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Stand basal area and solar radiation amplify white spruce climate sensitivity in interior Alaska: Evidence from carbon isotopes and tree rings

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Abstract

The negative growth response of North American boreal forest trees to warm summers is well documented and the constraint of competition on tree growth widely reported, but the potential interaction between climate and competition in the boreal forest is not well studied. Because competition may amplify or mute tree climate-growth responses, understanding the role current forest structure plays in tree growth responses to climate is critical in assessing and managing future forest productivity in a warming climate. Using white spruce tree ring and carbon isotope data from a long-term vegetation monitoring program in Denali National Park and Preserve, we investigated the hypotheses that (a) competition and site moisture characteristics mediate white spruce radial growth response to climate and (b) moisture limitation is the mechanism for reduced growth. We further examined the impact of large reproductive events (mast years) on white spruce radial growth and stomatal regulation. We found that competition and site moisture characteristics mediated white spruce climate-growth response. The negative radial growth response to warm and dry early- to mid-summer and dry late summer conditions intensified in high competition stands and in areas receiving high potential solar radiation. Discrimination against ^{13}C was reduced in warm, dry summers and further diminished on south-facing hillslopes and in high competition stands, but was unaffected by climate in open floodplain stands, supporting the hypothesis that competition for moisture limits growth. Finally, during mast years, we found a shift in current year's carbon resources from radial growth to reproduction, reduced ^{13}C discrimination, and increased intrinsic water-use efficiency. Our findings highlight the importance of temporally variable and confounded factors, such as forest structure and climate, on the observed climate-growth response of white spruce. Thus, white spruce growth trends and productivity in a warming climate will likely depend on landscape position and current forest structure.

KEYWORDS
boreal forest, carbon isotopes, climate change, climate-growth response, competition, dendroecology, *Picea glauca*

1 | INTRODUCTION

Forest structure and demography are changing with a warming climate. Widespread increases in tree mortality have occurred in the western United States (van Mantgem et al., 2009) and Canada (Luo & Chen, 2015; Peng et al., 2011; Zhang, Huang, & He, 2015), reducing stand basal area and shifting stand age. Changing disturbance regimes associated with climate warming further alter forest structure and demography (Barrett, McGuire, Hoy, & Kasischke, 2011; Johnstone, Hollingsworth, Chapin, & Mack, 2010). Forest structure and demography are a product of, and feed back to tree growth, death, and recruitment rates. In particular, competition is known to have large, effects on tree growth, recruitment, and mortality (Aakala, Fraver, D'Amato, & Palik, 2013; Alam et al., 2017; Coomes & Allen, 2007; Cortini, Comeau, & Bokalo, 2012; Fernández-de-Uña, Cañellas, & Gea-Izquierdo, 2015; Trugman, Medvigy, Anderegg, & Pacala, 2017; Zhang et al., 2015). Nonetheless, competition is frequently not considered in tree climate-growth analyses, though it has been getting more attention recently in a variety of forest types around the world (Alam et al., 2017; Cortini et al., 2012; Fernández-de-Uña et al., 2015; Fernández-de-Uña, McDowell, Cañellas, & Gea-Izquierdo, 2016; Piutti & Cescatti, 1997; Ruiz-Benito et al., 2014) including in the boreal forest in interior (Trugman et al., 2017) and southwest Alaska (Wright, Sherriff, Miller, & Wilson, 2018). Studies of productivity in mature stands in boreal forests have found negative growth responses to warm summer temperatures (Angert et al., 2005; Barber, Juday, & Finney, 2000; Beck et al., 2011; Bunn & Goetz, 2006; Girardin et al., 2016; Huang et al., 2010; Jiang et al., 2016; Juday & Alix, 2012; Juday, Alix, & Grant, 2015; Lloyd, Duffy, & Mann, 2013; Sullivan, Pattison, Brownlee, Cahoon, & Hollingsworth, 2017; Walker & Johnstone, 2014; Zhang et al., 2015), though these climate-growth responses can be variable within (Wilmking, Juday, Barber, & Zald, 2004; Wilmking, Juday, Terwilliger, & Barber, 2006) or across site physical (Nicklen, Roland, Ruess, Schmidt, & Lloyd, 2016), vegetative (Bunn & Goetz, 2006), and regional (Hellmann et al., 2016; Lloyd & Bunn, 2007) conditions.

Though the negative growth response of non-treeline boreal spruce forests to warm growing seasons is well documented (Barber et al., 2000; Juday & Alix, 2012) and the strong negative effect of competition on tree growth is known, the likely interactive effect of competition on climate-growth responses is poorly studied. The potential interactive effect of competition and climate may confound our understanding of climate-growth responses (e.g., negative growth responses attributed to climate may be partially related to stand competition levels), but if quantified, may elucidate unexplained variability in climate-growth response within and across boreal forest stands. The potential interactive effect between competition and climate may result in unexpectedly amplified or muted growth responses to climate affecting the future structure and demography of the boreal forest. This gap in our understanding of boreal forest climate-growth relationships is of particular concern for two reasons. First, the climate is warming at a faster rate in high latitude forests compared to lower latitude forests (Hinzman et al., 2005; IPCC, 2014) and the unknown interaction of this warming with tree growth presents greater uncertainly about future boreal forest structure and function. Second, the boreal forest represents nearly a third of the world's forests (Kuusela, 1990) and 22% of the carbon storage on Earth's land surface (IPCC, 2014). Thus, the growth response of trees in the boreal forest to climate change will greatly affect the future footprint of the boreal biome, carbon dynamics (Chapin et al., 2009; Cox, Betts, Jones, Spall, & Totterdell, 2000; Koven, 2013; Shaver, Billings, Chapin, Giblin, & Nadelhoffer, 1992), and albedo (Betts & Ball, 1997; Bonan, 2008; Euskirchen, McGuire, Rupp, Chapin, & Walsh, 2009) and influence habitat for flora and fauna over large areas.

White spruce (*Picea glauca*) is vulnerable to decreased water availability (Barber et al., 2000; McGuire et al., 2010; Yarie & Van Cleve, 2010; Yarie, Cleve, & Schlentner, 1990). Thus, white spruce in high basal area stands, where competition for water may be increased, could suffer exacerbated drought stress during warm, dry growing seasons relative to spruce in more open stands with less competition. Indeed, white spruce growth response to climate in western Canada was reduced when growing in stands with high aspen basal area (Cortini et al., 2012). Similarly, the correlation between growth and temperature for European beech changed from positive to negative as competition increased (Piutti & Cescatti, 1997). In central Canada, climate enhanced conspecific competition increased mortality in *Pinus banksiana* and *Populus tremuloides* (Luo & Chen, 2015). There is some evidence for similar climate–competition interactions for white spruce in interior Alaska: Growth was negatively correlated with soil moisture deficit in unthinned, but not thinned stands (Yarie et al., 1990) and more positively associated with precipitation in mature forests than in open treeline stands (Ohse, Jansen, & Wilmking, 2012).

Stable carbon isotopic ratios in tree rings record the balance between stomatal conductance and photosynthetic rate (Farquhar, O'Leary, & Berry, 1982; Francey & Farquhar, 1982) providing annually resolved information about physiological responses to environmental conditions (McCarroll & Loader, 2004). Thus, environmental conditions that influence stomatal conductance (soil water availability, vapor pressure deficit) and photosynthesis (air temperature, nutrient availability, irradiance) will also be recorded in the isotopic ratios of tree rings. During photosynthesis, ribulose-1,5-biphosphate carboxylase/oxygenase discriminates against the heavier ^{13}C in favor of ^{12}C contributing to a lower ^{13}C to ^{12}C ratio (δ^{13}C) in the leaves and wood of trees than in the atmosphere (Farquhar et al., 1982). When drought stressed, trees limit water loss from transpiration by closing stomata, which also limits the atmospheric CO_2 available for photosynthesis, forcing increased assimilation of ^{13}C during carboxylation and leading to greater intrinsic water-use efficiency (iWUE). Carbohydrates produced under drought stress conditions have a higher δ^{13}C value reflecting less ^{13}C discrimination (Δ^{13}C) and higher iWUE. This drought stress signature is preserved within the annual growth rings of trees. Arctic treeline white spruce stomatal closure has been observed in response to high vapor pressure deficit and is exacerbated by limited soil water availability (Sullivan &

Sveinbjörnsson, 2011). In Alaska and western Canada, white spruce carbon isotopic ratios are also correlated with temperature (Barber et al., 2000; Csank, Miller, Sherriff, Berg, & Welker, 2016; Holzkämper, Tillman, Kuhry, & Esper, 2012; Porter, Pisaric, Kokelj, & Edwards, 2009) and relative humidity (Porter et al., 2009).

