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Climate–growth relationships along a black spruce toposequence in interior Alaska

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A B S T R A C T

Despite its wide geographic distribution and important role in boreal forest fire regimes, little is known about the climate–growth relationships of black spruce (*Picea mariana* [Mill.] B.S.P.). We used *site-* and *tree-level* analyses to evaluate the radial growth responses to climate of black spruce growing on a north-facing toposequence in interior Alaska for the period A.D. 1949–2010. At the *site level*, correlations between growth and climate were negative for temperature and positive for precipitation. The signs and strengths of these correlations varied seasonally and over time. These *site-level* differences probably arise from tree interactions with non-climatic factors that vary with topography and include active layer thickness, soil temperature, solar radiation, microsite, and tree architecture. We infer that black spruce suffers from drought stress during warm, dry summers and that the causes of this moisture stress relate to topography and the seasonality of drought. *Tree-level* analyses reveal that divergent *inter-tree growth responses* among individual trees at the same site also occur, with the lower slope positions having the greatest frequency of mixed responses. The overall complexity of black spruce's climate–growth relationships reflects the plastic growth strategy that enables this species to tolerate harsh, high-latitude conditions across a transcontinental range.

INTRODUCTION

Boreal forests comprise a third of Earth's forests and occur in regions where climate is now changing rapidly (Wolken et al., 2011a). In interior Alaska, the largely forested region between the Alaska and Brooks Ranges, mean annual temperature has risen 1.4 °C since 1970 (Wendler and Shulski, 2009), and growing season length has increased by three days per decade over the same period (Euskirchen et al., 2010). These changes in climate are affecting tree

growth, fire regimes, and the geographic ranges of tree species (Beck et al., 2011; Kelly et al., 2013). Changes in forest composition have the potential to cause strong feedbacks to climate by altering the processes controlling trace gas sequestration and by altering land-surface energy budgets (Mann et al., 2012). To better predict future states of the boreal forest and assess global impacts of changes in forest composition it is essential to know how boreal tree species respond to climate under a variety of site conditions.

Black spruce (*Picea mariana* [Mill.] B.S.P.) has a transcontinental range spanning boreal North America and is the most abundant tree species in interior Alaska, where it grows in a variety of community types differing in floristic compositions, structures (open vs. closed canopy), soil properties (pH, moisture), altitudes, and slope positions (Hollingsworth et al., 2006). Black spruce is the dominant tree species growing at the cold, wet end of the continuum of soil temperature and moisture conditions present in interior Alaska (Yarie, 1983; Van Cleve et al., 1990).

The presence of black spruce on the landscape is strongly linked to the present-day fire regime of the Alaskan boreal forest (Johnstone et al., 2010). Its resinous foliage and wood, abundant fine branches that afford ladder fuels, and dense stand structure facilitate frequent burning (Hu et al., 1996). Black spruce's pyrogenic qualities led to a striking increase in fire frequency ca. 6000 years ago when this species first became abundant in interior Alaska during the initial stages of neoglacial cooling (Kelly et al., 2013). It follows that if black spruce's growth and distribution on the landscape change in the future, the regional fire regime may also change. Several lines of evidence suggest that the present black spruce-dominated forests in interior Alaska are undergoing changes in structure and composition (Beck et al., 2011; Mann et al., 2012; Kelly et al., 2013; Hollingsworth et al., in press).

Despite the ecological importance of black spruce in the Alaskan boreal forest, the majority of tree-ring studies in interior Alaska have involved white spruce growing near treeline (Lloyd et al., 2005, 2013). Dendrochronological studies in the Canadian boreal forest reveal that cool and wet conditions generally favor the radial growth of black spruce (Brooks et al., 1998; Subedi and Sharma, 2013). Radial growth of this species also correlates strongly with both the current and previous year's climate (Girard et al., 2011), and these relationships can vary along gradients in moisture (Trindade et al., 2011) and in response to site-specific characteristics, such as soil organic-layer thickness (Drobyshev et al., 2010).

Tree growth in the subarctic might be expected to be limited by cool summer temperatures, because temperature is an important factor controlling the latitudinal (Lloyd et al., 2011) and altitudinal (Et-

tinger et al., 2011) limits of many tree species. Indeed, conifers at treeline in Siberia have responded to recent warming by growing faster and shifting their geographic ranges northward (Lloyd et al., 2011; Berner et al., 2013). However, mounting evidence suggests that some trees in the circumboreal forest are becoming less sensitive to temperature, with the correlation between summer temperature and radial growth switching from positive to negative in recent decades (Briffa et al., 1998; D'Arrigo et al., 2008; Porter and Pisaric, 2011). In some cases, the negative response of white spruce to warming temperature is attributed to water stress replacing temperature as the most immediate factor limiting tree growth (Barber et al., 2000; D'Arrigo et al., 2009; Lloyd et al., 2013).

The decoupling of tree growth from temperature in high-latitude forests has been termed the *divergence problem* (D'Arrigo et al., 2008). Here we use the term *growth-climate divergence* because it more precisely describes this phenomenon and includes growth responses to both temperature and precipitation. Although *growth-climate divergence* is widespread in white spruce, its frequency among black spruce is unknown because the majority of dendrochronological studies in interior Alaska have involved white spruce growing at treeline, where it is the dominant tree species (Viereck, 1979; Lloyd et al., 2005).

Another type of growth divergence emerges when individual trees become the focus of study rather than the mean responses of all trees sampled at a site (Wilmking et al., 2004, 2005; Zhang et al., 2009). In traditional dendrochronology, the mean responses of large numbers of trees are used to reconstruct past climate (Carrer, 2011). While invaluable for climate studies, this approach ignores the fact that individual trees can display varying and sometimes opposing responses to the same climate drivers (Wilmking et al., 2005). Because this form of growth divergence involves differing *inter-tree growth responses*, here we use the term *inter-tree growth divergence* for this phenomenon. Previous studies have related *inter-tree growth divergence* to differences in meso- and microsite conditions including topographic position, soil fertility, soil temperature, and genotypic diversity associated with different aged cohorts (Szeicz and MacDonald, 1994; Wilmking and Juday, 2005; Wilmking and Myers-Smith, 2008). Though well documented in white

spruce (Driscoll et al., 2005; Wilmking et al., 2004, 2005) and observed in Alaskan black spruce (Wilmking and Myers-Smith, 2008, Walker and Johnstone, 2014), it is unclear how widespread *inter-tree growth divergence* is among black spruce growing in interior Alaska.

