

Local site conditions drive climate–growth responses of *Picea mariana* and *Picea glauca* in interior Alaska

E. FLEUR NICKLEN,^{1,2,†} CARL A. ROLAND,^{1,3} ROGER W. RUESS,²
JOSHUA H. SCHMIDT,¹ AND ANDREA H. LLOYD⁴

¹Central Alaska Network, National Park Service, 4175 Geist Road, Fairbanks, Alaska 99709 USA

²Department of Biology and Wildlife, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska 99775 USA

³Denali National Park and Preserve, National Park Service, 4175 Geist Road, Fairbanks, Alaska 99709 USA

⁴Department of Biology, Middlebury College, Middlebury, Vermont 05753 USA

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Abstract. The growth response of boreal forest trees to projected changes in climate will have wide ranging and cascading impacts on disturbance regimes, climate feedbacks, carbon storage, and habitat ranges for flora and fauna. Recent findings in Alaska suggest the boreal biome is shifting in response to changes in climate. It is unlikely such a shift will occur in a uniform manner over a landscape variable in topography and site conditions, although there is little consensus of how local site characteristics will interact with climate to alter tree growth patterns. Few studies of tree growth responses to climate in the boreal forest have used randomized study designs encompassing the full range of site conditions, leaving open the question of whether observed patterns in tree growth at local scales are wholly representative of the boreal forest. We addressed these issues using a systematic sampling design to quantify the landscape-scale patterns in annual growth for *Picea mariana* and *Picea glauca*, the two most abundant tree species in interior Alaska. We used measurements of annual tree growth based on increment cores taken from trees distributed across a 1.28 million-ha study area in Denali National Park and Preserve. We found site-specific variables, namely near-surface permafrost, slope angle, and elevation, strongly modified the magnitude, shape, and, in some cases, the direction of growth response to climatic conditions for both species. With predicted warming, our results suggest both *P. mariana* and *P. glauca* will decrease growth in areas underlain by shallow permafrost. *P. mariana* growth may increase on flat terrain, but decrease on steep slopes, while *P. glauca* growth will show the greatest increases at high elevations during very warm summers. Our results suggest future shifts in these species distributions in response to a changing climate will be conditional on variation in site factors operating at local scales.

Key words: boreal forest; climate–growth response; Denali National Park and Preserve; dendroecology; mixed-effects models; *Picea glauca*; *Picea mariana*.

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† **E-mail:** elizabeth_nicklen@nps.gov

INTRODUCTION

The boreal biome represents nearly 30% of the world's forested area (Kuusela 1990) and harbors 22% of the carbon contained in the terrestrial ecosystem (IPCC 2014). The impacts of predicted climate warming on the boreal forest are of particular concern because of amplified warming at

high latitudes. Alaska's boreal forest has warmed 1.9°C in the last half century, with an expected increase of 3–7°C by the end of the 21st century (Walsh et al. 2008, Bieniek et al. 2014, Chapin et al. 2014). Precipitation is also expected to increase, but not by enough to offset increased evapotranspiration caused by warmer temperatures and a longer growing season (Karl et al. 2009, Chapin

et al. 2014, Scenarios Network for Alaska and Arctic Planning [SNAP] 2014a). The boreal biome is expected to experience shifts in structure and function, potentially triggering feedbacks to the global climate system via changes in carbon cycling (Shaver et al. 1992, Cox et al. 2000, Schuur et al. 2008, 2015, Chapin et al. 2009, McGuire et al. 2009) and albedo (Euskirchen et al. 2009), further amplifying rapid changes in climate.

Alaska-wide analyses have generally shown decreased productivity in the interior boreal forest (Barber et al. 2000, Verbyla 2008, Beck et al. 2011, Juday et al. 2015) but increasing productivity in tundra areas (Verbyla 2008) and boreal-tundra ecotones (Beck et al. 2011, Juday et al. 2015) within the past half century. These results are consistent with findings from similar studies across boreal North America (Goetz et al. 2005, Bunn and Goetz 2006, Girardin et al. 2014) and circumpolar boreal forests, including Siberia (Lloyd and Bunn 2007, Lloyd et al. 2010). These changes in productivity have been broadly attributed to increases in summer air temperatures that promote growth in the colder and wetter areas of the region (Goetz et al. 2005, Verbyla 2008, Beck et al. 2011) and reduced growth as a result of increases in evaporative demand in the warmer reaches (Lloyd and Bunn 2007, Beck et al. 2011). Region-wide studies showing directional trends in productivity across climatic gradients are of fundamental importance for our broad sense of the current and future boreal biome footprint, but lack detail necessary for understanding how variable site conditions may modify directional trends in productivity. The response of the boreal forests in interior Alaska to climate change, at finer resolutions than regional scales, may depend on interactions among climate, topography, soil conditions (Sullivan et al. 2015, Swanson 2015), competition (Okano and Bret-Harte 2015), herbivory, species-specific responses, and disturbance history (Holtmeier and Broll 2007) and thus show different patterns than the global view of shifting biomes. Ignoring interactions between climate-growth responses and site conditions can lead to flawed predictions and biased conclusions (Sormunen et al. 2011) regarding the current growth and potential future footprint of the boreal forest.

Current studies of *Picea mariana* and *Picea glauca* offer conflicting evidence for the hypothesis that

local site characteristics will interact with climate to alter tree growth patterns. For instance, *P. mariana* in interior Alaska growing in low-lying peatlands were insensitive to interannual variation in temperature, while trees growing in nearby uplands were negatively affected by increased summer temperatures (Wilmking and Myers-Smith 2008). Similarly, the thickness of the soil organic layer can result in contrasting responses to summer warming (Gewehr et al. 2014). Yet others have found landscape position and stand characteristics to be poor predictors of *P. mariana* growth response to climate, with negative growth responses to warm growing seasons observed regardless of topography (Walker and Johnstone 2014). *Picea glauca* may respond differently to climate conditions depending on proximity to treeline, potentially as a result of reduced competition at higher elevations (Ohse et al. 2012, Okano and Bret-Harte 2015). Yet Wilmking et al. (2004) found no consistent relationship between landscape position in the Alaska and Brooks ranges and *P. glauca* growth response to climate. Conflicting results have also been reported with respect to how slope aspect mediates *P. glauca* response to climate (e.g., Wilmking et al. 2004, 2006, Johnstone et al. 2010). These conflicting findings demonstrate the potential for trees of interior Alaska to have site-specific response, suggesting that further analysis focusing on site-climate interactions across full landscape gradients is warranted.

Uncertainty about the magnitude and direction of the effects of climate on boreal tree growth in different site conditions highlights the need for an unbiased quantification of tree species growth response to climatic conditions across the full range of site variables. It is a primary principle in tree-ring science that site conditions largely dictate the degree to which annual tree growth varies in response to climate (Fritts 1976), and site selection governs the inferences that can be drawn about the relationship between forest growth and climate. Nonrandom site selection allows inferences to be drawn only about the fragments of landscape where trees were sampled. Global climate change affects the whole landscape, although few studies in the boreal forest have quantified climate-growth relationships across an extensive heterogeneous landscape using an unbiased and spatially balanced study

design (but see Girardin et al. 2012, 2016, Gewehr et al. 2014, DeRose et al. 2016, Foster et al. 2016). Studies with nonrandom selection of sample sites can provide significantly different results than studies with randomly chosen sample sites (Michalcová et al. 2011), demonstrating that true landscape-level inference requires randomized site selection across the full range of conditions within the sampling area.

Our goal was to quantify the annual radial growth of *P. glauca* and *P. mariana* in relation to site and climate factors using data gathered at the landscape scale via an unbiased, systematic sampling design. We predicted that warmer growing season temperatures would decrease the growth of both *P. mariana* and *P. glauca* in the warmer and/or drier locations within the landscape (south-facing slopes below treeline; e.g., Brooks et al. 1998, Barber et al. 2000, McGuire et al. 2010, Beck et al. 2011, Lloyd et al. 2013). We also predicted that increased precipitation would be positively associated with the growth of both spruce species when growing in the well-drained landscape positions (e.g., steep slopes), but that precipitation would have little or a negative association with the growth of both species growing in areas where drainage is poor. We also predicted that trees with perched root systems due to high water tables in valley bottoms or near-surface permafrost would show reduced growth during very warm growing seasons (e.g., Dang and Lieffers 1989, McGuire et al. 2010, Walker and Johnstone 2014), while the growth of *P. glauca* growing at treeline would be positively related to warm growing seasons (Lloyd and Fastie 2002, Roland et al. 2014, Okano and Bret-Harte 2015). To assess these predictions, we quantified the radial growth response of *P. glauca* and *P. mariana* to climate across the landscape to (1) determine the direction and magnitude of site variables' influences on the responses of both spruce species to climate conditions and (2) identify climate optima for the two species' growth across a range of landscape variables.

