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Climatic Sensitivity of a Mixed Forest Association of White Spruce and Trembling Aspen at Their Southern Range Limit

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Abstract: Climatic sensitivity of white spruce (*Picea glauca* (Moench) Voss) was examined growing in association with trembling aspen (*Populus tremuloides* Michx.) at their southern limit of distribution in a transitional ecotone between the southern boreal forest and northern prairie region. The study was carried out in the Spruce Woods Provincial Park (SWPP) located in southwestern Manitoba, Canada. The dry regional climate restricted trembling aspen growth during the growing season via moisture deficiency and temperature induced drought stress. Warm, mild winters also negatively affected radial growth of trembling aspen. Growth of white spruce was moderated by conditions within the aspen stands 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 of white spruce during the growing season via temperature induced drought stress. The findings of the study for white spruce support the stress gradient hypothesis in which facilitative interactions between tree species are expected under harsher environmental conditions.

Keywords: climate; dendrochronology; drought stress; *Picea glauca*; *Populus tremuloides*

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1. Introduction

Mixed species forest stands generally have higher overall long-term productivity rates due to niche segregation of competing tree species, particularly in terms of differences in functional traits such as shade tolerance [1,2]. For instance, shade tolerant species (e.g., white spruce: *Picea glauca* (Moench) Voss) can develop in the understory of a shade intolerant species (e.g., trembling aspen: *Populus tremuloides* Michx.) which established earlier during the phase of stand establishment which eventually leads to canopy stratification [3]. In the absence of disturbances, the shade tolerant species will succeed the shade intolerant species. Interspecific interactions between trees can be negative in the form of competition for resources such as light, moisture, and nutrients during forest stand development [4]. In hot and dry environments for tree growth, such as the southern limit of tree distributions gradating with grassland ecosystems, direct sunlight can raise temperatures and lead to increased rates of evapotranspiration [5]. In these harsh environments, trees can promote facilitative interactions whereby increased tree cover and shade can help reduce the rate of evapotranspiration. This follows the general principles of the stress gradient hypothesis in which facilitative interactions between different tree species in a mixed stand is expected more in harsher environments and that competitive interactions are more prevalent in more benign site conditions [6–9]. Studies have indicated that tree species growing in mixed stands can benefit via reduced sensitivity to climatic stress including drought stress [10–15].

White spruce is a transcontinental species that is present in every forest region in Canada except the Pacific coast [16]. Dendroclimatic analysis of white spruce in Canada has been carried out at its northern limit in sub-arctic regions where low temperature is a limiting factor to tree growth [17]. Furthermore, drought stress has also been shown to limit white spruce growth at its northern range limit [18,19]. In the Canadian prairies, dendroclimatological studies of white spruce have also been undertaken where climatic moisture deficiency has been identified as the principal factor that controls the southern distribution limit of coniferous tree species [20–25].

Trembling aspen is the most widely distributed tree species in North America that is abundant in the Canadian boreal forest [26] and also commonly found in the aspen parkland [27]. Since the early 1990s, mortality and dieback of aspen over its western interior range in Canada has been associated with drought conditions [28]. Since the first decade of the 21st century, decline of trembling aspen across North America has been linked to drought stress preceding each decline episode [29]. Interannual variation in radial growth of trembling aspen has been associated with drought stress in western Canada [30,31] and intersite differences in eastern Canada were related to thermal heat sums [32].

While a number of studies have examined mixedwood stands of white spruce and trembling aspen in the boreal forest region [1,3,33], comparatively less is known about mixedwood stands of white spruce and trembling aspen located at their southern range limit and their sensitivity to climatic stress. Tree species at their distributional range limit and at the interface between different vegetation types (i.e., forest vs. prairie) are expected to be sensitive to future changes in climate. A better understanding about how species respond to climate in association with each other will contribute to better insight into forest community assemblage patterns under future climate change. The objective of this study was to examine the climatic sensitivity of white spruce growing in association with trembling aspen at their southern limit of distribution within the forest-prairie transitional zone. Specifically, radial growth of white spruce growing in association with trembling aspen was examined using a dendroclimatic approach. It is expected that in the context of the stress gradient hypothesis, both aspen and white spruce will show reduced sensitivity to climatic stress from a moderated microclimate that limits evaporative water loss in the mixed-forests, which in turn could ameliorate the effects of the hot and dry regional climate.

2. Materials and Methods

2.1. Study Site and Field Sampling

The study was carried out in the Spruce Woods Provincial Park (SWPP) which is located in southwestern Manitoba (49°40′ N, 99°15′ W) (Figure 1). For the reference period of 1971–2000, the study area experienced an average annual temperature of 2.4 °C [34]. Average annual precipitation was 474.0 mm, with 78.3% occurring as rainfall and the remainder being snowfall.

