Spatial coherence and change of opposite white spruce temperature sensitivities on floodplains in Alaska confirms early-stage boreal biome shift

Glenn P. Juday  a,⇑, Claire Alix  b,1, Thomas A. Grant III  a,c

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Abstract

Since the mid 1970s, Interior Alaska white spruce trees experienced markedly lower growth than during the 19th and early 20th centuries. This observation raises the question of forest persistence on certain sites of lowland central and eastern Alaska. We analyzed white spruce growth across a 36-site network (540 trees) on three major river floodplains in boreal Alaska along a longitudinal gradient from eastern Interior to the southwest tree limit to test for the presence of tree growth patterns and climate sensitivities. Chronologies are compared for temperature sensitivity at both stand and individual tree levels, using data from Bethel, McGrath, and Fairbanks NWS stations during the common period of 1952–2001. Cross-dated stand-level ring width chronologies indicate three regions of common signal in tree growth across the gradient. Temperature sensitivity of stand- and individual-tree chronologies is spatially coherent. Most downriver chronologies correlate positively with spring mean monthly temperatures (MMT) at Bethel, mid- and upriver chronologies correlate negatively with MMT of May and previous year July at either McGrath or Fairbanks, and an area in between is a mixed population of positive and negative responders. In downriver positive responders, recent increases from suboptimal cool temperatures accelerated tree growth, while in mid- and upriver negative responders, recent increases from optimal or above-optimal temperatures decreased growth. Fairbanks negative responders are also negatively correlated with a 200-yr index of recorded and reconstructed Fairbanks summer temperatures, and recent sustained record high summer temperatures are associated with the lowest relative growth. Until the 1940s, absolute growth rate of negative responders was greater than positive responders, but from the 1970s the positive responders grew more. These results explain why northern ring width samples can display opposite temperature sensitivity and contribute to understanding recent “divergence” or loss of temperature sensitivity in a changing climate. We find that July MMT and annual precipitation at Fairbanks are now outside the limits that previously characterized the North American distribution of white spruce, and are near the reported physiological limits of the species. Our results of the spatial and temporal change of white spruce temperature sensitivity provide strong empirical evidence of previously proposed early stage biome shift in boreal Alaska due to clear climatic causes. Already, western Alaska, previously extending to tree limit, has become the optimum climate region for the species. With modest additional warming widespread tree death will be unavoidable on warmer lowland interior sites, where persistence of white spruce is unlikely.

1. Introduction

Boreal forest is susceptible to distinct thresholds or tipping points as well as a potentially rapid transition to alternative stable states, specifically in the transition from tundra/shrub to a colder biome or from steppe to a warmer and drier biome (Scheffer et al., 2012). Replacement of the boreal forest where it occurs today with woodland, shrub, or grassland would produce effects of considerable significance for albedo, carbon uptake and sequestration (Bonan, 2008), hydrologic regulation (Callaghan et al., 2011), wildlife habitat (Usher et al., 2005), and human use (Juday et al., 2005). Similarly, treeline advance into tundra has profound implications

⇑ Corresponding author. Tel.: +1 907 474 6717; fax: +1 907 474 7439.
E-mail address: gpjuday@alaska.edu (G.P. Juday).
1 These authors contributed equally to this manuscript.
for a range of ecosystem processes (Callaghan et al., 2005; Wilmking et al., 2006).

Negative sensitivity of white spruce (Picea glauca Moench Voss; hereafter PIGL) radial growth to summer temperatures is widely reported in a number of Interior Alaska and northwest Canada regions (Barber et al., 2000; Juday et al., 2003; Griesbauer and Green, 2012). This negative growth sensitivity suggests that during recent decades of elevated temperatures, carbon uptake capacity was reduced across a substantial part of the western North American boreal region. If additional temperature increases projected in some scenarios (Kirtman et al., 2013) were to occur, further growth reductions are likely (Juday et al., 2005), raising questions about the persistence of the species in much of the region where it occurs today (Ohse et al., 2009). Site types and subregions identified as supporting populations of negative responder PIGL populations include productive upland sites of eastern and central Alaska (Barber et al., 2000), treeline environments of the Brooks Range and Alaska Range (Wilmking et al., 2004), and floodplain sites in the Yukon Flats and mid Tanana River (Juday and Alix, 2012).

However, positive growth responses of PIGL to temperature are also known from northwestern North American high latitude and altitude sites, often in complex patterns mixed with negative responding populations. At Brooks Range treeline, a general trend in PIGL of decreasing proportion of negative temperature response and increasing proportion of positive response can be demonstrated from east to west with greater proximity to the Bering Sea coast (Wilmking and Juday, 2005). The question remains as to whether these limited observations (n = 7 stands) of decreasing negative responders from the eastern Interior toward the coastal and western portions of Alaska represents a true gradient, or is based on local site variability and the peculiarities of the types of forest sampled for dendrochronological analysis (e.g. treeline, upland, or floodplain forests).

In some locations, temperature sensitivity of northern PIGL growth has varied through time. Mountain treeline sites in east central Alaska and in the Alaska Range support both positive and negative responding PIGL populations, but a trend toward increasing negativity of growth to temperature began in the mid 20th century (Lloyd and Fastie, 2002). A similar pattern occurs in adjacent Yukon Territory (Griesbauer and Green, 2012). Across both the Alaska Range and Brooks Range, specific temperature thresholds are associated with a change from non-responsiveness to responsiveness of PIGL growth to temperature, both positive and negative. Since about 1950, these temperature thresholds have been more consistently exceeded, explaining why in these treeline environments temperature sensitivity has not been stable through time (Wilmking et al., 2004).

Overall growth trends of white and black spruce ring width chronologies across Alaska are broadly similar to trends in Normalized Difference Vegetation Index (NDVI) (Beck et al., 2011). However, only about 30 years of NDVI data is available. Direct comparisons of radial tree growth and temperature data over longer time periods and across a large spatial scale with control of site-to-site variability are needed to establish whether (1) a true spatial gradient in climate control of spruce growth occurs in the western North American boreal forest, and (2) whether temperature sensitivity is systematically shifting over time.

