

**Spatial patterns of white spruce (*Picea glauca*) in Eastern  
North America**

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### **Abstract**

Many species are responding to climate change by adjusting their spatial distribution and altering their growth patterns, especially near range limits. We studied historic growth of white spruce over two spatial scales. We studied populations in Michigan, Ontario, and New Brunswick to examine growth trends over distances of >1500 km, and then local populations separated by a distance of 5 km in Michigan. Trends in growth were compared to mean temperatures across sites. We demonstrate the use of regional climate, influenced at local scales by topographical features (e.g. presence of large water bodies), to study the effects of climate change.

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## Introduction

Global temperature increase resulting from climate change affects the growth and distribution of a large number of species, including many perennial plants (McKenney et al., 2007). For instance, in the boreal forest of North America, tree populations have responded positively to temperature increase over short periods of time, in terms of individual growth (Stinziano & Way, 2014) and temperature increase has been shown to foster treeline movement both northward latitudinally and upwards in altitude (Wilmking et al., 2004). High-latitude forests store up to 49% of the total carbon stored by forest ecosystems globally (Dixon et al., 1994), and these populations are important in mitigating the effects of climate change.

A pervasive boreal forest species in North America is white spruce (*Picea glauca*). Populations of this conifer species are found throughout much of Canada from the east coast to the west, and into northern Canada and Alaska (Figure 1). At high latitudes and at high elevation, annual growth rates of individual white spruce trees have increased in response to higher air and soil temperatures (Danby & Hik, 2006). However, precipitation plays an important role in tree growth as well. An increase in air temperature was found to negatively impact the radial growth of white spruce populations in Alaska; likely due to physiological stress resulting from moisture (usually available as runoff from melted snow), being less available due to the temperature increase (Barber & Juday, 2000).

Because the distribution of white spruce spans a large trans-continental spatial range, accurately describing the species' growth response to climate change is dependent on understanding how populations across specific regions respond to temperature and other environmental variables. Previous studies relating white spruce tree growth to weather conditions, such as temperature, precipitation, and humidity, have focused on sites at high

altitudes (Barber & Juday, 2000), and/or at high latitudes (Wilmking et al., 2004; Danby & Hik, 2006), near the species' northern range limit, in regions such as Yukon and Alaska. This project described populations near the southern range limit, where growing seasons are substantially longer than at higher latitudes (Rowe, 1972), and water availability is often provided by rainfall, rather than snowmelt (Holman et al., 2012; Notaro et al., 2015).

Our study sought to describe the effects of growing season temperature on annual growth of white spruce individuals near the southern limit of the species' range. Specifically, we focused on the radial growth of individuals per year. Two spatial scales were studied. First, large spatial extent, comparing populations that are separated from one another by distances of 600-1600 km. A second, local area within one site was also studied: i) lakeshore sites and ii) inland sites. In this region, a lake effect results in an average difference in temperatures of up to 2 °C between an area directly adjacent to Lake Superior and an area 5 km inland (Appendix; Hinkel & Nelson, 2012).

We hypothesized that annual growth rates would vary based on the location of individuals. Regions with greater correlation between growing season temperatures were expected to yield white spruce individuals with more similar annual growth rates. Additionally, warmer growing season temperatures were expected to result in decreased annual growth, as each population was located in temperate regions where higher annual temperatures often coincide with decreased precipitation (Trenberth & Jones, 2007; Cong & Brady, 2012; Betts et al., 2014), and cold temperatures are not extreme enough to restrict growth of white spruce individuals in these areas (Nienstaedt & Zasada; Rowe, 1972).

## Methods

### *Study sites*

At the large spatial extent, sites were located in Michigan, Ontario, and New Brunswick (Figure 1). The Michigan study site was located northwest of Powell, Michigan ( $46^{\circ}52'08.3''\text{N}$ ,  $87^{\circ}50'24.6''\text{W}$ ), and included land maintained by the Huron Mountain Wildlife Foundation. The region is largely undeveloped and is dominated by old-growth forests and small freshwater ponds and lakes. Annually, average temperatures range from  $6 - 11^{\circ}\text{C}$  and the average rainfall is 81 cm (Weather Underground). The presence of Lake Superior results in inland areas being relatively warmer than those along the lakeshore (Hinkel & Nelson, 2012). The Ontario site was located near North Bay ( $46^{\circ}18'58.2''\text{N}$ ,  $79^{\circ}28'07.1''\text{W}$ ), inland from Lake Nipissing. Annually, average temperatures range from  $0 - 9^{\circ}\text{C}$  and the average rainfall is 105 cm (Gov. of Canada). The New Brunswick site was located in Lorneville, NB, which is approximately 20 km southwest of Saint John, NB ( $45^{\circ}10'55.8''\text{N}$ ,  $66^{\circ}09'20.3''\text{W}$ ). The region is inland from the northern shore of the Bay of Fundy. Annually, average temperatures range from  $0 - 10^{\circ}\text{C}$  and the average rainfall is 143 cm (Gov. of Canada).