In this study, we investigate potential interactive effects of competition as well as site moisture characteristics with climate on white spruce radial growth and stomatal regulation. Using tree ring and carbon isotope data from a long-term vegetation monitoring program in Denali National Park and Preserve (see Roland, Schmidt, & Nicklen, 2013), we address the hypotheses that (a) white spruce growth response to climate can be mediated by stand competition and site moisture characteristics and (b) moisture limitation is the mechanism for reduced growth in warm, dry years. If competition does mediate climate-growth responses, we expect radial growth will have a less positive or more negative response to warm, dry growing seasons in high competition stands compared with radial growth in open stands. If competition for water (as opposed to nutrients or light) is driving the reduction in radial growth, we expect reduced ring growth and decreased ^{13}C discrimination (and increased iWUE) during warm, dry growing seasons in dry vs. moist sites and in high vs. low competition stands. If competition for nutrients or light limits growth rather than competition for water, photosynthesis may be reduced relative to stomatal conductance, and we expect reduced radial growth in high BA sites in concert with either no change in or increased Δ^{13}C (and decreased iWUE).

2 | MATERIALS AND METHODS

2.1 | Study area

The 1.28 million ha study area is situated in south-central interior Alaska within Denali National Park and Preserve (DNPP), almost entirely on the north side of the Alaska Range within DNPP (center near 63°41′N, 150°25′W; see Roland et al., 2013). The area includes steep Alaska Range hillslopes >2,400 m elevation, foothill ranges, and extensive lowland basins. Permafrost is continuous to discontinuous in the lowland basins and discontinuous to sporadic in the Alaska Range (Clark & Duffy, 2006). The study area experiences a continental climate with very cold, dry winters and short, warm summers. Temperature and precipitation are variable across the study area, which spans two climate regions (Bieniek et al., 2012). Mean January temperatures are ~−22°C in the lowland basins in the NW end of the park and ~−12°C in the Alaska Range. Mean July temperatures are ~16°C in the basins and ~8°C in the Alaska Range (1971–2000 monthly PRISM averages; Daly, 2009). Annual precipitation sums range from less than 400 mm in the lowlands to over 1,000 mm in the mountains (1971–2000 monthly PRISM averages; Daly, 2009), with the majority falling in June through August (Sousanes, 2008). Fire return intervals in the most fire-prone area of the park, the NW lowland basin, are around 200–300 years (Kasischke, Williams, & Barry, 2002). Fires are much less frequent at higher elevations.

Six tree species occur in our study area: white spruce (*Picea glauca*), black spruce (*Picea mariana*), Alaska birch (*Betula neoalaskana*), trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and tamarack (*Larix laricina*; Roland et al., 2013). Of these, white and black spruce are by far the most frequent and abundant trees in the study area. White spruce occupies 32% of plots in the study area with a mean basal area (BA) for occupied plots of 6.0 m^2/ha and occurs in a wide range of topographic positions, including being the most common treeline species in DNPP (Roland et al., 2013). The highest BA white spruce stands occur on warm, well-drained south-exposed mid-elevation slopes, in permafrost-free terrain. Black spruce occurs in 27% of plots with a mean BA of 1.0 m^2/ha for occupied plots and is generally restricted to the lowland basins and hills in DNPP primarily in areas affected by permafrost (Roland et al., 2013). The remaining four tree species each occur in 13% or fewer plots in the study area and are relative habitat specialists (Roland et al., 2013). Alaska birch and trembling aspen are strongly associated with burned areas, where aspen occurs in the warmest and driest sites. Balsam poplar is primarily found along rivers and in gravelly soils, and tamarack is found within a subset of black spruce habitat, generally in wet areas.

2.2 | Study design

As a part of the National Park Service's inventory and monitoring program, a systematic sampling grid was established across the study area (Roland et al., 2013; Roland, Oakley, Debevec, & Loomis, 2004). Grid spacing was 20-km, but with 10-km spacing within 6 km of the one park road (Figure 1). At each grid, intersection was a “mini-grid” consisting of five rows of five plots spaced 500 m apart. Each of the 25 points within a “mini-grid” entailed a circular 16 m diameter plot and an outer meta-plot extending another 10 m in radius.

At each plot, we measured a suite of topographic, edaphic, and vegetative variables (details in Roland et al., 2004, 2013). In addition to slope angle, elevation, and aspect, we recorded the diameter of each tree species at 1.37 m above ground level (DBH) within the plot and calculated plot basal area (BA; m^2/ha). We used point intercept transects to estimate percent tall shrub cover. At four cardinal directions within the meta-plot, we dug soil pits where, in addition to collecting soil for physical and chemical analysis, we measured the depth of the living mat and the soil organic layer (SOL) and recorded soil temperature at 10 cm below soil surface. We classified plots as either having growing season shallow frozen soil (GsSFS) or not. A plot was considered to have frozen soil during the growing season 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 at least one of the four soil pits or if the four soil temperatures taken at the plot were all <1°C. Otherwise, the plot was classified as free of near surface frozen soil during the growing season. We obtained potential solar radiation receipts for each of our plot locations using the Solar Analyst tool in ArcGIS 10.0 (Dubayah & Rich, 1995), which incorporates slope angle, aspect, latitude, sun angle, and surrounding landscape (based on the United States Geological Survey 60-m digital