METHODS

Study area

The study area is located almost completely on the north side of the Alaska Range in south-central interior Alaska DNPP and encompasses

12,800 km² with a center near 63°41' N, 150°25' W (Fig. 1). The study area experiences a continental climate compared with the area south of the mountain range with extreme low temperatures in the winter (mean January temperatures between −30° and −20°C in the Kuskokwim–Minchumina Basin to between −14° and −6°C in the Alaska Range) and warm temperatures in the summer (mean July temperatures range between 14° and 18°C in the lowland basins to between 2° and 10°C in the Alaska Range) (1971–2000 monthly PRISM averages [Fig. 1]; Daly 2009). Annual precipitation ranges from less than 400 mm in the lowland basins to over 1000 mm in the Alaska Range (1971–2000 annual PRISM averages; Daly 2009).

The terrain within the study area includes Alaska Range peaks over 2400 m in elevation, which grade northwest into foothills and eventually into the Kuskokwim–Minchumina Basin lying at 200 m in elevation (Fig. 1). Approximately one quarter of our study area is underlain by near-surface permafrost (Panda et al. 2014) with much of the continuous and discontinuous permafrost concentrated in the lowland basins in the northern part of the study area.

Within the study area, *Picea glauca* is the most common tree species, occurring most frequently and growing to greatest diameter on moderate slope angles at mid-elevations (450–500 m) in sites with high solar gain and no permafrost (Roland et al. 2013). *Picea mariana* is the second most common tree species in the study area. Although *P. mariana* achieves its greatest diameter in sites similar to where *P. glauca* occurs most frequently and grows best, *P. mariana* is most abundant on flat sites at low-elevation areas with cold, wet permafrost soils (Roland et al. 2013).

Sampling design

Plot locations were established using a two-stage systematic grid sampling design (Roland et al. 2013). In the first stage, a “macrogrid” of 20-km intervals was established, except within a 6-km buffer on either side of the DNPP road corridor the grid intervals were 10 km. In the second stage, a “minigrid,” consisting of five rows of five plots separated by 500 m, was set at each grid intersection of the macrogrid. Of the 43 minigrids and 1100+ plots visited, we cored (and cross-dated) 500 trees from a total of 28 minigrids

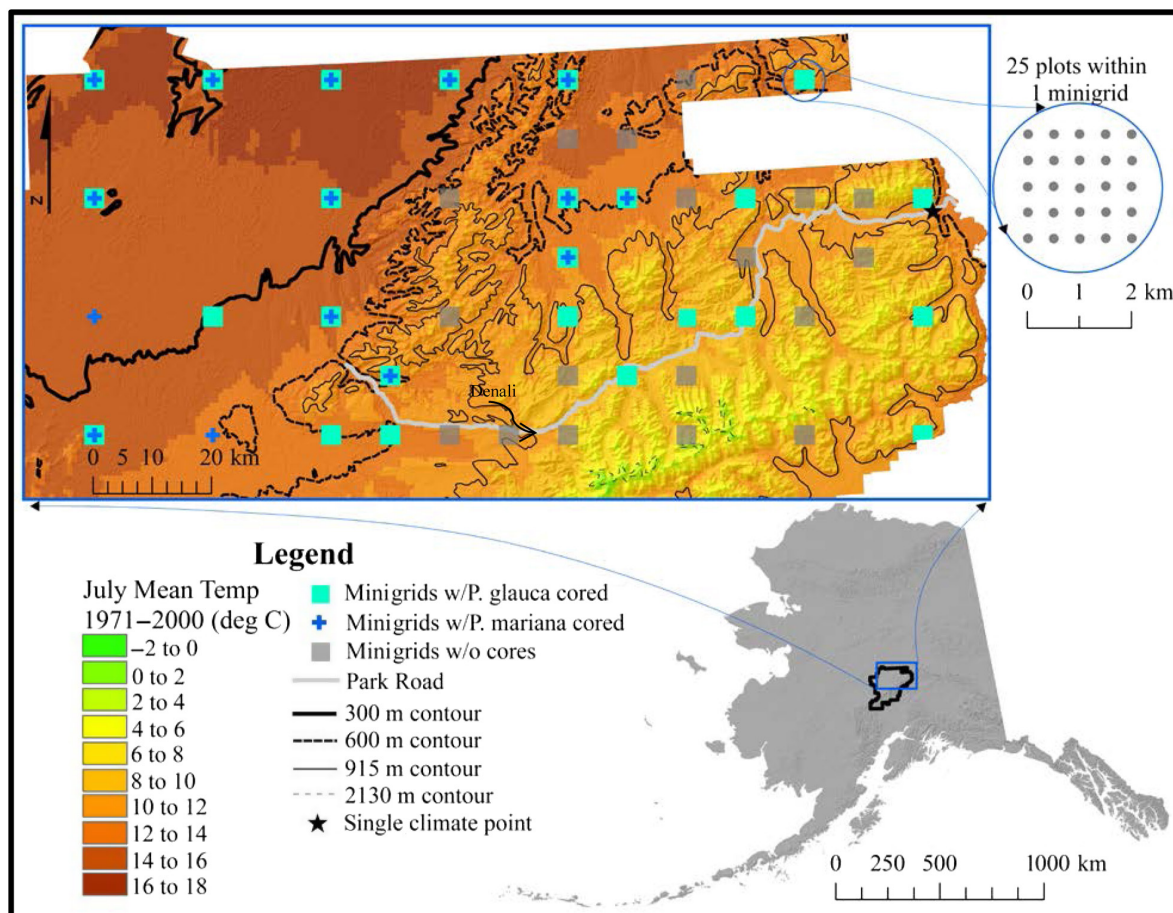


Fig. 1. A map showing location of plots with the study area of Denali National Park and Preserve. Information is provided about species cored (*Picea glauca* and *P. mariana*) at plots, mean July temperatures, major elevation contour lines, and the location of the single point climate data.

(Fig. 1) and 222 plots. Many of the minigrids and plots did not have trees because they were above treeline or contained areas too wet, or recently disturbed to support trees.

Each of the 25 points within a minigrid consisted of a 16 m diameter inner plot with an outer plot extending an additional 10 m radius. At each inner plot, we measured elevation, slope angle, and aspect. We used a 1.3-m soil probe to obtain the distance from the soil surface to an immovable object (either rock or frozen soil) in 16 locations. The outer plot area was divided into four quadrants. In each quadrant, we dug a soil pit to a 30-cm depth to measure soil characteristics. Soil temperatures were recorded at 10 cm depth at each soil pit. We sampled during the months of June–August in the years between 2003 and 2010.

Tree-ring measurements

We cored the largest tree within the four quadrants of outer plot area, although some of the sites had fewer than four trees to core or the trees were too small for coring (<5 cm at 1.37 m above ground surface). We extracted a bark-to-bark core (whenever possible) as low to the base as possible while avoiding buttressing or unusual growth to maximize the number of growth rings obtained. Dried, mounted and sanded cores were sent to the tree-ring laboratories at either Middlebury College in Vermont, United States, or Greifswald University in Germany where they were measured to the nearest 0.001 mm and cross-dated. Ring measurements were taken using WinDENDRO Image Analysis system (Regent Instruments) in the Middlebury College

tree-ring laboratory and with a Velmex sliding stage at Greifswald University. Cross-dating was validated using COFECHA and the Dendrochronology Program Library in R (dplR; Bunn 2010).

After averaging replicate ring widths by year from multiple radii taken from one tree, we used ring widths and tree radius to calculate basal area increment (BAI), the area of wood produced by each tree during each year of growth. In contrast to raw ring widths, BAI facilitates comparisons among trees of differing diameters. BAI also has a more direct relationship to area of wood produced by a tree than standardized ring widths. We used the tree diameter at the core location divided into half, with average bark width subtracted to estimate the radius. If the sum of the ring widths was larger than this radius, we used the ring width sum as the radius. We did this to avoid underestimated radius values that occur in cores with missing inner rings (due to rot or missing the pith). We used the radius to calculate the total basal area of the tree and then sequentially subtracted the ring width of the next inner ring from the radius and calculated the basal area of the previous year and so on. By subtracting the basal area of year $X - 1$ from the basal area of year X , we obtained the “washer”-shaped area of wood accreted at the core located in year X (i.e., BAI; following Johnson and Abrams 2009).

Site and climate variables

Based on results from a previous study of tree abundance in DNPP (Roland et al. 2013), we chose elevation and slope angle as explanatory site variables expected to influence spatial patterns in spruce growth while remaining relatively constant over the time period for which we have climate and BAI data. Elevation was recorded at the center of each plot with a global positioning system (GPS, GeoExplorer2; Trimble, Sunnyvale, California, USA). We measured slope angle both for the overall plot location and directly at the base of each cored tree (Tables 1 and 2).

We also calculated three variables related to plot aspect and solar gain (Tables 1 and 2). First, we calculated two measures of slope aspect: southness = $\cos(\pi \times (\text{aspect} + 180)/180)$ and eastness = $\sin(\pi \times \text{aspect}/180)$, following Pereira and

Table 1. Site variables tested in the first stage of the variable selection process.

