

Consistent negative temperature sensitivity and positive influence of precipitation on growth of floodplain *Picea glauca* in Interior Alaska

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Abstract: This paper calibrates climate controls over radial growth of floodplain white spruce (*Picea glauca* (Moench) Voss) and examines whether growth in these populations responds similarly to climate as upland trees in Interior Alaska. Floodplain white spruce trees hold previously unrecognized potential for long-term climate reconstruction because they are the source of driftwood that becomes frozen in coastal deposits, where archeological timbers and beach logs represent well-preserved datable material. We compared ring width chronologies for 135 trees in six stands on the Yukon Flats and Tanana River with temperature and precipitation at Fairbanks from 1912–2001. Our sample contains a stable common signal representing a strong negative relationship between summer temperature and tree growth. We developed a floodplain temperature index (FPTI), which explains half of the variability of the composite chronology, and a supplemental precipitation index (SPI) based on correlation of monthly precipitation with the residual of the temperature-based prediction of growth. We then combined FPTI and SPI into a climate favorability index (CFI) in which above-normal precipitation partially compensates for temperature-induced drought reduction of growth and vice versa. CFI and growth have been particularly low since 1969. Our results provide a basis for building longer chronologies based on archeological wood and for projecting future growth.

Résumé : Cet article quantifie le contrôle qu'exerce le climat sur la croissance radiale de l'épinette blanche (*Picea glauca* (Moench) Voss) de la plaine inondable et examine si la croissance dans ces populations réagit au climat de la même façon que les arbres des hautes terres de l'intérieur de l'Alaska. Les épinettes blanches de la plaine inondable possèdent un potentiel jusqu'à présent méconnu pour reconstituer le climat sur le long terme parce qu'ils sont la source de bois flotté qui finit gelé dans les dépôts côtiers où les bois archéologiques et les bois de plage constituent un matériau bien préservé et qui peut être daté. Nous avons comparé les séries dendrochronologiques de 135 arbres provenant de six peuplements des Yukon Flats et de la rivière Tanana avec les températures et les précipitations à Fairbanks de 1912 à 2001. Notre échantillon contient un signal commun stable qui représente une relation négative étroite entre la température estivale et la croissance des arbres. Nous avons développé un indice de température des plaines inondables (ITPI) qui explique la moitié de la variabilité de la série dendrochronologique composite et un indice de précipitation supplémentaire (IPS) fondé sur la corrélation des précipitations mensuelles avec les valeurs résiduelles de la prédiction de la croissance basée sur la température. Nous avons ensuite combiné l'ITPI et l'IPS dans un indice de climat favorable (ICF) dans lequel des précipitations plus élevées que la normale compensent en partie une réduction de la croissance due à la sécheresse provoquée par la température et vice versa. L'ICF et la croissance ont été particulièrement faibles depuis 1969. Nos résultats fournissent une base pour la construction de chronologies plus longues à partir de bois archéologiques et pour les projections de la croissance futures.

[Traduit par la Rédaction]

Introduction

Significant climate change impacts in high-latitude boreal ecosystems are already evident, and impacts are expected to become even more pronounced in the future (Juday et al. 2005), posing major challenges for boreal forest sustainability (Burton et al. 2010). The long-term response of boreal forests to climate change has important implications for the global carbon cycle, albedo, and canopy evapotranspiration, which, in turn, feed back into further climate change (ACIA 2005).

To properly interpret contemporary changes in the boreal forest and to be able to project future growth responses under further altered climate regimes, long-term climate controls must be identified.

Accurately calibrating climate parameters with tree growth response also allows reconstruction of past climates. Tree ring series used for far northern climate reconstructions traditionally have been collected at high elevations or northern latitudinal treelines. Alternatively, tree ring series from productive, low-elevation northern environments have been used

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to successfully reconstruct past climates (e.g., Barber et al. 2002). However, higher productivity ecosystems are poor preservation environments for the dead woody material necessary for extending the chronologies backward over long periods of time. Arctic driftwood is primarily made up of mature white spruce (*Picea glauca* (Moench) Voss) trees from high-productivity sites that have been eroded from the banks of the major rivers (Alix 2005). The wood can be sampled today as archeological timbers, much of it in an excellent state of preservation because it has remained frozen since abandonment (Giddings 1941).

The ability to crossdate and exploit this ancient, well-preserved driftwood depends on establishing and calibrating a common signal of growth sensitivity to climate during the period of instrument record and, further, demonstrating that the climate responsiveness is stable temporally. However, tree ring samples from older floodplain white spruce in the major drainages are rare, and long-term climate sensitivity has not been adequately investigated in these populations.

The goals of this study are to determine (i) whether a common signal is present in populations of white spruce on productive floodplain sites on the middle Tanana and Yukon rivers, areas with the warmest and driest summer climates in Alaska, and (ii) whether any signal can be related to climate parameters of the past century.

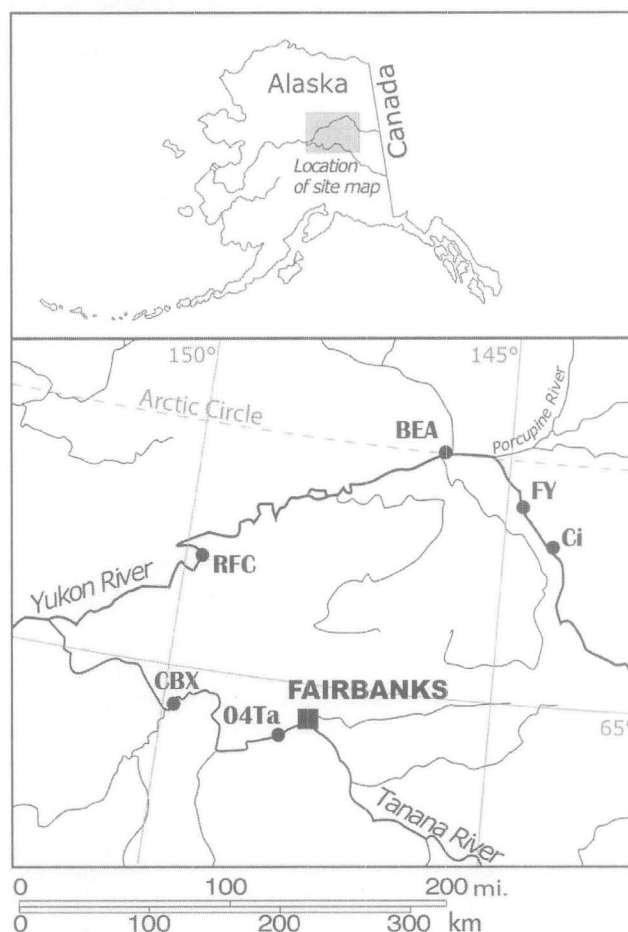
This investigation also provides the opportunity to determine whether floodplain white spruce growth displays the strong negative growth sensitivity to warm season temperatures found in productive uplands in Alaska (Barber et al. 2000), Yukon Territory (Szeicz and MacDonald 1996), and northeastern British Columbia (Zhang et al. 1999) and the decreasing trend of growth identified in satellite-derived normalized difference vegetation index (NDVI) values across much of boreal North America (Goetz et al. 2005).