Here we present a case study evaluating how climate differentially affects the radial growth of black spruce growing along a north-facing toposequence within the boreal forest landscape of interior Alaska. This toposequence incorporates steep gradients in solar radiation, soil drainage, and depth to permafrost. Specifically, we used *site-* and *tree-level* scales of study to explore three questions. First, how does topographic position affect the sensitivity of black spruce growth to variations in temperature and precipitation? To address this question we evaluated the radial growth responses to climate variability of black spruce growing at four different topographic locations along the toposequence. We hypothesized that trees at the comparatively well-drained *Summit* site are more sensitive to precipitation than to temperature compared to trees growing at the *Valley bottom* site, where soils are perennially moist and soil temperatures remain cold all summer. Second, how have the climate-growth relationships of black spruce changed over time? We hypothesized that the temporal changes in the sensitivity and sign of the *site-level* responses to different combinations of temperature and precipitation vary with topographic location. And third, do black spruce trees

growing at the same site differ in their growth responses to climate? To explore this question regarding *inter-tree growth divergence*, we evaluated the climate-growth relationships of individual trees growing at the same site. Specifically, we hypothesized that there is a greater diversity of *inter-tree growth responses* among trees at the *Valley bottom* versus the *Summit* site because microtopography tends to be more diverse at cold, moist sites underlain by permafrost than at dry sites lacking permafrost. We proposed that a greater understanding of *site-* and *tree-level* characteristics is required in order to develop a more complete picture of the underlying processes driving the growth responses of black spruce to variations in climate.

METHODS

Study Area

The toposequence at Babe Creek is located on a steep, north-facing hillslope in the Yukon-Tanana Uplands at 64°59'55"N and 147°39'25"W, approximately 40 km north of Fairbanks, Alaska (Fig. 1). Vegetation is the *Wet acidic black spruce* subtype within the *Acidic black spruce/lichen forest* community type described by Hollingsworth et al., (2006). The *Wet acidic* subtype is characterized by low-nutrient soils and a shallow active layer, which is the uppermost layer of ground that freezes and thaws annually. In interior Alaska, snow accumulates throughout the winter, and although maximum snowpack is shal-

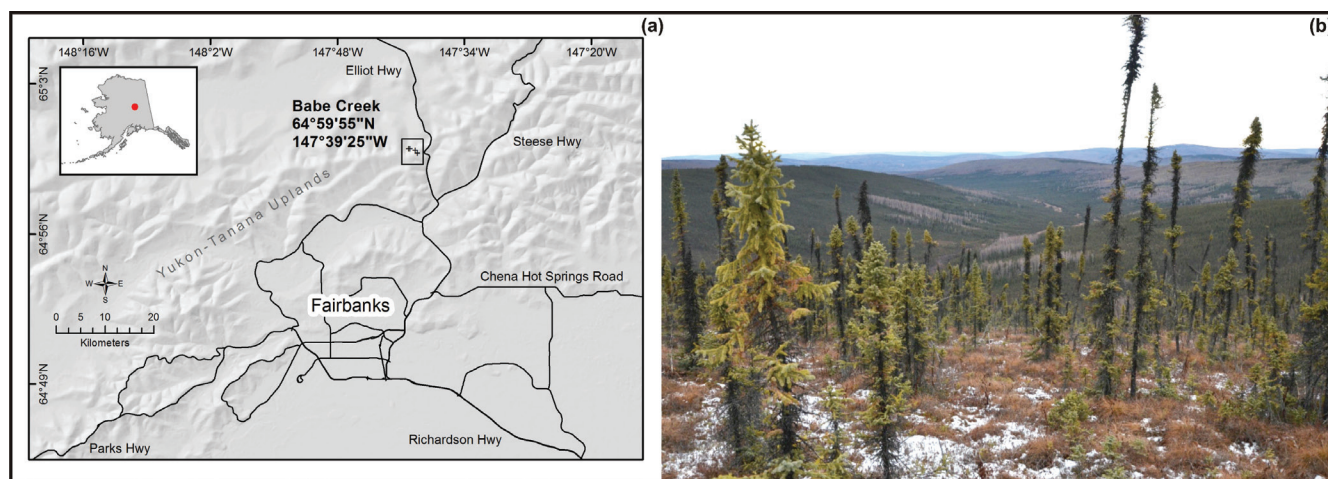


FIGURE 1. Babe Creek black spruce toposequence: (a) map of location relative to Fairbanks, Alaska, in the Yukon-Tanana Valley Uplands; and (b) view down the toposequence toward the north from the *Side slope* site in early October 2013.

low, it provides good thermal insulation, as winds are generally calm throughout the winter months (Hinzman et al., 2006). Ground- and shrub-layer vegetation is dominated by ericaceous shrubs and sphagnum mosses (Hollingsworth et al., 2006). The climate of interior Alaska is subarctic and continental, with warm summers and cold winters (Shulski and Wendler, 2007). Even in midsummer, steep gradients in solar insolation exist on this hilly landscape because of the low sun angles at this high latitude.

We sampled black spruce trees at four sites located along the 1-km-long toposequence: *Summit*, *Side slope*, *Toe slope*, and *Valley bottom*. Besides differing in topographic position and altitude, these sites differ in organic soil depth, active-layer thickness, site moisture, soil temperature at 40–50 cm depth, soil texture, solar radiation received during the snow-free season, and mineral soil pH (Table 1). Soil temperatures recorded at each site

between 2004 and 2012 reveal sizable differences in local microclimates (Table 1, Fig. 2). Soils are warmest at the *Summit*, where the active layer is deepest. Soil temperature at the *Summit* is 2 to 4 °C warmer than at the other sites in winter and 0.5 to 1.0 °C warmer in summer. Relative to the *Summit*, soils at the *Valley bottom* are the coldest of the three lower sites by as much as 0.5 °C in some summers. The *Side slope* and *Toe slope* sites are more similar to the *Valley bottom* than the *Summit* in terms of soil temperature. Consistent with the trend in soil temperature, active layers thin and solar radiation values decrease downslope of the *Summit* site.

Tree-Ring Samples

We collected two cores taken 180° apart from 20 trees at each of the four sites at 25–30 cm above

TABLE 1
Site characteristics of Babe Creek black spruce toposequence.

Site characteristic	<i>Summit</i>	<i>Side slope</i>	<i>Toe slope</i>	<i>Valley bottom</i>
Aspect	Northeast	Northwest	West	Northwest
Elevation ^a (m)	465	431	317	304
Basal area ^a (m ² ·ha ⁻¹)	6.6	2.4	14.9	2.5
Stand age ^a (yrs)	81–120	81–120	81–120	81–120
DBH (±standard deviation) ^b (cm)	7.8 (±1.2)	5.9 (±1.4)	7.3 (±1.2)	9.2 (±3.5)
Organic soil horizon depth ^a (cm)	26	30	23	30
Soil texture ^a	Silty loam	Organic	Sandy clay loam	Organic
Sand ^a (%)	23.2	23.2	Not measured	31.2
Silt ^a (%)	67.2	69.2	Not measured	61.2
Clay ^a (%)	9.6	7.6	Not measured	7.6
Soil pH ^a	5.24	4.83	4.60	4.83
Site moisture ^c	Subxeric	Mesic	Mesic	Subhygric
Active layer thickness ^d (cm)	90–>140	30–90	40–75	30–50
Soil temperature ^e (°C)	0.45	0.09	–0.05	0.01
Duration of direct solar radiation ^f (hrs)	2658	2472	2184	2200

^aMeasured by Hollingsworth et al. (2006). “Not measured” refers to samples in which there was not enough mineral soil available for the measurement.

