laboratory conditions have examined the response of juvenile plants to abiotic environmental changes in general, and the effect of $CO_2$ 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 $CO_2$, 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 $CO_2$. The effect of $CO_2$ over larger time scales has been shown to dissipate due to plant acclimation to increased levels of $CO_2$, a process which is also referred to as down regulation (Eamus and Jarvis, 1989). Such negative feedback mechanisms include an accumulation of starches in leafs, decrease in translocation of starches to tissue sinks, or a saturation in the activity of Rubisco. The level of $CO_2$ may lead to competitive displacement of one plant species over another. For instance, under current climatic conditions $C_4$ plants outcompete $C_3$ plants in xeric environments due to the higher WUE of the $C_4$ photosynthetic pathway. However, with increasing $CO_2$, $C_4$ plants lose this competitive edge which may translate into changes in species diversity and plant community composition.

The increased concentration of $CO_2$ 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 $CO_2$ 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 $CO_2$ 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 $CO_2$ by plants may have the potential to ameliorate the effect of climatic stress, and highlights the role of plants as future potential $CO_2$ sinks which can offset the magnitude and rate of $CO_2$ 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 $CO_2$ uptake and respiration, processes which underpin the primary