In the SWPP, the vegetation is classified as aspen parkland, which represents a transitional ecotone between the southern boreal forest and northern prairie [35,36]. White spruce and trembling aspen both occur as tree islands surrounded by mixed grass prairie [23,25]. White spruce seed from continuous forests and from adjacent spruce islands are dispersed by wind into the aspen stands. In the absence of disturbances such as fire, white spruce in the aspen understory will eventually replace aspen to form pure white spruce forests [3]. The SWPP occurs over an extensive belt of deltaic sands created about 12,000 years B.P. (Before Present) when a predecessor of the Assiniboine River connected into glacial Lake Agassiz [36].

A total of eight mixed forest stands containing an association of pole-sized, mid-rotation age white spruce and trembling aspen were sampled from across two prairie preserves (five stands in Aspen Bluff and three stands in Picnic prairie) within the SWPP (Figure 1). The three largest diameter white spruce and aspen trees were sampled from within each aspen stand and two increment cores were obtained per tree at breast height (1.3 m) from two opposite sides (180° separation).

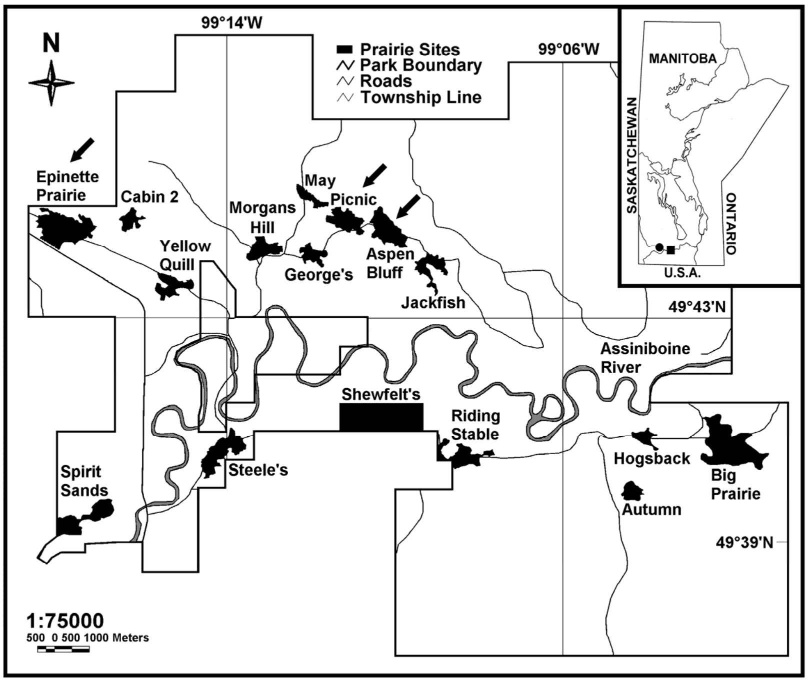

Figure 1. Regional setting of the Spruce Woods Provincial Park (SWPP) (■) and the Brandon Agriculture Station (●) in southwestern Manitoba and a map of the SWPP. Adapted from Schykulski and Moore [36].

2.2. Sample Processing, Cross-Dating, and Tree-Ring Measurement

Cores were prepared and crossdated following standard dendrochronological procedures [37,38]. Cores were mounted on grooved boards and all wood samples were sanded with progressively finer grades of sandpaper to highlight annual ring-width patterns. Crossdating involves matching relative ring-width variations (with a focus on narrow rings) among trees that have grown in nearby areas to identify the exact year in which each ring was formed [37,39].

The crossdated samples were measured to the nearest 0.001 mm using a VELMEX (stage micrometer) measuring system. The quality of the visual crossdating was further verified via statistical crossdating using the software program called COFECHA [40,41]. 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.

2.3. Climate Data

Primary climatic variables, including minimum, mean, and maximum monthly temperature [42] and total monthly precipitation [43], were obtained from the nearest meteorological station (Brandon Agriculture Station which is located 88.5 km from the study site) for the period of 1895–1999. The primary monthly meteorological data were converted into a secondary, synthetic variable that measures net water availability which is referred to as a moisture index. The moisture index is determined by subtracting monthly values of potential evapotranspiration (PET) from monthly precipitation (P) [44] and was calculated 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 19 km away from Brandon and combined into one series for a period of 1906–2000 [45].

2.4. Tree-Ring Analyses

Standardization of each ring-width series was performed using a 50-year cubic smoothing spline [46] using the software program called ARSTAN [41,47]. Tree-ring standardization generates dimensionless ring-width indices by dividing the observed values by the predicted values. This type of standardization amplifies the climatic signal and removes the effect of non-climatic factors (e.g., age-related trend) [39]. Autocorrelation was removed which makes tree ring measurements independent in order to meet the independence requirement of most statistical analyses [39,48]. Program ARSTAN develops autoregresive models of different orders to identify which order is the most effective at removing autocorrelation in the tree-ring series [41,47]. The standardized chronologies with temporal autocorrelation removed is referred to as the residual chronology. The residual chronology for white spruce and trembling aspen was created using a biweight robust mean.