“Organic” refers to sites where the mineral soil was not reached.

^bAverage diameter at breast height (DBH) of 20 sampled trees at the *Summit*, *Side slope*, and *Toe slope* sites and 26 trees at the *Valley bottom* site.

^c*Subxeric*: noticeable surface moisture on well-drained slopes or ridges; *Mesic*: moderate near-surface moisture on flat surfaces or in shallow depressions; and *Subhygric*: considerable near-surface moisture but with less than 5% standing water (Johnstone et al., 2008).

^dActive layer thickness was measured by Sergey Marchenko, Geophysical Institute, University of Alaska Fairbanks in Sept/Oct 2005–2010 with a calibrated metal rod inserted into the soil to the point of resistance.

^eMean soil temperature May–Sept 2004–2010 at 40–50 cm depth was measured by Sergey Marchenko, Geophysical Institute, University of Alaska Fairbanks, using data logger sensors installed in PVC pipes inserted into the soil to a standard depth near the lower limit of the active layer.

^fSnow-free period (May–Sept) solar radiation calculated from 1 May to 30 September 2011 using the ArcMap 10.0 Area Solar Radiation tool (Environmental Systems Resource Institute, Redlands, California) with a latitude setting of N65° and an ASTER (NASA Jet Propulsion Laboratory, California Institute of Technology) 20-m digital elevation model.

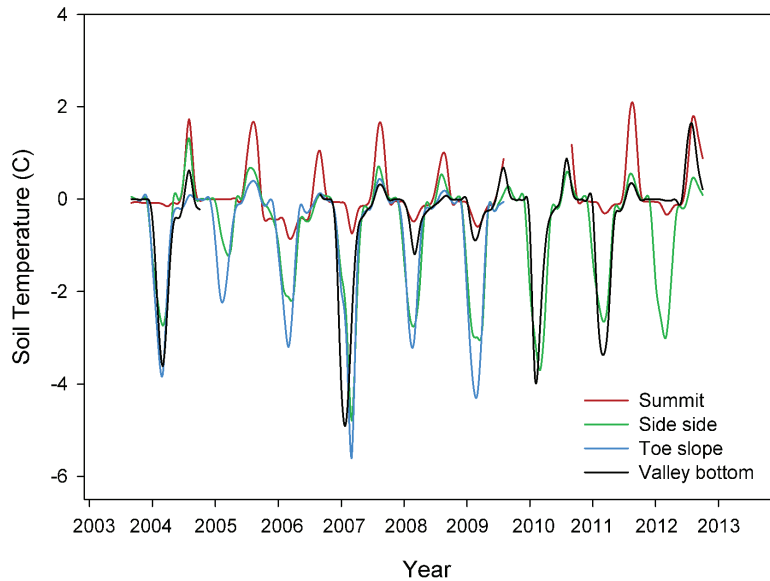


FIGURE 2. Mean monthly soil temperature recorded at each site at depth = 40–50 cm between 2004 and 2012. Measurements were made by Sergey Marchenko, Geophysical Institute, University of Alaska Fairbanks, using data logger sensors installed in PVC pipes inserted in the soil to a standard depth near the lower limit of the active layer. Breaks in some records are the result of instrument malfunction and/or frost heaving.

the ground to avoid deformities in tree rings located near the root-stem junction. The largest trees were selected for sampling to capture the longest temporal records, as historical studies of black spruce sites in interior Alaska indicate that the legacy effects of fire on stand structure result in the largest trees being the oldest (Hollingsworth et al., 2006, in press). Cross-sectional disks were collected from an additional six trees in the *Valley bottom* because the trees at this site were especially difficult to cross-date using cores. In the laboratory, tree cores and disks were mounted, sanded until individual xylem cells could be clearly distinguished under a stereomicroscope, and then measured to the nearest 0.001 mm using a Velmex TA unislide system (Velmex Inc., Bloomfield, New York) and Measure J2X software (VoorTech Consulting, Holderness, New Hampshire). The cores were first cross-dated visually and then statistically using the program COFECHA (Grissino-Mayer, 2001). At all four sites, 1969 was identified as a marker year, which corresponds to the occurrence of a widespread drought in interior Alaska (Xiao and Zhuang, 2007), when >1.6 million hectares burned in the region (Todd and Jewkes, 2006). Ring-width index (RWI) was deemed the response variable of choice rather than basal area increment (BAI), because our research questions did not involve a comparison of the absolute growth rates. We opted to conservatively detrend each ring-width series with either a negative exponen-

tial curve, a line of negative slope, or a horizontal line to remove the geometric growth trend using the *dplR* package (Bunn, 2008; Lloyd et al., 2011; Salzer et al., 2014) because we were interested in determining the growth responses (i.e., climate sensitivity) of black spruce to climate variability at both the *site-* and *tree-level*. This detrending strategy preserves the low-frequency (multi-decadal) trends in the ring-width data. The two detrended ring-width series from each tree were averaged to create the individual *tree-level* chronologies.

We developed *site-level* chronologies (Table 2) by averaging the *tree-level* chronologies from each site. The *detrendeR* package in the statistical program R was used to calculate the expressed population signal (EPS), which is a measure of the common variability in a chronology. We calculated the running EPS within a 50-year window for the period A.D. 1949–2010 that was used to classify the *site-* and *tree-level* responses (see Analysis of Climate–Growth Relationships below) because of the varying length of the chronologies (Table 2) and the low sample depths in the early part of the series. Although the EPS values (Table 2) for the *Side slope* (mean EPS = 0.77) and *Valley bottom* (mean EPS = 0.59) do not exceed the recommended 0.85 threshold to be considered a reliable and consistent signal (Wigley et al., 1984), we opted to evaluate the *site-* and *tree-level* climate-growth relationships of these sites anyway, since changing climate-growth relationships and *inter-*

TABLE 2
Summary of *site-level* chronologies.

Site	Number of trees (series)	Mean ring width (mm)	Series intercorrelation ^a	Mean sensitivity ^a	Start year range ^b	Mean EPS ^c
<i>Summit</i>	19 (31)	0.45	0.554	0.222	A.D. 1908–1940	0.88
<i>Side slope</i>	15 (27)	0.36	0.482	0.225	A.D. 1875–1943	0.77
<i>Toe slope</i>	18 (30)	0.43	0.546	0.221	A.D. 1895–1943	0.92
<i>Valley bottom</i>	13 (22)	0.44	0.474	0.219	A.D. 1857–1940	0.59

^aValues obtained from the program COFECHA output.