### *Core collection & processing*

White spruce trees were cored from sites near North Bay, Ontario and Lorneville, New Brunswick in 2016. Ten living trees were selected at each of these sites, and cores were collected at breast height (1.3 m) and stored in opaque plastic tubes for transportation and storage. In the lab, each core was transferred onto a core mount, rotated such that the rings faced directly upward, and secured with carpenter's glue. Once each core was secured in its mount, it was sanded down with 100, 150, and 250 grit sandpaper until a flat, smooth surface was formed

(Speer, 2010).

In Michigan, twenty-one white spruce cores were collected from six sites (three adjacent to Lake Superior (“lakeshore”), three approximately 5 km inland (“inland”)) (Figure 2) in the Huron Mountains of Michigan in summer of 2012. Tree selection was based on diameter, with only the largest three adult living individuals at each site selected for coring. Cores were collected at 30 cm above ground level. Preparation of each core for processing was performed once more by securing each core in a core mount and sanding it down with 100, 150, and 250 grit sandpaper (Speer, 2010).

#### *Data collection*

Each core was viewed and each tree’s radial growth increments were measured using a Velmex stage and dissecting microscope. These increments are indicated by distinguishable lines on the cores. MeasureJ2X software was used to record the width of rings from bark to pith. The measurements were checked for accuracy using COFECHA. Where dating errors were shown to be greater than 2-3 years, as reported by COFECHA, re-measurements of cores and adjustments using the program’s autoregression feature were completed until the measurements were indicated as reasonably accurate (Grissino-Mayer, 2001). The corrected individual series were then detrended using ARSTAN, allowing age effects and general trends spanning multiple years to be removed from analysis (Cook et al., 1986). Finally, residual chronology indices were tabulated using ARSTAN. The outputs from ARSTAN were in raw growth increments or the indexed residual increments, which were each used for analysis.

Historic temperature data for each of the sites were collected from weather stations nearest to each site. For the Michigan site, historic monthly temperature means were provided by

a weather station in Big Bay, MI (46°50'05.8"N, 87°42'42.6"W; <http://www.intellicast.com/Local/History.aspx?location=USMI0082>). The Ontario temperature data were provided by a weather station at the North Bay Airport (46°21'25.6"N, 79°25'43.0"W; [http://climate.weather.gc.ca/historical\\_data/search\\_historic\\_data\\_e.html](http://climate.weather.gc.ca/historical_data/search_historic_data_e.html)), and the New Brunswick temperature data were provided by a weather station in Saint John, NB (45°15'54.9"N, 66°03'11.9"W; <https://www.wunderground.com/history/airport/CYSJ>). Mean temperatures were calculated from April 1 – September 31 of each year from the earliest year available to the year of core collection. The growing season length was based on previous data collected by the United States Forestry Service (Nienstaedt & Zasada, 1990).

### *Data analysis*

Age effects on annual growth of individuals, which can result in the magnification of growth increments of older trees, were minimized by generating standardized indices for radial growth; annual growth residuals were used for analyses rather than raw ring width values (Cook & Peters, 1997). For the large spatial extent, comparing the growth of individuals between the New Brunswick, Ontario, and combined Michigan sites, annual residual growth was compared with mean growing season temperature at each site. To determine the spatial correlation between mean annual growing season temperature across distance classes of 500 km bin sizes, a modified, non-centered spatial correlogram was generated using the `correlog.nc` function in the NCF package in R version 3.3.1 GUI 1.68 for Mac OSX (Bjornstad, 2016). Similarly, a spatial correlogram was generated to determine the correlation between mean annual residual growth across distance classes of 500 km bin sizes.

For the local scale including only the Michigan sites, individual growth was divided by



diameter at breast height, so that a standardized measurement for annual growth could be used for analysis. This method of standardization was preferred over using the indices from before, so that long-term effects of the same regional temperature could be observed, while still accounting for age effects on growth. Mean growth per ring width was compared between the lakeshore and inland populations to determine whether proximity to Lake Superior influenced annual growth. Finally, a linear mixed model (ANCOVA) was used to test the effects of proximity to Lake Superior on the relationship between mean annual residual growth and mean regional growing season temperature. All analyses were performed in R version 3.3.1 GUI 1.68 for Mac OSX.