The boreal region of Alaska is characterized by major east to west gradients of temperature and precipitation, largely related to the transition from a strongly continental climate in the eastern Interior to a strong maritime influence at the limit of tree distributions near coastal regions in the west (Simpson et al., 2002). Along the major rivers in the interior, this transition occurs in a smooth uninterrupted gradient, in contrast to the northern Alaska treeline with its complex mosaic of site that differ in aspect, elevation, geology, and soils (Wilmking and Juday, 2005). Mature Interior floodplain forests have developed on the same soil type, from the same processes of primary floodplain succession (Viereck et al., 1993; Brabet et al., 2000; Magoun and Dean, 2000), occupy the same relatively narrow elevation band (maximum elevation = 305 masl at the Alaska/Canada border on the Yukon River to near sea level in the west), and do not vary in slope or aspect. As a result, a continuous river floodplain longitudinal transect of tree growth offers an ideal opportunity to test for a coherent pattern of temperature sensitivity. The purpose of this paper is to examine PIGL temperature sensitivity from the continental climate region of eastern Interior Alaska to the longitudinal treeline of maritime southwestern Alaska and determine whether temperature-related growth responses consistent with early-stage biome shift are underway on a common site surface.

1.1. Study area

The Yukon River basin occupies 832,700 km² across central Alaska and south-central Yukon Territory in Canada. The Tanana River within the Yukon River basin is a 980 km long tributary that enters the Yukon River a few kilometers above the Village of Tanana near the center of Alaska. The Kuskokwim river basin, in southwestern Alaska, is the second most prominent river basin of the state and covers an area of 124,319 km² (Fig. 1). All three rivers flow west or southwest, crossing Interior Alaska and emptying into the Bering Sea. Along these glacial meltwater rivers, a well-described process of forest succession culminates in the development of mature and old growth PIGL forests on well-drained high terraces (Van Cleve et al., 1996; Chapin III et al., 2006).

Three well-spaced National Weather Service (NWS) First Order stations – Fairbanks, McGrath, and Bethel – are located across the study area (Fig. 1). Annual precipitation is low in the interior of Alaska, and increases westward toward the downriver lower Yukon and Kuskokwim locations (Table 1). Mean summer and July temperatures follow the opposite pattern, with highest values in the Interior, and a gradient of cooler conditions toward the west (Simpson et al., 2005).

PIGL on floodplains sustain higher growth rates than on upland sites (McGuire et al., 2010), and on floodplains of central Alaska and the Yukon Flats, PIGL growth is mostly sensitive to high temperature limitation (Juday and Alix, 2012) and lack of summer precipitation (Yarie, 2008). Growth of mature PIGL on high floodplain terraces has been shown to benefit both from ground water proximity and precipitation. Extreme events such as floods that maintain high water during the growing season may impart distinctive patterns in annual ring width chronologies of boreal trees (Boucher et al., 2011).

Most older PIGL stands in the floodplain are assumed to have originated from primary succession following flooding disturbance. However, other disturbance factors also operate in floodplain PIGL stands. Fires are known to initiate succession in Alaska floodplain forests (Mann et al., 1995) but fire on floodplains is neither frequent nor extensive. Flooding also interacts with insect dynamics as a disturbance agent. Historically, PIGL on large river floodplains have been the focus of attacks of the northern spruce engraver beetle (Ips perturbaus (Eichhoff)), where a steady supply of suitable host trees weakened or injured by bank erosion are sustained (FS-R10-FHP, 2012, p. 10).

Starting in the late 19th century, the Yukon and Kuskokwim Rivers became major commercial travel routes, and riverbank trees were actively harvested and stacked by the river to be used as fuel for steam boilers on riverboats until the mid 20th century (Webb, 1990; Morse, 2003; Wurtz et al., 2006). Although this early history of wood harvesting along the major rivers of Alaska had a profound local impact, many of those harvested stands have eroded into the...
river, and we are confident that the stands we sampled are free of direct effects of tree harvest by humans.

2. Materials and methods

2.1. Sampling methods

We collected 540 penetrating cores or disks from floodplain PIGL trees at 36 distinct sites on high floodplains or terraces along the Yukon, Tanana and Kuskokwim Rivers (Table 2, Fig. 1). The sampled stands are irregularly spaced an average of 31.2 km apart along the Tanana, 60.4 km on the Yukon and 40.3 km on the Kuskokwim River. Samples were collected during summers of 2002, 2007 through 2010, and 2012 from the largest mature, dominant trees at each site, at or near breast height (137 cm). The smallest site sample included 5 trees and the largest 35 trees, with an average of 15 trees per stand (Table 2). The dataset includes six stands from the Yukon Flats and Tanana River analyzed in Juday and Alix (2012). All stands developed from flood-initiated primary ecological succession. As a result, our transect samples are influenced only minimally by site-to-site environmental differences other than climate and climatically related extreme events such as floods, mechanical damage, or insect outbreaks.

Radial growth was measured using a Velmex linear encoder and a laser measurement device with .001 mm resolution, producing raw ring width (RRW) series. All samples from a site were cross-dated using the program COFECHA (Grissino-Mayer et al., 1992). The few cross-dating problems were addressed through visual inspection of the sample, occasional re-measurement, and subsequent re-analysis using COFECHA until each site met quality control standards. The multiple radii measurements of individual year RRW were averaged to produce a tree mean RRW for a given year, which was used as the basis for subsequent analysis.