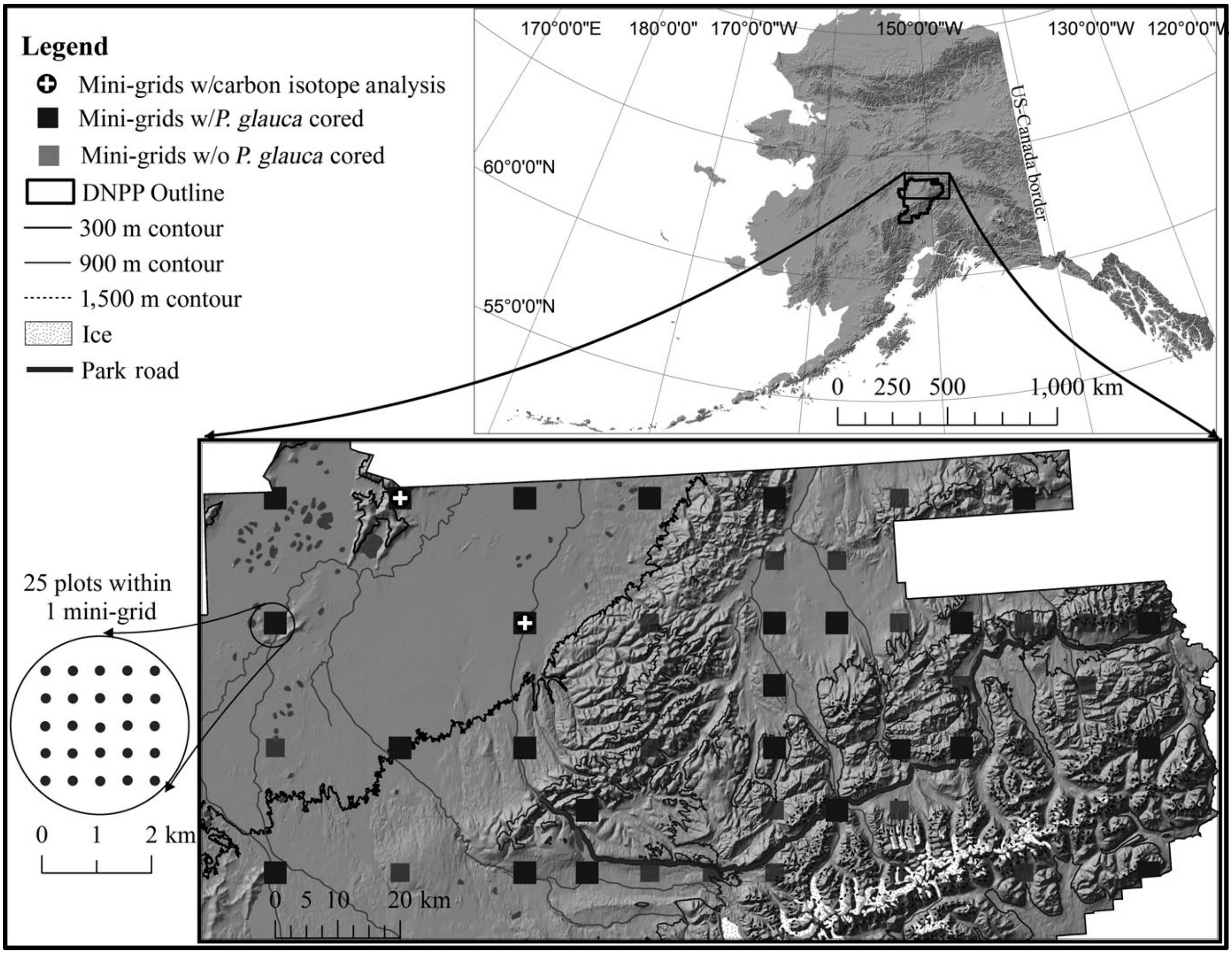

FIGURE 1 Map showing the location of sampled white spruce from minigrids in the Denali National Park and Preserve study area

elevation model from the National Elevation Dataset) into monthly radiation value estimates (Rich et al., 1994). We summed the monthly values into one potential solar radiation estimate per plot. We assigned each plot one of five lithology categories (bedrock, alluvium, drift, Nenana gravels, and eolian) based on the Denali Soil Map (Clark & Duffy, 2006). Sampling occurred between 2003 and 2010 during the months of June, July, and August.

2.3 | Tree sampling

Of the 43 mini-grids and 1,107 plots sampled, we cored and cross-dated 357 white spruce trees 10,347 growth rings) from a total of 26 mini-grids and 160 plots. We cored the largest tree within each of the four quadrants of the meta-plot, though often there were fewer than four trees to core or the trees were too small to core (<5 cm at 1.37 m from ground surface; see Supporting Information Figure S2 for size bias in cored trees). Many of the plots contained no trees as they were above treeline, too wet or too recently disturbed. We extracted penetrating cores whenever possible and cored as low to the ground as possible while avoiding bole deformities. Dried, mounted, and sanded cores were measured to the nearest 0.001 mm and cross-dated (see Nicklen et al., 2016). Dating was validated with COFECHA and the Dendrochronology Program Library in R (dplR, Bunn, 2008; Bunn & Korpela, 2016). We averaged replicate rings widths from individual trees by year. We used ring widths and tree radius to calculate basal area increment (BAI), an estimate of the area of wood produced by each tree in each year of growth (Nicklen et al., 2016). Because we were interested in the effect of biotic variables on growth, and biotic variables (moss depth, stand basal area) change over time, we limited our ring width sample to within 30 years of the sampling date as a balance between sample size and changing site conditions. The earliest years considered in our sample ranged from 1974 to 1981.

We selected six trees from each of two mini-grids for additional carbon isotope analysis (Figure 1). To target our interest in competition and drought stress, we selected trees and mini-grids based on (a) capturing a large gradient in tree BA across the plots (competition proxy), (b) one mini-grid was to be located in a floodplain and the other on a south-facing hillslope, and (c) other variables such as tree age and size, elevation, and general mini-grid location were to be kept as similar as possible, such that BA and site moisture were the focal covariates (Figure 1; Supporting Information Table S1). All selected trees were cored in 2009 or 2010, and $\Delta^{13}C$ analysis was conducted on each ring with sufficient wood going back to 1980. Each ring was sampled using a Foredom Flexshaft Drill (Foredom Electric Company, Bethel, CT, USA) fixed in place under a microscope. Samples were subsequently processed to α-cellulose using the modified version of the Brendel, Iannetta, and Stewart (2000) method recommended by Anchukaitis et al. (2008). Samples were weighed into tin capsules and analyzed for $\delta^{13}C$ using a Delta V Advantage with EA in the Organic Biogeochemistry Laboratory at the University of Notre Dame. The combustion reactor was run at 1,000°C, reduction reactor at 650°C, with the column at 65°C. Each run took 450 s with three reference gas peaks run at the beginning and end of the run (N2 at the beginning and CO_2 at the end). The CO_2 ran with a 75% dilution. Analytical precision was 0.2‰. Carbon isotope discrimination ($\Delta^{13}C$) was calculated as:

$$\Delta^{13}C = \frac{\delta^{13}C_a - \delta^{13}C_{tree}}{1 + \delta^{13}C_{tree}/1000}$$

Annual estimates of $\delta^{13}C_a$ are the $\delta^{13}C$ value of atmospheric CO_2 obtained from flask data collected at Point Barrow station for the years 1982 to 2009 (Keeling et al., 2001) and from McCarroll and Loader (2004) for 1980 and 1981. $\delta^{13}C_{tree}$ is the value of $\delta^{13}C$ measured from tree-ring cellulose for a given year. We calculated intrinsic water-use efficiency (iWUE) using two equations, from Farquhar et al. (1982):

$$\Delta^{13}C = a + (b - a) \times \left(\frac{C_i}{C_a}\right)$$

where a is the fractionation of $^{13}CO_2$ relative to $^{12}CO_2$ during diffusion (4.4‰), b is the biochemical fractionation during photosynthesis (27‰), and c_i/c_a is the ratio of CO_2 inside the leaf to CO_2 in the atmosphere. Solving for c_i and using the ratio of diffusivities of water vapor and c_a, we calculate iWUE (Farquhar, Hubick, Condon, & Richards, 1989):

$$\text{iWUE} = \frac{A}{G_s} = (c_a - c_i) \times (1/1.6)$$

2.4 | Model covariates

We focused on site and tree variables expected to represent or influence competition and moisture availability, but additionally

TABLE 1 Characteristics of covariates used in models of white spruce radial growth for the entire DNPP sample (for characteristics of subset trees used in $\delta^{13}C$ analysis, see Supporting Information Table S1)

Variable	Mean	*SD*	Min	Max	
Competition factors					Climate interaction tested?
Conifer basal area (m^2/ha)	11.0	11.9	0	66	Yes
Broadleaf basal area (m^2/ha)	3.2	6.9	0	35	No
Shrub cover above 1.5 m (%)	17.3	22.8	0	88	Yes
Drought stress/site moisture factors					
Slope angle (degrees)	9.0	7.8	1	36	Yes
Potential solar radiation (KWH/m^{2}[a])	680.4	66.0	486	839	Yes
Live mat depth (cm)	4.2	3.3	0	21	Yes
Soil organic mat (SOL; cm)	14.0	7.6	1	30	Yes
Tree size (DBH, cm)	22.7	9.7	5	54	Yes
Factors known to influence *P. glauca* growth in DNPP					
Lithology (five classes)	NA	NA	NA	NA	No
Growing season shallow frozen soil (GsSFS; binary)	NA	NA	NA	NA	No
Spruce mast year (binary)	NA	NA	NA	NA	No
Minimum age at time of coring	116	57.4	20	343	No
Climate factors					Prev. and/or current year?
Precip/snow Oct–Apr (mm)	182.9	67.8	57	430	Current
VPD May[b] (hPa)	5.5	1.1	2.3	10.1	Current
Precip. May (mm)	26.2	12.3	6	64	Current
VPD Jun–Jul[b] (hPa)	6.6	1.4	2.3	11.8	Previous & current
Precip. Jun–Jul (mm)	152.6	58.7	51	419	Previous & current
VPD Aug[b] (hPa)	4.0	1.2	1.1	8.9	Previous
Precip. Aug (mm)	76.5	27.8	20	172	Previous