Site covariates	Competing site covariate
Plot slope, plot slope ²	Tree slope, tree slope ²
Growing season shallow frozen soil (GsSFS)	Permafrost category (soil map)
Solar radiation	Southness/eastness
Elevation	
Lithology†	

Note: Highly correlated variables, shown in columns, were competed in separate models.

† Lithology was only included in the *Picea glauca* models as this variable is an important predictor of *P. glauca*, but not *P. mariana*, occurrence in DNPP (Roland et al. 2013).

Itami (1991). This calculation results in continuous values ranging from -1 to 1 , with maximum values for southness and eastness occurring on slopes with aspects of 180° and 90° , respectively (Table 2). Plots with slope angles $<4^\circ$ were considered flat and assigned 0 for both measures of aspect. Finally, we used the Solar Analyst tool in ArcGIS 10.0 (Dubayah and Rich 1995), which uses slope angle, aspect, latitude, sun angle, and surrounding topography (based on the United States Geological Survey 60-m digital elevation model from the National Elevation Dataset) to determine radiation values for a given topographic surface (Rich et al. 1994).

We also considered several substrate-related covariates. We used ArcGIS 10.0 to extract soil lithology type and permafrost status based on the work of Clark and Duffy (2006). We condensed soil lithology type to the following five types: bedrock, alluvium, drift, Nenana gravels, and eolian. Because soil lithology was an important predictor for the occurrence of *P. glauca*, but not *P. mariana* in DNPP (Roland et al. 2013), this categorical variable was considered only in the *P. glauca* candidate models (Table 1). We calculated permafrost status in two ways. First, we categorized each plot as continuous, discontinuous, or no permafrost based on the Denali Soil Map (Clark and Duffy 2006). Secondly, we created a yes/no “growing season shallow frozen soil” (GsSFS) based on field measurements. The plot was classified as having growing season shallow frozen soil if the average of 16 soil depths measured within each plot using a 130-cm soil probe was less than 50 cm and we found ice in the one of the four soil pits. The plot was also classified as

Table 2. The mean, SD, minimum, and maximum values observed for each continuous site and climate variable competed in the model selection process for *P. mariana* and *P. glauca*.

Variables	<i>Picea mariana</i>				<i>Picea glauca</i>			
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
Site variables								
Age proxy (ring count)	59	48	1	331	80	54	1	343
Plot elev (m)	308	190	154	874	618	220	162	1017
Plot slope (°)	4.5	5.7	0.0	25.0	9.0	7.8	0.0	36.0
Slope at tree (°)	4.6	6.6	0.0	28.0	9.0	8.4	0.0	35.0
May–Aug solar rad. (WH/m ²)†	496,988	21,620	400,531	567,660	519,370	40,613	388,882	607,380
Southness	0.0	0.4	−1.0	1.0	0.2	0.5	−1.0	1.0
Eastness	0.0	0.5	−1.0	1.0	0.1	0.5	−1.0	1.0
Climate variables								
T May	8.3	2.1	1.0	13.9	6.0	1.6	1.5	10.0
P May	25	13	2	91	25	16	2	85
T Jun–Aug	14.1	1.7	9.0	18.6	11.7	1.0	9.9	15.1
P Jun–Aug	175	58	59	530	193	54	95	337
T Sep	6.0	1.6	1	10.5	4.8	1.4	1.8	9.0
P Sep	43	24	6	180	42	24	4	124
P Oct–Apr	155	62	42	498	156	42	64	261

Notes: For *P. mariana*, there were 11,176 BAI measurements from 143 trees, 72 plots, and 15 minigrids, and for *P. glauca*, there were 30,425 BAI measurements from 357 trees, 159 plots, and 26 minigrids. The climate variables for *P. mariana* were interpolated for each plot; the climate data for *P. glauca* were from a single location. The spatially interpolated climate values were extracted from each plot location where *P. mariana* were cored and for each year for which we have a BAI value from that plot location. The single point climate values were extracted from one location (63.720103 N, −148.963606 W) near park headquarters around 880 m in elevation (Fig. 1). T = mean temperature (°C) and P = precipitation sum (mm).

† Units for solar radiation are the sum of watt hours per square meter.

having GsSFS if the four soil temperatures taken at the plot were all below 1°C. If these criteria were not met, the plot was classified as not having growing season shallow frozen soil.

We used two sources of climate data for analysis (Table 2). First, we considered downscaled spatially interpolated temperature and precipitation data provided by Scenarios Network for Alaska and Arctic Planning (SNAP 2014b; Retrieved in 2014 from <https://www.snap.uaf.edu/tools/data-downloads>; temperature version CRU TS 3.1 and precipitation version CRU TS3.1.01) for the years 1902–2009. These data provide estimates of historical monthly climatic conditions for any given location in Alaska at ~1-km spatial resolution. SNAP downscaled data for Alaska to a finer grid resolution (771 m) using PRISM (Parameter–elevation Relationships on Independent Slopes Model) which incorporates information on location, elevation, coastal proximity, topographic facet orientation, vertical atmospheric layer, topographic position, and orographic effectiveness of the terrain (Daly et al. 2008). For each plot location with cored trees and each year for which we had tree-ring data within

1902–2009, we extracted the monthly mean temperature (°C) and precipitation sum (mm). We also considered climate data from this same spatially interpolated data set, but from a single location within our study area (Table 2; Fig. 1; see *Model construction and data analysis* section for details).

We selected 13 climate variables for consideration based on past work (Table 3). Because many studies have found climate conditions in the previous growing seasons are correlated with spruce growth in the current year (Dang and Lieffers 1989, Barber et al. 2000, Wilmking et al. 2004, Lloyd et al. 2013, Walker and Johnstone 2014, Girardin et al. 2016), we included climate variables from June through August (Jun–Aug_{ringyr-1}) and September (Sep_{ringyr-1}) in the year prior to ring growth. Because some studies have found evidence of temperature-induced drought stress, particularly in spring (Juday and Alix 2012, Walker and Johnstone 2014), we included winter precipitation sum (October through April preceding ring development) as snow pack contributes to the recharging of water reserves in spring (Girardin and Wotton 2009).

Table 3. Climate covariates included in the second stage of the variable selection process: mean temperature (T, °C) and precipitation sum (P, mm).

Number	Climate variables tested
1	T Jun–Aug _{ringyr–1}
2	T Jun–Aug + T Jun–Aug ² _{ringyr–1}
3	P Jun–Aug _{ringyr–1}
4	T Sep _{ringyr–1}
5	T Sep + T Sep ² _{ringyr–1}
6	P Sep _{ringyr–1}
7	P OctApr
8	T May _{ringyr}
9	T May + T May ² _{ringyr}
10	P May _{ringyr}
11	T Jun–Aug _{ringyr}
12	T Jun–Aug + T Jun–Aug ² _{ringyr}
13	P Jun–Aug _{ringyr}

Note: The subscripts ringyr and ringyr–1 indicate climate from the year the annual ring was formed and from the year prior to ring formation, respectively.

Finally, we included mean temperature and precipitation sum for May and June through August in the year of ring growth. We expected a non-linear relationship between climate variables and BAI (Lloyd et al. 2013) and thus included quadratic terms for temperature variables (Table 3). Although a nonlinear relationship may exist between BAI and precipitation, this term was kept linear because gridded precipitation data are notoriously inaccurate (McAfee et al. 2014) and we wanted to avoid identifying spurious relationships in our models.

Age-related variable

We included a minimum age term to account for growth trends over time in the BAI series for each tree. The mean growth curves in our study area show increasing basal area when young and decreasing or variable basal area when older (Appendix S1: Fig. S3). We considered three alternative age curves: a straight line, a quadratic function, and a cubic function. Our minimum age term was the ring count, with the inner most ring assigned 1 and the outer most ring assigned the total ring count (Table 2). The count of rings is an underestimated approximation of tree age as we missed early rings by not coring directly at the ground surface and because we did not always hit the pith. Because the ring count does not accurately reflect actual age, we did not interpret the coefficient values for this term.

Model construction and data analysis

We used linear mixed-effects models to quantify the annual basal area growth response to site and climate variables for *P. glauca* and *P. mariana*. We log-transformed BAI for each species and modeled the growth response of the two species separately. Each of the continuous predictor variables was standardized to have a mean = 0 and SD = 1. Our base model included age proxy as a main effect and growth year and minigrid as random effects to account for nonindependence of BAI measurements within a given growth year and within plots spatially clustered into minigrids. The base model additionally included an autoregressive (AR1) random effect for each individual tree to account for temporal autocorrelation. All other candidate models were built upon this base model. We used the lme4 package (Bates et al. 2014, version 1.1-7) in program R for fitting mixed-effects models (R Development Core Team, 2014, version 3.1.1).