![Fig. 1. Map of Alaska with major rivers, forested area, sampled stands (n = 36), and the Fairbanks, McGrath, and Bethel First Order Weather Stations. Stands are color coded by predominant temperature response type (blue = positive, yellow = mixed and red = negative).](image-url)
2.2. Detrending

Tree-mean RW values were detrended in R using the dplR package (Bunn, 2008) to standardize tree ring widths and remove geometric bias and age related decline in growth. Each tree-mean RW chronology was detrended using three alternative curve form fits – horizontal mean, modified negative exponential, and cubic spline. Detrending in R followed default values for the cubic spline (frequency response of 0.5 at a wavelength of 0.67 multiplied by spline. Detrending in R followed default values for the cubic spline. The carbon-isotope ratio (\( \delta^{13}C \)) provides information on CO\(_2\) uptake and water vapor loss during photosynthesis (Barber et al., 2000). As a result, the correlation of \( \delta^{13}C \) to the three alternative RWI chronologies was significant (alpha = 0.05) either positively or negatively. When multiple detrending options were significantly correlated, we selected the option with the strongest correlation. When none of the three alternative RWI chronologies were significantly correlated, we selected the option with the strongest correlation, which was developed from a population of negative-responding upland PIGL in Bonanza Creek LTER (Barber et al., 2000) using a Pearson product-moment correlation. When none of the three alternative RWI chronologies were significantly correlated, we selected the option with the strongest correlation. When none of the three alternative RWI chronologies were significantly correlated, we selected the option with the strongest correlation, which was developed from a population of negative-responding upland PIGL in Bonanza Creek LTER (Barber et al., 2000) using a Pearson product-moment correlation. When none of the three alternative RWI chronologies were significantly correlated, we selected the option with the strongest correlation, which was developed from a population of negative-responding upland PIGL in Bonanza Creek LTER (Barber et al., 2000) using a Pearson product-moment correlation. When none of the three alternative RWI chronologies were significantly correlated, we selected the option with the strongest correlation, which was developed from a population of negative-responding upland PIGL in Bonanza Creek LTER (Barber et al., 2000) using a Pearson product-moment correlation. When none of the three alternative RWI chronologies were significantly correlated, we selected the option with the strongest correlation, which was developed from a population of negative-responding upland PIGL in Bonanza Creek LTER (Barber et al., 2000) using a Pearson product-moment correlation.
2.4. Climate sensitivity analysis

We analyzed both stand level and individual tree RWI (hereafter SL-RWI and IT-RWI respectively) chronologies to address the question of the type (positive or negative) and coherence of temperature control on the growth of the sampled PIGL trees across the longitudinal gradient. We compared the ST-RWI and IT-RWI chronologies to data from the three NWS First Order stations, and the master δ13C chronology of reconstructed summer temperatures from Bonanza Creek LTER (Barber et al., 2000).

We used temperature data from central Interior (Fairbanks), the upper Kuskokwim region (McGrath), and southwest Alaska (Bethel) (Fig. 1) to represent Interior, transition, and coastal regions respectively. Growth of Alaska white spruce has been shown to be responsive to a two-year lag period in temperature influence (Barber et al., 2000; Juday et al., 2005; Juday and Alix, 2012) and so we examined a period of three years prior to ring formation in our climate analysis to be certain to cover more than the minimum likely period of climate control.

The last year of correlation of tree growth with temperature data was determined by the year of sampling, with cutoff dates of 2001, 2006, and the years 2008 through 2012. As a result, the common period for all weather stations and tree ring data is 1952–2001. Other key time intervals that we examined are based on the availability of climate data for Interior Alaska (1906 to date of tree collection), the period of reliable Expected Population Signal (EPS) (1822–2006), and the earliest date with 50% of trees sharing a common signal and contributing to the mean (1860–2006).

To determine the influence of temperature at the three weather stations on the growth of the sampled floodplain trees, we correlated all SL-RWI chronologies with mean monthly temperatures at each weather station. As previously demonstrated (Juday and Alix, 2012), an index composed of the mean of monthly temperatures from Bonanza Creek LTER (Barber et al., 2000), the Fairbanks Flood Plain Temperature Index (FPTIF) (Barber et al., 2000; Juday et al., 2005; Juday and Alix, 2012) and the McGrath weather station, the same monthly temperature terms (May, -1 July, -2 July) were used to create a McGrath Flood Plain Temperature Index (FPTIMcG), and the earliest date with 50% of trees sharing a common signal and contributing to the mean (1860–2006).

To develop a Bethel Flood Plain Temperature Index (FPTIBeh), we identified Bethel Mean Monthly Temperatures (MMT) that were significantly correlated (95% CI) with mean SL-RWI of downriver stands. All significant correlations were positive in sign. We correlated Bethel MMT with each SL-RWI chronology sequentially, starting from the furthest downriver stand and proceeding upriver until no significant correlations with any MMT at Bethel occurred. This became the pool of nine positively responsive SL-RWI chronologies (AWC, ABI, BKS, BSI, JBA, UYS, UBE, BOW, ALC). This pooled 9–stand mean RWI chronology showed a significant (p < .01) positive correlation with four Bethel MMTs over a 36-month period (Fig. 2). FPTIBeh is defined as:

\[ FPTIBeh = \frac{(MMT_{May} + MMT_{Mar-1} + MMT_{Apr-2} + MMT_{Feb-2})}{4} \]

Where MMT = mean monthly temperature at Bethel, -1 = year prior to ring formation, and -2 = two years prior to ring formation. The resulting FPTIBeh is a combination of the MMT terms that maximizes the correlation of downriver SL-RWI chronologies using the fewest predictors.

We used the program DendroClim2002 to check for the potential occurrence of multicollinearity in the relationship between monthly climate predictors and responder type RWI, and to assist in the process of identifying the most appropriate months to use in the construction of the FPTIBeh. The set of months with significant DendroClim2002 coefficients of Bethel temperature to the 9–stand mean RWI during a 2-year window were essentially identical to months with significant Pearson correlation scores (p < .01), confirming that these are the principal months with long-term unique predictive power.