Notes. Whether the site or tree covariate's interactive effect with climate was tested is indicated as well as whether the climate variable used was for the year current with and/or previous to the year of ring formation.
[a]Solar radiation units are sum of kilowatt hours per square meter. [b]Quadratic terms evaluated in competing models.

included variables known to influence white spruce growth in DNPP (Table 1). Conifer BA was our primary metric of competition. Although BA is a measure of stand productivity, it has also been successfully used as a measure of plot crowding as it integrates both stand density and tree size (Martin & Ek, 1984; Trugman et al., 2017). We focused on within conifer competition for two reasons. First, competition within species or among congeners (e.g., *Picea glauca* and *Picea mariana*) is expected to be more intense than interspecific competition as different species or functional groups differ in resource use and phenology (Man & Lieffers, 1999). Second, there was considerably more conifer basal area across our study than broadleaf basal area (Table 1, Roland et al., 2013) making this dataset unsuitable for testing white spruce–broadleaf competition. We did include broadleaf basal area as a main effect to account for those few areas where there was high broadleaf BA. We included individual tree DBH both as a measure of tree relative dominance and as a potential variable in drought stress susceptibility, as larger trees can be more sensitive to drought than smaller trees (Bennett, Mcdowell, Allen, & Anderson-Teixeira, 2015). We assessed tall shrub cover as a possible competition factor as tall shrubs have been found to negatively affect white spruce growth (Cortini & Comeau, 2008). We evaluated plot slope angle and potential solar radiation estimates as site variables that may influence site moisture balance and tested depth of living mat and SOL as variables likely to influence soil moisture availability and climate-growth responses (Drobyshev, Simard, Bergeron, & Hofgaard, 2010; Gewehr, Drobyshev, Berninger, & Bergeron, 2014). Finally, we considered several variables known to influence white spruce growth in DNPP as main effects only: ring age (ring count), lithology type, and the presence or absence of growing season shallow frozen soil (Nicklen et al., 2016). We modeled ring age as a cubic function to account for growth trends related to age (Nicklen et al., 2016). We also included a binary variable to indicate mast seeding years in spruce as mast years are strongly associated with reduced radial growth of that year (Juday, Barber, Rupp, Zasada, & Wilmking, 2003). Mast data were based on records from interior Alaska (Juday et al., 2003; Roland, Schmidt, & Johnstone, 2014).

TABLE 2 Standardized coefficient estimates for significant relationships between log-transformed white spruce BAI and covariates in final selected model

Covariates and interactions	Estimate	Lower 95% limit	Upper 95% limit
Intercept	5.799	5.740	5.858
Age proxy	−0.126	−0.155	−0.096
Age proxy^2	−0.043	−0.060	−0.026
Age proxy^3	0.017	0.011	0.023
Broadleaf BA	0.047	0.007	0.086
DBH	0.224	0.188	0.260
Plot slope	−0.037	−0.072	−0.001
Potential solar radiation	−0.039	−0.067	−0.010
LiveMat_cm	−0.058	−0.086	−0.031
Eolian lithology	0.332	0.185	0.478
Mast Yr	−0.088	−0.101	−0.074
Precip/snow current Oct–Apr	−0.030	−0.036	−0.024
VPD current May	−0.015	−0.022	−0.009
VPD current May^2	0.016	0.012	0.019
VPD current Jun–Jul	0.017	0.008	0.027
VPD current Jun–Jul^2	−0.014	−0.018	−0.010
VPD previous Jun–Jul	−0.071	−0.081	−0.061
VPD previous Jun–Jul^2	0.021	0.016	0.025
Precip previous Jun–Jul	0.010	0.004	0.016
Precip previous Aug	0.028	0.022	0.033
VPD cur. May × solar rad.	−0.013	−0.021	−0.006
VPD cur. May^2 × solar rad.	−0.005	−0.009	−0.001
Precip. cur. May × solar rad.	0.009	0.004	0.014
Precip. prev. Aug × solar rad.	−0.008	−0.013	−0.003
Conifer BA × VPD prev. Jun–Jul	−0.011	−0.019	−0.004
Conifer BA × precip prev. Aug	0.010	0.005	0.016

Note. Covariates were scaled to have a mean of zero and a standard deviation of 1; thus, effects are relative. The marginal and conditional R^2 for the model were 0.15 and 0.92, respectively. N = 357 trees and 10,347 growth rings.

We considered the following climate variables: mean vapor pressure deficit (VPD) from June–July and August of the previous growing season and from May and June–July of the current growing season (Table 2). We also considered precipitation sums from the same time periods, as well as from the winter season (October–April) prior to ring formation. These data are downscaled and spatially interpolated climate data provided by Scenarios Network for Alaska and Arctic Planning (SNAP 2014; Retrieved in 2014 from https://www.snap.uaf.edu/tools/data-downloads; temperature and vapor pressure from CRU TS 3.1, precipitation from CRU TS3.1.01) for the years 1974–2009. The climate data are estimates of historical monthly climatic variables for any given locale in Alaska at 1-km resolution. SNAP downscaled monthly climate data for Alaska to a finer grid resolution using PRISM (Parameter–elevation Relationships on Independent Slopes Model) which integrates location, elevation, coastal proximity, topographic variables, vertical atmospheric layer, and orographic effectiveness of the terrain (Daly et al., 2008). For each plot and each year for which we had tree-ring data within 1974–2009, we extracted the monthly mean vapor pressure (hPa), temperature (°C), and precipitation sum (mm). We used the temperature data (Temp) to calculate mean monthly saturated vapor pressure (SVP) in hectoPascals (hPa) from Murray (1967):

$$\mathrm{SVP} = 610.7 \times 10^{(7.5 \times \mathrm{Temp})/(237.3+\mathrm{Temp})}/100$$

We then subtracted the mean monthly vapor pressure (VAP) value to obtain mean monthly vapor pressure deficit (VPD = SVP − VAP). Nonlinear climate-growth relationships have been found for white spruce (D'Arrigo et al., 2004; Lloyd et al., 2013; Nicklen et al., 2016; Sullivan et al., 2017; Wilmking et al., 2004); thus, we included nonlinear (quadratic) VPD terms (Table 2). As gridded precipitation data can be imprecise (McAfee et al., 2014), we included only linear precipitation–growth relationships to minimize detecting spurious precipitation–growth relationships.

2.5 | Modeling climate–competition effects on white spruce radial growth (full DNPP tree sample)

We used linear mixed-effects models to quantify the effect of competition–climate and site moisture–climate interactions on the BAI of white spruce. We log-transformed BAI and standardized continuous model covariates to have a mean of zero and a standard deviation of one. Thus, model coefficients were standardized and comparable. Because of the complexity of variables involved, we used a three-stage approach to model development. In the first stage, we established a "base" model by comparing models with the essential factors contributing to radial growth (ring age, tree size, reproductive effort, climate variables, and competition effects) and then tested whether the inclusion of climate–competition interactions improved model fit. Thus, we tested models with different ring age curves and iteratively included mast year, tree DBH, climate variables, conifer and broadleaf BA, and conifer BA in two-way interactions with climate variables. The model with the lowest AICc was selected as the best "base 1" model; it included a cubic ring age term, mast year, DBH, climate variables, broadleaf BA, and climate–conifer BA interactions (Supporting Information Table S2). The "base 1" model also contained two random effects: (a) minigrid ID to account for spatial non-independence of plots and (b) an individual-specific autoregressive (AR1) term to account for temporal autocorrelation and differences among individual trees. In the second stage of model selection, we tested our hypothesis that model fit would be improved by adding climate interactions with site factors associated with drought stress as well as adding main effects known to influence white spruce growth in DNPP (Table 1). Thus, we tested whether including climate interactions with tree DBH, percent tall shrub cover, plot slope angle, potential solar radiation, living mat depth, *or* SOL improved the "base 1" model. We tested a set of 88 competing models (Table 1, Supporting Information Table S2). For model simplicity, we limited the number of terms interacting with climate to two in a single model, one of which was always conifer BA, and we excluded quadratic terms from interactions with the aim of maintaining a sample size of approximately 10 sampled trees per model covariate. We found the addition of climate interactions with potential solar radiation, percent shrub cover, tree DBH, living mat depth, and SOL all improved the base model of BAI (lowered AICc); however, the addition of potential solar radiation–climate interactions produced the greatest reduction in AICc (Supporting Information Table S2). Thus, we selected potential solar radiation as the second variable (after conifer BA) to interact with climate terms. In stages 1 and 2, we used the full suite climate variables, while in stage 3 we assessed which of the climate variables and interactions should be in the final model. We compared 50 models with different combinations of climate variables interacted with conifer BA and potential solar radiation (Supporting Information Table S3). We also tested including some quadratic terms in the interaction terms. The final selected model was the most parsimonious model with an AICc value within two points of the lowest AICc value (Supporting Information Table S3).