Study area

The Yukon River basin occupies 832 700 km² across central Alaska and south-central Yukon Territory, Canada. One of the more prominent features of the watershed is the Yukon Flats, an area of 33 417 km² of low elevation (90 to 250 m), located some 1200 km from tidewater (USDA Forest Service 1994). In this region, the well-drained alluvial sites are characterized by a closed spruce-hardwood forest of white spruce, Alaska birch (*Betula neoalaskana* Sarg.), and balsam poplar (*Populus balsamifera* L.) (Vioreck and Little 2007). The Yukon River and its tributary, the Tanana, are mainly glacier-fed rivers. As a result, the shifting channels and deposition patterns are constantly initiating and destroying sites on which forests develop (Yarie et al. 1998). Waters of both the Yukon and Tanana rivers carry a high load of sediment and woody debris due to the high rate of bank erosion (Ott et al. 2001).

The Yukon Flats and middle Tanana River Valley experience the warmest summer temperatures and some of the lowest annual precipitation totals in Alaska. The mean monthly temperature for July is generally ~16.5 °C (1971–2000). The lowest average annual precipitation among Interior Alaska stations is 193 mm at Circle along the Yukon River, and most valleys in the region experience <280 mm (Shulski and Wendler 2007). As a result, the climate is semiarid, and the

Fig. 1. Location of study area and sampled stands, east-central Alaska (Yukon Flats and Tanana River), and city of Fairbanks, location of the UES/Fairbanks climate station.



highest evapotranspiration values in Alaska occur in the region (Patric and Black 1968).

Methods

We collected a single core from each of 101 white spruce trees from four stands along the Yukon River in 2002 and 34 trees from two stands along the Tanana River in 2004 and 2007 for a total of 135 cores (Fig. 1). All six stands were chosen as locations where mature white spruce trees in intact or eroding stands will become driftwood with additional bank erosion. All sites are within the range of the flood zone and all have been regularly flooded during spring river breakup or late summer high-water episodes. One stand (RFC) is at a slightly higher elevation in the Rampart Canyon section, and we sampled two localities (terrace and slope) there. Based upon the high interseries correlation, we combined the samples from terrace and slope (Table 1).

All trees that we cored were selected to represent the oldest–largest dominant trees on the site. Our coring attempt was abandoned for 21 trees because of wood decay. Consequently, our actual primary selection criteria for trees to sample became both age and soundness of the trunk. All trees were sampled at breast height as penetrating cores: from bark inward through the pith, continuing outward to bark.

Table 1. Sample tree and stand raw ring width (RRW) characteristics.

Site name	Site ID	First year	Last year	No. of years	No. of trees	Mean RRW (mm)	Mean interseries correlation ^a
Circle	Ci	1826	2001	175	19	1.15	0.609
Fort Yukon	FY	1830	2001	171	21	1.33	0.637
Beaver	BEA	1731	2001	270	26	0.94	0.736
Robert Fish Camps 1 and 2	RFC	1841	2001	160	35	1.02	0.748
Robert Fish Camp 1	RFC1	1841	2001	160	20	1.46	0.782
Robert Fish Camp 2	RFC2	1843	2001	158	15	1.12	0.723
Tanana River	04Ta	1835	2004	169	13	1.09	0.703
Caribou Crossing	CBX	1815	2006	192	21	1.137	0.780
All stands Yukon and Tanana rivers		1731	2006	185	135	1.175	0.537

^aMean interseries correlation calculated by COFECHA using the default setting of a 50-year window lagged by 25 years.

Raw ring widths (RRW) were measured using a Velmex sliding stage at 0.001 mm resolution. The crossdating and measurement verification of RRW was assisted by the identification of key pointer years present in the record such as 1969, 1954, 1924, which are especially small rings. Pointer years were somewhat variable from one site to the next or varied in strength or intensity. Measurement accuracy was verified by the crossdating program COFECHA (Grissino-Mayer et al. 1992), and very few dating errors were identified. Dating errors were corrected by examining and remeasuring the original specimen.

A number of trees in the stand 04Ta showed obvious evidence of growth release effect. In the affected trees, growth rate nearly doubled for one to three decades, followed by a return to characteristic previous growth rates. In every such case, growth rates returned to normal before the ring formed in 1912, the start of our climate record and analysis. For that stand, we cropped ring measurements from the series for 11 of 12 trees totaling 485 years (average 44 years per tree) during the period 1808 to 1911. The cropping procedure removed only ring width measurements of years before recorded climate data were available, so that it introduces the possibility of only a minor effect on the detrending equation form.

Measurements of RRW along both radii of the penetrating core were averaged to produce a tree mean value in a given year. The diameter size class distribution for the sample was generated as diameter inside bark (DIB), calculated as two times the sum of the mean annual radial growth measurements.

We examined RRW of the 135-tree floodplain sample to remove potential age-related trend and to construct a final mean index series for the entire sample (Cook et al. 1990). Previous results established that upland white spruce RRW series of mature trees in Interior Alaska contain little age-related trendedness from the beginning of the 20th century when climate records are first available (Barber et al. 2000). We detrended and normalized each tree's chronology with the program ARSTAN, using the dplR (Dendrochronology Program Library in the R environment, version 1.2.9; Bunn 2010). We generated a trial detrending of each of the 135 ring width chronologies using three alternative equation forms for each tree: modified negative exponential, smoothing spline, and horizontal mean. The modified negative exponential detrending option fits a classical nonlinear model of biological growth ($Y \sim a \times \exp(b \times 1:\text{length}(Y)) + K$)

with parameters based on Fritts (2001). The modified negative exponential fit was set to allow positive slope. The smoothing spline used a frequency response of 0.5 at a wavelength of 0.67 multiplied by the total number of years. When the nonlinear model cannot be fit, dplR defaults to standardizing the tree ring widths by a flat line of the mean values. We examined the growth trend of each individual tree series to determine evidence of age-related trend, particularly major, systematic decrease in ring width from the earliest one to three decades to a lower level throughout the remainder of the series. We then selected the equation form that generated a ring width index (RWI) chronology with the least evidence of age-related effects or which removed short-term distortions such as growth release events. Our detrending procedure resulted in a negative exponential detrending curve fit for five tree chronologies, smoothing spline for 16, and horizontal mean for 114.

We calculated EPS from the program ARSTAN (40-year window). The expressed population signal (EPS) is a statistic that represents the correlation between the series average and the "hypothetically perfect chronology" (Wigley et al. 1984). In effect, EPS represents the uncertainty in a tree-ring chronology when the number of cores is reduced, based upon the common variance of the sample, in particular the mean interseries correlation coefficient ($\bar{r}$) and the number of chronologies or time series (Briffa and Jones 1990). An EPS value of 0.85 has been suggested as a reasonable threshold to be reached by a given chronology to be considered a reliable, consistent signal (Wigley et al. 1984).

The analysis of the cores was based on correlation between climate data from University Experiment Station (UES 1906–1948) and Fairbanks Airport (1948–2001). The UES/Fairbanks record is a unique data set for Alaska and is of relatively high quality without major breaks (Wendler and Shulski 2009). It has been used in a number of successful dendrochronological reconstructions across a large portion of Interior Alaska (Juday et al. 2005). The Fairbanks temperature record is the longest in Interior Alaska and has been found to be highly correlated with the growth, isotopic content, and density of white spruce on upland sites across a wide longitudinal range of central Alaska (Barber et al. 2000).

