

Stand basal area and temperature interact to influence growth in white spruce in southwest Alaska

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Abstract. Warming temperatures are having a disproportionate effect on boreal ecosystems, influencing the establishment and growth of tree species across their respective ranges. However, less is known about how competitive interactions influence growth–climate relationships. We used tree-ring data from 26 study plots (836 trees) to investigate how the growth patterns of white spruce (*Picea glauca*) respond to variation in competition and climate in southwest Alaska. Using linear mixed-effects models, we compared growth against covariates for stand basal area, competition, climate (temperature, precipitation), and spruce beetle mortality. We characterized competition at the tree level using two distance-dependent competition indices: Hegyi index and a height advantage index. Furthermore, we assumed that stand-level competition increased with basal area. We found that high summer temperatures resulted in reduced growth in stands with higher basal area (i.e., the most crowded stands), but increased growth at sites with low basal area. Our results suggest that historically productive stands may show declines in growth under warmer conditions, with important implications for future stand structure and productivity.

Key words: competition; dendrochronology; dendroecology; environmental change; *Picea glauca*; tree growth.

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INTRODUCTION

Boreal forests comprise nearly a quarter of global terrestrial carbon (IPCC 2000) and over 30% of the world's forest carbon stores (Pan et al. 2011). Recent warming at high latitudes (Christensen et al. 2013) and the importance of boreal forests to global carbon storage highlight the need for a greater understanding of the effects that increasing temperatures have on tree establishment, growth, and mortality in these ecosystems. Understanding the extent to which competition may mediate climate–growth relationships is key to understanding the overall relationship between climate and growth. Competition has been shown to affect the growth–climate response in mid-latitude forests

(Sánchez-Salguero et al. 2015, Bottero et al. 2017, Ford et al. 2017), and there are indications that similar dynamics are taking place in high latitude forests (Wilmking and Juday 2005, Zhang et al. 2015). White spruce (*Picea glauca*) provides an ideal model to examine how intraspecific competition affects the expected growth–climate relationship because the species is widespread at northern latitudes, is well-studied in Alaska, and often occurs in monospecific stands. Recent work has demonstrated that the rapid warming already observed at northern latitudes has substantially influenced the growth (i.e., Barber et al. 2000, D'Arrigo et al. 2004, Wilmking and Juday 2005, Walker and Johnstone 2014, Sherriff et al. 2017) and establishment (Miller et al. 2017) of white spruce.

White spruce in Alaska have experienced contrasting patterns of growth near the western range limit of the species, suggesting that a biome shift may be underway (Beck et al. 2011, Juday et al. 2015). Coastally influenced (maritime) sites have generally displayed a positive response to warming (Sherriff et al. 2017), whereas many continental (interior) sites have shown a mixed growth response or declines in growth (e.g., Barber et al. 2000, Juday et al. 2015, Sullivan et al. 2017). In addition to the broadscale effects of climate and geography, finer-scale abiotic (e.g., soil, topography) and biotic (competition) conditions may influence growth patterns in forest stands (McGuire et al. 2010, Nicklen et al. 2016, Sullivan et al. 2017), but to date, this level of detail has received little attention in studies in Alaska, particularly at the individual tree level. Although there is some debate concerning the relative influence of climate and competition on tree growth in high latitude forests (Price et al. 2015, Zhang et al. 2015), recent work from southwest Alaska suggests that the relationship between temperature and growth in white spruce varies with stand density, whereby closed forest stands exhibit stronger growth declines in response to temperature than their more open-grown counterparts, especially in warmer than average years (Sherriff et al. 2017). If the relationship between climate and growth varies with stand basal area (e.g., Wilmking and Juday 2005) or competition, any effects of future warming are likely to be disproportionately large in the highest density stands, or in stands where competition otherwise is high.