## Results

### *Large spatial extent (up to 1500 km)*

At the Michigan site, the median age of individuals was 45 years, with the oldest individual dating back to 1916 and the youngest to 1993. The average core length at the Michigan site was  $180.7 \pm 63.5$  mm. At the Ontario site, individuals were much younger, with the median age being 13.5 years. The oldest individuals dated back to 2000, and the youngest to 2007. The average core length at the Ontario site was  $76.1 \pm 12.9$  mm. Finally, at the New Brunswick site, the median age of individuals was 35 years, with the oldest individual dating back to 1967 and the youngest individuals to 2006. The average core length at the New Brunswick site was  $96.1 \pm 43.0$  mm. The average core lengths were significantly different across each site (one-way ANOVA,  $df = 34$ ,  $F = 17.3$ ,  $P < 0.001$ ).

Growing season temperatures across each site were significantly different (one-way ANOVA,  $df = 94$ ,  $F = 26.2$ ,  $P < 0.001$ ), with New Brunswick being the warmest site and Michigan being the coolest site, on average. The mean regional growing season temperature at

the Michigan site was the coolest of the three sites at  $11.5 \pm 1.0$  °C between 1970 and 2012.

Annual residual growth was shown to have a negative relationship with mean growing season temperature at this site, but the relationship was not significant ( $R^2 = 0.01$ ,  $df = 29$ ,  $F = 1.6$ ,  $P = 0.2$ ) (Figure 3a & 3b). The mean regional growing season temperature at the Ontario site was  $12.6 \pm 0.5$  °C between 1970 and 2016. The relationship between annual residual growth and growing season temperature was also negative at the Ontario site, and was not significant ( $R^2 = 0.003$ ,  $df = 15$ ,  $F = 0.04$ ,  $P = 0.8$ ) (Figure 3c & 3d). Finally, the mean regional growing season temperature at the New Brunswick site was  $13.3 \pm 0.9$  °C between 1970 and 2016. The relationship between residual growth and mean growing season temperature at this site was positive, but the relationship was not significant ( $R^2 = 0.01$ ,  $df = 45$ ,  $F = 1.7$ ,  $P = 0.2$ ), (Figure 3e & 3f).

The spatial correlograms indicated that mean growing season temperature was positively and significantly correlated within the same site, while negatively and significantly correlated between the Michigan and Ontario sites (Figure 4a; separated by just over 600 km). The correlations between mean growing season temperature of sites separated by distances greater than 1000 km were not significant. (Figure 4b). A similar trend was observed when correlating mean residual growth of individuals at each site, though the scale in correlations was much smaller than for temperature. Individuals located within the same site had the greatest correlation between annual residual growth, and the correlation was significant, but was low in magnitude (Figure 4b). The correlation between residual growth of individuals at the Michigan site and those at the Ontario site was negative and significant. Correlations between individuals separated by distances greater than 1000 km were not significant.

### *Local scale (~5 km)*

From 1970 to 1997, inland individuals in Michigan had a greater mean growth than lakeshore individuals for all but one year (Figure 5). Between 1998 and 2012, however, there were several years of greater mean growth at the lakeshore site. Over the full 42-year span, individuals at the lakeshore site had a mean annual growth per core length of  $0.010 \pm 0.004$  mm, while individuals at the inland site had a mean annual growth per core length of  $0.012 \pm 0.003$  mm. The difference in mean annual growth per diameter was significant (paired t-test,  $df = 42$ ,  $T = -3.9$ ,  $P < 0.001$ ). Mean residual growth had a negative, non-significant relationship with mean annual growing season temperature for the region at both the lakeshore ( $R^2 = 0.06$ ,  $df = 29$ ,  $F = 1.7$ ,  $P = 0.2$ ) and inland ( $R^2 = 0.07$ ,  $df = 28$ ,  $F = 2.3$ ,  $P = 0.1$ ) sites (Figure 6). While the y-intercept for the inland site was significantly higher than that of the lakeshore site (ANCOVA,  $est. = 1.6$ ,  $T = 4.1$ ,  $P = 0.0001$ ), there was no significant effect of site on response to mean regional temperature (ANCOVA,  $est. = -0.13$ ,  $T = -0.232$ ,  $P = 0.8$ ).

## **Discussion**

For each of the large-extent sites, growing season temperature was shown to be a relatively weak predictor for residual growth of white spruce individuals. The Michigan site featured the strongest trend in relating annual growth to growing season temperature, with warmer temperatures resulting in relatively decreased growth in the same year. This relationship argues against the positive growth response of white spruce to warming temperatures, as presented in some prior studies (Danby & Hik, 2006), but reinforces the conflicting growth responses observed in other studies involving white spruce populations at more northern latitudes (Barber & Juday, 2000; Wilmking et al., 2004). In each of these studies, individual growth was

shown to change based on the primary limiting factor (either temperature or precipitation) within the studied populations' regions.