Climate analysis

Boreal evergreen conifers with a determinate growth habit

are constrained by a number of physiological factors and mechanisms that produce autoregressive effects, most of which occur no more than two years prior to the year of ring formation (Juday 2009). We examined correlation between the monthly climate data and ring widths for a period of 36 months backward in time beginning with August in the year of ring formation. Most of the year-to-year variability in growth of upland white spruce in Alaska has been explained previously by climate data from these 36 months (Barber et al. 2000).

We used the program DendroClim 2002 to check for the potential occurrence of multiple collinearity in the relationship between monthly climate predictors and RWI. DendroClim generates a set of coefficients that represent the median of 1000 runs in a bootstrap procedure based on linear correlation, Jacobian rotations for Eigenvalues, singular value decomposition, and solutions of linear systems accompanied by principal component regression significant at the 95% level (Biondi and Waikul 2004).

We constructed a floodplain temperature index (FPTI) to combine mean monthly temperature (MMT) terms to maximize the Pearson's correlation coefficient with mean sample RWI for the fewest predictors. Because a single MMT in each of the three years examined clearly dominated the scores of all months in the respective years, we constructed FPTI using the mean temperatures of these three months. The correlation of FPTI with RWI was examined for both annual values and for a five-year running mean of temperature versus a five-year running mean of RWI. We then introduced into FPTI on a trial basis other monthly temperatures that had significant independent correlation scores with RWI to test for unique and additive predictive value. None of these months with lower independent correlation scores added more than 0.05 to the correlation score, an improvement suggesting minimal information. Thus, we consider that the maximum predictive power of temperature for RWI with the fewest terms can be achieved by defining FPTI as

$$[1] \quad \text{FPTI} = (\text{MMT}_{\text{maxcorrelYr}} + \text{MMT}_{\text{maxcorrelYr}-1} + \text{MMT}_{\text{maxcorrelYr}-2})/3$$

where MMT represents mean monthly temperature, maxcorrel is the highest Pearson correlation score, Yr is the current year of growth, Yr - 1 is the previous year of growth, and Yr - 2 is two years prior to the current year of growth.

To explore the role of precipitation in the growth of these trees, we examined the correlation of monthly total precipitation (MTP) with the residual of the temperature-based prediction of RWI using both direct Pearson correlation and DendroClim output. The residual of the temperature-based prediction (rt-bp) is simply the difference between the observed and fitted values derived from a simple linear regression model in which the dependent variable is RWI and the independent variable is FPTI. Both FPTI and RWI were normalized using the subtraction method (observation minus mean, divided by standard deviation). We selected all months in which MTP was correlated at the 95% level, positively or negatively, with rt-bp. The monthly precipitation values were combined into a supplemental precipitation index (SPI):

$$[2] \quad \text{SPI} = (\text{MTP}_1 + \text{MTP}_2 + \dots + \text{MTP}_n)$$

where MTP is the monthly total precipitation and n is the total of all months with significant correlation (95%) of MTP and rt-bp.

Finally, we created a climate favorability index (CFI) combining FPTI and SPI. Both FPTI and SPI are normalized parameters expressed as units of standard deviation and so can be mathematically combined. Because FPTI is negatively correlated with RWI and SPI is positively correlated with rt-bp, CFI is calculated by subtracting the negative term from the positive:

$$[3] \quad \text{CFI} = \text{SPI} - \text{FPTI}$$

Once the CFI was established, we generated the Pearson correlation of CFI with each tree's RWI chronology to generate population statistics, including the percentage of the sample with significant correlation scores at the 95% and 99% confidence levels. Finally, we performed an explicit test for age-related decline in climate sensitivity by calculating the Pearson correlation score of each tree's age to the Pearson score of CFI to RWI.

Results

Sample depth, age, and growth

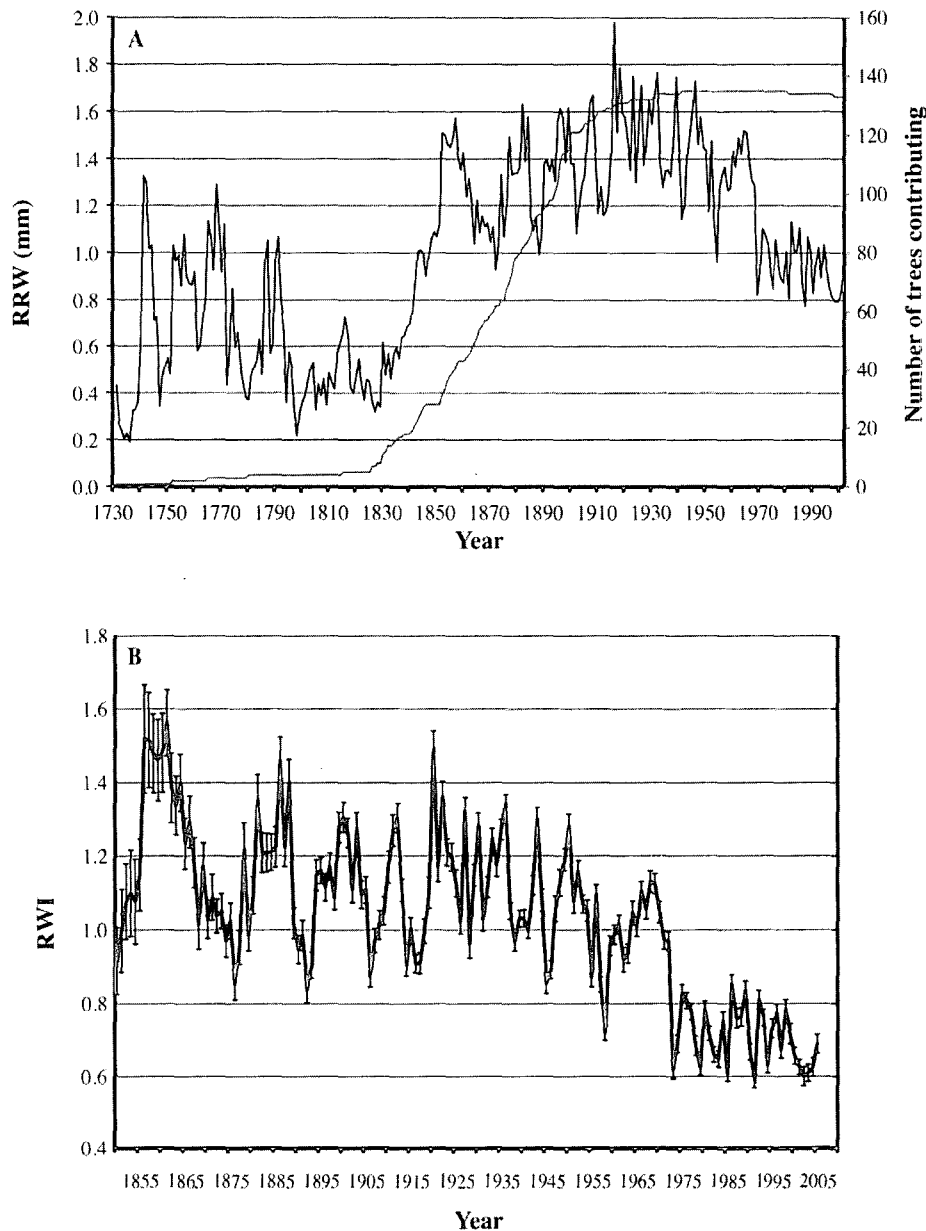
The great majority of the 135 trees in our sample have dates of origin in the 19th century. Based on earliest discernable ring (as contrasted with measurable rings), only 2% of trees have dates of origin in the 18th century and 4% in the 20th century. This age distribution minimizes the potential of age-dependent effects in climate-growth functions (Szeicz and MacDonald 1994). Diameter inside bark (DIB) size class distribution is essentially normal, with symmetry around the 30 to 35 cm class. Tree diameters in individual stands are also normally distributed. The relationship between DIB and age is not significant ($r^2 = 0.015$, $p = 0.152$). Sample depth varies only slightly (128 to 135 trees) between 1910, the date of uninterrupted temperature and precipitation records at Fairbanks, and the end of the chronology in 2001. The minimum EPS value from 1910 to 2001 is 0.969, indicating a reliable common signal in the sample through that time.