We expected site and climate variables to explain variation in growth in different ways, with site covariates explaining mean growth patterns across trees and climate and interaction terms explaining annual variability around the mean. For this reason, we found it most appropriate to separate the model selection process into two stages. In the first stage, candidate models were constructed and fit using nearly all possible combinations of site variables (57 different models for *P. mariana* and 51 for *P. glauca*). Highly correlated variables, such as the two measures of slope or measures of solar radiation and aspect, were never included in the same model but were instead competed in separate models (Table 1). We used Akaike information criterion (AIC) to select among competing site models (Burnham and Anderson 2002). A potential pitfall in selecting site variables in isolation from climate variables is that we may miss important site variables if strong site–climate interactions exist. To avoid this, we fit our top site models, those with AIC values within two points of the model with the lowest AIC value, with the full suit of climate and climate–site interactions. To avoid overfitting, the full suit of climate–site interactions included only the two most important site variables (highest estimate value) and excluded interactions with site variables with more than two categories.

From this subset of models we chose the site variables from the most parsimonious model with AIC values within two points of the lowest AIC value (Appendix S2: Tables S1 and S3). The site variables were then used in stage 2 of model selection.

In the second stage, we added the climate variables and interactions terms to the selected site variables from stage 1. Importantly, elevation is highly correlated with summer temperatures in the spatial climate data ($R^2 > 0.7$; Appendix S1: Fig. S1). If elevation was identified as an important site variable in the first stage, we used climate data from the single climate station located within the study area (Fig. 1) to avoid multicollinearity. If elevation was not an important site variable, we used the spatial climate data as we expected these data to be more representative of local climate at the plot locations. Using the same AIC selection process as in the first stage, we fit models with multiple combinations of climate variables and interaction terms ranging from the full model to models with only a few climate and interaction terms (Appendix S2: Tables S2 and S4). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity, normality, or temporal autocorrelation. Variables in the selected models were considered interpretable if the 95% confidence intervals (estimate $\pm 1.96 \times \text{SE}$ of estimate) around the estimate did not overlap zero or were not within 0.001 of zero. Unless specifically noted, we report model outputs with all other parameters set to mean values.

RESULTS

Site variables

The presence of growing season shallow frozen soil (GsSFS) significantly reduced the overall radial growth of both *Picea mariana* and *Picea glauca* (Table 4). Elevation was negatively related to *P. glauca* radial growth, but was not an important site variable for *P. mariana*. The addition of plot slope improved model fit only for *P. mariana*, although its influence on BAI prior to the addition of interactions was not significant (Table 4). For both species, the random autoregressive term by individual tree explained the most variance in BAI (Appendix S2: Table S5), while the random effects for year and minigrid explained considerably less variation.

Site by climate variables—*Picea mariana*

Site and climate main effects.—The presence of GsSFS reduced the estimated mean *P. mariana* BAI by 6% (11 mm²/yr). Elevation was not identified as an important predictor; therefore, the climate relationships were based on the spatial climate data. *Picea mariana* BAI was positively related to precipitation sums during May and Jun–Aug_{ringyr-1}. *P. mariana* BAI showed a “humped” response to mean Jun–Aug_{ringyr-1} and Sep_{ringyr-1}, but a positive response to Jun–Aug_{ringyr} temperatures (Table 4, Fig. 2; Appendix S1: Fig. S4). These responses to summer precipitation and temperature were modified by the presence of GsSFS and slope angle (interaction effects are detailed below). Increasing May temperatures had a negative effect on *P. mariana* radial growth irrespective of GsSFS or slope angle (Table 4).

GsSFS—climate interactive effects.—Although GsSFS had a net negative effect on *P. mariana* BAI, the negative effect was minimized or reversed in cool summers and maximized during very wet summers. During particularly cool summers, with mean Jun–Aug temperatures less than 12°C, the BAI of *P. mariana* in areas with GsSFS was similar or greater than BAI in areas without GsSFS (Fig. 3A). BAI of *P. mariana* growing in areas with GsSFS decreased linearly with increasing mean Jun–Aug_{ringyr-1} temperature, while *P. mariana* in areas without GsSFS increased with summer temperature until about 14°C after which radial growth declined (Fig. 3A). The presence of GsSFS substantially reduced the benefit of Jun–Aug precipitation to *P. mariana* wood accretion (Fig. 3B). During wetter than average summers, with Jun–Aug precipitation sums greater than 300 mm, *P. mariana* growing with GsSFS was estimated to have 11–20% less radial growth (22–38 mm²/yr) than trees on well-drained sites without GsSFS (Fig. 3B). Similarly, the presence of GsSFS reduced *P. mariana* radial growth with increasingly wet conditions in the September prior to ring formation (Fig. 3C).

Slope—climate interactive effects.—The shape of *P. mariana* radial growth response to prior growing season temperature and to a much lesser extent, precipitation, depended on plot slope angle. First, *P. mariana* BAI on steeper slopes had an overall negative response to increasing temperatures in the summer prior to

Table 4. Coefficient estimates (± 1 SE) for significant relationships between log-transformed basal area increment and model covariates in the final model for each species.

Covariates and interactions	<i>Picea mariana</i> (interpolated climate)	<i>Picea glauca</i> (single climate location)
	Estimate $\pm$ SE	Estimate $\pm$ SE
Site covariates		
Intercept	5.196 $\pm$ 0.196	5.870 $\pm$ 0.022
Age proxy	-0.023 $\pm$ 0.007	-0.027 $\pm$ 0.007
Age proxy ²		-0.024 $\pm$ 0.003
Age proxy ³		0.007 $\pm$ 0.001
Elevation of plot	(not included)	-0.046 $\pm$ 0.013
Slope of plot		(not included)
Growing season shallow frozen soil (GsSFS)	-0.054 $\pm$ 0.016	-0.061 $\pm$ 0.021
Lithology	(not included)	
Climate covariates		
T May _{ringyr}	-0.040 $\pm$ 0.016	
T May ² _{ringyr}		
P May _{ringyr}	0.019 $\pm$ 0.007	
T Jun–Aug _{ringyr-1}		
T Jun–Aug ² _{ringyr-1}	-0.023 $\pm$ 0.007	
P Jun–Aug _{ringyr-1}	0.021 $\pm$ 0.010	
T Jun–Aug _{ringyr}	0.056 $\pm$ 0.019	0.048 $\pm$ 0.013
T Jun–Aug ² _{ringyr}		
P Jun–Aug _{ringyr}		
T Sep _{ringyr-1}		0.024 $\pm$ 0.011
T Sep ² _{ringyr-1}	-0.009 $\pm$ 0.003	
P Sep _{ringyr-1}		
P Oct–Apr		
Site $\times$ climate interactions		
GsSFS $\times$ T May _{ringyr}		-0.012 $\pm$ 0.003
GsSFS $\times$ T May ² _{ringyr}		
GsSFS $\times$ P May _{ringyr}		
GsSFS $\times$ T Jun–Aug _{ringyr-1}	-0.046 $\pm$ 0.012	
GsSFS $\times$ T Jun–Aug ² _{ringyr-1}	0.021 $\pm$ 0.007	
GsSFS $\times$ P Jun–Aug _{ringyr-1}	-0.027 $\pm$ 0.006	
GsSFS $\times$ T Jun–Aug _{ringyr}		
GsSFS $\times$ T Jun–Aug ² _{ringyr}		
GsSFS $\times$ P Jun–Aug _{ringyr}		
GsSFS $\times$ T Sep _{ringyr-1}		-0.014 $\pm$ 0.003
GsSFS $\times$ T Sep ² _{ringyr-1}		
GsSFS $\times$ P Sep _{ringyr-1}	-0.018 $\pm$ 0.006	
GsSFS $\times$ P OctApr		
Slope $\times$ T May _{ringyr}		(Elev) -0.009 $\pm$ 0.002
Slope $\times$ T May ² _{ringyr}		(Elev)
Slope $\times$ P May _{ringyr}		(Elev)
Slope $\times$ T Jun–Aug _{ringyr-1}	-0.028 $\pm$ 0.005	(Elev) -0.006 $\pm$ 0.002
Slope $\times$ T Jun–Aug ² _{ringyr-1}	0.008 $\pm$ 0.002	(Elev)
Slope $\times$ P Jun–Aug _{ringyr-1}	-0.006 $\pm$ 0.003	(Elev) -0.003 $\pm$ 0.001
Slope $\times$ T Jun–Aug _{ringyr}		(Elev) 0.015 $\pm$ 0.002
Slope $\times$ T Jun–Aug ² _{ringyr}	-0.008 $\pm$ 0.002	(Elev)
Slope $\times$ P Jun–Aug _{ringyr}		(Elev) -0.007 $\pm$ 0.001
Slope $\times$ T Sep _{ringyr-1}		(Elev) -0.004 $\pm$ 0.002
Slope $\times$ T Sep ² _{ringyr-1}		(Elev) 0.003 $\pm$ 0.001
Slope $\times$ P Sep _{ringyr-1}		(Elev)
Slope $\times$ P OctApr		(Elev) 0.005 $\pm$ 0.002

Notes: The model for *P. mariana* includes climate data interpolated across the landscape, while the model for *P. glauca* includes elevation and climate data from a single location. Note that in this table, elevation replaces slope in the site-by-climate interactions for *P. glauca*. “Not included” indicates a variable was not included in the model selection process, while a blank cell indicates the variable was included and found not significant.