2.6 | Relationship among climate–competition effects, site, Δ^{13}C, iWUE, and radial growth in a subset of the DNPP tree sample

Our goals in the analyses of a subset of trees selected from a floodplain and south-facing hillslope were to (a) model the relationship of Δ^{13}C and iWUE in tree rings to mean June–July VPD, conifer BA, and site location (floodplain vs. hillslope), (b) determine whether radial growth response to climate and competition in these selected trees was similar to the overall sample, and (c) examine the relationship between radial growth and possible drought stress signals (Δ^{13}C and iWUE). We began by modeling Δ^{13}C and iWUE as a function of mean June–July VPD interacted with conifer BA and site. We included tree ID as a random effect. The iWUE model additionally included a term to account for the linear increase in iWUE over time. We then fit the same model to log-transformed BAI averaged over two years. We chose the mean of BAI concurrent with and following the current growing season year as radial growth is often related to conditions in both the current and previous growing seasons. Finally, we modeled the two-year BAI average as a function of Δ^{13}C interacted with conifer BA and site and separately as a function of iWUE interacted with conifer BA and site. The models of BAI included a tree-specific autoregressive (AR1) term to account for temporal autocorrelation and differences among trees. Tree age can significantly affect both growth rates as well as δ^{13}C values (McCarroll & Loader, 2004; Sullivan et al., 2017). For this reason, we tested including ring age in each of the models (Supporting Information Table S4). Continuous model covariates were standardized to have a mean of zero and a standard deviation of one. Thus, model coefficients were standardized and comparable.

We fit all mixed-effects models using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015, version 1.1–14) in program R (R Core Team, 2017, version 3.4.2). The correlation coefficients among model covariates were all between −0.6 and 0.6 (Supporting Information Figure S3). Residuals from each selected model were assessed for violations of normality, homoscedasticity, and temporal autocorrelation using the DHARMa package in R (Hartig, 2018). Residuals from models conformed to all model assumptions, save those from the full dataset BAI model, which showed some departure from normality (Supporting Information Figure S4). Variables in the selected models were considered interpretable if the 95% confidence intervals (estimate ± 1.96 × *SE* of estimate) around the estimate did not overlap zero or were not within 0.001 of zero. AICc values and conditional and marginal R^2 values were calculated with the Multi-Model Inference package (Bartoń, 2017, version 1.40.0).

3 | RESULTS

3.1 | Climate–competition effects on white spruce radial growth (full DNPP tree sample)

The addition of climate–competition interaction variables to the base climate model significantly improved model fit as measured by AICc (Supporting Information Table S2). The inclusion of climate interactions with potential solar radiation, percent shrub cover, tree DBH, living mat depth, and SOL all improved the base model of BAI, but potential solar radiation–climate interactions produced the greatest reduction in AICc (Supporting Information Table S2). Thus, in the final model we selected potential solar radiation as the second variable (after conifer BA) to interact with climate terms. The estimated effects of covariates included in the final model on BAI are described below.

The estimated mean white spruce BAI from the final selected model, for the period of observation, 1974–1980 to 2003–2009, was 330 mm^2/year. Living mat depth, potential solar radiation, and plot slope angle were negatively related to annual radial growth (Table 2). Thus, an increase of +2*SD* above the mean for each value would be expected to reduce annual BAI by 11%, 8%, and 7%, respectively. Additionally, radial growth was reduced by an estimated 8% in mast years relative to non-mast years. Radial growth was similar across lithology types except for eolian soils (loess), which were associated with high radial growth. Unsurprisingly, tree DBH was positively associated with radial growth. Plot conifer BA alone had no overall influence on radial growth (but see interactive effects below), while broadleaf BA +2*SD* above average was associated with an estimated 10% increase in white spruce annual radial growth (Table 2).

Without considering interactive effects, the climate conditions associated with the highest estimated BAI were low mean VPD values in June–July in the year prior to ring growth, followed by wet prior-year August conditions and low winter precipitation, low or high mean May VPD, and current June–July VPDs near or slightly above average. Only winter precipitation and mean June–July VPD

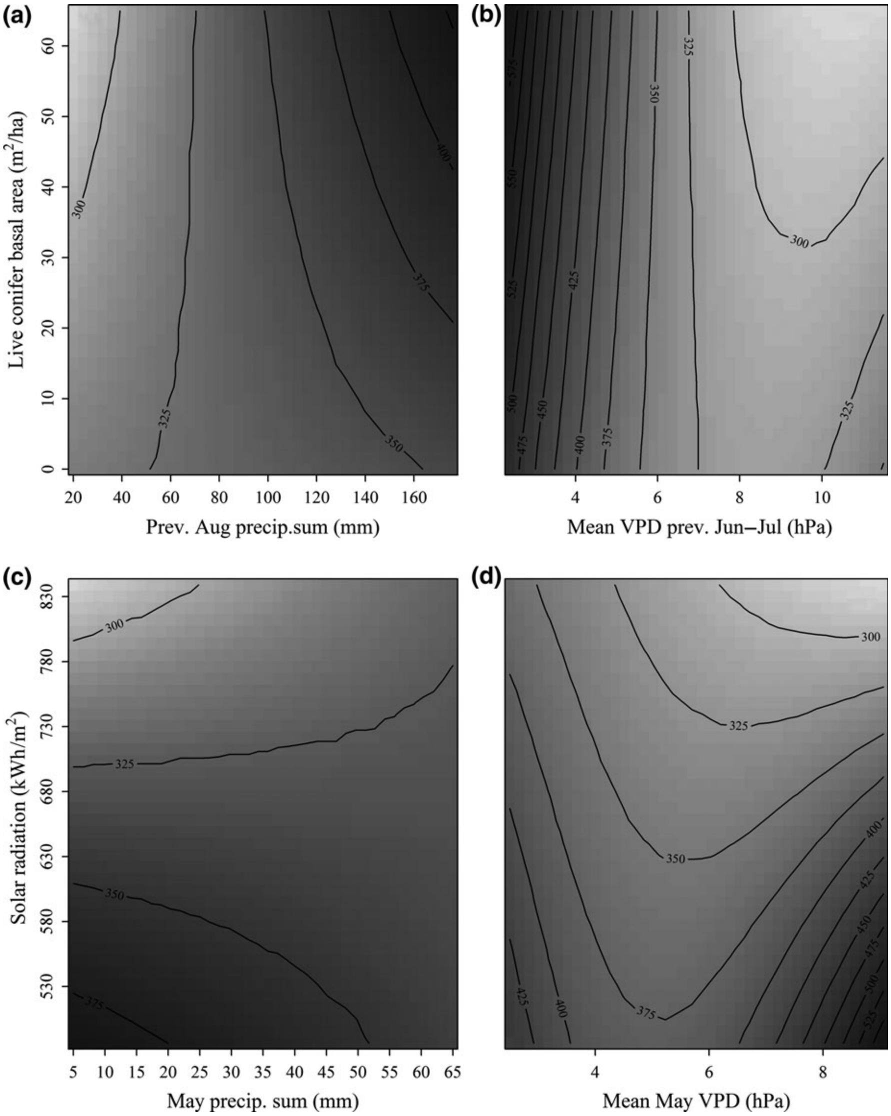

FIGURE 2 Estimated white spruce annual basal area increment (BAI, mm^2/year) as a function of live conifer basal area and previous year precipitation sum in August (a) and mean vapor pressure deficit in June–July (VPD; b) as well as a function of potential solar radiation and current May precipitation sums (c), and mean May vapor pressure deficit (d). Solar radiation, live conifer basal area, and climate values span the range observed within the sample. Model covariates not shown were held at mean values and a non-mast year is assumed