Mean RRW of the sample shows a distinct and sustained rise during the late 19th and early 20th centuries (Fig. 2A). Years of particularly high growth are 1916, 1939, and 1944–1946. The 25-year period of greatest growth in the sample occurred in the early to mid-20th century. Years of particularly low growth occurred in 1872, 1901, 1911, 1924, 1940–1941, 1954–1958, and 1969. Relative growth, as reflected by RWI, was also near or at a maximum in the early to mid-20th century (Fig. 2B). A sharp decrease in relative growth occurred in 1969, and it has remained low since (Fig. 2B). The last decades of the 20th century represent the lowest 25-year period of relative growth. Common growth signal across and within the sample population as indicated by mean interseries correlation — the average correlation of each series with a master chronology derived from all other series — is high (Table 1) and within the range considered useful for climate reconstruction (Grissino-Mayer 2001).

Temperature sensitivity

The set of months with significant DendroClim coefficients for temperature during the 36 months examined were

Fig. 2. (A) Annual ring increment and number of trees contributing to the chronology between 1731 and 2001. The thick line is raw ring width (RRW); the thin line is sample depth. (B) Ring width index (RWI) from 1846–2001 (minimum = 28 trees; maximum 135 trees) with ± 1 standard error (SE) bars.



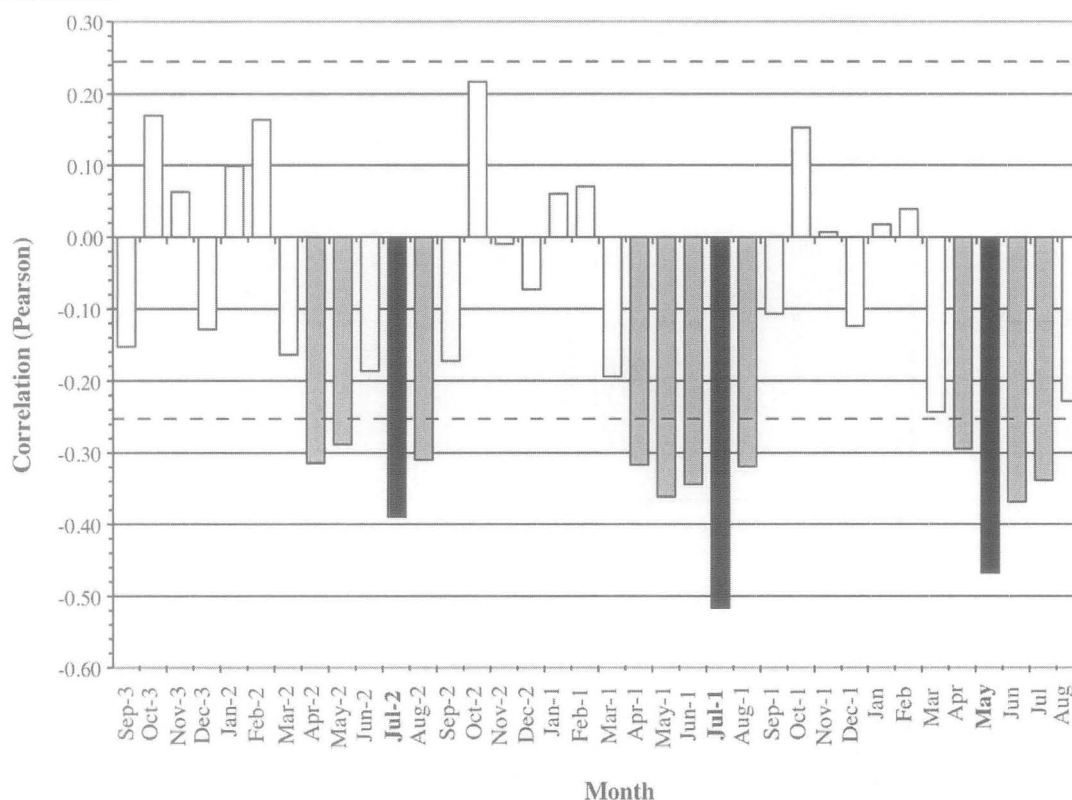
nearly identical (only one month different) to months with significant Pearson correlation scores (99% confidence level). The magnitude of differences (positive or negative) between the Pearson scores of the direct correlation of monthly climate variables versus RWI and DendroClim scores was minimal. The respective coefficients were highest in the same months of each year. As a result, either DendroClim or Pearson scores provided an equally reliable basis for constructing a floodplain temperature index (FPTI) to predict ring width of our floodplain white spruce population.

The set of months with significant correlation scores of mean monthly temperatures with the RWI chronology (Fig. 3) are clustered in (i) the warm season, or just before, in the year of ring formation (March through August), (ii) the year prior to ring formation (April through August), and

(iii) two years before ring formation (April–May and July–August). All significant monthly temperature correlations are negative. In each of the three years, a single monthly negative correlation achieves a score ≤ -0.39 and contains most of the predictive power during that year (Fig. 3).

The correlation of FPTI with RWI is -0.67 ($p < 0.001$). The smoothed values (five-year running mean) of both arrays is correlated at -0.82 ($p < 0.001$). The relationship between FPTI and RWI is dominated by a major trend of cool summers and high growth in the first half of the 20th century followed by a sustained period of low growth and warm summers that began in 1969 (Fig. 4). FPTI achieves year-to-year congruence with RWI in several periods, particularly the 1922–1927 and 1950–1969 sequences. During the early half of the 20th century, distinct short-term growth reductions as-

Fig. 3. Correlation of monthly temperature at UES/Fairbanks with mean ring width index (RWI; $n = 135$ trees; 1906–2001); broken lines indicate 99% significance level; black bars indicate the months used to create the floodplain temperature index (FPTI); grey bars indicate other significant months.



sociated with unfavorable (elevated) temperatures occurred in 1912–1913 and 1941–1942. Short-term growth spikes associated with favorable (low) predictive temperatures occurred in 1918, 1923, 1925, and 1926.

On an individual tree basis, RWI is significantly negatively correlated with FPTI in a large majority of trees: 85.2% at the 99% confidence level and 88.9% at the 95% confidence level. In only a few cases is RWI significantly positively correlated with FPTI: 3.0% of trees at both the 99% and 95% confidence levels. Periods of growth below FPTI occur more frequently since 1969, although a short period of growth in excess of FPTI is centered around 1982. However, the residuals of the prediction of RWI by FPTI are not randomly distributed, which suggests that another variable, common to the sample population, might add unique predictive power.