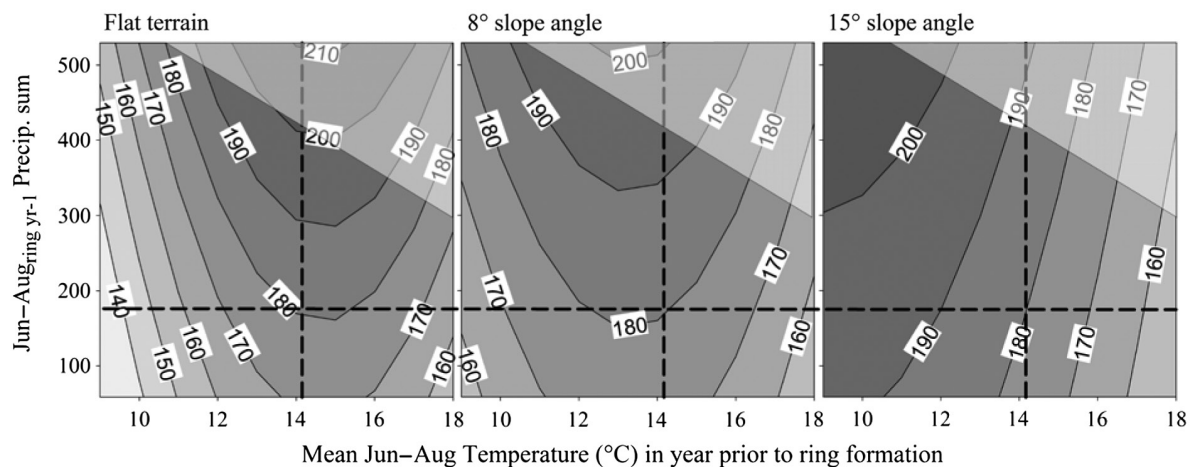


Fig. 2. The modeled relationship of *Picea mariana* basal area increment (BAI, mm²/yr; in white boxes) to climate conditions in Jun–Aug in the year prior to ring formation for trees growing on flat, 8°, and 15° slope angles. Mean temperature (°C) values and precipitation (mm) sums span the range experienced in the plot years (1902–2009) for which we had *P. mariana* BAI measurements; mean climate values are shown in dashed lines. The transparent triangular area represents combinations of high temperature and high precipitation that were unobserved in our sample. BAI values are for areas without GsSFS, and all model variables not shown were held at mean values.

growth, while the BAI of *P. mariana* on flat or moderately sloped surfaces increased radial growth with increasing summer temperatures to a certain point and then decreased growth (Fig. 2; Appendix S1: Fig. S4A). Second, optimum Jun–Aug temperatures for radial growth declined with increasing slope angle (Fig. 2; Appendix S1: Fig. S4A). Specifically, estimated optimum Jun–Aug_{ringyr-1} temperature for BAI growth dropped from 14.8°C on flat terrain to 13.5°C on 8° slopes to 9°C on 15° slopes. The positive radial growth response to current summer temperatures was only moderately influenced by slope angle: *P. mariana* radial growth on 15° slope angles did not increase above 16°C, while trees on flatter terrain increased linearly with current summer temperatures (Appendix S1: Fig. S4B). Overall, *P. mariana* had a strong positive growth response to increasing Jun–Aug precipitation regardless of slope angle, although sensitivity to precipitation did peak on flat terrain and modestly declined on steeper slopes (Fig. 2, Table 4).

Site by climate variables—*Picea glauca*

Site and climate main effects.—Mean predicted BAI for *Picea glauca* growing in average climatic conditions and without GsSFS was 354 mm²/yr.

This value is about double the predicted *P. mariana* mean BAI over the same period. The presence of GsSFS decreased mean *P. glauca* radial growth by an estimated 21 mm²/yr (6% decrease). Overall, elevation was negatively related to annual radial growth with *P. glauca* growing at 1000 m in elevation producing 18% less basal area annually than *P. glauca* growing at 200 m in elevation. Because elevation was determined to be an important site variable, climate data from a single location within the study area were used in place of the spatial climate data. Temperatures in the summer of ring formation and the September prior to ring formation were positively related to *P. glauca* radial growth, although the relationship changed depending on the presence of GsSFS and elevation.

GsSFS—climate interactive effects.—*Picea glauca* in areas with GsSFS had a different growth response to May and September temperatures than trees in areas without GsSFS (Fig. 4). An increase in mean May temperature from 1.5° to 10°C had no effect *P. glauca* radial growth in areas without GsSFS, but decreased radial growth by an estimated 6% in areas with GsSFS (Fig. 4A). *P. glauca* BAI responded positively to mean Sep_{ringyr-1} temperatures, but the presence of

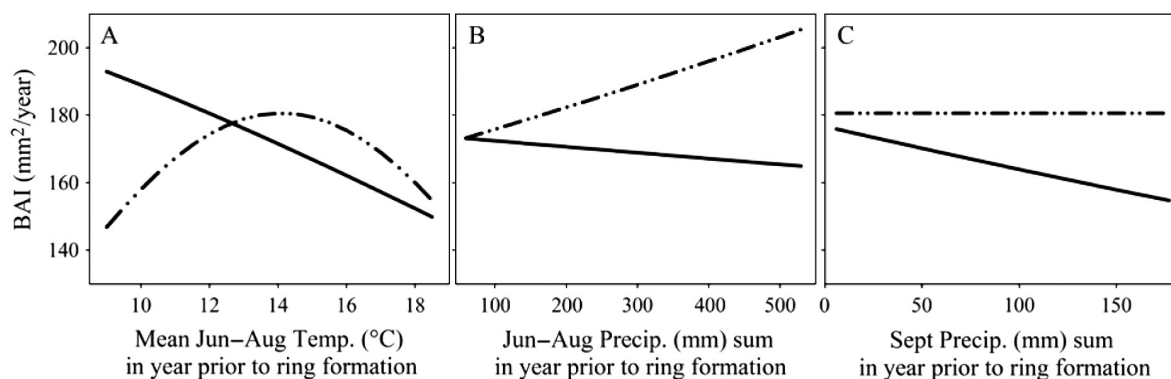


Fig. 3. Modeled *Picea mariana* basal area increment (BAI) response in areas with growing season shallow frozen soil (GsSFS, solid lines) and without GsSFS (dash-dot-dot lines) to (A) mean Jun–Aug temperature (°C), to (B) Jun–Aug precipitation (mm) sum, and (C) Sep precipitation sum (mm) in the year prior to ring formation. All model variables not shown were held at mean values. Temperature and precipitation values span the range experienced in the plot years (1902–2009) for which we had *P. mariana* BAI measurements.

GsSFS dampened this positive effect (Fig. 4B). *P. glauca* had the same estimated response to Jun–Aug temperature, regardless of the presence of growing season shallow frozen soil.

Elevation–climate interactive effects.—*Picea glauca* at all elevations produced more annual basal area when current summer temperatures were high, but this positive influence was amplified for *P. glauca* at higher elevations (Fig. 5A). When the mean Jun–Aug_{ringyr} temperature at the park headquarters area was warmer than 14.8°C, *P. glauca* at the limit of treeline (1000 m in elevation) was estimated to have radial growth surpassing that of lower elevation trees (Fig. 5A). Summer temperatures in the year before ring formation were positively related to radial growth for trees at low elevations, but had a weak negative effect on *P. glauca* at high elevations (Table 4). Summer precipitation was positively related to *P. glauca* BAI at low elevations, but the relationship was negative at high elevations (Fig. 5B). Increasing winter precipitation and colder May temperatures were estimated to increase high-elevation *P. glauca* radial growth, but reduce radial growth at low elevations (Appendix S1: Fig. S5).

DISCUSSION

We used tree-ring data collected in an unbiased, systematic sampling design over a 12,800-km² study area in DNPP to quantify the relationship

between annual radial growth of *Picea mariana* and *Picea glauca* and site and climate variables. We found that slope angle, elevation, and the presence of shallow frozen soil during the growing season govern how the two most common tree species in interior Alaska respond to climate. Overall, our results suggest the interactive effects of local site conditions may mediate species responses to changing climate regimes over large areas.