Descriptive statistics were determined for the chronologies of white spruce and trembling aspen for the full chronology length and for a shorter a period in which all series span the same time period (i.e., common interval analysis) and included mean sensitivity and standard deviation [39,48]. Statistics for the common interval analysis included the percentage of variation in the first principal component (PC1) shared by the ring-width series that makes up a chronology. The expressed population signal (EPS) values range from 0 to 1 and are a measure of the chronology signal as a fraction of the total chronology variance. The degree of a high common growth signal is represented by PC1, EPS, and intercore correlation. Intercore correlation is the average correlation between all possible pair-wise combinations of all cores sampled; intertree correlation is defined as the average correlation between all possible pair-wise combination of trees (calculated after an average chronology is determined between the two cores of each tree); and intratree correlation is the average of the correlation coefficient between the two cores of each tree.

2.5. Growth-Climate Analyses

Dendroclimatic relationships were examined between the residual growth chronology and the climatic variables (i.e., precipitation, moisture index, river discharge, and minimum, mean, and maximum monthly temperature). The dendroclimatic analysis was performed using both Pearson correlation analysis and response function analysis [44]. 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). These analyses were calculated using the software program called PRECON (version 5.17B) with 999 bootstrap iterations [49]. The period of comparison with the climate data was 1970–1999 for white spruce and 1949–1999 for trembling aspen. To examine the potential influence of longer-term effects of climate, the relationship between annualization periods for most of the climate variables (except for the moisture index) and radial growth were assessed using Pearson correlation analysis [18].

3. Results

3.1. Growth and Chronology Characteristics

White spruce showed few periods of reduced radial growth according to a running average (11-year) that summarized the growth indices (Figure 2a). The most prominent yearly growth reductions occurred in 1974, 1976, and 1979. In contrast, trembling aspen showed many years and periods of reduced growth (Figure 2b). The most prominent year of growth reduction was 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, although 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 ($r = 0.42$, $p < 0.05$). White spruce had a lower mean sensitivity and standard deviation than aspen (Table 1). The variance in PC1, the expressed population signal, intercore, intertree, and intratree correlation was lower in white spruce than in aspen.

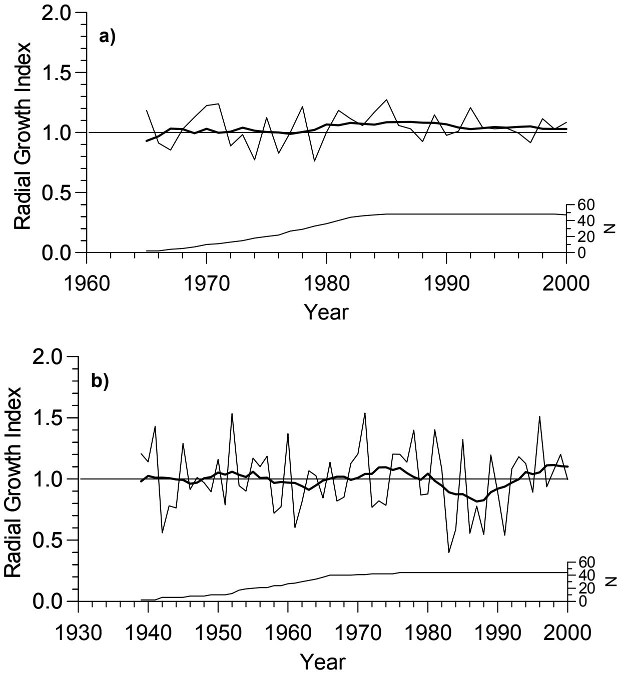

Figure 2. (**a**) The residual chronology of white spruce (1965–2000); (**b**) The residual chronology trembling aspen (1939–2000). The corresponding sample size (N, number of tree cores) is provided.

Table 1. General tree characteristics (mean and standard deviation in parenthesis) and statistics of the residual chronology of white spruce and trembling aspen.

Tree and Chronology Characteristics	White Spruce	Trembling Aspen
Tree diameter (cm)	20.5 (5.6)	16.0 (4.0)
Tree age (year)	30.4 (4.2)	51.6 (7.5)
Chronology Length	1965–2000	1939–2000
No. of trees (radii)	24 (48)	22 (44)
Mean ring width (mm)	3.11	1.27
Mean sensitivity	0.14	0.31
Standard deviation	0.13	0.27
Variance due to autoregression (%) [1]	45.00	4.2
Autoregressive (AR) model	2	1
Common Interval Analysis	1977–2000	1964–2000
No. of trees (radii)	17 (27)	18 (34)
Variance in PC1 (%)	39.28	50.69
Expressed population signal	0.89	0.94
Intercore correlation	0.33	0.48
Intertree correlation	0.32	0.47
Intratree correlation	0.58	0.67

[1] Refers to the standard chronology.