We calculated the correlation of FPTIBeh, FPTIMcG, and FPTIBeh with the mean of each of the 36 SL-RWI chronologies to examine climate sensitivity across the longitudinal gradient. We also calculated the correlation of the three temperature indices with all 540 IT-RWI chronologies to test for coherence of responses within stands and populations. The correlation scores of the IT-RWI chronologies (positive, negative, and non significant) formed the basis for assigning a response type to an individual tree. Responder types represent a label characterizing the maximum correlation of the tree RWI to station and sign (e.g. Fairbanks negative, Bethel positive, non-responder, etc.). All IT-RWI chronologies that achieved highest correlation scores with any of the indices for the common period 1952–2001 at the 99% CI were assigned to a responder type (positive or negative) for that station. IT-RWI chronologies that were not significantly correlated with any of the three temperature indices for the common period (99% CI, 1952–2001) were then correlated with FPTIBeh for the entire period of Fairbanks climate record (1906–2001). Any IT-RWI chronologies that were significantly correlated (99% CI) with this longer period were assigned to Fairbanks positive or negative responder type. The remainder of the IT-RWI chronologies were then examined for highest correlation scores at the 95% CI during the common period for the three temperature indices. IT-RWI chronologies that had previously failed a test of significance but whose correlation

![Fig. 2. Correlation of Bethel MMT to RWI of nine positively responding downriver stand level ring width index (SL-RWI) chronologies from 1952 to 2001. Histogram bars highlighted in black are months used to calculate the Floodplain Temperature Index for Bethel (FPTIBeh).](image)
scores were significant at 95% confidence level were assigned to the positive or negative responder type for the climate station with the highest correlation score. Any IT-RWI chronologies failing to qualify under these criteria were classified as non-responders. We generated Dendroclim2002 output for the “evolutionary” response function using a 42-year moving window from the first year of recorded temperature data to test for temporal stability.

We calculated EPS (Wigley et al., 1984) for the two principal responder groups, Fairbanks negative and Bethel positive populations, using the dplR package (Bunn, 2008) with a 40-yr window and a 39-yr overlap. In order to check the consistency of the temperature sensitivity of tree growth over longer time periods, we selected 51 of the oldest trees that showed negative sensitivity to FPTIB and developed a 256-yr (1750–2006) RWI chronology. RWI of this long-term negative responder chronology was compared with an index of Fairbanks summer temperature. The index is composed of a combination of recorded (1906–2006) and reconstructed data (1800–1905) derived from maximum latewood density and δ13C of upland PIGL with negative temperature sensitivity. The long-term temperature index is not based on individual monthly temperatures because the latewood density and δ13C values for the latewood are generally lower than those for the earlywood.

3. Results

3.1. Age, common signal and spatial structure

The mature and old-growth trees sampled in this study are strongly dominated by age classes from 100 to 240 years. Nearly two thirds of the trees (70%) in our sample have a first year of measured growth (FYOG) before 1900, indicating that the great majority of trees had a true date of origin in the 19th century and earlier. Half of the trees have FYOG in the half-century between 1840 and 1890 (Fig. 3). About a fifth of the sample (20%) includes younger trees with FYOG in the 20th century. Overall, the minimum chronology is 48 years and the maximum is 405, with an average of 154 years (Table 2). Tree age classes are relatively evenly distributed along the rivers, with no obvious geographic concentrations except for the youngest of the 36 stands (AWC, average age 84 years – Table 2), which is located near the western limit of PIGL on the lower Yukon River where expansion of tree distribution is most recent.

Mean interseries correlation of the 36 stands is relatively high, with values consistently above 0.5 (Table 2). CDI values and subsequent kriging interpolation allow the identification of three major areas of high crossdating, superimposed on a pattern of continuous change along the east–west longitudinal gradient (Fig. 4). The three regions are not necessarily consistent with or restricted to a single river basin. The easternmost region is composed of stands in the Yukon Flats and mid-Tanana River with CDI values as high as 95. In the center of the gradient, a region of high CDI (up to CDI = 84) is found along the Yukon River between the confluence of the Tanana River and the Koyukuk River. Finally, another area of high CDI is present among all lower-Yukon and Kuskokwim stands. CDI values for the comparison of the uppermost and lowermost river stand-level ring width chronologies are either very low or indicate no common pattern of tree ring signal.

3.2. Climate sensitivity in stand-level chronologies

The pattern of sensitivity of SL-RWI chronology to temperature displays a transition across the longitudinal gradient from Interior sites to downriver locations near the Bering Sea. FPTIB is highly negatively correlated with SL-RWI chronologies of central and eastern Interior Alaska during the common period of analysis (1952–2001) (Fig. 5A). The westernmost, downriver chronologies are either not significantly correlated or are positively correlated with FPTIB. The same geographical pattern of climate sensitivity is present, although at a weaker level, in the correlation of SL-RWI with FPTIB (Fig. 5B). Some of the downriver stands show a positive response of growth to both Fairbanks and McGrath temperature indices, although this positive correlation is inconsistent among those stands. The correlation of all 36 SL-RWI chronologies with FPTIB also varies in a coherent pattern across the gradient, but generally opposite in sign to Fairbanks and McGrath (Fig. 5C). The nine lower river SL-RWI chronologies are strongly positively correlated to FPTIB. In addition, positive correlations occur at mid Kuskokwim River stands (K3, K4) and two stands (MDI, YU) near Galena on the Yukon River.

3.3. Climate sensitivity in populations at the individual tree level

Overall, a strong majority (90%) of 540 IT-RWI chronologies are significantly correlated with one of the temperature indices; only 56 lack a significant correlation with any temperature index and are termed non-responders (Table 3). The majority of IT-RWI chronologies are assigned to responder type at opposite ends of the gradient, with 275 chronologies negatively correlated to FPTIB and 108 positively correlated to FPTIB. The third largest responder type (n = 55) is negative to FPTIB. There are no IT-RWI chronologies negatively correlated with FPTIB. Positive temperature sensitivity to Interior stations is relatively uncommon, with only 18 IT-RWI chronologies positively correlated with FPTIB and not with any other index, and 9 similarly positively correlated with FPTIB. Only two trees among the positive FPTIB or FPTIB occurred upriver from Fairbanks; the other 25 were in lower Tanana or mid- to downriver Yukon stands. These positive responding interior chronologies do not accelerate growth consistently in the same set of years and lack year-to-year congruence with the temperature index. They simply register an overall increased growth trajectory at some time in the second half of the period of analysis; a pattern of low-frequency variation that probably reflects individual tree growth acceleration in response to local events (e.g. death of neighbors) that released these trees from competition.