Implications of climate–site interactions on growth

While studies have shown trends of increasing spruce growth along the cooler and wetter margins of the boreal biome and decreasing growth within the interior Alaskan boreal forest (Beck et al. 2011, Juday et al. 2015), the growth responses of individual trees within stands often show a range of positive to negative correlations with warming (Wilmking et al. 2004, Beck et al. 2011, Juday et al. 2015). Our results, which demonstrate different growth responses to climate within our study area, help explain some of this within-region variability in growth responses to climate. In the former studies, gradients in climate regime were shown to drive broad patterns of growth responses, while our work shows how gradients in site conditions determine both the magnitude and shape of tree growth responses to climate. That is, topographic heterogeneity and site characteristics strongly influence an individual tree's growth response to climate such that trees within a given stand (containing

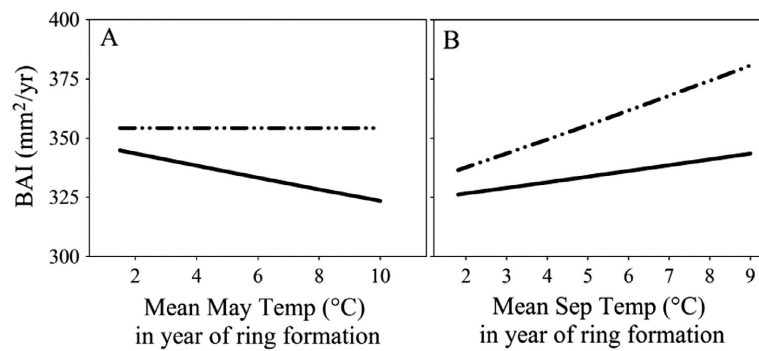


Fig. 4. Modeled *Picea glauca* BAI response to mean (A) May_{ringyr} and (B) Sep_{ringyr-1} temperature (°C) in areas with growing season shallow frozen soil (GsSFS, solid lines) and without GsSFS (dash-dot-dot lines). All continuous covariates not shown are held at mean values. Mean temperature values span the range experienced at a single location near Denali National Park headquarters between the years 1902 and 2009.

topographic and site variability) can show opposing responses to the same climate regime.

Climate thresholds for interior Alaska spruce growth

One of our objectives was to identify optimum or threshold climate conditions for both spruce species as thresholds may represent critical pivot points in growth trends as climate conditions warm. Although a growing number of studies have identified threshold temperatures for *P. glauca* radial growth, few have done this for *P. mariana*. Studies from Alaska and Canada have found temperature optima for *P. glauca* radial growth mostly between 11° and 14°C (D'Arrigo et al. 2004, Wilmking et al. 2004, Beck et al. 2011, Lloyd et al. 2013). We found linear temperature

relationships were better and more parsimonious predictors of BAI than nonlinear relationships, suggesting *P. glauca* in DNPP, even those at low elevations, have not reached a growth threshold due to temperature. The best explanation for this linear relationship is that although the mean June through August temperature across the plots where *P. glauca* were cored ranged from 7° to 18°C, the majority of years were below the 14°C threshold (Appendix S1: Fig. S1). The historical mean summer temperature from our plots with cored *P. glauca* (12.1°C) was within the range of optimum temperatures for growth observed in other studies, while the mean summer temperature in all of DNPP is quite a bit lower (7°C, SNAP 2014a, b),

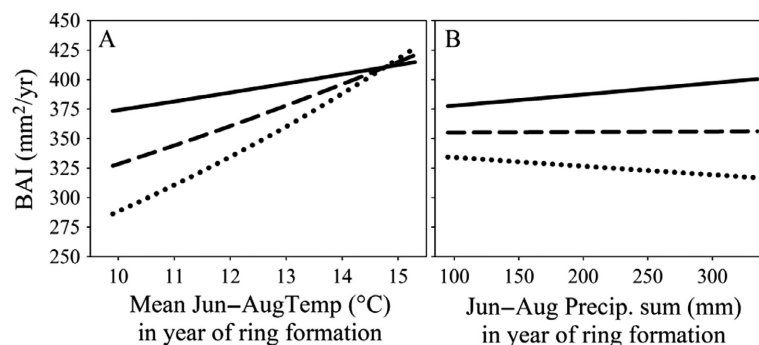


Fig. 5. Modeled basal area increment (BAI) response to (A) mean temperature (°C) and (B) precipitation sum (mm) in Jun–Aug during the year of ring formation for *Picea glauca* growing at 200 m (solid line), 600 m (dashed line), and 1000 m (dotted line) in elevation. Graphed estimates assume no growing season shallow frozen soil and mean values for all continuous covariates not shown. Mean temperature and precipitation values span the range observed at a single location near Denali National Park headquarters between the years 1902 and 2009.

suggesting future warming could improve growing conditions throughout much of our study area and DNPP.

Our *P. mariana* model suggested a mean prior June through August temperature optimum between 9° and 14.8°C, contingent on slope angle. The historical mean temperature of the plots with cored *P. mariana* (14.1°C) is within this range of optimum growth temperatures. One tree-ring study found threshold mean summer temperature values for *P. mariana* around 14°C (Girardin et al. 2014). Others found a minimum threshold of ~9°C and a linear decline in growth in relation to mean maximum summer temperatures starting at 18°C (Dang and Lieffers 1989). Measurement of *P. mariana* photosynthetic rates in response to temperature found a needle thermal optimum of 15°C for trees at treeline (Vowinckel et al. 1975). Each of these findings accords with the temperature optima identified for *P. mariana* in our study area.

Importance of random sampling designs

Our use of a randomized sampling design enabled us to draw inferences about *P. mariana* and *P. glauca* growth across a spatially extensive study area. Our finding that these species respond differently to climate depending on variable site conditions underscores the importance of randomized site selection when extrapolating to larger spatial extents. Nonrandomized sampling designs in tree-ring studies, where site selection is often intentionally nonrandom (Fritts 1976) and typically dominant, healthy trees are selected for coring, can result in strong biases in estimated forest growth and productivity (Nehrbass-Ahles et al. 2014). Although nonrandom site selection is clearly important when addressing targeted questions, the results of such studies often cannot be extrapolated beyond the selected (or similar) sites themselves.

Landscape context

To understand how our model results relate to tree growth across our study area, it is helpful to consider what percentages of the study area are characterized by different site conditions. Thirty-six percent of our study area is relatively flat (i.e., slope <5°). *Picea mariana* was disproportionately found on flat sites. Specifically, two-thirds of the plots in the study area containing measurable basal area of *P. mariana* and just fewer than 40%

of the plots with *P. glauca* had slope angles <5°. Thus, with modestly warmer summer temperatures and small increases in precipitation in DNPP (SNAP 2014a), about two-thirds of the DNPP *P. mariana* population would be expected to show no change or modest increases in growth (assuming no shallow permafrost). However, with the predicted increase of over 3°C in summer temperatures in DNPP by 2080 (SNAP 2014a), *P. mariana* may show widespread declines in radial growth in DNPP, although this decline may be offset by the positive influence of predicted increasing precipitation (again, assuming no shallow permafrost). Similar to the findings of Walker and Johnstone (2014), increasing May temperatures would be expected to diminish *P. mariana* growth on all slope angles. The contrasting effect of warming in May vs. warming in summer on BAI also highlights the significance of seasonality; the seasonal timing of warming conditions can have opposing effects on growth (Girardin et al. 2014, 2016).

Our results suggest there will be a shift to greater *P. glauca* radial growth in the 36% of the study area between 600 and 1200 m relative to the 52% of the study area below 600 m as mean summer temperatures rise above 14.7°C, which is predicted to have occurred by 2080 in DNPP (SNAP 2014a, b). Until then, we predict continued greater basal area production in the 52% of the study area below 600 m relative to higher elevation areas. However, our results suggest the amplified growth at higher elevations may be dampened by a slight, but significant, negative effect of very warm previous summer conditions on high-elevation trees. Indeed, others have found some trees growing at treeline show reduced or mixed growth responses to warm summer conditions in the last half century (Jacoby and D'Arrigo 1995, Lloyd and Fastie 2002, Wilmking et al. 2004, D'Arrigo et al. 2008). We found the *P. glauca* growing in the half of our study area at lower elevations (below 600 m) had positive BAI responses to both current and previous warm summers, which is in contrast to other studies in interior Alaska which have found reduced *P. glauca* growth in mature forests and lowland floodplains with increasing temperatures (Barber et al. 2000, McGuire et al. 2010, Juday and Alix 2012, Juday et al. 2015). The overall cooler, moister conditions in DNPP relative to

central interior Alaska (Roland et al. 2014) may contribute to this difference. Differences in competition, tree age, or stand successional stage in DNPP relative to other areas in interior Alaska may also play a role in the different growth responses observed.

Our results suggest that in the 22.5% of our study area now underlain with near-surface permafrost (Panda et al. 2014), BAI will decline in both *P. mariana* and *P. glauca* as growing season temperature increases (Figs. 3 and 4). Thus, as long as near-surface permafrost persists in DNPP, we expect reduced tree growth in these areas as growing season climate warms. However, models of permafrost in DNPP combined with global climate models predict less than 2% of our study area will have active layer depths thinner than 1 m by 2050 (Panda et al. 2014). This represents a dramatic change in near-surface permafrost, and opens the possibility of a substantial increase in spruce growth in these areas relative to the past. The presence of GsSFS reduced *P. mariana* and *P. glauca* growth by an estimated 6%; thus, as GsSFS degrades, we might expect greater productivity in these areas. Although the development of thaw ponds associated with degrading permafrost may preclude tree growth or cause shifts from forested areas to fens or bogs in some areas (Jorgenson et al. 2001), the edges of thaw ponds have drier soils than surrounding permafrost flats, potentially allowing the establishment of *P. glauca* stands (Lloyd et al. 2003). Thus, in our study area where permafrost is predicted to degrade, we may expect the margins of thaw ponds to show increases in spruce productivity. It is also possible areas with thawing permafrost could experience a shift in species dominance from stunted *P. mariana* forests to more productive *P. glauca* stands (e.g., Wirth et al. 2008).