in year of ring formation showed no interactive effects with conifer BA or solar radiation. Estimated BAI decreased with increasing winter precipitation (Table 2). It may be that high snow cover is related to shorter growing seasons or growing seasons shifted to later in the spring/summer when drought stress is greater. Growth response to current and previous June–July VPD was nonlinear. White spruce BAI was predicted to increase with current year June–July VPD until an estimated 7.5 hPa, above which BAI decreased (Table 2; Supporting Information Figure S5). In contrast, BAI was predicted to decrease strongly with increasing previous year June–July VPD, but at VPD values above 9 hPa BAI no longer decreased with increasing VPD (Figure 2).

Increasing conifer BA was predicted to amplify the negative effects of previous August drought and June–July VPDs on white spruce radial growth (Table 2; Figure 2a). Specifically, BAI increased from an estimated 300 mm^2/year to over 400 mm^2/year with increasing precipitation levels in high conifer BA stands, while white spruce in open stands was only predicted to increase BAI from an estimated 325 to 350 mm^2/year under the same August precipitation gradient (Figure 2a). Similarly, white spruce growing in high conifer BA stands were more sensitive to previous mean June–July VPD than trees in low conifer BA stands (Figure 2b).

Current year May precipitation was positively associated with BAI in high potential solar radiation (south-facing slopes with no sun-obstructing topography) sites, but negatively associated with BAI in low solar radiation sites. In years with dry May conditions, BAI varied an estimated 75 mm^2/year depending on site potential solar radiation receipts, while in wet May conditions estimated radial growth was nearly uniform across the range of site solar radiation levels (Figure 2c). White spruce growth in low solar radiation sites was predicted to benefit the most from high mean May VPD, while white spruce in high solar radiation sites reduced BAI in years with high mean May VPD (Figure 2d). White spruce in low solar radiation sites showed the lowest estimated radial growth when May VPD was average, while growth was higher in either cool (low VPD) or warm (high VPD) years. Counterintuitively, previous year August precipitation benefited white spruce more in low rather than high solar radiation sites. It is possible white spruce growth in high solar radiation sites ceases for the year before these trees can benefit from August rainfall. Alternatively, August rainfall may run off and/or evaporates in high solar radiation sites before it is available for next year's growth.

3.2 | Relationship among climate–competition effects, site, $\Delta^{13}C$, iWUE, and radial growth (subset of DNPP tree sample)

Discrimination against ^{13}C ($\Delta^{13}C$) in annual tree rings was predicted to decrease with increasing current mean June–July VPD values and during mast years (Table 3; Figure 3), but was not influenced by estimated ring age (Supporting Information Table S4). Stand competition (conifer BA) and site (floodplain vs. hillslope) had no direct influence on $\Delta^{13}C$ levels; however, $\Delta^{13}C$ was more sensitive to mean June–July VPD in high vs. low conifer BA stands and in hillslope vs. floodplain trees (Table 3; Figure 3). Patterns in iWUE were the inverse of those for $\Delta^{13}C$ (Table 3).

The two-year BAI mean (mean of current and subsequent year BAI) was predicted to decrease with increasing current mean June–July VPD and with mast year (Table 3). Unlike the larger DNPP sample, radial growth in this subset was directly and negatively related

TABLE 3 Standardized coefficient estimates for models

Covariates and interactions	$\Delta^{13}C$ model	iWUE model	2-year BAI model	2-year BAI ~Δ13C	2-year BAI ~iWUE
Intercept	16.487[a]	105.47[a]	7.261[a]	7.3[a]	7.33[a]
Mast year	−0.301[a]	2.694[a]	−0.084[a]	−0.066[a]	−0.064[a]
VPD current Jun–Jul	−0.455[a]	4.395[a]	−0.091[a]	NA	NA
Conifer BA	0.205	−2.038	−0.180[a]	−0.14[a]	−0.139[a]
Site	−0.066	1.085	0.685[a]	0.375[a]	0.382[a]
Conifer BA × VPD curr. Jun–Jul	−0.160[a]	1.629[a]	−0.007	NA	NA
Site × VPD curr. Jun–Jul	0.301[a]	−3.222[a]	0.041	NA	NA
$\Delta^{13}C$[b]	NA	NA	NA	0.035	−0.059[a]
Site × $\Delta^{13}C$[b]	NA	NA	NA	−0.04	0.090[a]
Conifer BA × $\Delta^{13}C$[b]	NA	NA	NA	0.019	−0.032[a]
Marginal R^2/conditional R^2	0.14/0.47	0.40/0.63	0.22/0.90	0.21/0.81	0.21/0.83

Notes. The first three models share the same covariates, with the first estimating $\Delta^{13}C$, the second estimating iWUE, and the third estimating log-transformed white spruce BAI (average of current and subsequent growth years). The fourth and fifth models estimate the relationship between two-year BAI average and $\Delta^{13}C$ and iWUE, respectively. Covariates were scaled to have a mean of zero and a standard deviation of 1. NA indicates the covariate was not in the model. Each model has tree as a random effect. BAI models additionally have a cubic ring age term that is not shown (see Supporting Information Table S4) and an autoregressive term (AR1) by individual tree as a random effect. $N = 12$ trees, 360 growth rings and 247 $\Delta^{13}C$ and iWUE measurements. Estimates for "Site" are for the floodplain trees relative to the hillslope trees.

[a] Estimate significant (upper and lower 95% confidence interval do not overlap zero). [b] Covariate is iWUE for 2-year BAI~iWUE model and × $\Delta^{13}C$ for the 2-year BAI~Δ13C model.