^bStart year ranges underestimate tree age, as the pith was not always captured in the cores, and the tree age at core height was not estimated.

^cEPS is the expressed population signal calculated from A.D. 1949–2010 using the detrendR package in the R statistical program.

tree growth divergence within a site could themselves be the reason for the low EPS values.

Analysis of Climate–Growth Relationships

To evaluate the climate–growth relationships of black spruce through time, we analyzed a 50-year moving interval analysis (i.e., 50 years of radial growth correlated with 50 years of mean monthly temperature [MMT] and 50 years of total monthly precipitation [TMP] data) for the period A.D. 1949–2010 using the program DENDROCLIM2002. This computer program uses 1000 bootstrapped samples to compute correlation coefficients for each 50-year interval (i.e., first interval 1949–1999, second interval 1950–2000, etc.) and assesses significance at $p < 0.05$ (Biondi and Waikul, 2004). We correlated *site-level* chronologies with climate records from the Fairbanks Station, a first-order weather station located at the Fairbanks International Airport. The same climate data has been used previously in dendrochronological reconstructions in interior Alaska, and it is highly correlated with growth patterns in upland white spruce (Barber et al., 2000; Juday and Alix, 2012; Juday et al., 2015). Since our black spruce chronologies have limited temporal depths in the early part of the series, we limited the climate–growth analysis to the period A.D. 1949–2010. We selected an 18-month climate window (18 months of temperature data and 18 months of precipitation data) because the radial growth of black spruce has been correlated with climate variables from both the previous and current year (Girard et al., 2011; Trindade et al., 2011). The 50-year moving inter-

val analysis correlated 50 years of radial growth at each site in year t with MMT and total TMP for the period from April of year $t-1$ to September of year t for the period A.D. 1949–2010. Following Lloyd et al. (2011), we classified each site’s response to MMT for the period A.D. 1949–2010 (because of the low sample depths in the early part of the *site-level* chronologies) into one of four response-types based on the number of positive, negative, or non-significant correlation values determined by DENDROCLIM2002 for all year and monthly combinations. These four response-types are: positive (“+”: >67% of significant correlations with temperature are positive), negative (“-”: >67% of significant correlations with temperature are negative), mixed (“m”: between 33% and 67% of significant correlations with temperature are positive), or none (no significant correlations with temperature). This method of categorizing each site into response-types for MMT was then repeated for correlations between radial growth and TMP. We made qualitative comparisons between different sites along the toposequence by evaluating the significance and direction of the DENDROCLIM2002 results.

To evaluate the climate–growth relationships of individual trees within each site, we correlated individual *tree-level* chronologies with MMT and TMP using the 50-year moving interval analysis described above. The 50-year moving interval correlations between each tree’s radial growth and climate (both MMT and TMP) were then categorized into one of the four response-types described above. For consistency with the *site-level* classification of responses, we limited the *tree-level* analyses to the period A.D. 1949–2010. We then deter-

mined the percentage of trees at each site exhibiting each temperature-precipitation response-type combination (e.g., +Temperature and +Precipitation (+T+P), -Temperature and +Precipitation (-T+P)). Within- and between-site comparisons were made qualitatively by evaluating the percentage of trees exhibiting each response-type combination. A rigorous statistical analysis of the multivariate *inter-tree growth responses* to temperature and precipitation was not deemed appropriate because the number of trees sampled at each site was relatively small.

RESULTS

Site-Based Variations in Climate Sensitivity

The black spruce chronologies we studied are 100 to 155 years long (Table 2; Fig. 3). The youngest trees grow at the *Summit* site and established there between A.D. 1908 and 1940. The oldest sample trees grow in the lower slope positions where they established between A.D. 1857 and 1943. Al-

though two cores were collected from 20 trees at each site, the number of sample trees that we were able to successfully cross-date varied by site.

At the *site-level*, the overall sensitivity of black spruce growth to climate for the period A.D. 1949–2010 at all four sites was negative for temperature and positive for precipitation (Fig. 4). Trees growing at different sites along the toposequence varied in their sensitivity to the seasonality of climate (Fig. 4). At the *Summit*, tree growth was positively correlated with temperatures in December of the previous year and negatively correlated with temperature in April and May of the current year (Fig. 4, part a). Precipitation in April of the current year and in August of both the previous and current years was positively correlated with growth at the *Summit* (Fig. 4, part a). The *Side slope* climate-growth relationships resemble the *Summit* more than the lower slope sites, where temperature in April and May of the current year was negatively correlated with tree growth and where correlations with precipitation in August of the previous year were positive (Fig. 4, part b). At the *Toe slope*, tree growth throughout the growing season in both the previous and current