Evidence for a boreal biome shift?

Although radial growth alone is not an adequate metric of shifting biome distributions, it is one important component in shifting species distributions. Our estimates of radial growth suggest that while the prediction of a “biome shift” within Alaska (e.g. Beck et al. 2011) may be true with respect to the expansion of forests into areas currently occupied by tundra, they do not necessarily support the idea that forests will evacuate their current footprint in DNPP (Juday et al. 2015) for

three reasons. First, we found *P. glauca* growth at all elevations responded positively to increasing summer temperatures. Furthermore, we estimated optimum *P. mariana* growth in flat areas without shallow permafrost at temperature values slightly higher than the historical average, suggesting modest warming would benefit *P. mariana* growth in these site conditions. Finally, our results suggest the predicted reduction of shallow permafrost in DNPP in the coming decades (Panda et al. 2014) may stimulate tree growth over large segments of this landscape relative to the past as suggested for this area by Roland et al. (2013), depending on climate and other site factors.

Conclusions

Our work yields insight into how site-specific characteristics and climate interact to determine tree growth at the landscape scale in DNPP. Our results show that annual productivity of both *Picea* species occurring in interior Alaska does not respond uniformly to variation in climate, but instead responds to multiple interacting environmental and climatic gradients, and that climate optima for growth are dependent on landscape position. Thus, it may not be valid to discuss a uniform climate–growth response across the interior boreal forest region for *P. mariana* or *P. glauca*. Rather, predictions about future growth responses of these species to climate should be conditional on variation in site factors operating at local scales. As we found contrasting responses to climate within DNPP, it is possible, if not likely, that there are similar influences of site factors on larger regional patterns within interior Alaska and elsewhere in the North American boreal forest.

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LITERATURE CITED

- Barber, V. A., G. P. Juday, and B. P. Finney. 2000. Reduced growth of Alaska white spruce in the twentieth century from temperature-induced drought stress. *Nature* 405:668–673.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using eigen and S4. R package version 1.1-7. <http://CRAN.R-project.org/package=lme4>
- Beck, P. S. A., G. P. Juday, C. Alix, V. A. Barber, S. E. Winslow, E. E. Sousa, P. Heiser, J. D. Herriges, and S. J. Goetz. 2011. Changes in forest productivity across Alaska consistent with biome shift. *Ecology Letters* 14:373–379.
- Bieniek, P. A. J. E., R. L. Walsh, and U. S. Bhatt Thoman. 2014. Using climate divisions to analyze variations and trends in Alaska temperature and precipitation. *Journal of Climate* 27:2800–2818.
- Brooks, J. R., L. B. Flanagan, and J. R. Ehleringer. 1998. Responses of boreal conifers to climate fluctuations: indications from tree-ring widths and carbon isotope analyses. *Canadian Journal of Forest Research* 28:524–533.
- Bunn, A. G. 2010. Statistical and visual crossdating in R using the dplR library. *Dendrochronologia* 28:251–258.
- Bunn, A. G., and S. J. Goetz. 2006. Trends in satellite-observed circumpolar photosynthetic activity from 1982 to 2003: the influence of seasonality, cover type and vegetation density. *Earth Interactions* 10:1–12.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.
- Chapin III, F. S., J. McFarland, A. D. McGuire, E. Euskirchen, R. W. Ruess, and K. Kielland. 2009. The changing global carbon cycle: linking local plant-soil carbon dynamics to global consequences. *Journal of Ecology* 97:840–850.
- Chapin III, F. S., S. F. Trainor, P. Cochran, H. Huntington, C. Markon, M. McCammon, A. D. McGuire, and M. Serreze. 2014. Alaska. Pages 514–536 in J. M. Melillo, T. C. Richmond, and G. W. Yohe, editors. *Climate change impacts in the United States: the Third National Climate Assessment*. U.S. Global Change Research Program, Washington, D.C., USA. <http://dx.doi.org/10.7930/J00Z7150>
- Clark, M. H., and M. S. Duffy. 2006. Soil survey of Denali National Park area, Alaska. National Cooperative Soil Survey, NRCS, and USDA, Palmer, Alaska, USA.
- Cox, P. M., R. A. Betts, C. D. Jones, S. A. Spall, and I. J. Totterdell. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408:184–187.
- Daly, C. 2009. Alaska PRISM climate Maps 1971–2000. PRISM Climate Group; National Park Service. Map 2193235. <https://irma.nps.gov/App/Reference/Profile/2193235>
- Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis, and P. P. Pasteris. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology* 28:2031–2064. <http://dx.doi.org/10.1002/joc.1688>
- Dang, Q. L., and V. J. Lieffers. 1989. Climate and annual ring growth of black spruce in some Alberta peatlands. *Canadian Journal of Botany* 67:1885–1889.
- D'Arrigo, R. D., R. K. Kaufmann, N. Davi, G. C. Jacoby, C. Laskowski, R. B. Myneni, and P. Cherubini. 2004. Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada. *Global Biogeochemical Cycles* 18:GB3021.
- D'Arrigo, R., R. Wilson, B. Liepert, and P. Cherubini. 2008. On the 'Divergence Problem' in northern forests: a review of the tree-ring evidence and possible causes. *Global and Planetary Change* 60:289–305.
- DeRose, R. J., J. D. Shaw, and J. N. Long. 2016. Building the forest inventory and analysis tree-ring data set. *Journal of Forestry* 114:1–9.
- Dubayah, R., and P. M. Rich. 1995. Topographic solar radiation models for GIS. *International Journal of Geographic Information Systems* 9:405–413.
- Euskirchen, E. S., A. D. McGuire, T. S. Rupp, F. S. Chapin III, and J. E. Walsh. 2009. Projected changes in atmospheric heating due to changes in fire disturbance and the snow season in the western Arctic, 2003–2100. *Journal of Geophysical Research: Biogeosciences* 114:G04022.
- Foster, J. R., A. O. Finley, A. W. D'Amato, J. B. Bradford, and S. Banerjee. 2016. Predicting tree biomass growth in the temperate-boreal ecotone: Is tree size, age, competition, or climate response most important? *Global Change Biology* 22:2138–2151.
- Fritts, H. C. 1976. *Tree rings and climate*. Blackburn, Caldwell, New Jersey, USA.
- Gewehr, S., I. Drovyshev, F. Berninger, and Y. Bergeron. 2014. Soil characteristics mediate the distribution and response of boreal trees to climatic variability. *Canadian Journal of Forest Research* 44:487–498.
- Girardin, M. P., X. J. Guo, P. Y. Bernier, F. Raulier, and S. Gauthier. 2012. Changes in growth of pristine boreal North American forests from 1950 to 2005 driven by landscape demographics and species traits. *Biogeosciences* 9:2523–2536.
- Girardin, M. P., X. J. Guo, R. de Jong, C. Kinnard, P. Bernier, and F. Raulier. 2014. Unusual forest growth decline in boreal North America covaries

