DENDROCLIMATIC ANALYSIS OF WHITE SPRUCE AT ITS SOUTHERN LIMIT OF DISTRIBUTION IN THE SPRUCE WOODS PROVINCIAL PARK, MANITOBA, CANADA

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ABSTRACT

We examined the radial growth—climate association of a disjunct population of white spruce (*Picea glauca* (Moench) Voss) at its southern limit of distribution. Forty-four white spruce tree islands were sampled over four mixed-grass prairie preserves in the Spruce Woods Provincial Park located in the forest-prairie boundary of southwestern Manitoba. Reduced radial growth occurred during the 1910s, 1930s, early 1960s, and the late 1970s to the early 1980s and corresponded to periods of drought on the Canadian prairies, and the Great Plains of the United States. Correlation and response function coefficients indicated that 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. Growth was positively correlated with August–September (t-1) and May–June–July (t) precipitation and moisture index (precipitation minus potential evapotranspiration). Radial growth was positively associated with June–July–August (t) river discharge. Growth was most correlated with maximum and mean temperature compared with minimum temperature. Precipitation and maximum temperature accounted for the greatest variation in radial growth (61%). The results suggest that white spruce growth is sensitive to climatic fluctuations because growth is restricted by moisture deficiency exacerbated by temperature-induced drought stress.

Keywords: aspen parkland, climate change, dendroclimatology, drought stress, mixed-grass prairie, *Picea glauca* (Moench) Voss, prairie-forest boundary, response function.

RÉSUMÉ

L'association entre l'accroissement radial et le climat fut examinée chez une population disjointe d'épinette blanche croissant à sa limite sud de distribution. Quarante-quatre épinettes ont été échantillonnées dans quatre réserves de la prairie d'herbes mixtes du Parc Provincial Spruce Woods situé au sud-ouest du Manitoba, à l'interphase entre la forêt et la prairie. De faibles accroissements radiaux furent observés au cours des années 1910, 1930, au début des années 1960 et de la fin des années 1970 au début des années 1980. Ces épisodes correspondent tous à des périodes de sécheresse survenues dans les prairies canadiennes et les grandes plaines américaines. Les coefficients de corrélation et des fonctions de réponse ont démontré que les conditions encourues durant l'été et l'automne antérieurs (t-1) à la formation du cerne et durant l'été de la formation du cerne (t) influencent fortement la croissance radiale de l'épinette blanche. L'accroissement fut positivement corrélé aux précipitations des mois de août–septembre (t-1) et des mois de Mai–Juin–Juillet (t) de même qu'à un indice d'humidité (précipitation moins évapotranspiration potentielle). L'accroissement radial fut positivement associé aux débits fluviaux des mois de Juin–Juillet–Août (t). La croissance était aussi plus fortement corrélée aux températures maximales et moyennes qu'aux températures minimales. Les précipitations et les températures maximales ont expliqué 61% de la variation de la croissance radiale. Ces résultats suggèrent que l'épinette blanche est sensible aux fluctuations du climat car l'accroissement radiale est affecté par un manque d'humidité lequel est accrue lors des sécheresses reliées aux températures élevées.

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INTRODUCTION

Projections of future climate change based on climate models indicate a warming of 1.5°C–4.5°C upon a doubling of atmospheric CO₂ emissions by A.D. 2071–2100 (Houghton *et al.* 2001). The effect of global warming is expected to be most apparent at mid- to high-latitudes, and for disjunct tree populations and tree species at their edge of distribution (Rizzo and Wiken 1992; Lenihan and Neilson 1995). In Canada, most dendroclimatological studies of white spruce (*Picea glauca* (Moench) Voss) have been conducted at its northern limit in sub-arctic regions where low temperature (Szeicz and MacDonald 1995) 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).

In the prairie provinces of Canada, the southern limit of white spruce occurs in the aspen parkland, a transitional vegetation zone (ecotone) between prairie to the south and boreal forest to the north (Bird 1961; Zoltai 1975; Nienstaedt and Zasada 1990). Ecotones are expected to be sensitive to climatic change (Rizzo and Wiken 1992). The environment of the 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 direct 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 at its southern limit of distribution within the forest-prairie transition in response to past climatic

fluctuations. Specifically, the radial growth-climate association of white spruce was explored.