To date, the effects of competition between individuals and stand condition (e.g., stand basal area, disturbance) on spruce growth have not been explicitly quantified or ranked at fine spatial scales near the species' range limit. If growth response to climate depends on the intensity of local competition, variation in competitive stress at the tree level may lead to within-stand heterogeneity in growth that is independent of other variables such as tree size or topography. Likewise, stand structure, a key component controlling competitive interactions, varies over time, and structural changes due to disturbance can lead to changes in the growth patterns of surviving individuals (Sherriff et al. 2011, 2017). For example, the removal of competitors following bark beetle outbreaks makes resources that were

previously in short supply more readily available to surviving trees, which in turn can result in a rapid growth release in the survivors (Romme et al. 1986, Veblen et al. 1991, Berg et al. 2006, Sherriff et al. 2011). Greater access to resources following the removal of competitors may also alter the climate–growth relationship, potentially mitigating growth declines under warm or dry conditions, or resulting in a positive growth response when conditions are favorable.

In this study, we hypothesized that the effect of summer temperature on white spruce growth would vary with between-tree competition and stand basal area. Specifically, we expected an interaction between competition and temperature such that the negative effect of increasing temperatures on radial growth would be stronger (i.e., associated with smaller rings) where trees were subject to higher levels of competition. Furthermore, we expected an interaction between stand basal area and temperature, where unfavorable climatic conditions would have stronger effects in stands where basal area was higher. We included precipitation in the analysis, but decided against including an interaction term between precipitation and competition because we assumed that competition has a seasonal (summer) influence on growth in this region, and thus, summer temperatures were more likely to influence its effect.

METHODS

Study area and field data collection

The study sites were located in Lake Clark National Park and Preserve and Katmai National Park and Preserve, between approximately 58° and 61° latitudes (Fig. 1). The regional climate is shaped by storms arriving from the Bering Sea and Northern Pacific Ocean, and cold air masses from the Alaskan interior. Moving along a southwest to northeast gradient, mean annual precipitation ranges from 336 to 495 mm, while average maximum and minimum July temperature ranges from 17.7° to 19.7°C and −12.9° to −13.6°C, respectively (NOAA/NCDC, <http://www.ncdc.noaa.gov>). Most precipitation falls during the growing season as rain, though winter snow is common in both ecoregions. On average, September is the rainiest month, though the wet season extends from July through October.