Within stands, IT-RWI chronologies generally register the same type of temperature sensitivity. Overall, twenty-two stands contain a majority of trees assigned a negative response type, and eight stands contain a majority of trees assigned a positive response (Fig. 6). The eight stands with a majority positive responder population are generally in the lowermost river locations (Fig. 1, Table 3). The twenty-two stands with a majority of negative
responders to either FPTIF or FPTIM are upriver stands (Yukon Flats and mid-Tanana River). The six stands made up of trees without a majority of either positive or negative responders are labeled mixed response stands (Figs. 1 and 6). With one exception (AYC), these six stands are located west of 156°/C176 west longitude, downriver from the Galena and McGrath areas (Fig. 1).

The moving interval bootstrapped correlative analysis (DendroClim “evolutionary” response) during the 1952–2001 common period provides perspective on temporal changes in the strength of temperature sensitivity. DendroClim output for the downriver Bethel positive responding population (n = 108) indicates consistently high positive correlation of temperature with growth for the months of March and April in the year before ring formation. In recent years the positive correlation became significant with May and June temperature in the year of ring formation. These results demonstrate that in coastward populations, early and warm springs, associated with the first availability of liquid water, have remained the principal positive growth factor, but recent summer temperature increases have passed a threshold to become a positive influence on growth as well.

At mid-river locations where McGrath negative responders are concentrated, the negative influence on tree growth of previous July became more decisive as temperatures increased in recent decades. For McGrath negative responders (n = 55), negative sensitivity to current June through August temperatures strengthened since the mid 1970s climate regime shift as well. Finally, in the Fairbanks negative responder population (n = 275), negative sensitivity to previous July temperature remained very strong throughout the period of analysis. However, negative sensitivity to current May temperature increased and also became significant for April in the most recent decades.

During the period 1952–2006, FPTIF values shifted to high levels (favorable for growth) and since then growth remained at its highest sustained levels for the period of temperature record. Growth of the Fairbanks negative responder population is effectively modeled by FPTIF values also increased to high levels, which in this case was unfavorable for growth. Growth of Fairbanks negative responders has remained generally low since the shift. In addition, single or short-term peak years of high temperature favorability – including 1971, 1982, 1992 and 2000–2004 – have not been matched by a commensurate increase in the growth of this population.

3.4. Growth performance of positive and negative responders from the longer-term perspective

Fairbanks summer (May–Aug.) temperature index captures the main features of low frequency variance present in the old-tree (n = 51) chronology (Fig. 7C). Fairbanks summer temperature index is significantly correlated with growth of the Fairbanks negative responder population (r² = 0.39) for the entire period of 1802–2006, for the period of instrument record (1906–2006; r² = 0.43), and for the period of temperature reconstruction (1802–1905; r² = 0.34) (Fig. 7C). At the beginning of the 19th century, growth...
of this population was moderately high and temperatures were favorable with relatively cool summers. From the 1830s to the 1880s growth was generally low during a period of sustained relatively warm summers. The favorable (cool) summer temperature index values and high growth of the first half of the 20th century represent the optimum period of growth from this 200+ year perspective. High summer temperatures of the late 20th century and early 21st century reach the most extreme unfavorable values. The highest maximum single summer temperature index value at Fairbanks occurred in 2005, and the sustained period of below-average growth since 1969 is unprecedented. The failure of growth to match short-term periods of cooler, more favorable, summer temperatures in the early 1980s and early 2000s also occurred in the period 1909–1915, but not earlier.

The overall growth trajectories (5-yr smoothed values) of the Fairbanks negative and the Bethel positive populations were generally consistent until the 1970s (Fig. 8A and B). The Fairbanks negative responders sustained a greater relative growth (RWI) rate (Fig. 8B) than the Bethel positive responders (Fig. 8A) from the earliest years of record until about 1960. Decade-averaged absolute growth (RRW) since 1860 shows a similar pattern. From the decades of the 1860s through the 1930s the Fairbanks negative responders grew at a distinctly greater absolute rate than the Bethel positive responders (Fig. 8C). In the 1940s through 1960s the two populations grew at a similar absolute rate. Beginning in the 1970s the Bethel positive responders grew at a substantially greater rate than the Fairbanks negative responders. The later registered their lowest growth performance of the past 150 years in the post-1970s regime shift period, about 30% less than in the peak decades of the 1920s through 1940s (Fig. 8C). By the 1990s the absolute growth rate of the positive responders was about 40% greater than that of the negative responders.

4. Discussion

4.1. An overall perspective on climate sensitivity

Our results greatly expand previously defined areas of Alaska known to have high levels of climatic sensitivity in floodplain
are strongly climate-driven and generally applicable to mature and across a wide range of mature tree age classes (Fig. 3), these results and effectively modeled temperature responses (Fig. 7) shared our samples. Based on spatially coherent regional signals (Fig. 4) all our samples, drastically reducing the influence of site and sub-climate trends because the floodplain site surface was common to ent. Our results are particularly robust for analysis of longitudinal negative, Bethel positive) identified across the longitudinal gradi-ent. The specific temperature terms that we identified as significant controls of PIgL growth have been reported in other studies of boreal North American forest, both on floodplain and non-floodplain sites. Growth of floodplain PIgL at tree limit on the Mackenzie River Delta in Yukon Territory is negatively correlated with previous July temperature (Porter and Pisaric, 2011). A July temperature control of growth of negatively sensitive PIgL has been identified previously in treeline populations in the Brooks Range and Alaska Range (Wilmking et al., 2004; Wilmking and Juday, 2005). A spring (March or April) maximum correlation of temperature factors and tree ring density response to temperature (Wilmking et al., 2004). Positive growth sensitivity to other tem-perature factors and tree ring density response to temperature are also reported from treeline Brooks Range PIgL (D’Arrigo et al., 2005). The consistency and widespread occurrence of these two fundamental temperature sensitivity response types (positive and negative), the relative rarity of non-responder types, the fact that similar responses occur across a large geographic area, and the high amount of total variance explained suggests that the operative climatic control is not as complex on large river floodplains as on dry south bluffs in central Alaska (Lloyd et al., 2013) or in the varied mountain landscape of adjacent Yukon Territory (Griesbauer and Green, 2012). Between the two ends of the river gradient, sites lacking a majority of trees with either positive or negative temperature