Individuals within the same local-scale sites had the highest correlation in mean annual growth, and the correlation was negative between individuals from the Michigan and Ontario sites, which were separated by a distance of just over 600 kilometers. However, the correlation between individuals within the same site was just under 0.1, indicating that a high degree of variation exists even over a very small distance scale. This variation could result from the density of the forest surrounding each individual, as boreal individuals in less-dense areas often have greater annual growth (He & Duncan, 2000). Additionally, tree growth can be affected by the types of vegetation present in the undergrowth (Callaway & Walker, 1997; Nilsson & Wardle, 2005), which can vary over short distances.

Previous temperature studies at our sites near Lake Superior showed that inland areas are warmer during the summer than those directly alongside the lakeshore (Appendix; Hinkel & Nelson, 2012). Therefore, if temperature were a substantially limiting factor in this region, white spruce populations further inland would be expected to grow more, on average, than the lakeshore populations, and both should indicate a positive growth response to regional temperature. While inland individuals were shown to have grown more than lakeshore individuals between 1970 and 2012, both populations indicated a negative growth response to temperature. Consequently, it was determined that temperature must not be the primary limiting factor for white spruce individuals in this region.

One potential explanation for why temperature is not limiting is the size of the individuals selected. Mature white spruce are relatively large, and able to compete effectively for access to direct sunlight. This allows individuals to be less limited by regional temperature

fluctuations, so long as the range in temperature is not extreme (Wilmking et al., 2004).

Furthermore, we chose the largest individuals at each site, which emerge through the forest canopy and are therefore less likely to be limited by temperature than individuals occupying the undergrowth, where temperatures are cooler due to restricted sunlight (Louis et al., 2005). A much more plausible limiting factor for these individuals would be access to water. Temperature and precipitation are often inversely related; a warmer growing season likely corresponds with decreased precipitation in the same year (Trenberth & Jones, 2007; Cong & Brady, 2012; Betts et al., 2014). Because water availability is likely a primary limitation on growth of white spruce along the species' southern range limit (Goldstein et al., 1985), a negative relationship would be expected between temperature and annual growth of individuals.

At higher latitudes, where temperatures range into extreme lows, temperature is the primary limiting factor, and warmer growing seasons will benefit the growth of individuals (Danby & Hik, 2006). However, in regions with milder annual temperatures, precipitation is the primary limiting factor for growth of white spruce. Increasing temperatures resulting from climate change will likely result in decreased individual growth of individuals near the southern limit of the species' range, due to the negative relationship observed between temperature and precipitation within the region (Trenberth & Jones, 2007; Cong & Brady, 2012; Betts et al., 2014). Because of the increased growth expected at high latitudes and decreased growth expected at lower latitudes, the overall effect of warming temperatures could likely be a shift northward in the overall distribution of white spruce.