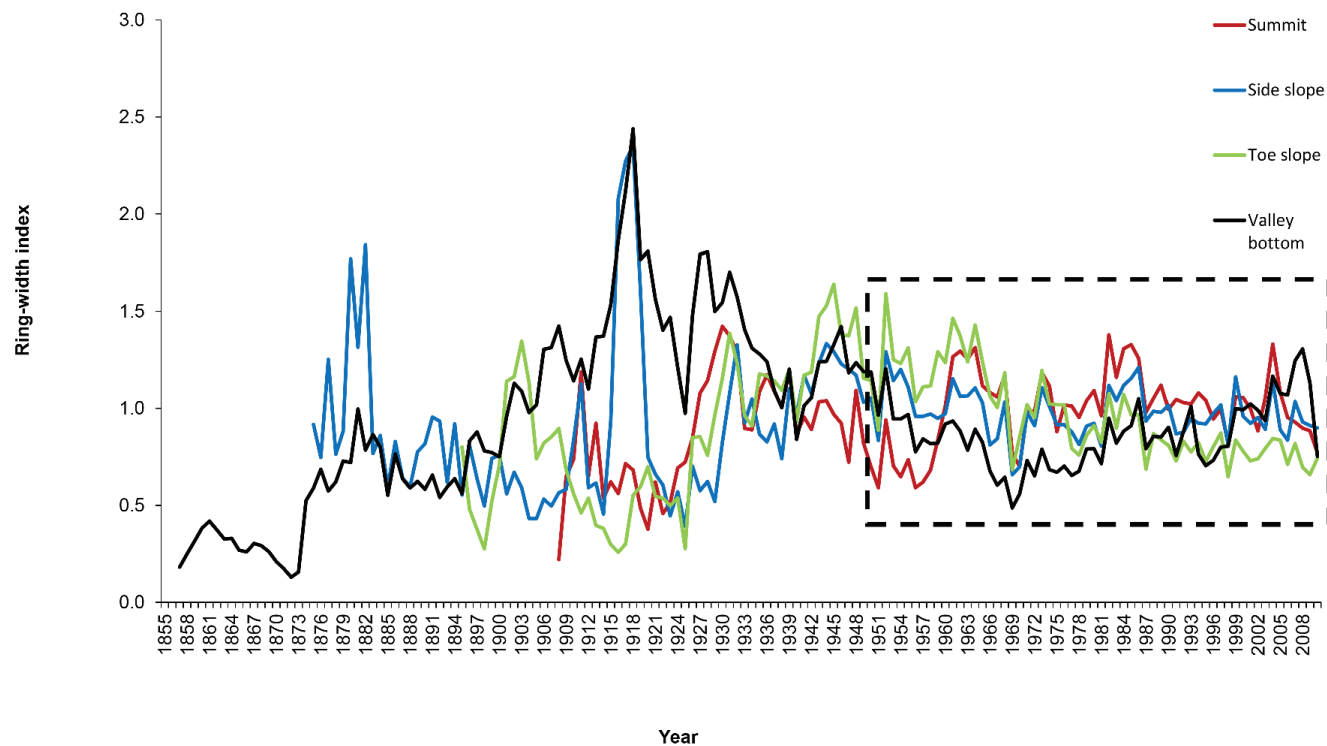


FIGURE 3. Site-level detrended mean ring width indices for the *Summit*, *Side slope*, *Toe slope*, and *Valley bottom*. The dashed box delineates the analysis period (A.D. 1949–2010), where all individual *tree-level* chronologies are included.

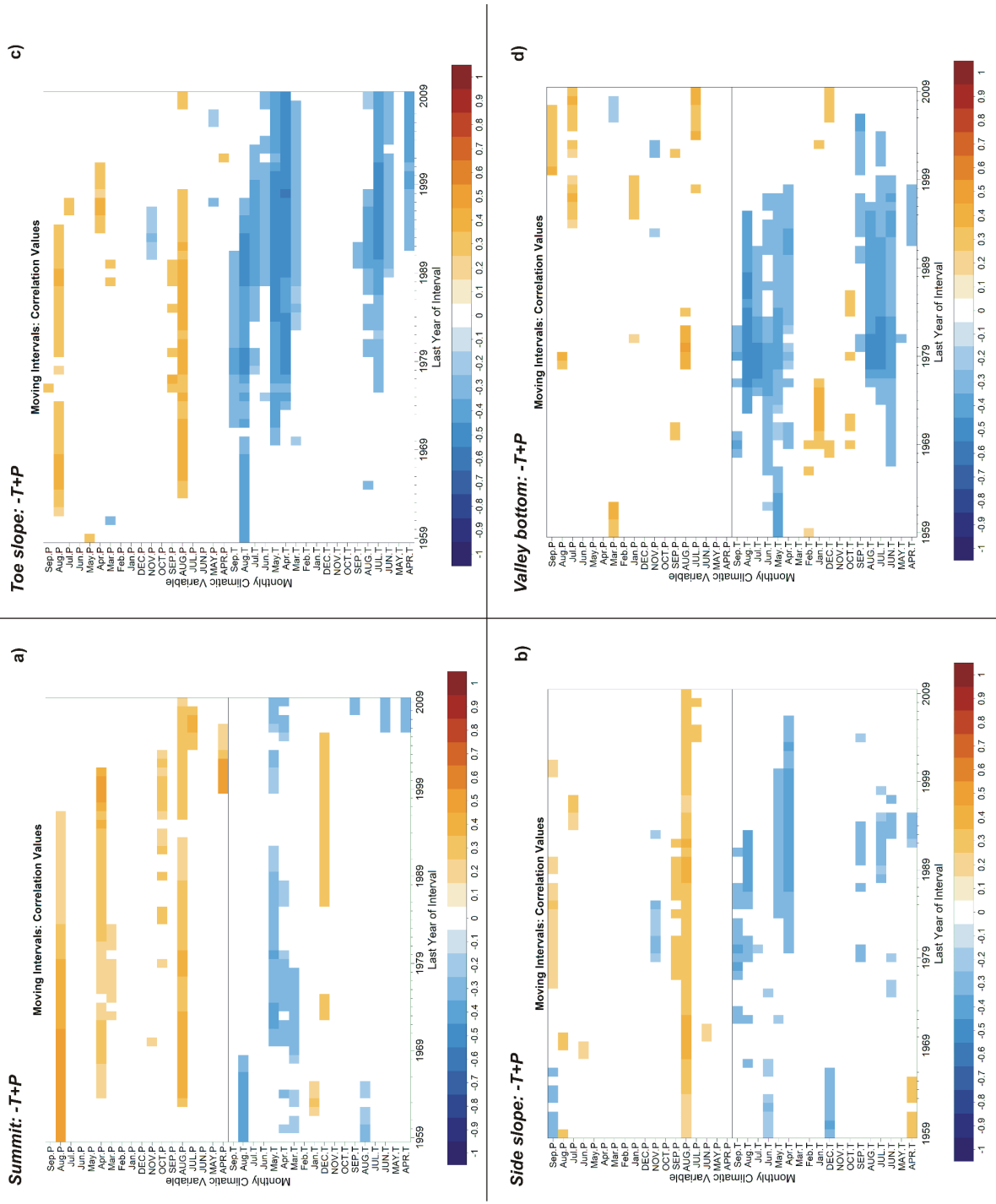


FIGURE 4. Correlations between black spruce radial growth and temperature (T) and precipitation (P) vary along the toposequence for the period A.D. 1949–2010. Capitalized months (e.g., APR) refer to previous year of growth and lowercase months (e.g., Apr) refer to current year of growth. Correlation values are the result of a 50-year moving interval analysis performed in DENDROCLIM2002 using an 18-month window extending from April of the previous year of growth to September of the current year of growth. The multivariate responses to both temperature and precipitation (i.e., positive [+], and negative [–]) for the period A.D. 1949–2010 are indicated for each site. Significant correlations are represented by blue shades for negative correlations and orange shades for positive ones. All non-significant correlations are set to 0.0 and appear white.

years was negatively correlated with temperature, while correlations between growth and August precipitation in both the previous and current years were positive (Fig. 4, part c). At the *Valley bottom*, tree growth throughout the growing season in both the previous and current years was negatively correlated with temperature, and positively correlated with July precipitation in both the previous and current years (Fig. 4, part d).

Changing Climate–Growth Relationships over Time

The climate–growth relationships of black spruce trees varied through time in patterns seemingly correlated with topographic position. At the *Summit*, significant positive correlations with temperature in December of the current year have diminished during the past decade, as have significant positive correlations with precipitation in April and August of the current year (Fig. 4, part a). At the *Side slope*, significant positive correlations with September precipitation of the previous and current years have disappeared in recent decades (Fig. 4, part b). At the *Toe slope*, significant correlations with April temperature in both the previous and current years remained strong throughout the past two decades (Fig. 4, part c). In contrast, significant negative correlations with spring and growing season (May–September) temperatures in both the previous and current years have diminished in the last decade at the *Valley bottom* at the same time that significant positive correlations with precipitation in July of the previous and current years, and September of the current year have developed there (Fig. 4, part d).