METHODS

Study Area

The study was conducted in the Spruce Woods Provincial Park (SWPP), which is located in southwestern Manitoba (49°40'N, 99°15'W) (Figure 1). 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 (Figure 1). The area experiences, for the reference period of 1971–2000, an average annual temperature of 2.4°C (Environment Canada 2002; Table 1). Average annual precipitation amounts to 474.0 mm, with 78.3% as rainfall and the remainder as snowfall. Precipitation peaks in June (Figure 2). In the mixed-grass prairie region, soil moisture is depleted by late July when temperature is the highest (Coupland 1950; Figure 2), reaching a daily maximum of 25.9°C (Environment Canada 2002).

The SWPP resides over an extensive belt of deltaic sands 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). 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). 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. Two successional pathways exist for white spruce in this landscape and are believed to ultimately converge to form pure white spruce forests in the absence of disturbances such as fire and severe grazing (Bird 1961). In the first successional pathway, white spruce is considered a pioneer species because 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),

Figure 1. Regional setting of the Spruce Woods Provincial Park (SWPP) (■) and the city of Brandon (●) in southwestern Manitoba shown in the inset map. The southern continuous limit of white spruce according to Farrar (1995) is indicated by the dashed line. The arrows in the enlarged map of the SWPP indicate the mixed-grass prairie preserves in which white spruce islands were sampled (Source: Schykulski and Moore 1997).

Table 1. Location and characteristics of climatic and hydrological stations.

Station	Location	Distance from SWPP (km)	Elevation or Drainage Area	Period of Records	¹ Missing Data (%)	² Mean Annual Temp. (°C)	² Mean Annual Precip. (mm)
Brandon CDA	48°52'N 99°59'W	88.5	363 m a.s.l	1895–1999	1.3 ³	2.4	474.0
Assiniboine River at Brandon	49°51'N 99°56'W	81.7	93800 km ²	1906–1973	3.3	—	—
Assiniboine River Near Brandon	49°52'N 100°06'W	100.7	93700 km ²	1974–2000	0	—	—

¹Proportion of missing monthly values that could not be estimated because of the lack of neighboring stations with a corresponding period of climate data.

²For the reference period of 1971–2000 (Environment Canada 2002).

³Proportion of missing monthly precipitation values; there were no missing temperature values.

Figure 2. Climate diagram of the Brandon CDA station showing mean monthly temperature (bold line) and total monthly precipitation (open bars) for the reference period of 1971–2000 (Source: Environment Canada 2002).

which is also a pioneer species commonly distributed on dry, rocky sites. Creeping juniper is believed to assist white spruce establishment by reducing mortality of white spruce seedlings from 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 that are surrounded by mixed-grass prairie. The islands have an asymmetric spatial structure because white spruce regeneration is concentrated on the northern aspect of the tree islands (Chhin and Wang 2002). The white spruce islands proceed to form continuous white spruce forests in the absence of disturbances. In the second successional pathway, the role of juniper is 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 in the open prairie (Bird 1961). The progressive recruitment of aspen leads to the development of aspen groves surrounded by mixed-grass prairie; the aspen groves in turn develop to form continuous aspen forests. White spruce seed from adjacent spruce islands and forests may be dispersed by wind into the aspen groves and forests. White spruce is considered shade tolerant and thus can grow in the understory of aspen and can regenerate in its own shade (Nienstaedt and Zasada 1990). Consequently, white spruce in the aspen understory will eventu-

ally replace aspen to form pure white spruce forests in the absence of disturbances.

Natural and anthropogenic disturbances have contributed to the landscape mosaic of the aspen parkland (Bird 1961). In pre-European settlement 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 through 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 preserves protected under the mandate of the Prairie Management Plan of Manitoba Conservation (Schykulski and Moore 1997). Agriculture continues within privately owned land within the centre of the park, and livestock grazing has been relegated to Shewfelt's grazing lease (Schykulski and Moore 1997).

Field Sampling

A total of forty-four white spruce tree islands were sampled from four mixed-grass prairie preserves (Epinette, Picnic, Aspen Bluff, and Jackfish) within the SWPP (Figure 1). The criteria for selection included that islands were 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 had similar topography. Twenty-four islands were selected in the largest prairie (Epinette), eight islands in each of the medium sized prairies (Picnic and Aspen Bluff) and four islands in the smallest prairie (Jackfish) (Figure 1). Epinette Prairie experienced severe burning in 1997 (Schykulski and Moore 1997). Within each of the burned islands of Epinette Prairie a disc was collected at breast height (1.3 m) on the largest dominant dead tree for a total of 24 trees (48 radii). Within the islands of the other prairie preserves, two dominant trees

were cored at breast height (1.3 m) with an increment borer, and 2 cores were obtained per tree. Dead material was also sampled. The total number of trees (radii) sampled in Picnic, Aspen Bluff, and Jackfish Prairies were 16 trees (32 radii), 16 trees (32 radii), and 8 trees (16 radii), respectively.