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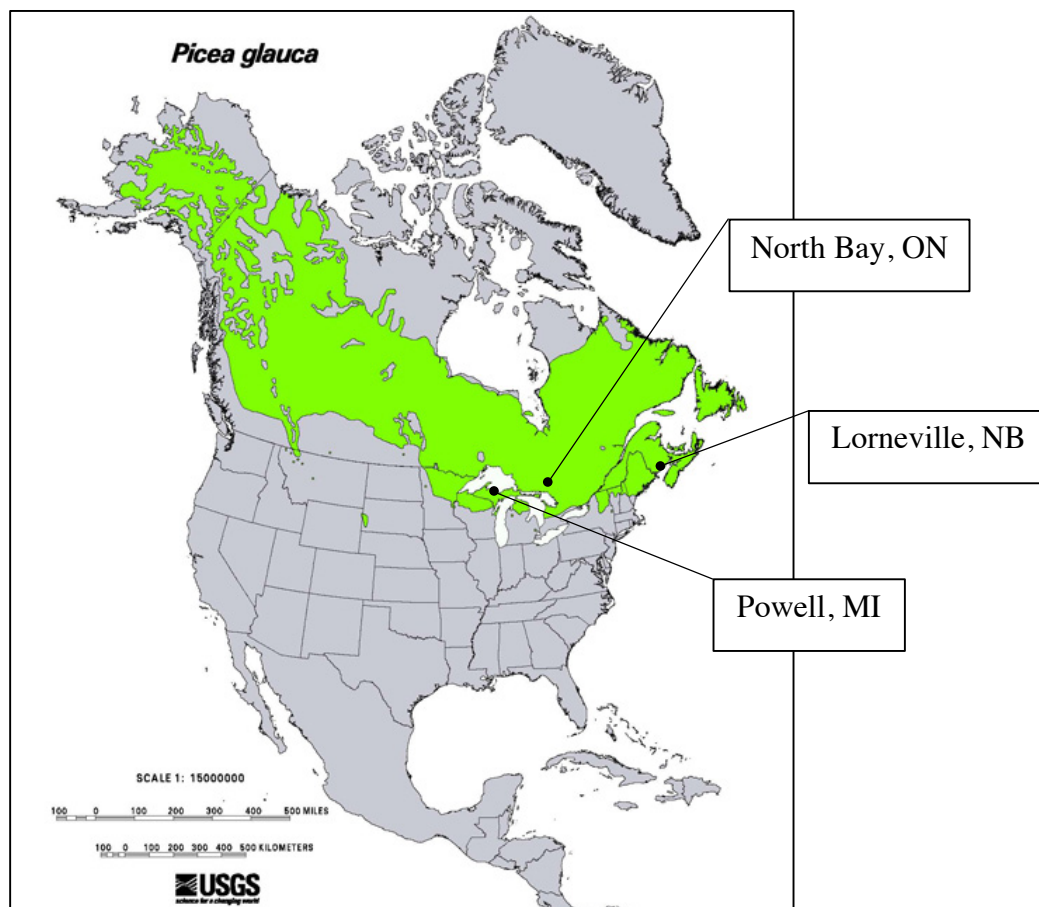
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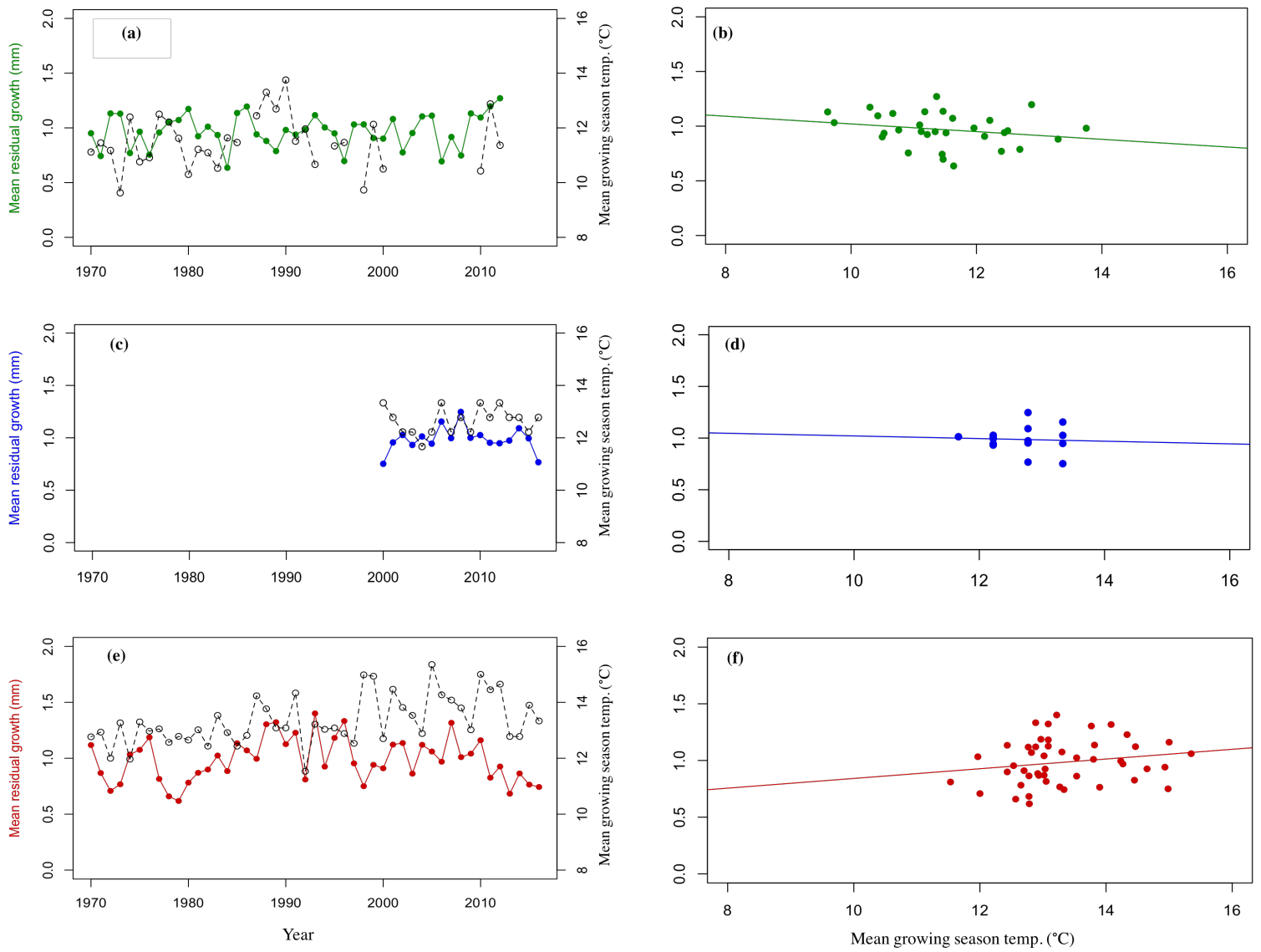
## Figures