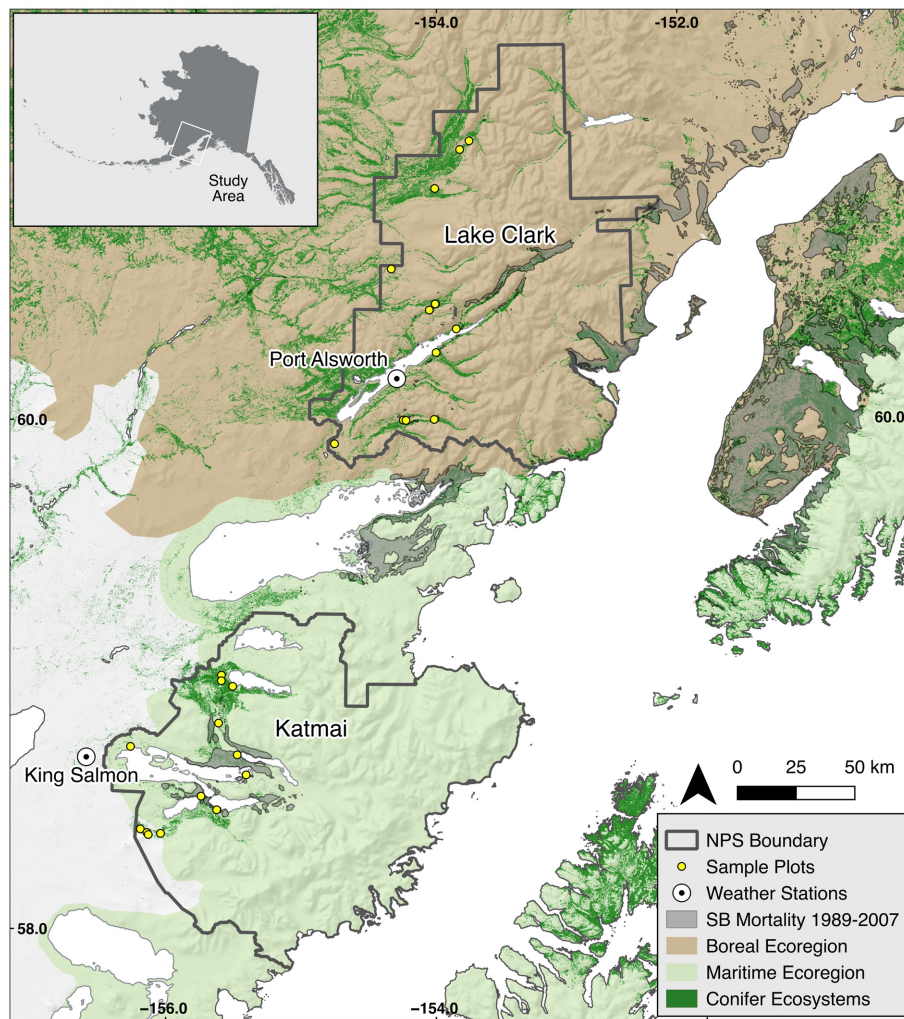


Fig. 1. Study area.

Twenty-six representative sites were drawn from a larger sample population using a generalized random tessellation stratified (GRTS) sample design, which was augmented as needed with randomly stratified samples (Miller et al. 2017). The sites were evenly distributed between Lake Clark ($n = 13$) and Katmai ($n = 13$) National Parks and Preserves, and across a range of stand densities. Lake Clark National Park is located in the Lime Hills (hereafter “boreal”) ecoregion, and Katmai National Park is located in the Alaska Peninsula (hereafter “maritime”) ecoregion (Nowacki et al. 2003). The boreal ecoregion, located at the eastern end of the longitudinal gradient, is characterized by a moderate

continental climate typical of Interior Alaska (warm summers, cool winters) due to its proximity to the Bering Sea and North Pacific Ocean, while the maritime ecoregion, to the west, has a cooler summer climate and milder winter temperatures (Nowacki et al. 2003).

Between 2009 and 2012, a permanent 30×30 m (0.09 hectare) plot was established at each site. Plots were sampled across a range of stand densities, a majority of which were either closed forest (>50% canopy cover) or woodlands (~10–25% canopy cover; Viereck et al. 1992). All trees with dbh ≥ 4 cm were cored over a contiguous area within each plot to attain a representative sample of tree ages. The number of cored

trees varied per plot, ranging between 30 and 60 individuals, and the cored area generally comprised a census of at least half of the 30 × 30 m plot. Cored trees therefore included live and dead stems from a full range of diameter classes and canopy positions. We recorded dbh, height, and condition (live or dead), as well as the within-plot location (x and y , in meters) for every cored tree.

We recorded the elevation (m), slope (°), aspect (°), and geographic coordinates for each plot. Plots were 22–550 m elevation and <9° slope. We assumed that because slope values were low and did not vary considerably among plots (see Sherriff et al. 2017), neither slope nor aspect would contribute to variation in site productivity, and thus would have a limited influence on growth. We therefore elected not to use the slope or aspect values in the final analysis. Elevation increased along a longitudinal gradient in the study area, with higher elevations in the eastern (boreal) sites, though we only included sites at lower elevations (not treeline, Sherriff et al. 2017).

Growth and age data

We processed all cores using standard dendrochronological techniques (Fritts 1976, Speer 2010). The cores were statistically cross-dated using COFECHA (Holmes 1983). We estimated establishment year for each core by correcting for coring height (see Miller et al. 2017). When possible, we estimated years-to-pith with ring curvature for the cores that did not include the pith. We elected to use raw ring widths for radial growth, because the similarity between the BAI (basal area index) and ring width models was close enough that the inference concerning climate and competition would be largely the same (Appendix S1: Fig. S1). We used static competition indices which were measured during the sample year, which necessitated that we limit our analysis to a time period during which we could assume that competition metrics were relatively uniform. To meet this assumption, we constrained our study period to include growth years from 1986 to the year the samples were collected, which ranged from 2009 to 2012. We selected this time period because it represents a period of increased growth in white spruce in both ecoregions and it includes years with average summer temperatures exceeding 11–13°C,

which has been shown to be an upper threshold for growth (e.g., D'Arrigo et al. 2004, Wilmking et al. 2004, Sherriff et al. 2017). We could not estimate establishment year for a small subset of cores ($n = 45$), so these cores were not considered in the final analysis. Our final data set included 18,974 annual growth rings from 836 trees distributed among 26 plots. While our ring width measurements are almost certainly affected by the well-known relationship between tree size and annual ring width (Fritts 1976, Cook 1987), our period of interest was relatively short (1986–2010), suggesting that error due to this trend would be minimized. However, we included year of establishment (a proxy for tree age) in every fitted model to account for variation due to age.