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responses (mixed stands) occur intermittently. In general terms, mixed response stands are most common in locations from near Galena and McGrath downriver to locations not far from tree limit near Bethel (Fig. 1). This western region of mixed responses can be described as a transition zone both in terms of temperature and precipitation, from the warm summers and dry condition of the interior to the maritime-influenced zone of cooler summers and higher precipitation in the west. The value of McGrath mean July temperature is intermediate between the July temperature at both ends of the gradient (Fairbanks and Bethel), yet McGrath annual precipitation is twice the Fairbanks total (Table 1). Based on the geographical distribution of mixed response stands, most of them receive higher precipitation as well as cooler July temperatures compared to the warm, dry interior lowlands. At the same time, the mixed response stands are located upriver from the area dominated by positive responders, and thus experience warmer summers than the stands at the transition to treeless tundra (Fig. 1). As a result, in the mixed response stands, climatic factors are not close to the extreme values either at the warm or the cool end of the longitudinal gradient. In such conditions, local site-specific factors may be the decisive influence on whether a given tree within a stand is a positive or negative responder.

One mixed response stand (AYC) is located within the group of 20 strongly negative responding stands (Table 3) and appears as an anomaly. The AYC site is in the canyon section of the Yukon River, within a mountain region where precipitation is higher (Simpson et al., 2002) than either in the Yukon Flats (upriver) or the Tanana-Yukon lowlands (downriver). The cooler, moister environment of the AYC stand locality compared to the surrounding broad lowlands appears to explain the almost equal number of positive and negative responding individual trees found in the AYC sample. A similar diversity of climate sensitivity occurs in Yukon Territory in areas of complex mountain terrain (Griesbauer and Green, 2012).

4.2. Environmental niche parameters of PIGL and implications in Alaska

In theoretical terms (Fig. 9A), the growth response to temperature of most plant species, including PIGL, follows a normal distribution with clear suboptimal cold and warm ranges (Grossnickle, 2000). Temperature and precipitation values derived from climate stations across the North American PIGL distribution (Thompson et al., 1999) are in good agreement with physiological data on growth performance of the species, when adjusted for the difference between mean monthly ambient air temperature versus instantaneous temperature used in physiological studies. Optimum temperature (in controlled environments) for growth of interior British Columbia PIGL at constant vapor pressure deficit is achieved between 15 and 23 °C (Grossnickle, 2000). PIGL seedlings experience a sharp drop in net photosynthesis at air temperatures above 23 °C. Net photosynthesis remains depressed up to 30 °C, and ceases completely at 35 °C. The combination of moisture stress together with heat stress is an even more serious limitation.

![Fig. 6. Proportion of individual tree ring width index (IT-RWI) chronologies classified by predominant temperature response type.](image-url)
to net photosynthesis in the northern spruces than high temperatures alone (Grossnickle, 2000). The niche space occupied by the entire North American population of PIGL can be described by July MMT between about 10 and 21°C, and total annual precipitation between about 270 and 1100 mm (Thompson et al., 1999). The distribution field of these two parameters for PIGL is centered on July temperatures of about 15.5°C, and annual precipitation of 450 mm and above. These parameters provide a perspective on the portion of climatic niche space occupied by the spruce populations along our longitudinal gradient.

In conceptual terms, temperature increases that start from opposite ends of the temperature gradient should have opposite effects on growth of PIGL trees. Initial temperatures below the optimum for a species followed by temperature increases should produce increased growth (Fig. 9A, left). Initial temperatures at or above the optimum followed by increases should result in decreased growth (Fig. 9A, right). The three main responder groups in our sample are generally arrayed along a gradient of July temperatures, thus allowing a test of the theoretical model of PIGL growth response. The reference period of temperature can be divided into two halves, corresponding to a cooler first half (1952–1979), and a warmer second half 1980–2006 (Table 1).

Annual precipitation at both Bethel and McGrath weather stations during the 1951–2006 time period was near 450 mm (Table 1), well above the minimum for PIGL. July temperature at Bethel over the same period was well below the optimum, but clearly above the 10°C isotherm limit that roughly defines the North American treeline (Sirois, 1992). Based on these values, positive growth responses to increasing temperatures in the downriver portion of the gradient would be logical and consistent with

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**Fig. 7.** Temperature and averaged individual tree ring width index (IT-RWI) for opposite ends of the longitudinal transect. (a) Mean Bethel positive responding IT-RWI chronology (dark line; n = 108) vs. Floodplain Temperature Indices for Bethel (FPTIBEH, gray line) for 1952–2006 (r² = 0.45); (b) Mean Fairbanks negative responding IT-RWI chronology (dark line; n = 275) vs. FPTIFAI (gray line) for 1952–2006, (r² = 0.48); (c) Mean Fairbanks negative responding IT-RWI chronology of oldest trees (dark line; n = 51) vs. Fairbanks summer (May–August) temperature index (gray dashed line = reconstructed values; gray solid line = recorded data) for 1750–2006 (r² = 0.39). Note that RWI scale is inverted for Fairbanks negative responders.
the physiological data. During the first half of the climate reference period, positive-responding trees, primarily occurring in downriver locations, occupied an environment that was well below the optimum July temperature for PIGL growth, as indicated by Bethel Weather station data (Fig. 9B). During the second half of the climate reference period the distribution cloud of July temperatures at Bethel and the associated relative growth of positive responders shifted distinctly higher and upward respectively.