3.2. Growth-Climate Relationships

White spruce responded more strongly to maximum temperature ($R^2 = 0.45$) than to total precipitation ($R^2 = 0.41$) and to moisture index ($R^2 = 0.24$) (Figure 3). Growth was negatively correlated to February of the current year (−, t) precipitation (Figure 3a). White spruce growth was not significantly correlated with the moisture index (Figure 3b). 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) (Figure 3c). Of the temperature variables, growth responded more to maximum temperature ($R^2 = 0.45$) (Figure 3f) than to mean ($R^2 = 0.40$) (Figure 3e) and minimum temperature ($R^2 = 0.37$) (Figure 3d). Growth was correlated with June (−, t) maximum temperature.

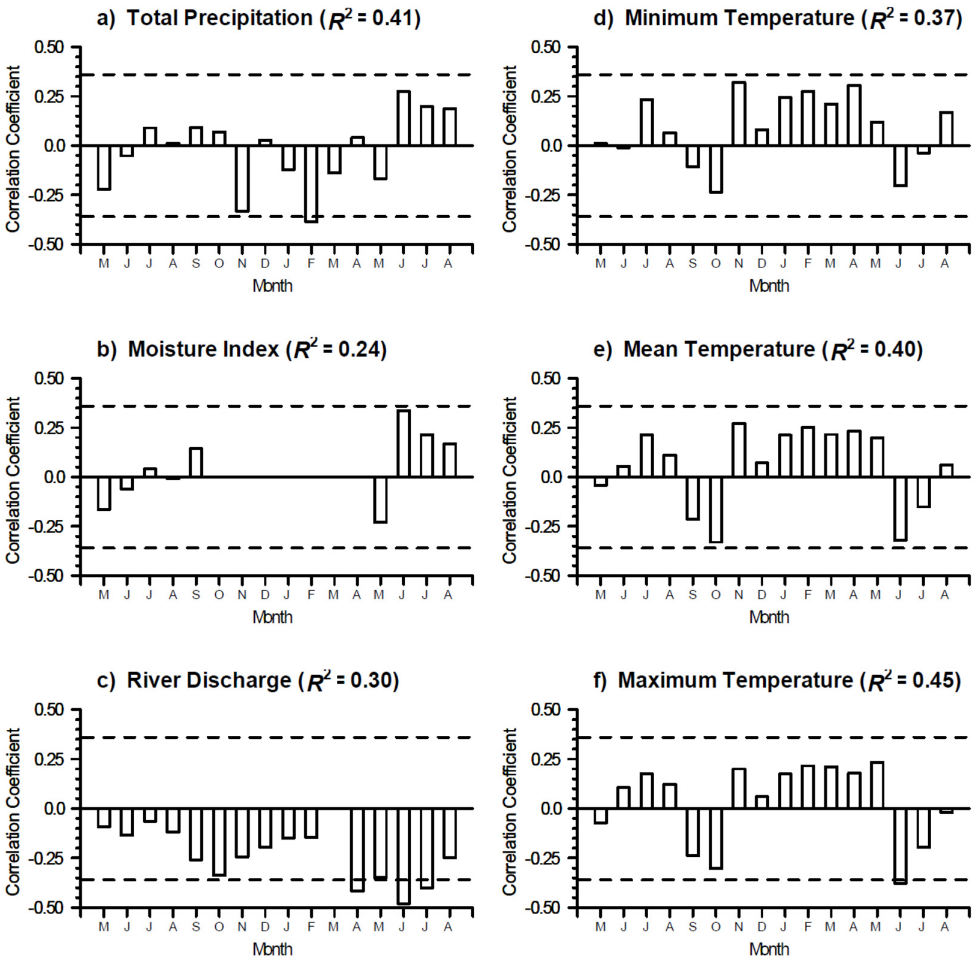

Figure 3. Pearson correlation coefficients between the residual chronology of white spruce and (**a**) total precipitation; (**b**) moisture index; (**c**) river discharge; (**d**) minimum temperature; (**e**) mean temperature; and (**f**) maximum temperature. Significant correlations ($p < 0.05$) determined 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 function model for each climate variable is indicated.

Trembling aspen responded more to maximum temperature ($R^2 = 0.43$) than to total precipitation ($R^2 = 0.40$) and the moisture index ($R^2 = 0.30$) (Figure 4). Growth was correlated with June (+, t) precipitation (Figure 4a) and moisture index (Figure 4b). Response to river discharge was almost absent in aspen ($R^2 = 0.09$) (Figure 4c). Trembling aspen was affected more by maximum temperature ($R^2 = 0.43$) (Figure 4f) than either mean ($R^2 = 0.39$) (Figure 4e) and minimum temperature ($R^2 = 0.30$) (Figure 4d). Growth was correlated with January (−, t) minimum, mean, and maximum temperature. Furthermore, growth was correlated with June (−, t) mean and maximum temperature.

White spruce showed no significant correlations with any of the annualized precipitation periods (Table 2). Instead, white spruce 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 of trembling aspen 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 (t) precipitation.