Spruce beetle mortality data

The spruce beetle (*Dendroctonus rufipennis*) is the leading cause of mortality in our study area. Spruce beetle-related mortality was present in 16 of the 26 plots. Spruce beetle activity remained at a low-level (<6%) until 2000, when the most recent outbreak began. We created a tree-level indicator for spruce beetle mortality based on the status of each tree when it was sampled. Although we were not interested in the effects of spruce beetle mortality per se, we needed to account for the known variation in growth caused by beetle kill, including growth reductions in affected trees prior to death (Csank et al. 2016, Sherriff et al. 2017), and growth releases in surviving trees (Sherriff et al. 2011). We assumed that spruce beetles were the mortality agent for trees that were dead at the time of sampling because we found evidence of beetles (entry holes, galleries, and/or blue stain fungi) and no evidence of other disturbance (e.g., fire or wind-throw) at the study sites (Sherriff et al. 2011, 2017). For every cored tree that was dead at the time of sampling, we used the last year of ring formation (determined based on cross-dating of cores) as an approximate date for tree death, which we considered a single mortality event. We estimated annual spruce beetle mortality intensity (an estimate of annual spruce beetle mortality rate) at the plot level by dividing the total number of plot-level mortality events in each year by the total number of trees in the plot. We could only estimate mortality events for cored trees, which may slightly underestimate

mortality intensity in some stands. Beetle-related mortality peaked at our sites between 2003 and 2005.

To test for lag effects influencing growth release, we created a series of lagged mortality intensities for each year, ranging from one to five years preceding ring formation, and compared their effect on growth using Pearson correlation coefficients with log ring width for all plots that experienced spruce beetle mortality. We assumed that the mortality intensity from 0 to 5 yr before ring formation would most influence growth for two reasons: (1) These windows lie within previously established release periods for white spruce in this region (Sherriff et al. 2011), and (2) the largest outbreak during the study period was centered around 2005, five years prior to the last recorded year of growth. The four-year mortality intensity had the strongest negative relationship to growth, so we included it in all subsequent calculations. We ran the final model with and without data from dead trees, with little change in the results (Appendix S1: Fig. S1). Therefore, we elected to combine data from both live and dead trees in the single analysis.

Spruce beetle mortality was confined almost exclusively to forested sites. Woodland plots had only 9% (37 dead trees) mortality at the time of sampling, while forested plots had 33% (163 dead trees) mortality. Of the 201 trees that died, 78% (157) died between 1986 and 2011. A majority (69%) of the beetle kill was concentrated at the western end of the gradient, in the maritime ecoregion. During the height of the recent spruce beetle outbreak, as many as 22 trees died in sampled plots per year, mostly during the period from 2003 to 2007.

Competition indices.—We modeled the effects of competition on growth at two scales. We characterized stand-level crowding with basal area calculated for each plot (m^2 per hectare). While stand basal area is not a direct measure of competition per se, we assumed that stand-level competition would be higher in stands with higher basal area and that competitive pressure would be likely increase when resources became more limited, as might occur during periods of increased temperature. We also calculated two tree-level competition indicators that characterize competition between a focal tree and its immediate neighbors. The first was based on the

size and distance-dependent competition index developed by Hegyi (1974), the second was modeled after a height advantage index developed by Weber et al. (2008). The Hegyi index is calculated with the equation:

$$\text{Hegyi}_i = \sum_{j=1}^n \frac{\text{dbh}_j / \text{dbh}_i}{\text{Dist}_{ij}}$$

Hegyi_i is the competitive strain on the focal tree i , dbh_i is the dbh of the focal tree, dbh_j is the dbh of competitor tree j , and Dist_{ij} is the distance between them. We assumed that higher values on the index equated to higher levels of neighborhood competition for the focal tree. We calculated the Hegyi index using the tree diameter at the time of sampling, which assumes that the effect of competition between trees was relatively unchanged throughout the sample period.