The role of precipitation

Direct Pearson correlations between RWI and monthly total precipitation are marginally significant (positive) for six months at the 99% confidence level and 12 months at the 95% confidence level. These direct correlations are identical or temporally similar to significant months in DendroClim scores. We added the six months of precipitation most highly correlated with RWI into a direct precipitation index, but we found that it was a considerably less effective predictor than FPTI.

We found that rt-bp was also significantly correlated with several MTP values (Fig. 5). As a way to explain the remaining variability in growth not predicted by FPTI alone, we combined MTP to produce the following SPI:

$$\begin{aligned}
 [4] \quad \text{SPI} = & (\text{MTP}_{\text{Apr}0} + \text{MTP}_{\text{Mar}0} + \text{MTP}_{\text{Feb}0} \\
 & + \text{MTP}_{\text{Aug}-1} + \text{MTP}_{\text{Jul}-1} + \text{MTP}_{\text{Mar}-1} + \text{MTP}_{\text{Feb}-1} \\
 & + \text{MTP}_{\text{Aug}-2} + \text{MTP}_{\text{Mar}-2} + \text{MTP}_{\text{Feb}-2} + \text{MTP}_{\text{Jan}-2}) \\
 & - (\text{MTP}_{\text{Dec}-3} + \text{MTP}_{\text{Nov}-3})
 \end{aligned}$$

The linear regression of SPI with rt-bp is highly significant across the range of values and explains nearly half of the remaining variability of RWI (Fig. 6). Overgrowth, or higher values of growth than modeled by FPTI, is associated with high values of SPI, and undergrowth, or lower values of growth than modeled by FPTI, is associated with low values of SPI. A disproportionate share of the error in the regression of SPI with rt-bp is due to outlier values in 1926 and 1991.

Climate favorability index

As defined in the Methods section, the climate favorability index (CFI) represents a simple mathematical combination of FPTI and SPI into a new variable that is positively correlated with RWI (Fig. 7A). CFI correlates with RWI at 0.747 (0.878 for five-year running mean), an improvement of 0.077 over the FPTI. In addition, the residuals of CFI-based prediction of RWI do not display trendedness, suggesting that precipitation does play an important supplemental role in determining growth of this population and that the remaining departures of growth not explained by the selected temperature and precipitation terms are most likely random.

The temporal pattern of CFI reflects the same principal features of FPTI, including sustained high favorability during

Fig. 4. Floodplain temperature index (FPTI) and ring width index (RWI) by year (1906–2001); the thick line represents RWI; the broken line represents FPTI ($r = -0.67$).

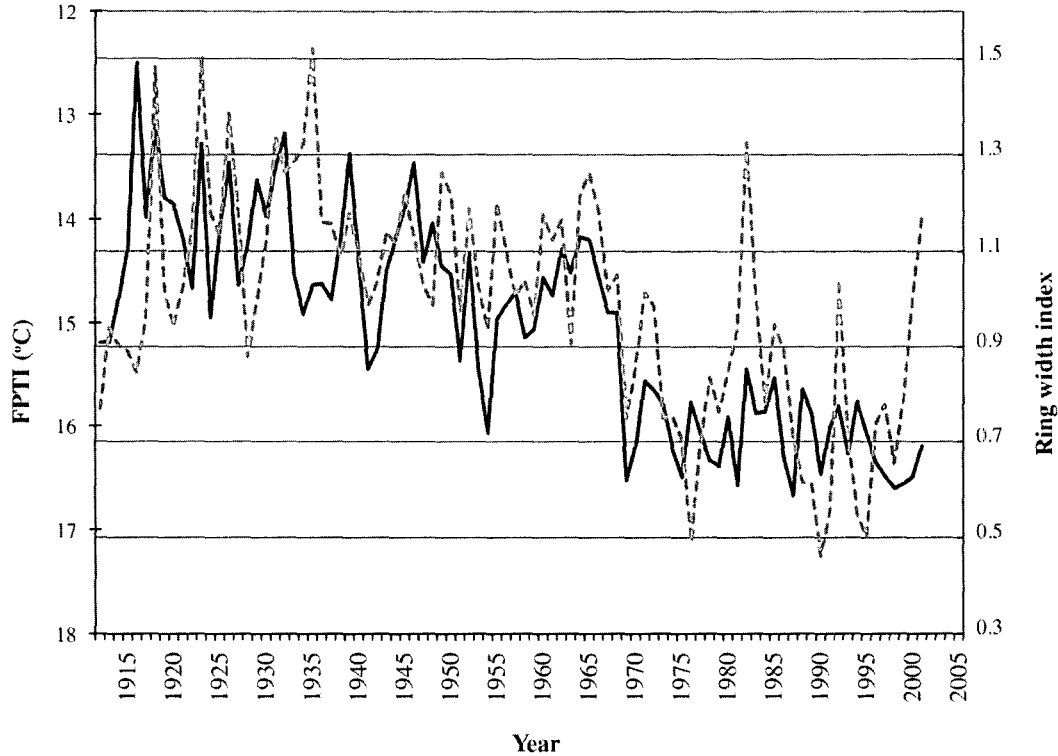


Fig. 5. Correlation of monthly precipitation at Fairbanks with residual of temperature-based prediction (rt-bp) of growth; broken lines indicate 95% significance level: (A) late winter – early spring; (B) late summer; (C) early winter.