At the opposite upriver end of the longitudinal gradient, central and eastern Interior Alaska populations are vulnerable to high temperature growth limitation (McGuire et al., 2010). Fairbanks annual precipitation (271 mm) during the 1951–2006 reference period was at the lower limit for the species in North America (Table 1). Fairbanks July MMT, from the earliest continuous temperature record (1906) until the start of our common period of analysis (1951), was 15.7 °C. PIGL does not occur naturally at July MMT above 15.7 °C without substantially more than 270 mm precipitation, or at least it did not during the 20th century calibrating period used by Thompson et al. (1999). In fact, during our 1952–2006 reference period the Fairbanks July MMT of 16.7 °C and annual precipitation of 271 mm (Table 1) were outside the field of joint temperature and precipitation values that characterized the North American distribution of PIGL during the late 20th century (Thompson et al., 1999). During the first half of the climate reference period, the negative-responding population, primarily occurring in upriver locations, occupied an environment that was either at the optimum temperature for PIGL growth as indicated by the McGrath station data (Fig. 9C) or well above optimum as indicated by Fairbanks station data (Fig. 9D). During the second (warmer) half of the climate reference period, the distribution clouds of index temperature and associated growth response in the McGrath and Fairbanks negative responding populations shifted lower and downward (Fig. 9C and D). In the warmest years, the Fairbanks negative responding population experienced July precipitation, or at least it did not during the 20th century calibrating period used by Thompson et al. (1999). In fact, during our 1952–2006 reference period the Fairbanks July MMT of 16.7 °C and annual precipitation of 271 mm (Table 1) were outside the field of joint temperature and precipitation values that characterized the North American distribution of PIGL during the late 20th century (Thompson et al., 1999). During the first half of the climate reference period, the negative-responding population, primarily occurring in upriver locations, occupied an environment that was either at the optimum temperature for PIGL growth as indicated by the McGrath station data (Fig. 9C) or well above optimum as indicated by Fairbanks station data (Fig. 9D). During the second (warmer) half of the climate reference period, the distribution clouds of index temperature and associated growth response in the McGrath and Fairbanks negative responding populations shifted lower and downward (Fig. 9C and D). In the warmest years, the Fairbanks negative responding population experienced July
daytime temperatures near the physiological upper limit, and trees achieved the lowest level of relative growth of all populations or time periods (Fig. 9D).

The Fairbanks climate station itself is situated within the extreme lower limit of a local rain shadow effect in Interior Alaska, and so is not representative of the complex mountain landscape, including upland and mountain sites with cooler temperatures and higher precipitation (Simpson et al., 2002), where suitable environments for spruce would likely persist if further warming were to occur. Still, the elevated temperatures of recent years have shifted this part of the Interior Alaska environment to a point that persistence of the species, or the current local distribution of the species, is challenged. It is difficult to see how further temperature increases in that Interior region would make the persistence of PIGL anything other than problematic, because the species historically has not occurred in such conditions and its physiology is not well adapted to such warmth.

The decline in relative and absolute growth performance of the Fairbanks negative responders does not appear to be due primarily to age-related growth changes (e.g. Szeicz and MacDonald, 1994). Since 1800, growth of Fairbanks negative responders was consistently closely aligned with summer (May–August) temperature (Fig. 7C). In the several centuries before 1800, a period which represents the Little Ice Age, reconstructed boreal Alaska temperatures (Hu et al., 2001; Anchukaitis et al., 2013) were notably cooler than temperatures at the time of the PIGL positive/negative responder growth rate reversal of the late 20th century. Based on the strong and consistent temperature controls we have identified, it is unlikely that the growth rate of positive responders in western Alaska exceeded the growth rate of upriver negative responders since at least the Medieval Climate Anomaly (or Warm Period) of A.D. ∼1000 to 1350 (Díaz et al., 2011). This inversion of the growth rate performance of the positive and negative responder populations represents an historical change clearly related to the 1976 Pacific climate regime shift (Ebbesmeyer et al., 1991). A decrease in PIGL growth rate coincident with the regime shift has been reported previously in negative-responding populations (Barber et al., 2000; Wilmking et al., 2004; Juday et al., 2005), and our results now demonstrate a simultaneous acceleration in growth of positive-responding populations.

4.3. Implications for biome shift

Our findings offer a useful perspective on the “divergence” problem (Jacoby and D’Arrigo, 1995; Wilmking et al., 2005; D’Arrigo et al., 2008) in dendrochronology. Divergence is generally considered to be the systematic temporal decrease in climate sensitivity of tree ring width series, particularly beginning in the late 20th century. Divergence generally has been of greatest concern in ring width chronologies positively correlated with temperature at treeline (e.g. Carrer, 2011). According to our model, for tree ring samples collected in locations where the initial temperature was near optimal, temperature increases would produce no further growth increases, or even switch the growth response from positive to negative (Fig. 9A). Recent strong temperature increases in the northwestern North American Arctic and Subarctic have apparently crossed this threshold. Our results appear to fit the criteria identified by D’Arrigo et al. (2014) for better explaining the divergence phenomenon – large-scale and regional coverage, along with physiological and ecological mechanisms.