The height advantage index ranged from 0 to 1 depending on whether or not the focal tree was taller than its competitors (1), shorter than its competitors (0), or ranked somewhere in between. The index was calculated using the equation:

$$\text{Height}_i = \frac{\sum_{j=1}^n h_j}{n}; \text{ if } (h_i > h_j, h_j = 1), \\ \text{else } (h_j = 0)$$

Height_i refers to the index for each focal tree, h_i is the focal tree height, and h_j is the height of each competitor (out of n competitors, Weber et al. 2008). We assumed that higher values of the index indicated that the focal tree had a greater competitive advantage than the other trees in its neighborhood, and thus was under less competitive pressure. Tree height was not recorded for a subset of the data, mostly in uncored competitor trees (27 individuals within three plots). We used plot-specific models to estimate parameters in the Chapman-Richards function to estimate heights for these individuals,

$$\text{Height} = A(1 - e^{-k \cdot \text{dbh}})^p$$

where model parameters A (maximum possible height), k , and p (scaling parameters) were estimated using robust non-linear regression (Appendix S1: Table S1). Although there were other tree species present in the study area, white spruce was by far the dominant species. We

therefore assumed that all species were competitively equivalent, and did not specify species when calculating competition indices.

We determined the optimal neighborhood competition radius (beyond which neighboring trees were assumed to be outside the competition radius) by analyzing correlations between the competition indices and ring width, calculated for neighborhoods with radii in 1 m increments between 1 m and 5 m surrounding each tree. The selected radius was 5 m for the Hegyi index and 3 m for height advantage, and these values were used in all subsequent analyses. To correct for errors in the competition indices for trees near the plot edge, we used a translation edge correction, which has been shown to have less bias than other edge correction methods such as buffering or reflection (Pommerening and Stoyan 2006).

Climate data.—We estimated annual temperature and precipitation values for each plot using climate data from the Daymet data set (Version 3; Thornton et al. 2018). Daymet is a 1 km resolution gridded climate data set, with estimated daily climate observations from 1980 to the present (Thornton et al. 2018). For each water year, we used Google Earth Engine (Gorelick et al. 2017) to extract maximum daily temperature (°C) for the summer months (June and July) and total winter–spring (January–April) precipitation (mm) for each plot location. We aggregated the temperature and precipitation to annual resolution by summing the daily precipitation observations and averaging maximum daily temperatures. We elected to use winter–spring precipitation (hereafter precipitation, which mostly falls as snow) and average maximum summer temperature (hereafter temperature) as covariates because they

have low collinearity and both have been shown to be good predictors of growth in this region (Miller et al. 2017, Sherriff et al. 2017).

Statistical analysis

To quantify the effects of stand basal area, competition (Hegyi index, height advantage), climate (precipitation and temperature), and their interactions on annual growth, we fit linear mixed-effects models (package nlme, Pinheiro et al. 2016) that regressed ring width against tree and climate attributes. We specified tree nested within plot as the random effects, and all other variables were treated as fixed effects. Growth data are continuous-positive (greater than 0) and non-linear by nature. They become normal upon transformation, so we log-transformed ring width prior to analysis.

Along with climate, stand basal area, and competition, we included covariates for tree characteristics (establishment year, tree-level mortality) and 4-yr lagged spruce beetle mortality intensity in each model because these variables have been shown to influence annual growth and to account for heterogeneity between plots. Additionally, we fit each model with and without dbh to test for the effects of size. We fit 16 models in total, with and without interaction terms for temperature and both stand basal area and tree-level competition variables (Table 1). We elected to test for interactions between temperature and both stand basal area and tree-level competition, because we hypothesized that these effects might vary with scale. We also decided that we would not include interaction terms between winter–spring precipitation and competition or basal area metrics, because while precipitation has been shown to

Table 1. AIC, Delta AIC, model parameters (K), and marginal and conditional r^2 for the models evaluating ring width response, ranked by Delta AIC.

