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Divergent responses to permafrost and precipitation reveal mechanisms for the spatial variation of two sympatric spruce

E. Fleur Nicklen,[1,2,]† Carl A. Roland,[1,3] Roger W. Ruess,[2,4]
Tobias Scharnweber,[5] and Martin Wilmking[5]

[1]Central Alaska Network, National Park Service, Fairbanks, Alaska 99709 USA
[2]Department of Biology and Wildlife, University of Alaska, Fairbanks, Alaska 99775 USA
[3]Denali National Park and Preserve, National Park Service, Fairbanks, Alaska 99709 USA
[4]Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775 USA
[5]Institute of Botany and Landscape Ecology, University of Greifswald, Greifswald 17489 Germany

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Abstract. The ranges of black and white spruce are largely sympatric, suggesting both species have similar climate requirements. The two species, however, are highly segregated across the landscape with black spruce most common on nutrient-poor sites with cold, poorly drained soils and white spruce more common on productive sites with warmer, well-drained soils. Because site conditions influence tree climate–growth responses, it is difficult to compare white and black spruce climate–growth responses as these responses are confounded by the differences in site conditions in which the two species naturally occur. As the climate warms dramatically in northern latitudes, it is critical to understand how a changing climate and associated changes in permafrost and fire regimes will interact to shape future species composition and ecosystem functioning in the boreal forest. In this study, we examined the climate–growth responses of black and white spruce growing in the same sites. This approach eliminates the confounding factor of site conditions and facilitates our understanding of how these two species respond to climate. We included standardized thaw depth of the active layer in our analysis as a representation of permafrost, which is a key factor delineating these two species' habitat preferences and is actively warming and thawing as the climate warms. Our most important finding was that the climate–growth responses of the two species, but especially white spruce, hinged on the thaw depth of the active layer. Specifically, with increasing June–July temperatures white spruce radial growth increased in areas with deep thaw or no near-surface permafrost, but strongly decreased when growing in areas with near-surface permafrost. Black spruce radial growth was less sensitive to June–July temperature than white spruce but had a consistent and more positive response to summer precipitation. These findings point to a primary mechanism potentially driving the positioning of these two tree species within the landscapes of boreal interior Alaska and imply widespread thawing of permafrost may foster expansion of white spruce in this region at the expense of black spruce, but that in a wetter climate, black spruce may gain competitive advantage over white spruce in some landscape positions.

Key words: climate change; dendroecology; permafrost; *Picea glauca*; *Picea mariana*.

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

INTRODUCTION

In interior Alaska, black spruce (*Picea mariana*) and white spruce (*Picea glauca*) share a similar geographic footprint but are largely spatially segregated on the landscape (Viereck et al. 1993, Roland et al. 2013). Black spruce trees most commonly occupy more acidic and nutrient-poor sites at lower elevations often on colder, more waterlogged soils than white spruce. In contrast, white spruce tends to occupy warmer, more productive areas and treeline locations. The site conditions where the two species attain maximum live biomass, however, are very similar and generally describe the areas where white spruce is most commonly found (Roland et al. 2013, 2019). That black spruce is less common where it appears to grow best has been interpreted as competitive exclusion of black spruce by the faster growing white spruce (McGill 2012, Roland et al. 2013). Black and white spruce geographic distributions largely overlap, suggesting the two species have similar climate envelopes; however, black spruce extends further south on the eastern edge of its distribution and white spruce extends further south along the Rocky Mountains in the west. Because site conditions can strongly influence tree climate–growth responses (Drobyshev et al. 2010, Gewehr et al. 2014, Nicklen et al. 2016, Wright et al. 2018), it has been difficult to directly compare white and black spruce climate–growth responses as these responses are confounded by the differences in site conditions in which the two species naturally occur.

The spatial distribution of these two species is linked to macroclimate, fire, and substrate (Lloyd et al. 2005, 2007, Roland et al. 2013, 2019). Key life history characteristics such as black spruce's tolerance of nutrient-poor soils and partial dependence on fire for sexual reproduction and white spruce's larger seed mass (Liu et al. 2013) and ability to capitalize on soil nutrients (Chapin 1986) to out-compete black spruce are likely primary factors of these species' current footprint on the landscape. The two species' growth and reproductive responses to climate, however, may also be an important driver in their distribution patterns. Indeed, fossil and pollen evidence of past white and black spruce population fluctuations indicate climate played an important role in the species past distributions and may point to potential differences in the two species' climate preferences (Hu et al. 1998). The expansion of white spruce into northern and central Alaska during the early to mid-Holocene, around 9500 yr before present (BP), occurred following an increase in moisture, but still during a period when climate was drier (Hu et al. 1998), but not necessarily warmer than present (Clegg et al. 2011). In the mid-Holocene, ~5500–7000 yr BP, black spruce replaced white spruce as the dominant forest species in central and eastern Alaska (Anderson and Brubaker 1994, Tinner et al. 2006). This transition in species dominance coincided with an increase in effective moisture (Hu et al. 1998). Thus, climate patterns in the past seem to have been important drivers of white and black spruce abundance and there is some indication that an increase in effective moisture was at least partially responsible for the mid-Holocene shift from white spruce to black spruce dominance (Hu et al. 1998). Fire frequency increased during the late Holocene, generally following the increase in effective moisture and the increase in black spruce abundance (Lynch et al. 2004, Hu et al. 2006, Lloyd et al. 2006, Tinner et al. 2006). It is speculated that the shift to a black spruce-dominated forest, a more flammable forest type than white spruce, was at least one of the causes of increased fire frequency on the landscape during the cooler, wetter conditions of the late Holocene (Hu et al. 1998, Brubaker et al. 2007, Higuera et al. 2009, Hoecker et al. 2020).