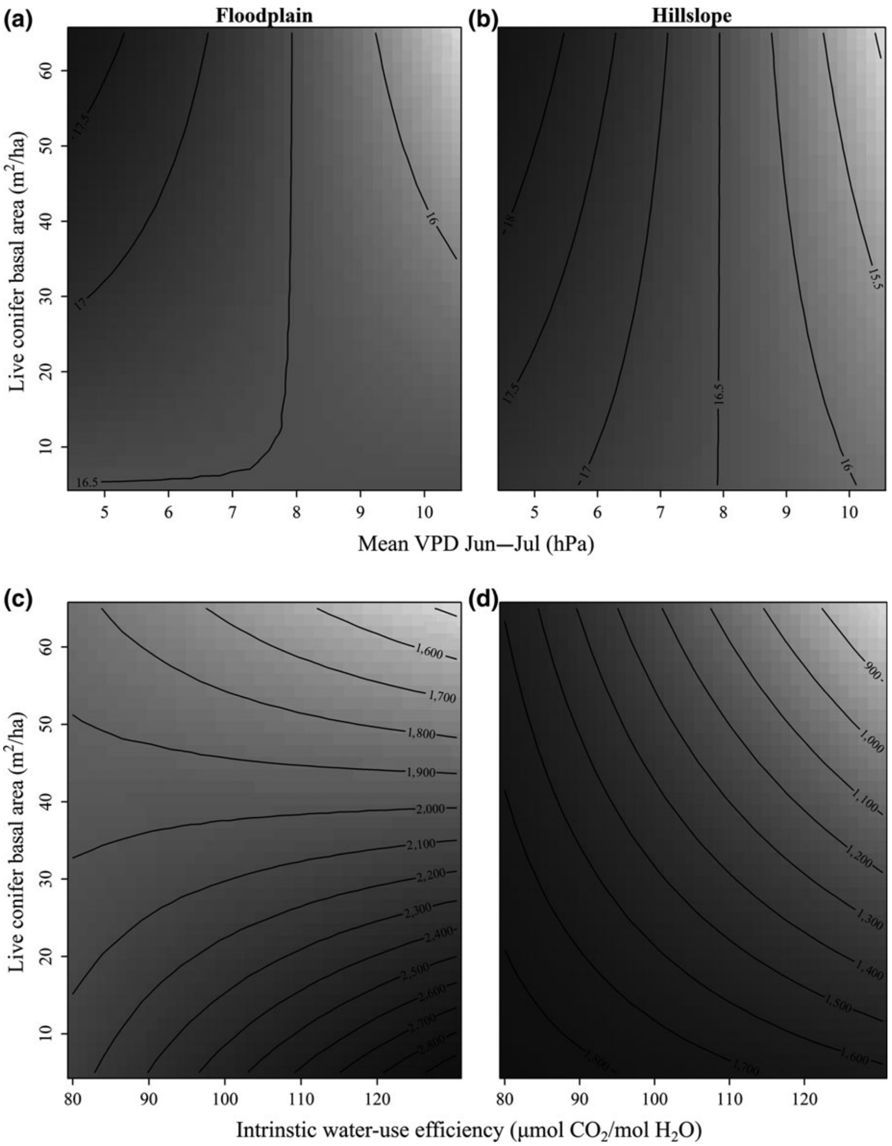

FIGURE 3 Estimated $\Delta^{13}C$ as a function of live conifer basal area and current year mean June–July vapor pressure deficit (VPD; a, b), and estimated 2-year mean BAI as a function of live conifer basal area and intrinsic water-use efficiency (iWUE; c, d) at the floodplain (a, c) and south-facing hillslope site (b, d). Model covariates not shown were held at mean values, and a non-mast year is assumed

to conifer BA and showed no variation in response to summer VPD across gradients of conifer BA or site location. The average two-year BAI mean from the floodplain trees was an estimated 50% larger than the hillslope trees. For context, the mean BAI from the six floodplain and hillslope plots was 311% and 184% larger than the mean BAI from the entire DNPP sample, respectively. These were both relatively productive areas, with the floodplain site being the most productive in the DNPP sample (Supporting Information Figure S1). The relationship between the two-year BAI mean and $\Delta^{13}C$ was not significant, though there were some apparent trends. These same trends, though in the inverse, were significant in the relationship between 2-year BAI mean and iWUE. The 2-year BAI mean generally decreased with increasing iWUE, but this negative trend was amplified by stand competition and strongly dependent on site location (Figure 3c–d). While trees in the hillslope site significantly decreased growth with increasing iWUE, trees in the floodplain site showed only minor growth decreases with increasing iWUE and only at the highest stand competition levels. At low stand competition levels, floodplain trees actually increased growth with increasing iWUE (Figure 3c).

4 | DISCUSSION

We found that white spruce climate-growth response was contingent on stand BA and site moisture characteristics. High competition (stand BA) and high potential solar radiation intensified the negative BAI response to warm and dry early to mid-summer and dry late summer conditions. The results of our carbon isotope analysis supported the hypothesis that moisture limitation is the mechanism for reduced growth in warm dry years, particularly in high competition stands and in the drier portions of the landscape. Discrimination against ^{13}C diminished with high June–July VPD, and this response was amplified in trees on south-facing hillslopes and in high BA stands, in keeping with our hypothesis. In productive locations where competition for water may not be limiting, however, we report evidence that growth is positively related to increased iWUE.

Finally, during mast years, we found decreased radial growth, reduced ^{13}C discrimination, and increased intrinsic water-use efficiency. Our findings demonstrate the significant role of temporally variable and confounded factors, such as forest structure and climate, on the observed climate response of white spruce in interior Alaska.

We found tree growth was interactively influenced by factors related to succession (moss depth and conifer BA), tree aging, and climate. This confounded and interacting nature of climate change and other directionally changing factors on tree growth has several implications. First, disentangling growth trends related to successional processes and tree aging from growth trends related to climate change requires a sampling design that encompasses a wide range of tree ages and sizes growing in similar sites (Bowman, Brienen, Gloor, Phillips, & Prior, 2013) and analysis procedures that account for the influence of succession or tree aging on growth (e.g., utilizing appropriate detrending methods or including age-related growth curves and succession-related factors in growth models). Our findings that growth declined with increasing moss depth and showed greater declines in high conifer BA than low conifer BA stands in warm, dry summers suggest that if factors related to succession and tree age are not accounted for, the result will likely be declining spruce radial growth rates over time and it will not be possible to discern whether this is due to climate changes, succession, tree aging, or some combination thereof. This accords with the finding that detrending methods influence the apparent growth trends in white and black spruce (Sullivan et al., 2017; Sullivan, Pattison, Brownlee, Cahoon, & Hollingsworth, 2016). It is important to note that we did not explicitly examine trends over time in this paper, but found that site factors that do change over time significantly influence white spruce climate-growth responses.

Another implication of interacting climate and succession factors is that sampling location is an important consideration when drawing inferences from the results of tree-ring studies. We found that white spruce in high conifer BA stands showed a more negative growth response and decreased Δ^{13}C to June–July VPD than white spruce in more open stands. Thus, studies conducted in mature, closed-canopy forests in interior Alaska may find more pronounced white spruce growth responses to increasing summer drought than white spruce in young, open-canopy forests (e.g., Barber et al., 2000).

An important implication of the interactive effect of climate and stand BA is that the maximum density of mature forests in interior Alaska may be reduced, such that a “fully stocked” forest in a warmer and drier future could have a lower BA than in the past. If this were the case, we would expect to see an increase in white spruce mortality in high BA stands associated with warm, dry climate conditions. There is mixed evidence that this reduction in stand BA is currently occurring. For example, Trugman et al. (2017) found white spruce mortality in interior Alaska was associated with high spring temperatures and to a lesser extent, July moisture availability, and competition, but found no evidence of increased mortality between 1994 and 2013. It may be that this was too short a time period to detect change in mortality rates. Indeed, longer term studies from Canada have found increased mortality rates for white spruce and other boreal tree species resulting from competition (Luo & Chen, 2015; Zhang et al., 2015) and drought (Peng et al., 2011). The inconsistent or uncertain evidence of increased white spruce mortality may indicate that other factors are countering the negative impacts of increasing summer drought and successional processes such as shifting foliage to root ratios, and/or increasing atmospheric CO_2 (Angert et al., 2005; Sullivan et al., 2017). It may also be that long-term, competition-induced increases in tree mortality in high basal area stands associated with warm, dry conditions help counter the negative impacts of a warming climate in these locations.

We show that trees in high BA sites are more sensitive to climate than those growing in more open stands. The greater climate sensitivity of trees in mature, high competition sites may increase vulnerability to disease and insect induced mortality (Anderegg et al., 2015; Cahoon et al., 2018; Csank et al., 2016; Mcdowell et al., 2008) and reduce resilience to disturbance (Johnstone, McIntire, Pedersen, King, & Pisaric, 2010) relative to trees in younger, less drought-stressed stands.

Mast years, years with high cone and seed production, are recorded as relatively narrow rings in white spruce tree-ring series (Juday et al., 2003). A novel and noteworthy result of our work is that mast years are recorded as particularly low Δ^{13}C and high iWUE values in white spruce tree rings in DNPP. Similarly, current year shoots in *Fagus crenata* showed ^{13}C enrichment during fruiting (Han, Kagawa, Kabeya, & Inagaki, 2016). Reduced radial growth during mast years is likely due to a shift toward reproduction at the expense of stem growth. It is possible the reduced Δ^{13}C and increased iWUE during mast years is a result of increased photosynthesis and/or greater stomatal closure resulting from the high demand for photosynthate and water required for cone and seed maturation. This pattern could also result from a shift in the timing of resource allocation, with reproductive effort occurring early in summer when water is more available and wood production occurring later when temperatures are higher and drought stress is greater. There is some evidence from temperate trees that nutrients for cone and seed production come from multi-year accumulated reserves, but that carbon comes from current year photosynthesis (Han & Kabeya, 2017). That both radial growth and Δ^{13}C are reduced in the mast year supports the idea that current year's carbon, and not stored carbon is being redirected from radial growth to reproduction. Given that masting events in white spruce are climatically driven (Krebs, LaMontagne, Kenney, & Boutin, 2012; Roland et al., 2014) and exert a tax on white spruce radial growth, there may likely be future interactions or trade-offs between growth and reproduction which may play out differently across the landscape (Roland et al., 2014).