Sample Processing

Cores and discs were prepared and crossdated following standard dendrochronological techniques (Yamaguchi 1991; Stokes and Smiley 1996). Cores were mounted and all wood samples were sanded with progressively finer grades of sandpaper to highlight ring-width patterns. Cross-dating was conducted using the list method of Yamaguchi (1991), which involves the listing of narrow rings of each tree core and subsequently comparing all increment cores for shared narrow rings. 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).

Chronology Development

Each ring-width series was detrended with a 50-year cubic smoothing spline with a 50% frequency response (Cook and Peters 1981) using the program ARSTAN (Cook 1985; Holmes 1992). A 50-year spline preserves 99% of the variation in each ring-width series at a wavelength of about 15 years. Consequently, common trends (1–15 years) between trees are conserved. Each measured series was thus converted into dimensionless ring-width indices through standardization (*i.e.* 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). The open-grown nature of the white spruce islands minimizes the role of stand dynamics in affecting radial growth trends. The standardized ring-width series were also prewhitened with autoregressive (AR) modeling to remove temporal autocorrelation. Auto-

regressive modeling thus makes observations independent to meet the condition of most statistical analyses (Legendre and Legendre 1998). Furthermore, autoregressive modeling removes low-frequency variation and enhances the common growth signal, which is usually better correlated with yearly climatic fluctuations. The residual chronology was created using a biweight robust mean of the ring-width series pooled from the four mixed-grass prairie preserves. The expressed population signal (EPS) was determined and it represents the chronology signal as a fraction of the total chronology variance, *i.e.* it quantifies the degree to which a particular sample chronology portrays a hypothetically perfect chronology (Briffa and Jones 1990).

Growth-Climate Relationships

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; Table 1) for the period of 1895–1999. 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). Missing precipitation values in Table 1 represent the proportion of monthly values that could not be estimated because of the lack of neighboring stations with a corresponding period of climate data. These missing monthly values were estimated with the mean for that month. 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 as a function of mean air temperature using an empirical formula developed by Thornthwaite (1948). The moisture index was determined for the months of May to September. Untransformed mean monthly river discharge (m^3s^{-1}) was obtained from two hydrological stations located on the Assiniboine River, one at Brandon (1906–1973) and the other 20 km upstream (1974–2000) (Water Survey of Can-

ada 2002; Table 1). The flow of water in most river systems in Manitoba, including the Assiniboine River, are affected by upstream regulation (*e.g.* affected by dams) (Water Survey of Canada 2002). The impact of regulation is assumed to be minimal, but hydrological stations are highlighted if the effects of regulation are known to be substantial (Water Survey of Canada 2002). There was no substantial regulation affecting the two hydrological stations selected (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 1913–2000.

Radial-growth climate relationships were examined between the residual chronology and the climatic variables (*i.e.* minimum, mean and maximum monthly temperature, total monthly precipitation, moisture index, and river discharge) extending over two 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 (Briffa and Cook 1990). Response function analysis was performed with the program PRECON (version 5.17B) using 999 bootstrap iterations (Fritts *et al.* 1991) over the period of 1913–1999 for river discharge, and 1900–1999 for the other climatic variables. Response function analysis was conducted on separate climatic variables, and with total precipitation in combination with minimum, mean and maximum temperature data. As the climatic variables may have cumulative or long-term effects, the relationship between annualization periods of the climate data (except for the moisture index) and radial growth was also examined using Pearson correlation analysis (Szeicz and MacDonald 1996; St. George and Nielsen 2002). The annualization periods included May ($t-1$)–April (t), June ($t-1$)–May (t), July ($t-1$)–June (t), August ($t-1$)–July (t), and September ($t-1$)–August (t).

RESULTS

General Chronology Statistics

The residual chronology (1881–2000) showed reduced radial growth during the 1910s,

Figure 3. The residual chronology of white spruce and the corresponding sample size (N = number of tree radii). The bold line indicates an 11-yr running average of the growth indices.