Inter-tree Growth Responses to Climate among Individual Trees

The climate–growth relationships (A.D. 1949–2010) of individual trees were not homogeneous. Examination of the *tree-level* climate–growth relationships revealed that trees at each site varied widely in their growth responses to climate (Fig. 5). Although the majority of trees at all four sites were negatively correlated with temperature (Fig. 5, part a) and positively correlated with precipitation (Fig. 5, part b), negative responses to temperature increased downslope, and positive responses

to precipitation tended to increase upslope. Hence, although the $-T+P$ multivariate response–type was common at all four sites, the percentage of trees exhibiting this particular growth response varied with topographic position (Fig. 5, part c). At the *Summit*, 59% of sampled trees were $-T+P$ responders, whereas 35% were $+T+P$ responders. At the *Side slope*, the two dominant response–types occurred in similar proportions, with 27% of trees being $+T+P$ responders and 27% of trees being $-TmP$ responders. Climate responses were particularly diverse among trees growing at the *Toe slope* and *Valley bottom* sites, where mixed responses to precipitation were more frequent than at the *Summit* and *Side slope* (Fig. 5, part c). At the *Toe slope*, the dominant response–type was $-TmP$ (39%), whereas at the *Valley bottom* the two dominant response–types occurred in similar proportions, with 25% of trees being $+T-P$ responders and 25% of trees being $-TmP$.

DISCUSSION

Our findings along the Babe Creek toposlope demonstrate that the climate–growth relationships of black spruce vary widely across topography, over time, and among individual trees within a site, and that both *growth–climate divergence* and *inter-tree growth divergence* are common occurrences. Collectively, *site-* and *tree-level* climate–growth relationships provide complimentary information describing the climate sensitivity of Alaska’s most abundant tree species.

Varying Sensitivity of Growth to Climate with Topography

These results complement dendrochronological studies elsewhere in the boreal forest that indicate the growth of black spruce is favored by cold and wet conditions (Brooks et al., 1998; Subedi and Sharma, 2013; Walker and Johnstone, 2014). In contrast, the growth of black spruce at treeline in the Brooks Range is limited by cool summer temperatures (Lloyd et al., 2005).

The *site-level* differences we observed in the growth responses of black spruce to climate are probably responses to differences in non-climatic factors such as hydrology, active layer thickness, soil temperature, and incoming solar radiation. All these factors vary according to topographic posi-

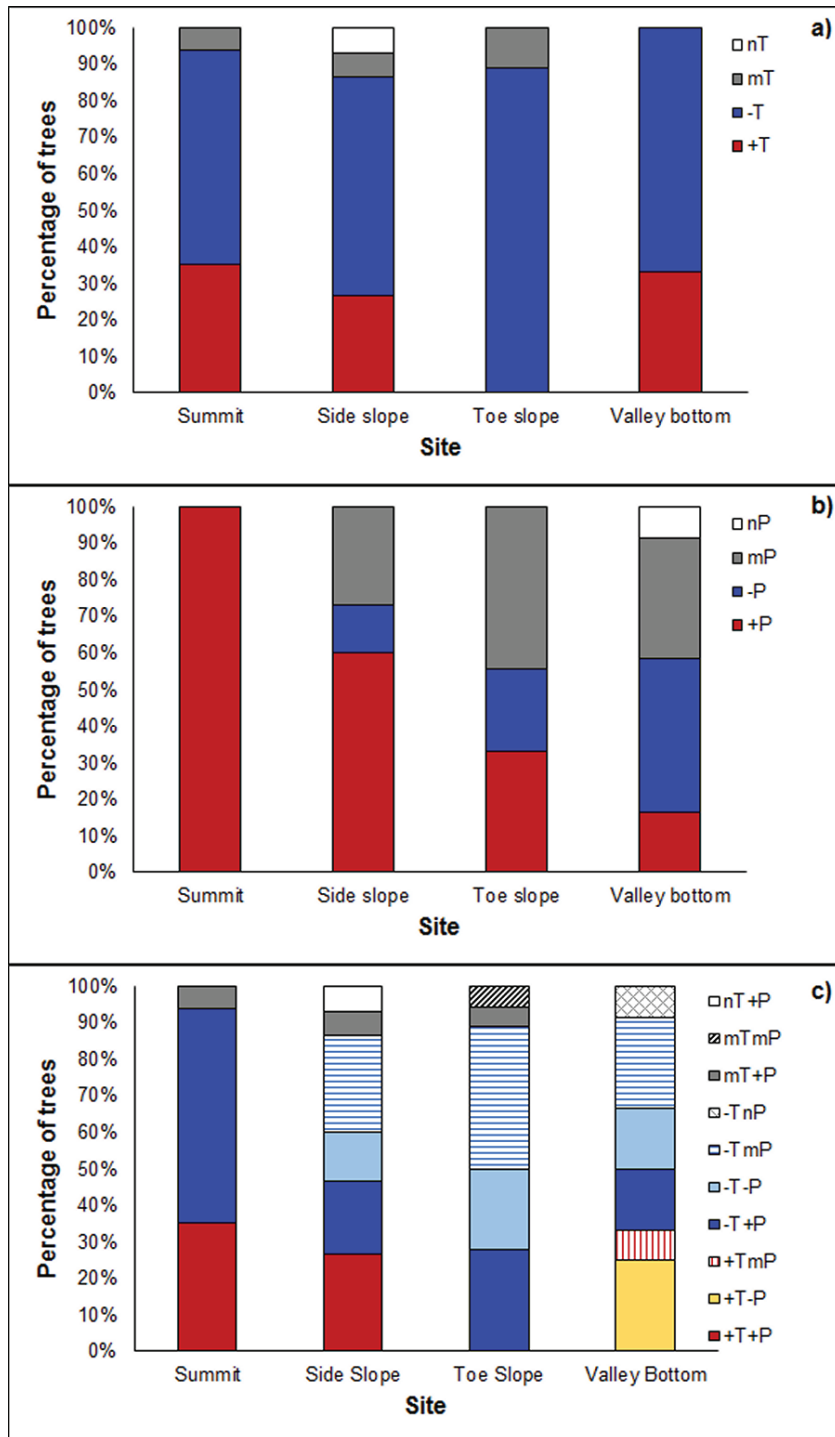


FIGURE 5. Individual trees differ in how they respond to climate, and these differences are associated with topographic position. Percentages are the trees at each site exhibiting positive (+), negative (-), mixed (m), and non-significant (n) responses to temperature (T) and precipitation (P). Trees were categorized by their univariate (e.g., +T refers to trees with a positive response to temperature) responses to (a) temperature and (b) precipitation, and (c) multivariate responses to both temperature and precipitation based on the results of a 50-year moving interval analysis for the period A.D. 1949–2010.