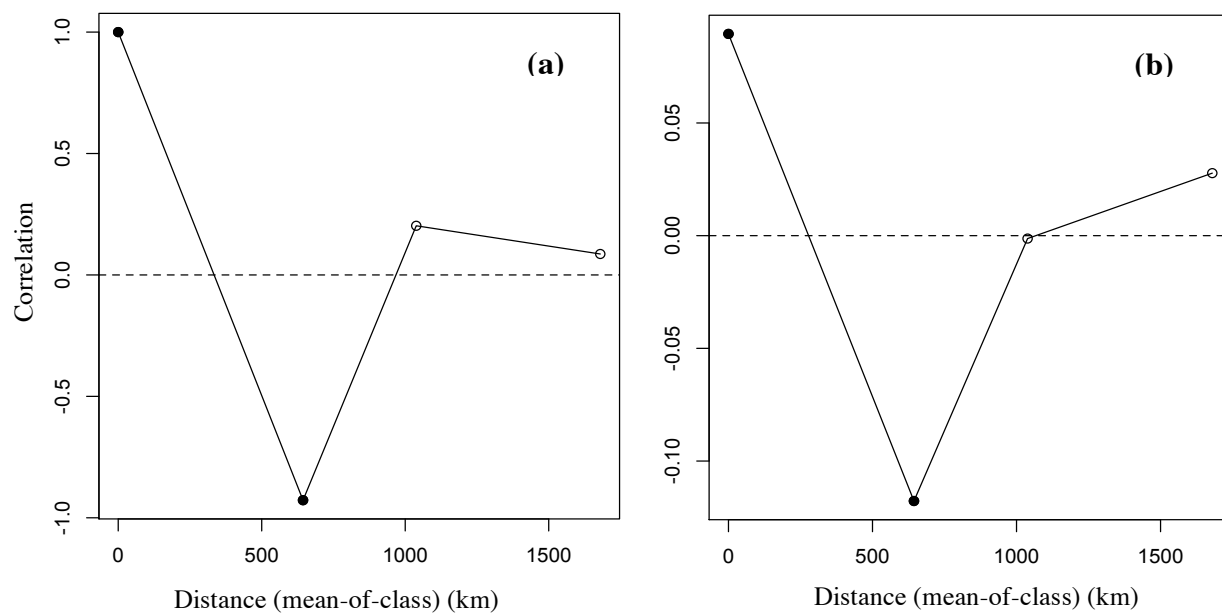
**Figure 1.** Range of *Picea glauca* distribution, with locations of study sites indicated.