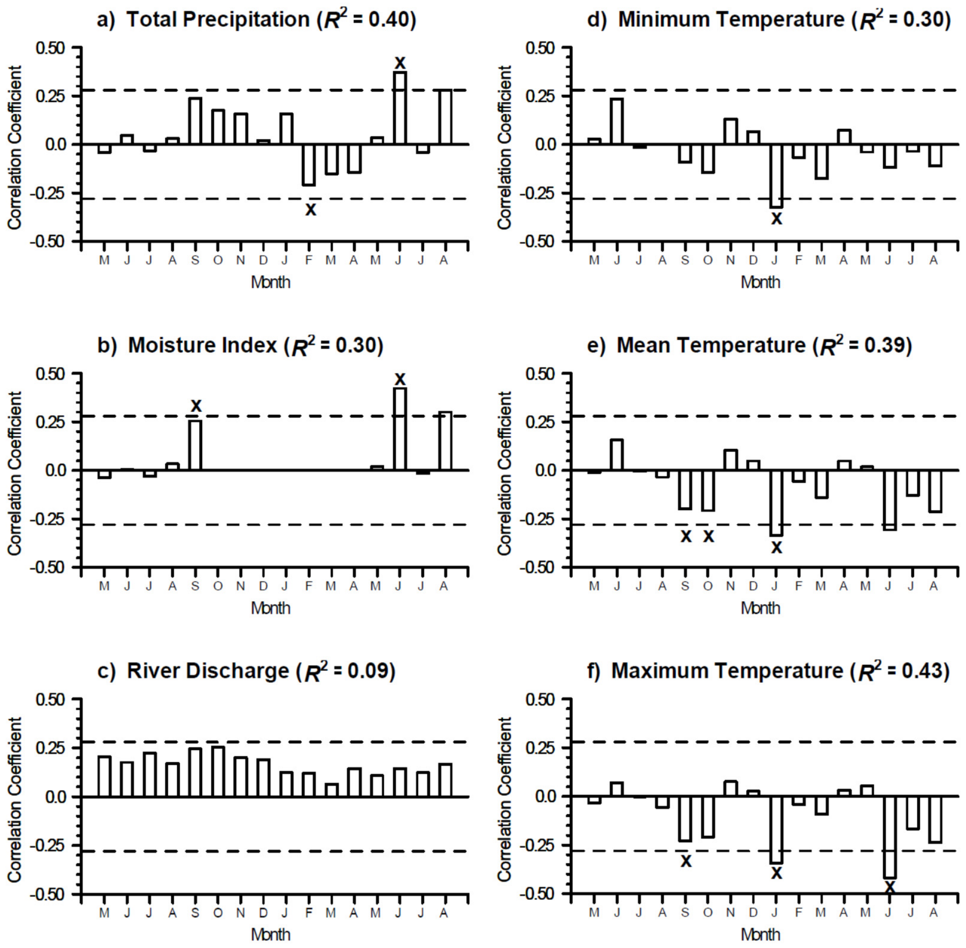

Figure 4. Pearson correlation coefficients between the residual chronology of trembling aspen and (**a**) total precipitation; (**b**) moisture index; (**c**) river discharge; (**d**) minimum temperature; (**e**) mean temperature; and (**f**) maximum temperature. Significant correlations ($p < 0.05$) determined from correlation analysis extend past dashed lines. Significant climatic variables ($p < 0.05$) determined from the response function analysis are denoted with an X. The R^2 value of the response function model for each climate variable is indicated.

Table 2. Pearson correlation coefficients between the residual chronology of white spruce and trembling aspen with the annualization periods of climatic variables.

Annualization Period	Total Precip.	River Discharge	Min. Temp.	Mean Temp.	Max. Temp.
White spruce					
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
Trembling aspen					
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

[1] t−1 denotes the previous year. *: $p < 0.05$.

4. Discussion

White spruce showed few instances of reduced growth. Furthermore, growth did not correspond with the 1980 regional drought [50] and corresponded very minimally to the 1988 regional drought [51]. 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 [52] who examined mixedwood 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 [52] also concluded that the effect of climate was secondary to the influence of insect infestations on aspen growth.

The low standard deviation and mean sensitivity of white spruce growing in association with trembling aspen underscores the low degree of interannual variation of spruce in this environment due to the moderated microclimate of the aspen groves. In contrast, 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 [53] who showed that in contrast to trees at the xeric forest border, trees within the mesic forest interior (i.e., far away from the stand edges) were not sensitive to climate.

The dendroclimatic analyses (i.e., correlation analysis and response function analysis) indicated that white spruce 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 suggest that white spruce trees benefited from the moderated microclimate of aspen groves. These results are very much in contrast to white spruce growing in pure tree island stands which had a strong and direct association with precipitation [24]. The reduced effect of drought stress on white spruce supports the stress gradient hypothesis in which facilitative interactions between tree species are expected under harsher environmental conditions [6–9]. Similarly, mixed stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst) had higher growth and yield compared to their respective monoculture counterparts in Poland under conditions of drought stress [13]. Mixtures of European beech (Fagus sylvatica L.) with either Norway spruce or silver fir (*Abies alba* Mill.) were more productive than their monospecific counterparts on sites with low productivity in France [15]. This stress gradient hypothesis also applies to mixed stands of silver fir in France [10], mixed stands of European beech in Germany [11], and mixtures of Douglas-fir (Pseudotsuga menziessi (Mirb.) Franco) in Germany [12].