tion (Fig. 6), as site moisture is largely determined by topographic drainage, which in turn is controlled by permafrost (i.e., soil temperature and active layer thickness) and soil texture (Johnstone et al., 2008). For instance, the *Valley bottom* site has the wettest soils because it intercepts water moving downslope, which facilitates the rapid growth of mosses, which in combination with topograph-

ic shading and cold-air drainage creates the coldest soils with the thinnest active layers anywhere along the toposquence (Table 1). Cold soil temperatures and shallow active layers at both the *Toe slope* and *Valley bottom* probably restrict rooting depth to the top 20 cm of the soil profile (Van Cleve et al., 1983) and inhibit root growth (Ruess et al., 2003), which in turn may slow rates of water

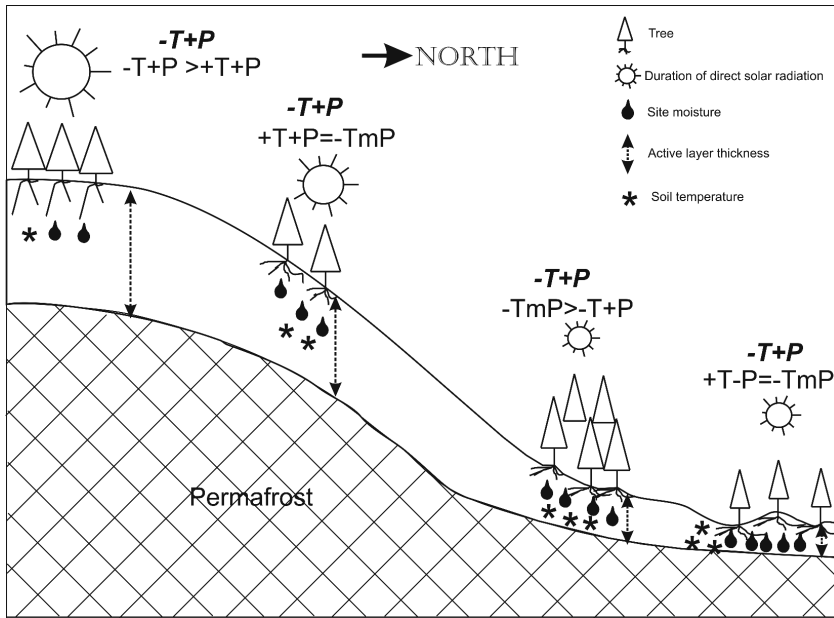


FIGURE 6. Schematic of north-facing Babe Creek toposequence illustrating the *site-level* (bold and italics) and dominant *tree-level* response-types observed, where “-,” “+,” and “m” refer to negative, positive, and mixed responses to temperature (T) and precipitation (P) (see also Fig. 4). Relative differences between sites are depicted for the density of trees, duration of direct solar radiation (size of symbol corresponds to the duration of direct solar radiation received throughout the 2011 snow-free season), site moisture (number of symbols corresponds to the amount of soil moisture), active layer thickness, and soil temperature (number of symbols corresponds to coolness of soil for May–Sept 2004–2010). Refer to Table 1 for exact values.

uptake (Wolken et al., 2011b) as well as lead to more rapid paludification during post-fire succession (Crawford et al., 2003).

Do Topography and Tree Architecture Interact to Determine Growth Responses to Climate?

Tree architecture differs markedly along the toposequence at Babe Creek (Fig. 7), and we speculate these differences may contribute to the observed variations in the growth responses to climate. By *tree architecture* we mean the integrated structure of root

and shoot anatomy incorporating all elements of vascular systems, support structures, and canopy arrays. This architecture is the product of the climate, microsite, and disturbance history that a tree has experienced over the course of its life (Pereg and Payette, 1998). It reflects the physiological stresses experienced in the past and partly determines how a tree responds to these stresses in the future.

Although the following studies document the phenotypic plasticity of black spruce, dendro-architectural studies of the above- and belowground growth of black spruce at the northwestern extreme of its range in Alaska are non-existent. Significant architectural dif-

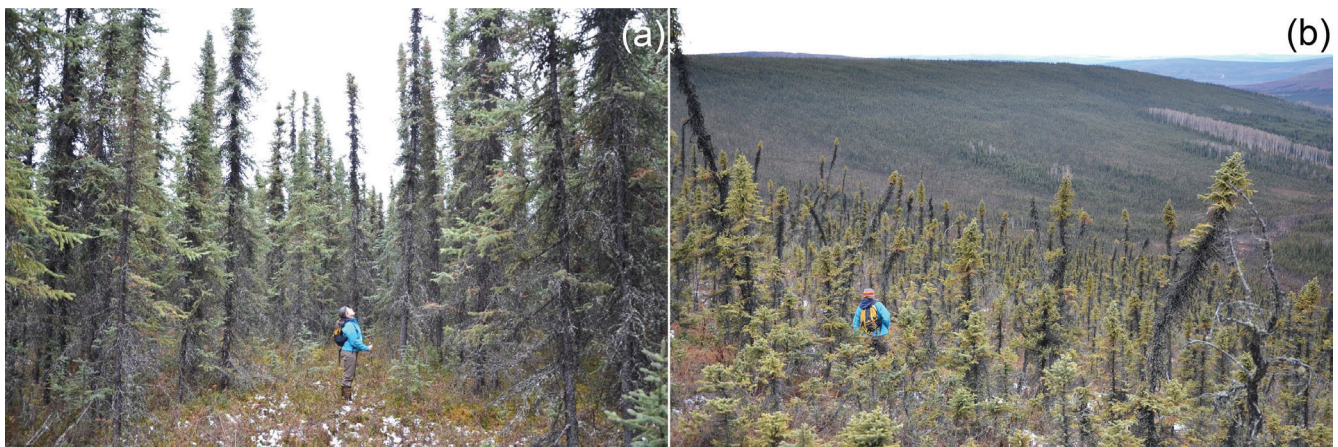


FIGURE 7. The architecture of individual black spruce trees differs widely between sites at Babe Creek: (a) *Summit*; and (b) *Side slope*. These differences likely contribute to the divergent ways these trees respond to climate at both the *site-* and *tree-level*.

ferences have been previously shown in black spruce in Interior Alaska, with more carbon being allocated to roots at lowland sites underlain by permafrost than at upland permafrost-free sites (Noguchi et al., 2012). In northern Manitoba, black spruce growing on discontinuous permafrost have greater total above- and belowground biomass than trees at wet sites (Wang et al., 2003). In the Québec subarctic, the aboveground growth and growth form of black spruce are strongly influenced by defoliation events that include both growing season frost events and mechanical defoliation caused by snow and ice abrasion (Payette et al., 1996). In a greenhouse study, black spruce established and grown at warmer air temperatures were shorter and also allocated more carbon to aboveground growth than to root growth than did trees grown under cooler conditions (Way and Sage, 2008). Decreased allocation of carbon to root growth can increase the susceptibility of trees to drought stress under a regime of periodic soil drying and thus decrease competitiveness for soil nutrients (Way and Sage, 2008). Pairing tree-ring studies with architectural studies similar to those described above may greatly expand our understanding of the processes by which black spruce modulates its growth in response to climate variability.