Despite the very different site conditions (floodplain vs. hillslope) and a large gradient in conifer BA across the subset plots, the mean Δ^{13}C and iWUE were not significantly different between the floodplain and hillslope trees and across conifer BA levels (Table 3). This finding is consistent with the set point theory of homeostatic gas exchange (Brooks & Mitchell, 2011; McDowell, Adams, Bailey, Hess,

& Kolb, 2006; Whitehead, Jarvis, & Waring, 1984). Under this theory, the floodplain and hillslope trees in high and low conifer BA stands may have adjusted their architecture (e.g., leaf size, sapwood porosity, root development) to maximize photosynthesis while minimizing risks of cavitation (Fernández-de-Uña et al., 2016; McDowell et al., 2006; Tyree & Sperry, 1988) to ultimately achieve a homeostatic level of $\Delta^{13}C$ and iWUE. However, during hot, dry summers $\Delta^{13}C$ decreased and iWUE increased in trees in high competition sites relative to low competition and in hillslope relative to floodplain, suggesting the former trees operate on a much thinner safety margin (lower soil water potential) and close their stomata more quickly during warm dry periods than the latter trees. The ability of white spruce to maintain a constant ratio between water loss and photosynthetic gain across these disparate site conditions highlights the phenotypic plasticity of these trees in the face of incrementally changing conditions; however, the greater sensitivity of both growth and $\Delta^{13}C$ of the trees on high competition, south-facing slopes points to potential future break points in this plasticity.

In water-limited environments, increasing summer drought is expected to lead to stomatal closure, resulting in decreased $\Delta^{13}C$ and reduced transpiration relative to photosynthesis, and thus increased iWUE. Prolonged stomatal closure during drought conditions reduces carbon uptake (Mcdowell et al., 2008; Sala, Woodruff, & Meinzer, 2012; Sevanto, Mcdowell, Dickman, Pangle, & Pockman, 2014). Given this, we expected to see reduced BAI with decreasing $\Delta^{13}C$ and increasing iWUE. In general, we found these expected patterns, with one exception: Floodplain trees in open stands increased growth with increasing iWUE. This finding suggests these trees may have increased iWUE as a result of increased photosynthesis rather than decreased stomatal conductance. This highlights the need to interpret iWUE in concert with growth patterns and not to assume it is metric of drought stress. We emphasize these results are from a very small subset of trees from a productive floodplain and cannot be extrapolated to the full landscape. Rather, these findings point to the highly dynamic mosaic of tree growth responses to climate and importance of stand competition and landscape position in mediating climate-growth responses.

We found a positive association between BAI and broadleaf BA. This is likely driven by the site conditions associated with broadleaf species in DNPP that are also conducive to white spruce productivity: deep active layers (Alaska birch), south-facing slopes (aspen), and river terraces (balsam poplar; Roland et al., 2013). Further, soil temperatures and nutrient cycling may be higher in areas with high broadleaf BA (Chapin et al., 2006). In broadleaf dominated forest stands, high radiation input during spring thaws the ground earlier than in conifer dominated stands (Chapin et al., 2006) and leaf litter inhibits moss development, keeping soils warmer than in areas with thick living mats (Roland, Stehn, Schmidt, & Houseman, 2016). Broadleaf trees, however, take up considerably more soil water than coniferous trees (Young-Robertson, Bolton, Bhatt, Cristóbal, & Thoman, 2016) and, thus, could have a significant impact on white spruce climate-growth relationship. Indeed, Cortini et al. (2012) found this to be the case in mixedwood forests in western Canada. Because broadleaved trees constitute a small fraction of the DNPP forest mosaic, we were unable to test the effect of broadleaf BA on white spruce growth response to climate. This should be a focus of future work in study areas with greater broadleaf presence and representation in different site conditions than found DNPP.

It is not surprising that we found that large diameter trees showed higher annual BAI than small diameter trees. It is worth noting, however, that tree DBH had an effect size two to forty times larger than the climate and interaction variables. Similarly, ring age also had a nearly twofold to 25-fold larger effect than climate and interaction variables. Our model results are consistent with the finding that mass growth rate increases with individual tree size (Foster, Finley, D'Amato, Bradford, & Banerjee, 2016; Stephenson et al., 2014) and that tree size and age have larger impacts on tree productivity within a region than climate (Foster et al., 2016). The strong positive influence of tree size on growth underscores the need to interpret climate-growth responses from within the context of current forest physical structure. If predictions of forest productivity or carbon storage were based only on dendroecological studies using dimensionless ring width indices to determine climate-growth, the large and significant effect of current tree size and age would be lost resulting in exaggerated climate effects on future productivity. There is likely some interactive effect between climate and tree size as has been found with climate and tree age (Carrer & Urbinati, 2011; Szeicz & MacDonald, 1994). We found including climate–DBH interactive effects in our growth model improved the model fit (Supporting Information Table S2), but for simplicity, we only included interactions with the one variable in addition to conifer basal area that *best* improved the model fit; thus, climate–DBH interactions were not included in our final growth model. Our understanding of white spruce growth in interior Alaska would benefit from an explicit examination of climate and tree size interactions.

There are several limitations to our models of white spruce growth. First, our estimates of growth are limited to stem growth. Thus, we are unable to determine whether a change in radial growth represents an overall change in productivity or a reallocation of carbon among stems, roots, branch elongation, or needles. We did, however, include reproductive effort into our growth, $\Delta^{13}C$, and iWUE models, which revealed significant trade-offs between radial growth and reproduction as well as distinct $\Delta^{13}C$ and iWUE patterns associated with masting. Second, although our study design ensured a random sample of plot locations across the study area, at the plot level our cored trees tended to be slightly larger than the average tree within the plot (Supporting Information Figure S2) indicating a tree size bias. This bias may have led to an underestimated competition effect in our model, assuming larger trees are less negatively affected by competition with smaller trees and perhaps to an overestimated climate effect, assuming larger trees are more drought sensitive than smaller trees (Bennett et al., 2015). Finally, we did not core dead trees, so our sample may be affected by "modern sample bias." However, because we limited the time frame of our study to 30 years and our sample includes a large range in tree ages from a random placement of plots, with relatively few dead trees, our sample should be relatively robust and buffered from some of the biases associated with sampling only living trees.

In summary, we found stand BA mediates the influence of climate on the annual radial growth of white spruce in DNPP, amplifying the negative effect of previous summer VPD and moderating the positive influence of previous August rainfall. Our carbon isotope analysis suggests the mechanism behind these modified climate-growth responses may be increased competition for moisture in high basal area stands and dry sites. We also found that large reproductive events (mast years) both reduce radial growth and strongly decrease $\Delta^{13}C$ (and increase iWUE) of white spruce trees, suggesting trade-offs between growth and reproduction for current year's photosynthate. Our finding that high BA stands show greater sensitivity and negative growth responses to warming climate conditions than open stands may ultimately portend lower white spruce stand densities and increased vulnerability to insects and disease in future interior Alaska mature forests. Our findings also point to the need for studies examining growth trends to address the confounded nature of climate change and other directionally changing factors that influence tree growth (succession, tree aging, atmospheric CO_2). Overall, our results suggest highly dynamic individual tree growth responses to future climate change that are dependent on both landscape position and stand competition and likely to result in feedbacks on future forest structure.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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