Model	AIC	Δ AIC	Marginal r^2	Conditional r^2
BA temp interaction only with dbh	9749.46	0.00	0.24	0.72
BA & height temp interaction with dbh	9757.92	8.46	0.24	0.72
BA & Hegyi temp interaction with dbh	9758.14	8.68	0.24	0.72
Full model with dbh	9766.70	17.24	0.24	0.72
No interactions with dbh	9780.22	30.76	0.24	0.72
Hegyi temp interaction only with dbh	9789.00	39.54	0.24	0.72
Height temp interaction only with dbh	9789.11	39.65	0.24	0.72
Hegyi & height temp interaction with dbh	9797.41	47.95	0.24	0.72

Notes: Models are named according to their temperature–competition interactions, if any were included. The selected model is given in bold.

influence annual growth (Sherriff et al. 2017), we assumed that the effects of competition are more likely to occur during the summer growing season and thus are more likely to interact with summer temperatures. We compared the relative support for each model using Akaike information criterion (AIC). The model with the lowest AIC has the most support in the given data set, and models with ΔAIC ($\Delta\text{AIC}_i = \text{AIC}_i - \text{AIC}_{\min}$) less than 2 contain a similar amount of information (Burnham and Anderson 2004). We performed all data analyses in the R statistical computing environment (version 3.4.1, R Core Team 2016).

We scaled and centered all continuous predictor variables prior to model fitting by subtracting the mean and dividing by two standard deviations (Gelman 2008). Standardizing variables in this fashion allows for a more intuitive interpretation of interaction terms, as it puts variables on a common scale (Gelman 2008). Model results can be interpreted as a change in the response for a change of two standard deviations of the predictor for continuous variables, which roughly corresponds to the change from lowest to highest value, and a change in category for binary variables (Gelman 2008). We tested for multicollinearity by estimating variance inflation factors. We visually assessed each model for temporal

autocorrelation with autocorrelation plots of the normalized residuals (Pinheiro and Bates 2000). We found temporal autocorrelation between years in the initial models, so we included a continuous-time autocorrelation term to account for correlated growth between subsequent years. We used marginal r^2 (variance explained by fixed effects) and conditional r^2 (variance explained by fixed and random effects together) to estimate the variance explained by each candidate model (Nakagawa and Schielzeth 2013).

RESULTS

All of the linear mixed-effects models, including the top-ranked (lowest AIC) model evaluating growth response included a combination of tree, stand basal area, tree-level competition, site, and climate attributes (Table 1). The top-ranked AIC model included an interaction term between temperature and stand basal area, suggesting that crowding mediates the response to warming (Fig. 2; Appendix S1: Table S2). The marginal r^2 for the selected model was 0.24, and the conditional r^2 was 0.72 (Table 1). Models without the temperature $\times$ basal area interaction term all had ΔAIC values >30 , which suggests that models including this interaction term had much

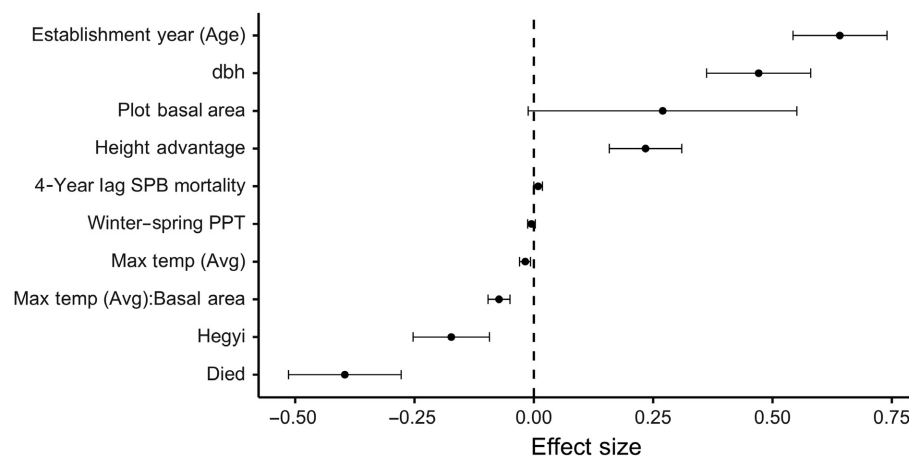


Fig. 2. Regression estimates (effect size) from the linear mixed-effects model with lowest AIC value. Estimates are ordered smallest to largest (negative to positive) according to effect size. With the exception of tree condition (live or dead), which is binary, all predictor variables were standardized prior to analysis by subtracting the mean and dividing by two standard deviations, which put all estimates on a common scale interpretable as the change in response ± 2 two standard deviations of the predictor for continuous variables, or a change in category for binary variables. Ring width was log-transformed prior to analysis. Interactions between variables are indicated by (:). Points refer to standardized regression coefficients; lines are 95% confidence intervals.

stronger support from the data than any of the other models we evaluated (Burnham and Anderson 2004).