Negative sensitivity to temperature has been reported for Alaska birch (Betula neoalaskana Sargent), black spruce (Picea mariana (Miller) Britton Sterns, et Poggenburg 1888), and PIGL on upland sites in central Alaska (Barber et al., 2000; Juday et al., 2005; FS-R10-FHP, 2007). The climatic distribution envelope for black spruce and Alaska birch is quite similar to PIGL (Thompson et al., 1999). This multi-species consistency supports the interpretation that a broadly similar climatic adaptation is involved in the distribution limits for these three species that dominate the Alaska
boreal region, and that temperature increases of recent decades are depressing growth of the entire set. Across Alaska a broad pattern of “browning” and “greening” (decreasing and increasing temporal trend in NDVI) has been demonstrated for black spruce and PIGL during the period 1982–2008 (Verbyla, 2008; Beck et al., 2011; Baird et al., 2012). Our study demonstrates a true gradient of coherent and year-to-year temperature sensitivity of PIGL trees at this statewide scale. Floodplain spruce populations closest to the western Alaska tundra, an NDVI “greening” area, overwhelmingly belong to the positive responding population. Spruce populations within the mid- and upriver, interior boreal forest, an NDVI “browning” area, overwhelmingly belong to the negative responding population. Locations between “browning” and “greening” areas are characterized by tree populations of mixed temperature sensitivity responses. The preponderance of McGrath negative responders in a mixed response environment (Table 3) characterized by twice the precipitation of Fairbanks suggests that more precipitation will not necessarily reverse a temperature-driven negative growth response.

It is particularly noteworthy that the short-term occurrence of extreme unfavorable temperatures has become chronic in the eastern interior. The July MMT at Fairbanks increased one degree C from the first to the second half of the period of climate analysis (Table 1). Since 2006, Fairbanks July MMT have remained elevated, with the years 2007, 2009, 2013 ranked 2nd, 13th, and 15th warmest in the 109-year record respectively. Recent temperature and precipitation levels typical of Fairbanks climate station already appear unsuitable for long-term PIGL persistence, and at the least are typical of environments at the very margin of the persistence of PIGL (e.g. Scheffer et al., 2012). However, low elevation stations, such as Fairbanks and McGrath, experience warmer summers and lower precipitation than surrounding hills and mountains. As a result, even in the landscapes surrounding weather stations that record submarginal climate conditions, PIGL may be able to survive in favorable microenvironments (e.g. AYC).

If growth-predicting index temperatures for PIGL, especially July temperatures, continue to increase at the same rate (~1 °C) as during our period of analysis, and if annual precipitation does not increase in lowland eastern and central Alaska, then it is difficult to see how PIGL can remain broadly distributed across the landscape. On south bluffs, the warmest and driest environments where spruce occurs, an eventual contraction of PIGL forest distribution appears inevitable (Lloyd et al., 2013).

Extreme events may in fact, ultimately be more important in the process of ecosystem change induced by climate change than the gradual evolution of mean temperatures and precipitation (Jentsch et al., 2007). The consistency and widespread nature of weakened positive responsiveness to favorable temperatures in negative responding Alaska PIGL populations, occurring after prolonged exposure to temperatures at the upper limit of the species tolerance, suggests that species decline and elimination is near. PIGL is capable of quickly recovering from moderate drought stress, but severe drought causes a slower recovery of its gas exchange capability (Grossnickle, 2000). Short term growth reduction of PIGL in central Alaska, particularly in 1993, may have been caused by spruce budworm defoliation, itself triggered by warm temperature anomalies (Régnière, 1987; FS-R10-FHP, 2007). But other years with climatically anomalous PIGL growth deficit (1982, 2001–2004) have no apparent relationship with insect or disease other than chronic high temperature/drought stress levels. The failure of growth recovery during recent short-term periods of favorable temperatures and precipitation suggests a hormetic process in the detrimental zone of response to a stressor (Costantini et al., 2014).

The boreal conifer forest has been identified as the global biome most vulnerable to climate change based on current distribution, broad climate parameters, and scenarios of climate change (Gonzalez et al., 2010). Our results show that at the same time that climatically related reduced growth performance occurred across a large portion of the white spruce distribution in the productive heart of Interior Alaska in the late 20th and early 21st centuries, a large area of improved temperature suitability occurred coastalward in western Alaska. The coherence of these changes across space, through time, and in line with the physiology of PIGL and associated species, provides confirming evidence that climatic change in a large portion of the western North America boreal forest has passed a tipping point, and that an early stage of biome shift is now underway.

4.4. Applications to forest management in Alaska

Since statehood in 1959, the state of Alaska has gradually received a land entitlement of over 42 mill ha from the federal government. Much of this land base has been classified through administrative procedures for forest management and from 1983 on, the Alaska Division of Forestry has proposed new state forests for establishment by the Alaska Legislature (http://forestry.alaska.gov/stateforests.htm). The Alaska State Constitution (Article 8, Section 4) requires that the state’s replenishable resources must be “… utilized, developed, and maintained on the sustained yield principle, …”

In order to accurately project future forest growth and yield or ecosystem services such as carbon uptake under specified climate scenarios, model projections of white spruce and trees responding similarly, need to be assigned the appropriate temperature sensitivities (negative or positive). Consequently, forest growth/carbon uptake projections would have to be area-weighted according to the geographic extent or proportion of the positive, mixed, and negative responses zones to temperature within the area under evaluation. A critical piece of information to perform such calculations is a more precise geographical placement of the boundary between positive vs. negative responding populations than is available now.

Temperature-driven temporal changes in growth of both positive and negative responders in recent decades are not small. Mean ring width of positive responders in 1970–1999 compared to 1920–1949 increased 35%, while ring width of negative responders decreased 29% in between the same two time periods. As a result, under a continuation of the current climate regime, forest inventories and productivity models that are calibrated with historical data from the past one or two centuries will overstate the growth potential of trees within areas of predominant negative responders and underestimate the growth potential of positive responders. Additional temperature increases would further amplify the error.

Our results demonstrate that as long as recent high temperatures persist, literally achieving sustainable forest production will not be possible in the predominant negative response region of central and eastern Alaska when compared to the past two centuries. Eastern and central Alaska was previously the region of highest forest productivity in boreal Alaska, and state forests and land classifications for forest management are currently concentrated there. By contrast, western Alaska, a region long seen as marginal for forest production, was not a priority for state forest designations. Now, much of western Alaska has strong potential for sustainable forest management for the first time, and thus should receive serious consideration for state forest establishment.

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