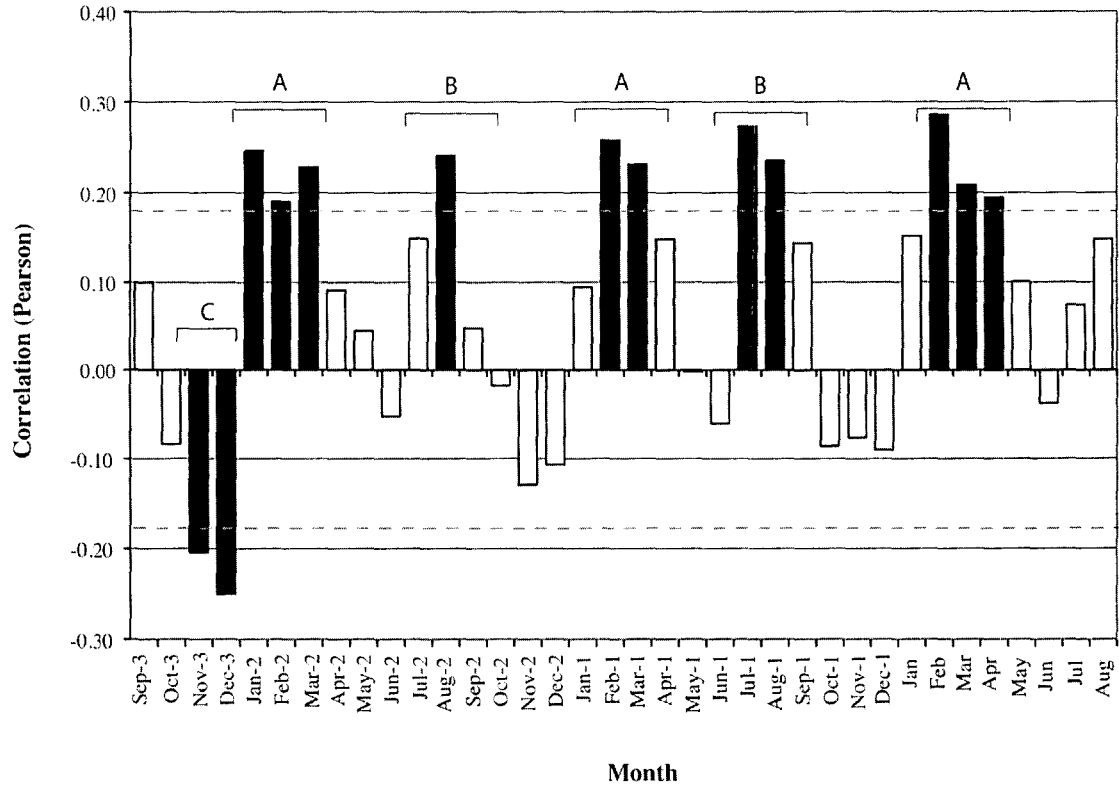
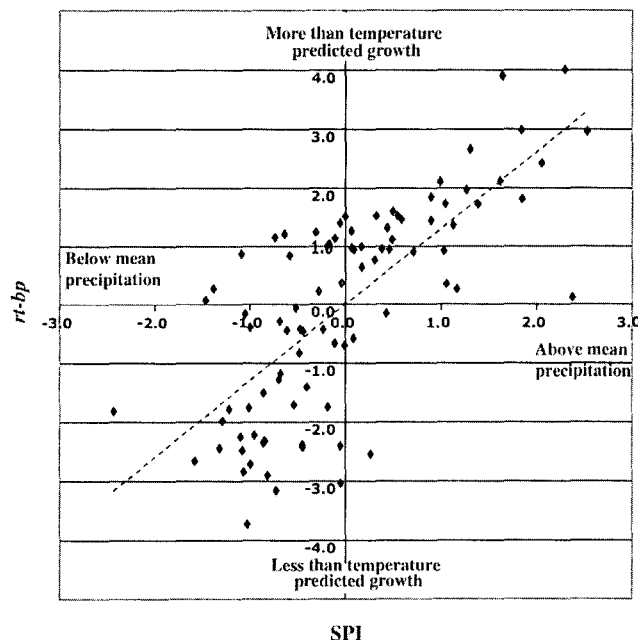


Fig. 6. Precipitation influence on residual of temperature-based prediction (rt-bp) of growth, expressed as scatterplot of rt-bp vs. supplemental precipitation index (SPI). Both axes represent units of standard deviation; $r^2 = 0.53$; $y = 1.3023 \times 0.0104$ (data plotted without largest negative and positive outliers — 1991, 1926).



the 20th century until 1969, sustained low climate favorability since then, and good year-to-year congruence except for a few periods of two to three years (Fig. 7A). Until 1969, RWI is congruent with CFI with a brief period of underprediction of growth centered at 1928–1929. Since 1970, CFI is low and includes overprediction of growth at 1982 and 1992 (Fig. 7A). The five-year running mean smoothing resolves most of the remaining variability into a pattern that includes a quasi-decadal cycling and an overall decline in growth and climate suitability to sustained low values since 1970 (Fig. 7B).

A strong majority of individual trees have significant Pearson correlation scores of RWI with CFI, 85.9% at the 99% confidence level and 91.1% at the 95% confidence level. Over half of all individual trees are correlated with CFI at scores 0.50 and higher. Only 2.2% (99% confidence level) of trees were negatively correlated with CFI.

Discussion

The apparently fundamental and consistent climate predictive relationships presented in this paper can be related to the ecology of white spruce in Interior Alaska. The absolute level of the growth of white spruce within a given climatic zone in central Alaska is largely determined by soil and site conditions (Van Cleve et al. 1996; Van Cleve and Yarie 1986). However, on upland sites across a broad area of east-central Interior Alaska, the year-to-year variation in radial growth of white spruce is controlled by temperature-induced drought stress (Barber et al. 2000). Negative growth response to summer temperatures is also present among a substantial portion (>40%) of trees at treeline (Wilmking et al. 2004). Radial growth of our floodplain populations of older white

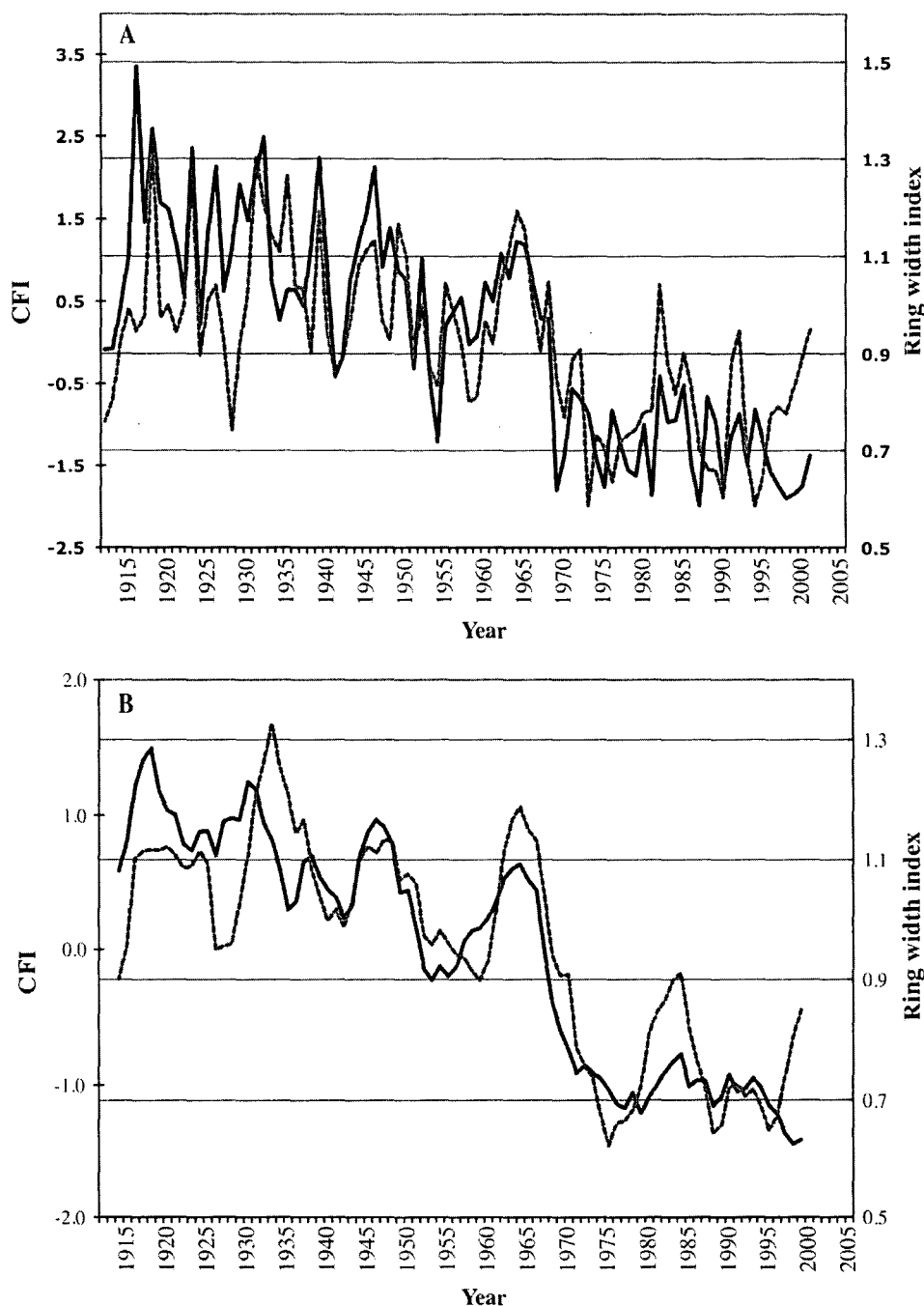
spruce follows a pattern of negative sensitivity to temperature largely similar to that of upland and treeline populations. All three white spruce populations (upland, treeline, and here floodplain also) share the following features of temperature sensitivity: (i) maximum correlation of radial growth is with $MMT_{JulYr-1}$; (ii) the strongest monthly correlation is < -0.5 ; (iii) a significant correlation exists between MMT and RWI for the year of ring formation and two or more prior summers; and (iv) in the year of ring formation, the greatest amount of unique explanatory power is in a month prior to July (May on floodplain and productive upland sites and March or April at treeline sites).