Annual diameter growth ranged from 0.02 to 5.27 mm (mean = 0.73 mm). Our model indicated that annual growth was greater overall for trees with a more recent establishment year (younger trees, effect size = 0.64, 95% CI = 0.54–0.74; Fig. 2).

Tree diameters ranged from 1.4 to 45.8 cm (mean 15.1 cm). Diameter at breast height, which was positively related to growth, had the strongest effect on ring width of any of the structural traits included in the model (effect size = 0.47, 95% CI = 0.36–0.58).

As expected, the Hegyi index was negatively related to radial growth (effect size = -0.17 , 95% CI = -0.25 – 0.09), while height advantage had a positive effect on growth (effect size = 0.23 , 95% CI = 0.16 – 0.31).

The temperature: plot basal area interaction term in the selected model suggests that the effects of temperature are conditional on plot basal area (effect size = -0.07 , 95% CI = -0.01 to -0.05). At sites with plot basal area values on the lower end of the spectrum, such as those in woodland ecosystems, high summer temperatures lead to increased growth (Fig. 3). However, in sites with basal area were near the average or higher (i.e., closed forest systems), warmer summer temperatures resulted in reduced annual growth (effect size = -0.02 , 95% CI = -0.03 to >-0.01 for average plot basal area levels). The selected model suggested that winter–spring precipitation did not have a consistent effect on ring width (effect size = >-0.01 , 95% CI = -0.013 to >0.01 ; Fig. 2).

The effect of spruce beetle mortality on growth varied. Trees that died from spruce beetle showed reduced growth when compared to those that survived (effect size = -0.40 , 95% CI = -0.51 to -0.28 ; see also Csank et al. 2016 and Sherriff et al. 2017). We did not detect evidence of an increase in growth due to competitive release following beetle-related mortality (effect size <0.01 , 95% CI = 0 to 0.02).

DISCUSSION

Our results indicate that climate influenced the growth of individual trees regardless of competitive intensity, but as predicted, the direction and

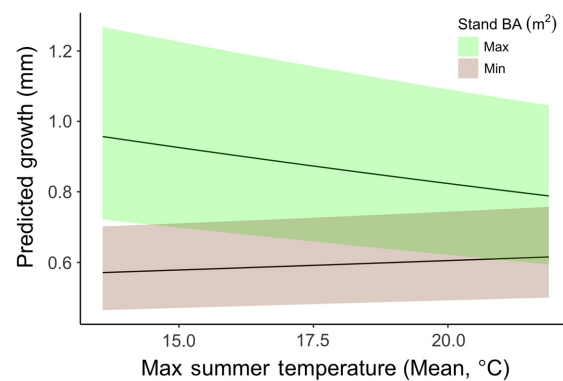


Fig. 3. Predicted change in growth (mm) for live trees as a function of mean summer temperature at minimum and maximum crowding index for each ecoregion. Predictions are for population-level response and do not incorporate random effects. All other variables were held to their mean or mode. Shaded areas are 95% confidence intervals, which were calculated as 1.96 times the standard error.

strength of this effect varied with stand basal area. Tree growth did not vary consistently with stand basal area under average summer temperatures, yet we found that trees in stands with higher basal area (i.e., crowded forest) sites showed growth declines when maximum summer temperatures increased, while trees in stands with lower basal area (i.e., less crowded woodland) sites responded positively under similar conditions.