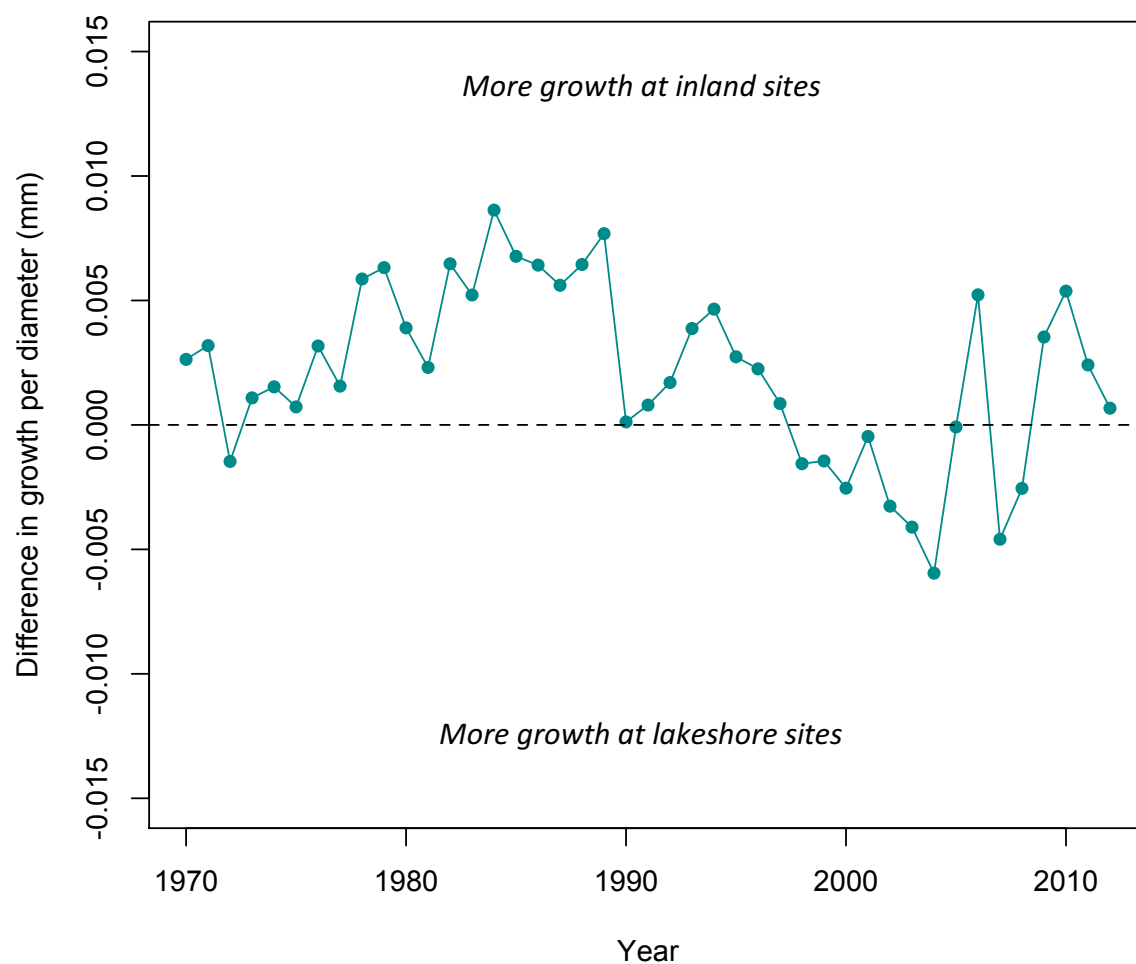
**Figure 2.** Michigan site map. Sites 1, 2, and 3 are inland, while sites 4, 5, and 6 are near the lakeshore.



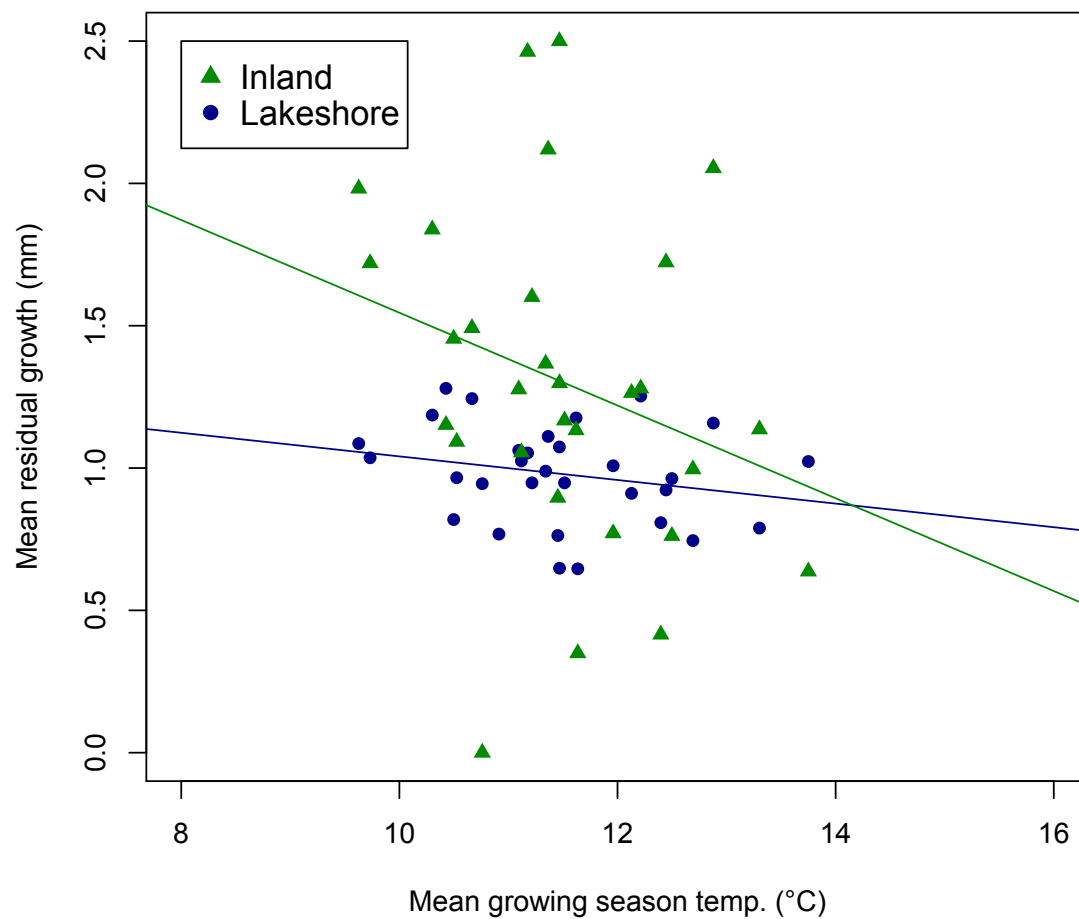
**Figure 3.** Mean residual growth of white spruce and mean growing season temperatures at the (a) Michigan, (c) Ontario, & (e) New Brunswick sites. Residual growth of white spruce vs mean growing season temperatures for the (b) Michigan, (d) Ontario, & (f) New Brunswick sites.