Even though CFI has been mathematically set to have a positive relationship to RWI, white spruce in our sample are nearly all “negative responders” to warmth and dryness in the sense used in Wilmking et al. (2004). It is true that positive, rather than negative, correlations of white spruce radial growth to temperature can be found among trees in the Alaska landscape, particularly where summer temperatures are coolest and precipitation is most abundant (e.g., Beck et al. 2011). However, the number of white spruce that have been demonstrated to contain the negative response to temperature now includes, e.g., all of the 269 sampled trees on low-elevation uplands in eastern and central Interior Alaska (Barber et al. 2000), 461 negative responders at treeline in the Brooks Range and Alaska Range mountains (Wilmking et al. 2004), 83 of 118 trees sampled on the Kuskokwim River floodplain (Winslow 2008), and now 123 of the 135 trees sampled in the current study. The consistency of a broadly similar negative response of white spruce growth to temperature across these large sampling areas, in a number of habitats and sites and for the 100+ years of climate record available, strongly supports the view that a negative temperature response is one of, if not the most, typical forms of climate control of white spruce in Interior Alaska, at least at temperatures typical of the last century or so.

We evaluated the climate sensitivity on an individual-tree basis across our 135-tree sample to determine how consistent the climatic signal is within the population. Removing from the sample the 12 trees that are not significantly ($p < 0.05$) positively correlated with CFI only changes the overall Pearson correlation score with mean RWI by 0.005. The reason that individual trees that have poor correlation scores with CFI do not degrade the correlation with the sample mean is that their departures from CFI-predicted growth are random across time within individual-tree chronologies and random between trees. As a result, in terms of their effect on the sample mean, the departures of the trees that are not significantly positively correlated cancel each other out. We currently have no basis to conclude that there is an opposite “positive responder” or alternate signal present in the growth of the population that we sampled. This differs from findings of positive temperature responses in some treeline white spruce populations (Wilmking et al. 2004) and low-elevation, coastward white spruce populations on the Kuskokwim River (Winslow 2008).

The temperature responsiveness of our sample is stable during the period of instrument-based weather records (1912+). Specifically, there is little evidence of the “divergence” phenomenon (Wilmking et al. 2005) in our chronology in which previously common growth trends within

Fig. 7. (A) Climate favorability index (CFI) and ring width index (RWI) by year ($r = 0.747$); (B) five-year running mean of CFI and RWI ($r = 0.878$). In both, the thick line is RWI, and the dotted line is CFI.



samples of northern conifers diverge among members of the population. A sliding 30-year correlation of RWI to CFI is significant ($p < 0.05$) for all but the three most recent calculation years. Divergence arises when growth of some trees in a sample remains well correlated to calibrating temperatures while in others it either decreases in temperature sensitivity markedly, or even changes from positive to negative or vice versa. The presence of divergence makes samples that contain it either suspect or not suitable for reconstructing past temperatures from calibrating relationships during the period of recorded climate data. The stabil-

ity of climate predictive relationships in our sample represents minimal divergence in our sample, suggesting that similar floodplain trees may be better candidates for ring width based climate reconstruction than high-elevation trees that traditionally have been used.

As a further test of the validity and strength of CFI, which includes a precipitation component in addition to temperature, we compared each tree's correlation score of RWI with CFI to the same tree's correlation of RWI with a chronology of $\delta^{13}\text{C}$ values. The $\delta^{13}\text{C}$ chronology was developed from a population of negative-responding upland white spruce in

Bonanza Creek LTER (Barber et al. 2002). Values of $\delta^{13}\text{C}$ are not directly affected by ring width. The carbon-isotope ratio ($\delta^{13}\text{C}$) provides information on CO_2 uptake and water vapour loss during photosynthesis, and so, under limiting conditions, registers drought stress (Barber et al. 2000). As a result, this comparison constitutes a broad independent test of the presence of a common moisture stress signal. The high degree of agreement of these independent sets of correlation scores ($R^2 = 0.80$) confirms that a common climate signal related to moisture stress and temperature is widespread in upland and floodplain white spruce populations in central Interior Alaska.

Considering especially the range of nonclimatic factors that could limit tree growth in these populations, our results suggests that in similar populations, such nonclimatic influences on radial growth variability are substantially lower than climatic controls. This finding is applicable to intact, healthy, canopy-dominant trees. It likely does not apply to trees that have experienced variable levels of canopy suppression during their life such as trees that emerged from canopy suppression or trees that experienced changes in secular trend of growth from events such as mechanical trauma.

The relationship of tree age with climate sensitivity, defined as the correlation score between CFI and RWI, is negative and significant ($r = -0.29$, $p > 0.01$), suggesting that there is a weak age-related tendency toward decreased climate sensitivity similar to results demonstrated in the western Northwest Territories, Canada (Szeicz and MacDonald 1994). The mean correlation of RWI with CFI is significant (negative) for the oldest half of the population but not significant for the youngest half. Even allowing for this relationship, older trees are still well distributed across the upper range of CFI correlation scores. Senescence of trees is not necessarily the only explanation for weakened climate sensitivity with increasing age. Older trees have been exposed to stochastic processes such as wind or snow breakage of stems or canopy tops for a longer time than younger trees. Stem and canopy breakage (and any growth-release effect following it) would necessarily degrade climate-based predictions of ring width. The greater cumulative exposure to such processes with increasing tree age could easily produce a weak trend of reduced climate sensitivity, even among trees that have otherwise retained equivalent abilities to physiologically respond to climate controls.

Another important finding in our study is the supplemental role of precipitation in influencing the growth of this population of floodplain trees. Given the high degree of common signal, a similar effect potentially could explain some of the residual non-temperature-related variability in upland trees as well. Only a few studies in boreal North America have established direct correlations of precipitation with radial growth at significant levels (e.g., black spruce; Brooks et al. 1998). Our direct correlation with precipitation was only marginally significant by itself, and a much less effective predictor than FPTI. This is not surprising as temperature and precipitation are correlated in Interior Alaska (Mock et al. 1998). However, our results show that although precipitation does not play an important direct role in controlling growth, it does have a significant and indirect role in influencing growth. We believe that this approach holds promise for other species

and sites where previous interpretations of climate sensitivity have been based solely on temperature.