1930s, early 1960s, and late 1970s to early 1980s (Figure 3). Descriptive statistics of the residual chronology of white spruce for the entire chronology length and common interval analysis are shown in Table 2. High-frequency interannual variation in radial growth was reflected by a high mean sensitivity (0.33). A strong common growth signal was reflected by a large percentage of the total variance being explained by the first principal component (PC1) (66.2), and high intercore correlation (0.66).

Growth-Climate Relationships

Response function analysis showed that relative to total precipitation ($r^2 = 0.48$) (Figure 4A) and the moisture index ($r^2 = 0.49$) (Figure 4B), river discharge ($r^2 = 0.15$) (Figure 4C) explained a small proportion of the variance in radial growth. Correlation analysis showed that radial growth of white spruce was positively associated with both total precipitation and Thornthwaite's moisture index 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 positively correlated with June (t), July (t), and August (t) river discharge. Relationships between radial growth and temperature indicated that the strongest climate response model was with maximum ($r^2 = 0.34$) (Figure 4F), followed by mean ($r^2 = 0.20$) (Figure 4E) and then minimum ($r^2 = 0.16$) (Figure 4D) temperature. Growth was negatively correlated with July ($t-1$) minimum temperature; July ($t-1$), June (t), and July (t) mean

Table 2. General statistics of the residual chronology of white spruce.

White Spruce Descriptive Statistics	
Chronology Length	1881–2000
No. of trees (radii)	64 (128)
Mean ring width (mm)	2.07
Mean sensitivity	0.33
Standard deviation	0.27
Variance related to autoregression (%) ¹	12.3
Autoregressive (AR) model ¹	1
Expressed population signal (EPS)	
0.85	1881–2000 (4) ²
0.90	1883–2000 (5)
0.95	1885–2000 (10)
Common Interval Analysis	1917–1995
No. of trees (radii)	39 (79)
Variance in first principal component (PC1) (%)	66.2
Expressed population signal (EPS)	0.99
Intercore correlation	0.66
Intertree correlation	0.66
Intratree correlation	0.84

¹Refers to the standard chronology.²The time period and the number of radii in parentheses to reach an EPS level.

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 ($r^2 = 0.61$; Figure 5). Significant response function coefficients occurred in September (t-1), May (t), June (t) and July (t) for both total precipitation and maximum temperature. The combination of total precipitation and maximum temperature explained more variance in growth than the moisture index, which is an integration of precipitation and mean temperature.

The relationship between climatic annualization periods and radial growth showed that total precipitation for the period of July (t-1) to June (t), August (t-1) to July (t), and September (t-1) to August (t) all had a significant, positive effect on radial growth (all $p < 0.001$; Table 3). Of these annualization periods, the period of August (t-1) to July (t) had the strongest correlation with growth. Similarly, river discharge showed a positive effect on growth for August (t-1) to July (t) ($r = 0.21$, $p = 0.054$), and September (t-1) to Au-

gust (t) ($r = 0.23$, $p < 0.05$) (Table 3). Of the temperature variables the strongest correlation was a negative response to August (t-1) to July (t) maximum temperature ($r = -0.19$, $p = 0.052$).

DISCUSSION

Chronology Strength

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 expressed population signal (EPS) of 0.85 is considered a benchmark of the signal strength of a chronology (Briffa and Jones 1990). An EPS of 0.85 or greater was achieved for the entire chronology length (1881–2000) with a sample of as few as 4 radii, which is characteristic of trees in extremely arid site locations (Briffa and Jones 1990). 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 ex-

Figure 4. Pearson correlation coefficients between the residual chronology of white spruce 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. Dashed lines indicate significant correlations at $p < 0.05$. Significant climatic variables determined from the response function analysis are denoted with an X. The r^2 value of the response model indicates the proportion of the variance in radial growth accounted for by the full set of monthly climate variables.

plained by climate ranges from 60 to 65% (Fritts 1974; Case and MacDonald 1995).