**Figure 4.** (a) Correlation of mean growing season temperature over distance class. (b) Correlation of mean residual growth over distance class. Note change in scale on y-axis.

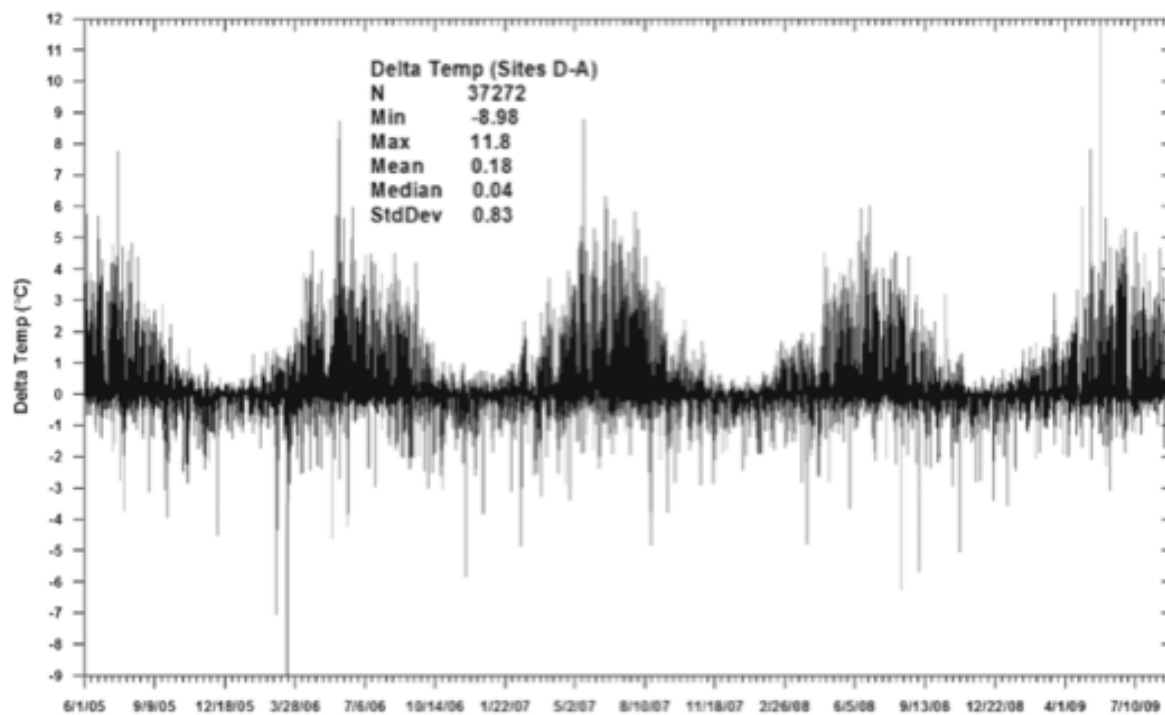


**Figure 5.** Difference in mean growth of white spruce per diameter between inland and lakeshore sites. Positive values indicate growth at inland sites was greater than at lakeshore sites. Negative values indicate growth at lakeshore site was greater than at inland sites.



**Figure 6.** Mean residual growth of white spruce at lakeshore and inland sites vs. regional growing season temperature from 1970-2012.

## Appendix 1



Difference in monthly temperature between inland and shoreline near Lake Superior. Positive values indicate inland site was warmer than lakeshore site. From Hinkel & Nelson, 2012.