The negative relationship of white spruce growth to February precipitation suggests that high winter snowfall has a negative impact on growth. High snowfalls can potentially cause abrasion of the cuticle layer of needles and lead to winter desiccation injury [54]. Furthermore, high winter snowfall levels can potentially increase the mechanical load on tree crowns leading to branch and twig breakage. Since trees generally prioritize repair of damaged crowns, diameter growth would suffer.

Of the temperature variables, growth of white spruce 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, and this was also observed in white spruce growing in pure stands [24,39]. 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. It is possible that given the higher water demands of trembling aspen [26] relative to white spruce, the growing season periods of high water availability could benefit trembling aspen growth at the expense of white spruce.

Correlation and response function analysis of trembling aspen indicated that growth was limited by moisture deficiency as growth was correlated with both moisture index and precipitation in June (+, t). The influence of moisture deficiency was also reflected in the correlation of growth of trembling aspen with the September (t−1) to August (t) precipitation period. The strong response to summer precipitation and moisture index indicates that the dry regional climate of the aspen parkland has negatively affected growth of aspen. This corresponds to other studies which have indicated that interannual variation in radial growth of trembling aspen has been associated with drought stress in western Canada [30,31].

Growth of trembling aspen 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 [54,55]. In other words, Tranquillini [54] and Havranek and Tranquillini [55] reported that while the cold hardiness 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 [54,55]. 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 [52].

5. Conclusions

Climate does contribute directly to the conditioning of tree growth particularly at climatic extremes at the range limit of tree species [56]. In this study, the dry regional climate restricted trembling aspen growth during the growing season via moisture deficiency and temperature induced drought stress. Furthermore, warm, mild winters also negatively affected radial growth of trembling aspen. The radial growth-climate associations of white spruce growing in mixed stands with trembling aspen further underscores the importance of temperature induced drought stress as a major determinant of the southern range limit of white spruce. Notably, this mixed forest association can also ameliorate the degree of direct moisture stress for white spruce. The findings of the study for white spruce support the stress gradient hypothesis in which facilitative interactions between tree species are expected under harsher environmental conditions.

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Author Contributions: S.C. and G.W. conceived and designed the experiments; S.C. performed the experiments; S.C. led and G.W. assisted with data analysis; S.C. led and G.W. assisted with writing and revising the paper.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Man, R.; Lieffers, V.J. Seasonal photosynthetic responses to light and temperature in white spruce (*Picea glauca*) seedlings planted under an aspen (*Populus tremuloides*) canopy and in the open. *Tree Physiol.* **1997**, *84*, 437–444. [CrossRef]
2. Cavard, X.; Bergeron, Y.; Chen, H.Y.H.; Pare, D.; Laganiere, J.; Brassard, B. Competition and facilitation between tree species change with stand development. *Oikos* **2011**, *120*, 1683–1695. [CrossRef]
3. Huang, J.-G.; Stadt, K.J.; Dawson, A.; Comeau, P.G. Modelling growth-competition relationships in trembling aspen and white spruce mixed boreal forests of western Canada. *PLoS ONE* **2013**, *8*, e77607. [CrossRef] [PubMed]
4. Oliver, C.D.; Larson, B.C. *Forest Stand Dynamics*; John Wiley and Sons: New York, NY, USA, 1996; p. 544.
5. Chhin, S.; Wang, G.G. Growth of white spruce, *Picea glauca*, seedlings in relation to microenvironmental conditions in a forest-prairie ecotone of southwestern Manitoba. *Can. Field Nat.* **2007**, *121*, 191–200.