Boreal conifers in northern Eurasia begin growth at the time of the introduction of snowmelt into the soil until that source of soil moisture is depleted and the trees first encounter moisture stress of sufficient severity to restrict physiological activity (Vaganov et al. 1999). As "determinate-growth" species, evergreen conifers, including white spruce, cease height elongation and, in their radial growth, switch from the production of large earlywood cells to the production of small latewood cells when they first encounter their threshold level of moisture stress (Grossnickle 2000). In most evergreen conifer species, the seasonal switch in height and lateral growth appears to be one-way and cannot be restarted (Vaganov et al. 2006). Summer temperatures that are consistently cool from the start of the growing season deplete the initial moisture supply gradually so that the active growth season is extended, allowing more annual growth. High temperatures early in the growth season cause the stress threshold to be encountered more quickly and less annual growth is accomplished (e.g., Bigras 2000). These established temperature-driven physiological controls match our findings. In addition, temperatures or precipitation in the calendar year of ring formation that occur after the determinate-growth switch happens have minimal influence on that year's growth and primarily will exert influence on the following year's growth. This contributes to the observed one-year time lag in maximum correlation of climate predictive factors with growth.

The SPI that we developed is made up of a set of summer and winter months that would, in fact, deliver water to the tree at the most advantageous times for its physiological benefit to counteract these limitations. Precipitation values of late winter months are the principal terms in SPI (Fig. 5). Snow accumulation in these months represents the initial moisture supply for the growing season. The second major component of SPI includes precipitation of mid- and late-summer months (Fig. 5). This represents the other critical time for delivery of water to avoid the one-way growth switch as moisture stress is increasing. Direct experimental evidence is now available to confirm that summer precipitation is a limiting factor for floodplain white spruce within the sampled area. At Bonanza Creek LTER, a long-term (1989–2005) exclusion of summer precipitation (through fall) resulted in a significant reduction of white spruce growth compared with controls on a Tanana River floodplain white spruce site (Yarie 2008). The final component of SPI is a negative influence of November and December, which we have determined to be almost entirely due to strong effects of the highest precipitation totals in four particular years. We interpret that pattern as the effect of stem breakage due to heavy snow, similar to results seen in *Abies maresii* forests in Japan (Kajimoto et al. 2002).

An 18-year experimental study of moisture limitation at the Bonanza Creek LTER began with the hypothesis that soil moisture limitation controls forest growth, but that augmentation of soil water supply from high river stages might be a unique moisture source on the Tanana River floodplain (McGuire et al. 2010). We cannot rule out some additional contribution of an improved river discharge record in explaining white spruce growth. However, there are good reasons to

believe that this effect is genuinely limited. Floodplain sites where mature white spruce trees occur often contain a substantial fraction of sand and are well drained. At the same time, white spruce roots generally are shallow and so are susceptible to early and rapid drying. If an influence of water stage on growth occurred, it would more likely happen through extreme events. By definition, the outlier years in the regression of CFI with RWI are not explained by the climatic predictive factors that we used. Instead, shorter term meteorological data such as local extreme winter precipitation, flood events, and tree-damaging insect outbreaks may account for these discrepancies.

Our interpretation of the environmental controls and recent trends in white spruce growth is further supported by comprehensive classification of trends in gross primary productivity across Alaska as represented by NDVI values obtained from the NASA GIMMS data set (Beck et al. 2011). Tree growth as represented by an extensive set of black and white spruce ring width chronologies, including the 135 trees analyzed in this study, demonstrates a high degree of spatial and temporal coherence with NDVI values (Beck et al. 2011). Finally, the MODIS satellite NDVI product at a finer (1 km²) pixel resolution became available starting in 2000. The area with the strongest MODIS negative NDVI trends (browning) in Alaska from 2000–2009 is centered in the Yukon Flats. This indicates that climate-related stress in vegetation has not been relieved since our cutoff date of 2001 and even may have intensified (Parent and Verbyla 2010).

Three factors in our study point to the strong potential for improved and extended archeological dating and climate reconstruction. First, our sample is representative of large trees that have fallen into the major river system in Alaska as the result of bank erosion and, through river and coastal transport, have been incorporated into beach deposits from which desirable specimens were selected and preserved in human structures or reworked material. Second, the widespread and consistent negative growth response to warmth and drought in our sampled tree population, which occupies a substantial portion of the driftwood source area, suggests that the material should be datable with sufficient overlap in time and that there is a reasonable probability that preserved archeological logs or natural deposits can be located that carry a tree ring signal useful for climate reconstruction. Third, the consistency and stability of the climate–growth relationship through time suggests that this population of trees or logs may be less affected by uncertainties in climate reconstruction introduced by the divergence phenomenon than some populations that have been used in Alaska to date (Wilmking et al. 2005).

In the mid-1950s, one of the early tree ring researchers in North America, J.-Louis Giddings, observed “The climatic meaning of certain local belts or blocks of strong cross-dating has not yet been solved. The most striking such area is that of the Yukon Flats region of the middle Yukon River...” (Giddings 1954). We believe that we have provided an explanation of the climatic meaning he sought.

Conclusions

1. We have developed a white spruce ring width chronology that extends from 1731 to 2001, with a reliable signal for the period of climate data from 1912–2001. Our sample

of 135 trees is representative of older and mature dominant trees of the floodplain environment of the mid-Yukon and Tanana rivers that will become driftwood in future years.

2. The climatic signal that we have established contains a strong negative relationship between summer temperature and tree growth, centered on May in the year of ring formation and July in the two years preceding. A significant relationship between our floodplain temperature index (FPTI) and ring width index (RWI) is present not only in the sample mean, but also in the great majority of individual trees and in the mean of all stands. FPTI explains over half of the year-to-year variability in the growth of our sample during the 90 years of climate data analyzed.
3. By comparing monthly precipitation data against the residual of temperature-based prediction (rt-bp), our analysis shows that precipitation plays an important supplemental role in controlling growth of floodplain white spruce, consistent with recent experimental results (Yarie 2008). We combined FPTI with a supplemental precipitation index (SPI) into an overall climatic favorability index (CFI), which explains the majority of the year-to-year variability in the growth of white spruce so that remaining variability is likely to be due to non-climatic or extreme meteorological events.
4. The climatic responsiveness of our sample does not increase or decrease during the period of instrument-based weather records (1912+). There is no evidence of a period of divergence between the tree growth and temperature predictor, unlike results from treeline populations (Wilmking et al. 2005). This suggests that similar floodplain trees that do not exhibit divergence may be better candidates for ring width based climate reconstruction than high-elevation trees traditionally sampled.
5. The period of reliable common signal in the sample includes a prolonged period of optimum climate and high growth in the first half of the 20th century and a prolonged period of low growth starting in 1969 and continuing to the present.
6. Tree ring growth trends and climate sensitivity identified in this study are highly consistent with satellite-derived NDVI growth trends for the last two decades of the 20th century in which the two data sets overlap (Beck et al. 2011).
7. Finally, the strong climatic signal demonstrated in this renewed analysis of Yukon River floodplain white spruce provides a solid basis for the task of building longer chronologies based on archeological wood and other undated specimens that were transported as driftwood from interior rivers to the coasts of Alaska.

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