The negative effect of the interaction between basal area and temperature showed that continued warming could lead to declines in productivity and/or forest health in this region of Alaska. Our findings are consistent with studies that report declining growth patterns observed across interior Alaska and western Canada (Barber et al. 2000, Beck et al. 2011, Juday et al. 2015, but see Sullivan et al. 2017) and with recent studies that argue for the importance of competition in mediating the effects of climate on growth (D'Amato et al. 2013, Zhang et al. 2015, Bottero et al. 2017, Ford et al. 2017). Where they have been reported, growth declines in white spruce have been attributed in part to temperature-induced drought stress: As high temperatures increase evaporative demand, competition for soil water increases and trees show signs of moisture stress (Barber et al. 2000, Csank et al. 2016).

While site conditions may explain why some stands were more densely stocked to begin with, our results suggest that competition that arises from these high stocking levels can result in growth declines at more extreme summer temperatures. When the most crowded stands experience warmer and possibly drier conditions, site productivity decreases (e.g., McGuire et al. 2010), and radial growth declines more sharply than in stands where fewer or smaller trees are competing for available resources.

Competition among trees at the individual (tree) level also influenced growth. Trees with a greater height advantage than their neighbors exhibited more radial growth than individuals of lower stature and likely also exerted a greater competitive effect on their neighbors. Size–distance relationships also had an effect. Trees growing near many competitors of larger diameter (i.e., trees with a higher Hegyi index) showed reduced growth relative to trees under less competitive conditions. The positive growth response we observed in focal trees that were taller or of larger diameter than their neighbors may be due to a competitive advantage in the focal tree, such as better access to light or a deeper root system. Alternatively, the positive growth response recorded in some focal trees could simply be the result of a less competitive environment, where there are fewer neighbors to interact with. Determining the exact mechanism behind the relationships between competition indices and growth is difficult in observational studies (Weber et al. 2008), because where an individual falls within competitive hierarchies determines its ability to access available resources.

The absence of an interaction between these tree-level competition metrics (Hegyi index and height advantage) and temperature was unexpected. Our results suggest that temperature-related growth limitations are occurring at broader scales than individual trees, affecting all trees within a site regardless of the competitive interactions among neighboring trees. Neighborhood-level competition is a function of localized clumping in the spatial distribution of individual trees and is independent of the overall crowding and/or tree density within a given site. Even though competitive advantage allows an individual to obtain more of a shared resource than its neighbor, the lack of a relationship between

tree-level competition and plot-level crowding metrics suggests that trees can have a competitive advantage and still be affected by resource scarcity.

Counter to our expectations, winter–spring precipitation did not have a consistent effect on growth. Sherriff et al. (2017) found that the effect of precipitation received between January and April was positively correlated with growth, but the effects were spatially variable. The spatial variability of the effect of precipitation may explain its lack of effect in our models. Our results also suggest that winter–spring precipitation alone may have less of an effect on growth than other factors, such as temperature, competition, or site other conditions. Csank et al. (2016) found indications of early-season drought stress in one of the sites included in this study, presumably due to late-thawing soils, suggesting that the insensitivity of growth to precipitation here could be attributed to site-level variables other than competition (e.g., edaphic factors). In interior Alaska, the growth response of white spruce to temperature has been found to vary with topography and seasonal soil thaw (Nicklen et al. 2016), exemplifying the importance of fine-scale variation for climate–growth dynamics.

The lack of a strong effect from lagged spruce beetle mortality might be due to the short lag times between outbreaks and growth in our study area. Disturbance plays an important role in stand dynamics, but its influence may be limited relative to broadscale factors such as climate (Csank et al. 2016) and competition. Climate drives both growth and spruce beetle mortality (Berg et al. 2006, Sherriff et al. 2011). Here, the largest spruce beetle outbreak during our study period began in the early 2000s, following a prolonged period of warm and dry years in the late 1990s. High summer temperatures may contribute to more spruce beetle outbreaks in the future (Sherriff et al. 2011), and dense stands may experience declining growth, regardless of background beetle activity.

Our results suggest that climate-driven competition at the stand level is an important factor that will influence the relationship between rising temperatures and radial growth in white spruce. On average, the densest forest stands in our study were in at the eastern end of the gradient (boreal ecoregion), and these areas also

experienced the warmest and driest growing season conditions of any in the study area. Given the growth declines observed in these forested sites (Sherriff et al. 2017), we could expect further reductions in growth, and potentially declining stand conditions with continued warming, consistent with model forecasts for the region (Krist et al. 2014).

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LITERATURE CITED

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Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2462/full>