6. Condes, S.; del Rio, M. Climate modifies tree interactions in terms of basal area growth and mortality in monospecific and mixed *Fagus sylvatica* and *Pinus sylvestris* forests. *Eur. J. For. Res.* **2015**, *134*, 1095–1108. [CrossRef]
7. Forrester, D.I. The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. *For. Ecol. Manag.* **2014**, *312*, 282–292. [CrossRef]
8. Maestre, F.T.; Callaway, R.M.; Valladares, F.; Lortie, C.J. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J. Ecol.* **2009**, *97*, 199–205. [CrossRef]
9. Jucker, T.; Avacaritei, D.; Barnoaiea, I.; Duduman, G.; Bouriaud, O.; Coomes, D.A. Climate modulates the effects of tree diversity on forest productivity. *J. Ecol.* **2016**, *104*, 388–398. [CrossRef]
10. Lebourgeois, F.; Gomez, N.; Pinto, P.; Merian, P. Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, Western Europe. *For. Ecol. Manag.* **2013**, *303*, 61–71. [CrossRef]
11. Pretzsch, H.; Schutze, G.; Uhl, E. Resistance of European tree species to drought stress in mixed versus pure forests: Evidence of stress release by inter-specific facilitation. *Plant Biol.* **2013**, *15*, 483–495. [CrossRef] [PubMed]
12. Thurm, E.A.; Uhl, E.; Pretzsch, H. Mixture reduces climate sensitivity of Douglas-fir stem growth. *For. Ecol. Manag.* **2016**, *376*, 205–220. [CrossRef]
13. Bielak, K.; Dudzinska, M.; Pretzsch, H. Mixed stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce [*Picea abies* (L.) Karst] can be more productive than monocultures. Evidence from over 100 years of observation of long-term experiments. *For. Syst.* **2014**, *23*, 573–589. [CrossRef]
14. Pretzsch, H.; del Rio, M.; Ammer, C.; Avdagic, A.; Barbeito, I.; Beielak, K.; Brazaitis, G.; Coll, L.; Dirnberger, G.; Drossler, L.; et al. Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. *Eur. J. For. Res.* **2015**, *134*, 927–947. [CrossRef]
15. Toigo, M.; Vallet, P.; Pero, T.; Bontemps, J.-D.; Piedallu, C.; Courbaud, B. Overyielding in mixed forests decreases with site productivity. *J. Ecol.* **2015**, *103*, 502–512. [CrossRef]
16. Nienstaedt, H.; Zasada, J.C. White spruce [*Picea glauca* (Moench) Voss]. *Silvics of North America: 1. Conifers*; Burns, R.M., Honkala, B.H., Technical Coordinators, Eds.; US Department of Agriculture, Forest Service: Washington, DC, USA, 1990.
17. Szeicz, J.M.; MacDonald, G.M. Dendroclimatic reconstruction of summer temperatures in northwestern Canada since A.D. 1638 based on age-dependent modeling. *Quat. Res.* **1995**, *44*, 257–266. [CrossRef]
18. Szeicz, J.M.; MacDonald, G.M. A 930-year ring-width chronology from moisture-sensitive white spruce (Picea glauca Moench) in Northwestern Canada. *Holocene* **1996**, *6*, 345–351. [CrossRef]
19. Barber, V.A.; Juday, G.P.; Finney, B.P. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* **2000**, *405*, 668–673. [CrossRef] [PubMed]
20. Zoltai, S.C. *Southern Limit of Coniferous Trees on the Canadian Prairies*; Information Report NOR-X-128; Canadian Forestry Service: Edmonton, AB, Canada, 1975.
21. Hogg, E.H. Climate and the southern limit of the western Canadian boreal forest. *Can. J. For. Res.* **1994**, *24*, 1835–1845. [CrossRef]
22. Sauchyn, D.J.; Beaudoin, A.B. Recent environmental change in the southwestern Canadian Plains. *Can. Geogr.* **1998**, *42*, 337–353. [CrossRef]
23. Chhin, S.; Wang, G.G. Spatial and temporal pattern of white spruce regeneration within mixed-grass prairie in the Spruce Woods Provincial Park of Manitoba. *J. Biogeogr.* **2002**, *29*, 903–912. [CrossRef]
24. Chhin, S.; Wang, G.G.; Tardif, J. Dendroclimatic analysis of white spruce at its southern limit of distribution in the Spruce Woods Provincial Park, Manitoba, Canada. *Tree Ring Res.* **2004**, *60*, 31–43. [CrossRef]
25. Chhin, S.; Wang, G.G. Climatic response of *Picea glauca* seedlings in a forest-prairie ecotone of western Canada. *Ann. For. Sci.* **2008**, *65*, 207. [CrossRef]
26. Perala, D.A. Quaking aspen (*Populus tremuloides* Michx.). *Silvics of North America: 2. Hardwoods*; Burns, R.M., Honkala, B.H., Technical Coordinators, Eds.; US Department of Agriculture, Forest Service: Washington, DC, USA, 1990.
27. Peterson, E.B.; Peterson, N.M. *Ecology, Management, and Use of Aspen and Balsam Poplar in the Prairie Provinces*; Canadian Forest Service, Northern Forestry Center: Edmonton, AB, Canada, 1992.
28. Hogg, E.H.; Brandt, J.P.; Michaelian, M. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. *Can. J. For. Res.* **2008**, *38*, 1373–1384. [CrossRef]