Drought Signal

The periods of growth reduction corresponded to documented periods of drought on the Canadian prairies (Case and MacDonald 1995; Sauchyn and Beaudoin 1998; Nkemdirim 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). The decades of the 1930s and 1980s have been described as the driest decades of this century in the Canadian prairies. The 'dust bowls' of the 1930s were widespread both in the Canadian prairies and the Great Plains of the United States (Meko 1992), and are distinct in the pattern of re-

Figure 5. Response function coefficients between the residual chronology of white spruce and both total precipitation (open bars) and maximum temperature (solid bars). Significant climatic variables are denoted with an X.

duced radial growth of white spruce in the 1930s. Nkembirim and Weber (1999) also place the decade of the 1910s as comparable to the 1930s and 1980s in severity of drought. The dry decade of the 1910s also corresponded to a period of reduced radial growth but less so than the 1930s and 1980s. Furthermore, Chhin and Wang (2002) demonstrated that recruitment of white spruce in the SWPP showed a decline during the 1930s and early 1960s, which correspond to periods of reduced growth. Therefore reduced radial growth may increase the probability of mortality for white spruce in the SWPP. In addition to dry periods, severely reduced 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). Previous analyses of drought reconstructions in prairie regions have indicated asynchronous regional differences

(Meko 1992; Case and MacDonald 1995; Case 2000; St. George and Nielsen 2002). For instance, Blasing and DuVick (1984) and Stockton and Meko (1983) have described the 1890s as a dry period. This period did not correspond to a reduction in radial growth in white spruce in the SWPP; however, greater sample depth of older trees may be required to uncover the drought of the 1890s. Overall, the correspondence of reduced radial growth to dry years and periods demonstrates the strong role of drought in conditioning tree growth.

White Spruce Responses to Climate

Correlation and response function coefficients indicated that 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 condition 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 minimum and mean temperature of the previous year. High temperatures may increase evapotranspiration 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

Table 3. Pearson correlation coefficients between the white spruce residual chronology and annualization periods of climatic variables for the period of 1913–1999 for river discharge, and 1990–1999 for the remaining climate variables.

Annualization Period	Total Precip.	River Discharge	Mean Temp.	Min. Temp.	Max. Temp.
May ($t-1$)–April (t)	0.09	0.03	–0.01	0.07	–0.09
June ($t-1$)–May (t)	0.19	0.11	–0.02	0.08	–0.12
July ($t-1$)–June (t)	0.41***	0.16	–0.04	0.09	–0.16
August ($t-1$)–July (t)	0.54***	0.21	–0.04	0.12	–0.19
September ($t-1$)–August (t)	0.49***	0.23*	–0.03	0.13	–0.18

¹ $t-1$ denotes the previous year.

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

drought. The strong effect of drought stress was exemplified by the strong positive relation between radial growth and May, June and July precipitation, summer river discharge, and 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. Because of 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. Future reconstructions have the potential to account for about 29% of the variance of August (t-1) to July (t) precipitation given the high correlation ($r = 0.54$) of white spruce growth with this precipitation period. In the prairie region 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 in an arid climate, pre-European settlement fires, and post-settlement demand for wood. Nonetheless, Sauchyn and Beaudoin (1998) were able to construct a chronology greater than 200 years using older material of white spruce from archeological sources (*i.e.* log buildings constructed by early European settlers). Despite the lack of older material, fossil pollen records indicate that after the late Wisconsin glaciation (18,000 years B.P.) and the subsequent receding and melting of the ice sheets, white spruce was one of the early colonizing plant species of the Western Canadian Interior plains

(Ritchie and MacDonald 1986). White spruce reached the northern prairie region around 12,600 years B.P. (Ritchie and MacDonald 1986).

Determinants of Tree Distribution Limits

The establishment of conifer species at their northern and southern range limits is 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.* 1987; Szeicz and MacDonald 1995; 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.* 1987). 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 northwestern limit of distribution in Manitoba (Tardif and Stevenson 2001). Tardif and Stevenson (2001) postulate 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) speculate that *P. mariana* is unable to establish on lichen mats at its northern limit while determinants of their southern limit are poorly understood.

Notwithstanding the influence of nonclimatic factors (*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), climate does con-

tribute directly to the conditioning of tree growth. 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 1995), 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 strong radial growth-climate associations of white spruce in the SWPP further underscore the importance of moisture deficiency intensified by temperature-induced drought stress as a major determinant of white spruce growth at its southern range limit.

CONCLUSIONS

In summary, the drought sensitivity of white spruce reinforces the basic principles of undertaking feasible dendroclimatological studies 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 ameliorates the research gap for conifers at their southern limit of distribution. Given older material from archeological sources, white spruce in the SWPP has great potential in future drought reconstructions of the Canadian prairies. Moreover, the growth-climate relationships will assist in the parameterization of models of forest growth in response to climatic change.

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