What Causes Black Spruce's Negative Growth Responses to Warm Spring and Growing Season Temperatures?

Trees at all four topographic locations generally responded negatively to warmer temperatures and positively to increased precipitation (Figs. 4 and 5). These negative responses to temperature are probably the result of reduced photosynthesis caused by water stress. This is the explanation given in previous studies for the negative effect of above average spring and summer temperatures on the radial growth of black spruce (Walker and Johnstone, 2014) and white spruce (Beck et al., 2011; Juday and Alix, 2012; Lloyd et al., 2013) in interior Alaska. In the case of white spruce, the occurrence of water stress is less surprising because this species can be found growing at the warmest, driest sites in the region. In contrast, black spruce can grow at the coldest, wettest sites including the north-facing toposequence at Babe Creek.

We speculate that two different mechanisms create drought stress in black spruce trees at Babe Creek

and that their importance depends on topographic position. The first mechanism is well documented in non-permafrost terrain and occurs when evapotranspiration outstrips the supply of soil moisture during periods of drought accentuated by above-average summer temperatures. This first mechanism is probably the most frequent cause of drought-induced reductions in growth at the relatively warm and well-drained *Summit* site where trees respond positively to increased precipitation in the spring and in late summer of both the previous and current year (Fig. 4, part a).

A second mechanism of drought stress may occur at the *Toe slope* and *Valley bottom* sites where cold, wet, and poorly aerated soils may cause water loss via transpiration to exceed the capacity of the roots to uptake water (Dang et al., 1991). Possible evidence for this rhizosphere-mediated drought stress at Babe Creek may be the downslope decline in the responsiveness of trees to enhanced summer precipitation and the downslope increase in negative responses to warm growing seasons (Fig. 5). Although soil water is not in short supply at these lower slope positions, physiological limitations on the uptake of this water may inhibit the growth of black spruce when air temperatures are unusually warm. Further evidence for the occurrence of drought stress arising in poorly aerated, cold soils comes from the negative response of tree growth to warm spring temperatures in the current year at all four sites (Fig. 4). Lloyd et al. (2013) observed similar negative growth responses of white spruce to warm air temperatures in March and April, which they attributed to drought stress caused by limitations on water uptake through roots in cold soils. This same phenomenon may explain the finding of Walker et al. (2015) that black spruce trees growing on north-facing slopes are more moisture limited than trees growing on south-facing slopes.

Changing Climate–Growth Relationships over Time

The climate–growth relationships of black spruce trees at Babe Creek have changed over time, varying with topographic position (Fig. 4). The complexity in these relationships may be compounded by interactions between environmental/ecological characteristics unique to each site (Table 1; Fig. 6),

such as active layer thickness, soil temperature (Fig. 2), solar radiation, and tree architecture occurring at the *site-* and *tree-level*. Snow depth and duration would also influence these relationships, as this north-facing toposequence would be snow covered for one to two weeks longer than south-facing slopes (Hinzman et al., 2006). Regional scale variables (e.g., May–September mean monthly temperatures) may further complicate these relationships.

Inter-tree Growth Responses to Climate among Individual Trees

Although many high-frequency, year-to-year responses to climate are shared among the trees we studied, the long-wavelength growth trends manifested at decadal time scales differed (see Pisaric et al., 2007). Accordingly, although there was a dominant response-type at each site, there was also considerable variability in the proportion of trees exhibiting each response-type (Fig. 5). We attribute our ability to cross-date trees within sites, despite the fact that individual trees displayed a variety of multivariate response-types, to the fact that cross-dating relies on the high-frequency responses of individual trees to annual and intra-annual variations in climate (Grissino-Mayer, 2001). These high-frequency responses are shared among most trees even though these same trees may be exhibiting divergent, low-frequency trajectories in their growth responses to climate.

Variability in *inter-tree growth responses* tends to be greater in lower slope positions at Babe Creek, with trees at the *Side slope*, *Toe slope*, and *Valley bottom* possessing more mixed responses to temperature and precipitation than trees at the *Summit* (Fig. 5, part c). A possible explanation for why response-type diversity increases downslope includes an increase in microtopographic variation (Fig. 6), which Wilmking and Myers-Smith (2008) suggested is an important factor in determining *inter-tree growth responses* among black spruce to climate. Even though black spruce can grow in cold, wet soils, it is sensitive to slight variations in soil moisture (Wolken et al., 2011b). At the *Valley bottom*, hummock and hollow topography has been created by a combination of frost heaving and the localized accumulation of *Sphagnum*-peat hummocks. These hummocks and hollows, together with patches of *aufeis* (overflow

ice) and occasional *palsas* (frost mounds), create a wider range of substrate conditions than are present in higher slope positions.

Evidence of Both Types of Growth Divergence

Black spruce trees at Babe Creek exhibit both *inter-tree growth divergence* and *growth-climate divergence*. The former is well illustrated by the high frequency of mixed growth responses to climate at the *Toe slope* and *Valley bottom* (Fig. 5, part c). *Growth-climate divergence* is evident in the changing signs and strengths of correlations between tree growth and temperature/precipitation over the life span of individual trees (Fig. 4). Clearly, divergence phenomena are characteristic of black spruce growing along this toposequence and probably occur throughout the range of this species. This interesting complexity may be one reason why dendrochronologists have tended to avoid using black spruce to construct climate-proxy records. It remains to be seen whether general patterns in black spruce's response to climate variability will emerge after accounting for site conditions, tree age, and tree architecture.

CONCLUSIONS

Simply identifying drought stress as the main climatic control over black spruce growth fails to reveal the full complexity of black spruce's responses to climate variability within the topographically complex, permafrost landscapes of interior Alaska. In this case study, the sensitivity of black spruce growth to climate varies over short distances in response to topography (Fig. 4) and differs strikingly among trees growing at the same sites (Fig. 5). This *inter-tree growth divergence* is especially pronounced at the coldest, wettest sites. We speculate that the cause of the differing climate-growth relationships relates to microsite variability and architectural differences between individual trees, which in turn reflect the highly plastic growth strategy that enables black spruce to exist in some of the most extreme settings for tree growth.

Our results also illustrate that even at the coldest, wettest sites in the boreal forest of interior Alaska, site moisture may limit the growth of black spruce (Figs. 4 and 5). The causes of this moisture stress

relate to topography and the seasonality of climate. With continued warming, this moisture-mediated sensitivity to warm temperatures may eventually inhibit black spruce productivity (Walker and Johnstone, 2014) and thus contribute yet another mechanism to the ecological regime shift predicted for the interior Alaskan boreal forest (Beck et al., 2011; Mann et al., 2012; Kelly et al., 2013).

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