29. Worrall, J.J.; Rehfeldt, G.E.; Hamann, A.; Hogg, E.H.; Marchetti, S.B.; Michaelian, M.; Gray, L.K. Recent declines of *Populus tremuloides* in North America linked to climate. *For. Ecol. Manag.* **2013**, *299*, 35–51. [CrossRef]
30. Hogg, E.H.; Brandt, J.P.; Kochtubajda, B. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951–2000. *Can. J. For. Res.* **2005**, *35*, 610–622. [CrossRef]
31. Leonelli, G.; Denneler, B.; Bergeron, Y. Climate sensitivity of tembling aspen radial growth along a productivity gradien in northeastern British Columbia, Canada. *Can. J. For. Res.* **2008**, *38*, 1211–1222. [CrossRef]
32. Lapointe-Garant, M.-P.; Huang, J.-G.; Gea-Izquierdo, G.; Raulier, F.; Bernier, P.; Berninger, F. Use of tree rings to study the effect of climate change on trembling aspen in Quebec. *Glob. Chang. Biol.* **2010**, *16*, 2039–2051. [CrossRef]
33. Jiang, X.; Huang, J.-G.; Stadt, K.J.; Comeau, P.G.; Chen, H.Y.H. Spatial climate-dependent growth response of boreal mixedwood forest in western Canada. *Glob. Planet. Chang.* **2016**, *139*, 141–150. [CrossRef]
34. Environment Canada. *Canadian Climate Normals*; Environment Canada: Ottawa, ON, Canada, 2002.
35. Bird, R.D. *Ecology of the Aspen Parkland of Western Canada in Relation to Land Use*; Canada Department of Agriculture, Research Branch: Ottawa, ON, Canada, 1961.
36. Schykulski, K.; Moore, J. *Spruce Woods Provincial Park: Prairie Management Plan*; Manitoba Department of Natural Resources: Winnipeg, MB, Canada, 1997.
37. Stokes, M.A.; Smiley, J.L. *An Introduction to Tree-Ring Dating*; The University of Chicago Press: Chicago, IL, USA, 1968.
38. Yamaguchi, D.K. A simple method for cross-dating increment cores from living trees. *Can. J. For. Res.* **1991**, *21*, 414–416. [CrossRef]
39. Fritts, H.C. *Tree Rings and Climate*; Academic Press: London, UK, 1976.
40. Holmes, R.L. Computer-assisted quality control in tree-ring dating and measurement. *Tree Ring Bull.* **1983**, *43*, 69–78.
41. Holmes, R.L. *Dendrochronology Program Library*, 1st ed.; Laboratory of Tree-Ring Research, University of Arizona: Tucson, AZ, USA, 1992.
42. Vincent, L.A.; Gullett, D.W. Canadian historical and homogeneous temperature datasets for climate change analyses. *Int. J. Climatol.* **1990**, *19*, 1375–1388. [CrossRef]
43. Mekis, E.; Hogg, W.D. Rehabilitation and analysis of Canadian daily precipitation time series. *Atmos. Ocean* **1999**, *37*, 53–85. [CrossRef]
44. Thornthwaite, C.W. An approach toward a rational classification of climate. *Geogr. Rev.* **1948**, *38*, 55–94. [CrossRef]
45. Water Survey of Canada. *National Water Data Archive (HYDAT CD-ROM)*; Version 2000-2.01; Water Survey of Canada, Environment Canada: Downsview, ON, Canada, 2002.
46. Cook, E.R.; Peters, K. The smoothing spline: A new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree Ring Bull.* **1981**, *41*, 45–53.
47. Cook, E.R. A Time Series Analysis Approach to Tree-Ring Standardization. Ph.D. Thesis, University of Arizona, Tucson, AZ, USA, 1985.
48. Cook, E.R.; Kairiukstis, L.A. *Methods of Dendrochronology: Applications in the Environmental Sciences*; Kluwer Academic Publishers: Dordrecht, The Netherlands, 1990.
49. Fritts, H.C.; Vaganov, E.A.; Sviderskaya, I.V.; Shashkin, A.V. Climatic variation and tree-ring structure in conifers: Empirical and mechanistic models of tree-ring width, number of cells, cell-size, cell-wall thickness and wood density. *Clim. Res.* **1991**, *1*, 97–116. [CrossRef]
50. Stockton, C.W.; Meko, D.M. Drought recurrence in the Great Plains as reconstructed from long-term tree-ring records. *J. Clim. Appl. Meteorol.* **1983**, *22*, 17–29. [CrossRef]
51. Meko, D.M. Dendroclimatic evidence from the Great Plains of the United States. In *Climate since AD 1500*; Bradley, R.S., Jones, P.D., Eds.; Routledge: London, UK, 1992; pp. 312–330.
52. Hogg, E.H.; Schwarz, A.G. *Tree-Ring Analysis of Declining Aspen Stands in West-Central Saskatchewan*; Information Report NOR-X-359; Canadian Forest Service, Northern Forestry Centre: Edmonton, AB, Canada, 1999.
53. Fritts, H.C. Tree-ring characteristics along a vegetation gradient in northern Arizona. *Ecology* **1965**, *46*, 393–401. [CrossRef]

54. Tranquillini, W. *Physiological Ecology of the Alpine Timberline: Tree Existence at High Altitudes with Special Reference to the European Alps*; Springer: Berlin, Germany, 1979.
55. Havranek, W.M.; Tranquillini, W. Physiological processes during winter dormancy and their ecological significance. In *Ecophysiology of Coniferous Forests*; Smith, W.K., Hinckley, T.M., Eds.; Academic Press: San Diego, CA, USA, 1995; pp. 95–124.
56. Woodward, F.I. *Climate and Plant Distribution*; Cambridge University Press: Cambridge, UK, 1987; p. 174.