- with the retreat of Arctic sea ice. *Global Change Biology* 20:851–866.
- Girardin, M. P., E. H. Hogg, P. Y. Bernier, W. A. Kurz, X. J. Guo, and G. Cyr. 2016. Negative impacts of high temperatures on growth of black spruce forests intensify with the anticipated climate warming. *Global Change Biology* 22:627–643.
- Girardin, M. P., and B. M. Wotton. 2009. Summer moisture and wildfire risks across Canada. *Journal of Applied Meteorology and Climatology* 48:517–533.
- Goetz, S. J., A. G. Bunn, G. J. Fiske, and R. A. Houghton. 2005. Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. *Proceedings of the National Academy of Sciences USA* 102:13521–13525.
- Holtmeier, F., and G. Broll. 2007. Treeline advance—driving processes and adverse factors. *Landscape Online* 1:1–33.
- IPCC. 2014. Climate Change 2014: synthesis report. Contribution of Working Groups I, II, and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.
- Jacoby, G. C., and R. D'Arrigo. 1995. Tree-ring width and density evidence of climatic and potential forest change in Alaska. *Global Biogeochemical Cycles* 9:227–234.
- Johnson, S. E., and M. D. Abrams. 2009. Basal area increment trends across age classes for two long-lived tree species in the eastern U.S. Pages 129–134 in R. Kaczka, I. Malik, P. Owczarek, H. Gartner, G. Helle, and I. Heinrich, editors. *Tree rings in archaeology, climatology and ecology*. Volume 7. Scientific Technical Report STR 09/03. GFZ Potsdam, Potsdam, Germany.
- Johnstone, J. F., E. J. B. McIntire, E. J. Pedersen, G. King, and M. J. F. Pisaric. 2010. A sensitive slope: estimating landscape patterns of forest resilience in a changing climate. *Ecosphere* 16:1–21.
- Jorgenson, M. T., C. H. Racine, J. C. Walters, and T. E. Osterkamp. 2001. Permafrost degradation and ecological changes associated with a warming climate in central Alaska. *Climate Change* 48:551–579.
- Juday, G. P., and C. Alix. 2012. Consistent negative temperature sensitivity and positive influence of precipitation on growth of floodplain *Picea glauca* in interior Alaska. *Canadian Journal of Forest Research* 42:561–573.
- Juday, G. P., C. Alix, and T. A. Grant III. 2015. Spatial coherence and change of opposite white spruce temperature sensitivities on floodplains in Alaska confirms early-stage boreal biome shift. *Forest Ecology and Management* 350:46–61. <http://dx.doi.org/10.1016/j.foreco.2015.04.016>
- Karl, T. R., et al. 2009. Global climate change impacts in the United States: a state of knowledge report from the U.S. Global Change Research Program. Cambridge University Press, New York, New York, USA.
- Kuusela, K. 1990. The dynamics of boreal coniferous forests. Finnish National Fund for Research and Development (SITRA), Helsinki, Finland.
- Lloyd, A. H., and A. G. Bunn. 2007. Responses of the circumpolar boreal forest to 20th century climate variability. *Environmental Research Letters* 2:1–13. <http://dx.doi.org/10.1088/1748-9326/2/4/045013>
- Lloyd, A. H., A. G. Bunn, and L. Berner. 2010. A latitudinal gradient in tree growth response to climate warming in the Siberian taiga. *Global Changes Biology* 17:1935–1945. <http://dx.doi.org/10.1111/j.1365-2486.2010.02360.x>
- Lloyd, A. H., P. A. Duffy, and D. H. Mann. 2013. Nonlinear responses of white spruce to climate variability in interior Alaska. *Canadian Journal of Forest Research* 43:331–343.
- Lloyd, A. H., and C. L. Fastie. 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change* 52:481–509.
- Lloyd, A. H., K. Yoshikawa, C. L. Fastie, L. Hinzman, and M. Fraver. 2003. Effects of permafrost degradation on woody vegetation at arctic treeline on the Seward Peninsula, Alaska. *Permafrost and Periglacial Processes* 14:93–101.
- McAfee, S., G. Guentchev, and J. Eischeid. 2014. Reconciling precipitation trends in Alaska: 2. Gridded data analyses. *Journal of Geophysical Research: Atmospheres* 119:13820–13837. <http://dx.doi.org/10.1002/2014JD022461>
- McGuire, A. D., L. G. Anderson, T. R. Christensen, S. Dallimore, L. Guo, D. J. Hayes, M. Heimann, T. D. Lorenson, R. W. Macdonald, and N. Roulet. 2009. Sensitivity of the carbon cycle in the Arctic to climate change. *Ecological Monographs* 79:523–555.
- McGuire, A. D., R. Ruess, A. Lloyd, J. Yarie, J. Clein, and G. Juday. 2010. Vulnerability of white spruce tree growth in interior Alaska in response to climate variability: dendrochronological, demographic, and experimental perspectives. *Canadian Journal of Forest Research* 40:1197–1209.
- Michalcová, D., S. Lvončík, M. Chytrý, and O. Hájek. 2011. Bias in vegetation databases? A comparison of stratified random and preferential sampling. *Journal of Vegetation Science* 22:281–291.
- Nehrbass-Ahles, C., F. Babst, S. Klesse, M. Nötzli, O. Bouriaud, R. Neukom, M. Dobbertin, and D. Frank. 2014. The influence of sampling design on tree-ring-based quantification of forest growth. *Global Change Biology* 20:2867–2885. <http://dx.doi.org/10.1111/gcb.12599>
- Ohse, B., F. Jansen, and M. Wilmking. 2012. Do limiting factors at Alaskan treelines shift with climatic regimes? *Environmental Research Letters* 7:1–12.

- Okano, K., and M. S. Bret-Harte. 2015. Warming and neighbor removal affect white spruce seedling growth differently above and below treeline. *SpringerPlus* 4:79.
- Panda, S. K., S. S. Marchenko, and V. E. Romanovsky. 2014. High-resolution permafrost modeling in Denali National Park and Preserve. Natural Resource Technical Report. NPS/CAKN/NRTR—2014/858. Published Report 2208990. National Park Service, Fort Collins, Colorado, USA.
- Pereira, J. M. C., and R. M. Itami. 1991. GIS-based habitat modeling using logistic multiple regression: a study of the Mt. Graham red squirrel. *Photogrammetric Engineering and Remote Sensing* 57:1475–1486.
- R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>
- Rich, P. M., R. Dubayah, W. A. Hetrick, and S. C. Saving. 1994. Using viewshed models to calculate intercepted solar radiation: applications in ecology. Pages 524–529 in *American Society for Photogrammetry and Remote Sensing Technical Papers*. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland, USA.
- Roland, C. A., J. H. Schmidt, and J. F. Johnstone. 2014. Climate sensitivity of reproduction in a mast-seeding boreal conifer across its distributional range from lowland to treeline forests. *Oecologia* 174:665–677.
- Roland, C. A., J. H. Schmidt, and E. F. Nicklen. 2013. Landscape-scale patterns in tree occupancy and abundance in subarctic Alaska. *Ecological Monographs* 83:19–48.
- Scenarios Network for Alaska and Arctic Planning [SNAP], University of Alaska. 2014a. Projected climate change scenarios for Denali National Park. Climate change summary reports of National Parks, Preserves and Monuments. <https://www.snap.uaf.edu/sites/default/files/denali.pdf>
- Scenarios Network for Alaska and Arctic Planning [SNAP], University of Alaska. 2014b. Historical monthly temperature, precipitation and vapor pressure products. <https://www.snap.uaf.edu/tools/data-downloads>
- Schuur, E. A. G., et al. 2008. Vulnerability of permafrost carbon to climate change: implications for the global carbon cycle. *BioScience* 58:701–714.
- Schuur, E. A. G., et al. 2015. Climate change and the permafrost carbon feedback. *Nature* 520:171–179.
- Shaver, G., W. D. Billings, F. S. Chapin III, A. E. Giblin, K. J. Nadelhoffer, W. C. Oechel, and E. B. Rastetter. 1992. Global change and the carbon balance of arctic ecosystems. *BioScience* 42:433–441.
- Sormunen, H., R. Virtanen, and M. Luoto. 2011. Inclusion of local environmental conditions alters high-latitude vegetation change predictions based on bioclimatic models. *Polar Biology* 34:883–897.
- Sullivan, P. F., S. B. Z. Ellison, R. W. McNow, A. H. Brownlee, and B. Sveinbjörnsson. 2015. Evidence of soil nutrient availability as the proximate constraint on growth of treeline trees in northwest Alaska. *Ecology* 96:716–727.
- Swanson, D. K. 2015. Environmental limits of tall shrubs in Alaska's Arctic National Parks. *PLoS ONE* 10:e0138387.
- Verbyla, D. 2008. The greening and browning of Alaska based on 1982–2003 satellite data. *Global Ecology and Biogeography* 17:547–555.
- Vowinkel, T., W. C. Oechel, and W. G. Boll. 1975. The effect of climate on the photosynthesis of *Picea mariana* at the subarctic treeline. 1. Field measurements. *Canadian Journal of Botany* 53: 604–620.
- Walker, X., and J. F. Johnstone. 2014. Widespread negative correlations between black spruce growth and temperature across topographic moisture gradients in the boreal forest. *Environmental Research Letters* 9:064016.
- Walsh, J. E., W. L. Chapman, V. Romanovsky, J. H. Christensen, and M. Stendel. 2008. Global climate model performance over Alaska and Greenland. *Journal of Climate* 21:6156–6174.
- Wilmking, M., G. P. Juday, V. A. Barber, and H. J. Zald. 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Global Change Biology* 10:1–13.
- Wilmking, M., G. P. Juday, M. Terwilliger, and V. Barber. 2006. Modeling spatial variability of white spruce (*Picea glauca*) growth responses to climate change at and below treeline in Alaska – a case study from two National Parks. *Erdkunde* 60: 113–126.
- Wilmking, M., and I. Myers-Smith. 2008. Changing climate sensitivity of black spruce (*Picea mariana* Mill.) in a peatland-forest landscape in Interior Alaska. *Dendroecologia* 25:167–175.
- Wirth, C. L., W. Lichstein, J. Dushoff, A. Chen, and F. S. Chapin III. 2008. White spruce meets black spruce: dispersal, postfire establishment, and growth in a warming climate. *Ecological Monographs* 78: 489–505.

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