Alaska's climate has warmed at twice the rate of the global average since the mid-20th century (Markon et al. 2018). Interior Alaska's mean annual temperature has warmed at rate of about 0.1°C/dec between 1925 and 2012 (Bieniek et al. 2014, Vose et al. 2017). This upward trend is superimposed upon low-frequency variability associated with Pacific sea surface temperatures. The low-frequency variability is manifested as a warm period during the 1920s to early 1940s that transitioned to a cool period from the late 1940s to mid-1970s with no clear trend (Bieniek et al. 2014, Markon et al. 2018) followed by a strong upward trend starting in the late 1970s, which briefly dipped in the mid-2000s, but continued upward at a rate of 0.4°C/dec through at least 2016 (Markon et al. 2018). There is disagreement on precipitation trends in Alaska, though most studies find little to no significant trends in interior Alaska (McAfee et al. 2013, Bieniek et al. 2014, Vose et al. 2017), but Wendler et al. (2017) find precipitation has increased with increasing temperature. Precipitation is spatially variable and difficult to measure, and the trends are dependent on time period and data sources (McAfee et al. 2013). Historically unprecedented warming is projected by the end of the 21st century with mean annual temperatures in interior Alaska projected to increase by 2.2–4.4°C and precipitation projected to increase by 5% to over 15% relative to the 1971–2000 means under the intermediate RCP4.5 (Sun et al. 2015).

The impacts of increasing temperature and precipitation on black and white spruce growth are still not well understood. In lowland areas of interior Alaska, both black and white spruce generally show negative climate–growth responses to increases in summer temperature and positive climate–growth responses to increases in summer precipitation (Barber et al. 2000, Beck et al. 2011, Lloyd et al. 2013, Walker and Johnstone 2014, Sullivan et al. 2017, Cahoon et al. 2018), although these responses often (but not always; Walker and Johnstone 2014) vary depending on site conditions (Lloyd and Fastie 2002, Wilmking et al. 2006, Wilmking and Myers-Smith 2008, Johnstone et al. 2010*b*, Nicklen et al. 2016, Wolken et al. 2016). While these negative responses to higher summer temperatures could result in overall reduced growth of both species as the climate warms, other factors, such as increasing precipitation, increasing CO_2, or shifting resource allocation within a tree, may mitigate these negative effects. A few studies in interior Alaska have examined climate–growth relationships and growth trends of both black and white spruce (Beck et al. 2011, Nicklen et al. 2016, Sullivan et al. 2016, 2017, Cahoon et al. 2018), but none have directly compared the two species growing in the same site conditions. Results from these studies suggest the two species respond very similarly to climate, though black spruce tends to show a different response to May weather conditions with a more positive response to May precipitation (Sullivan et al. 2016, Cahoon et al. 2018) and a more negative response to May temperature (Nicklen et al. 2016). Given that black spruce is considerably more common than white spruce on sites with shallow active layer thickness (generally >50 cm), where hot, dry May conditions may be most stressful to trees in shallow, frozen soil with little access to water, these results may reflect site-mediated tree responses rather than differences in underlying species-based responses to climate.

As the climate warms, several indirect effects of warming will likely also influence the future growth and distribution of the two species. Climate warming over the last half century, in combination with sporadic years with deep snow, has led to an increase in permafrost temperature (Osterkamp and Romanovsky 1999, Brown and Romanovsky 2008, Romanovsky et al. 2010), which has led to a deepening of the active layer (Åkerman and Johansson 2008). As permafrost continues to degrade and active layers deepen across interior Alaska (Panda et al. 2014), edaphic conditions may facilitate increased white spruce growth relative to black spruce and a transition to a white spruce-dominated landscape may be likely (Wirth et al. 2008, Roland et al. 2013). A shift from black to white spruce dominance could reduce the flammability of the landscape (Hu et al. 1998, Brubaker et al. 2007, Higuera et al. 2009, Hoecker et al. 2020) and increase aboveground carbon stores as white spruce stands tend to have greater basal area than black spruce stands (Roland et al. 2013, 2019). While the growth of the two species across landscapes of varying active layer thickness may be a function of individualistic responses to site conditions, it is also likely that there is an interactive role of site conditions and climate, such that the two species respond to climate differently in different site conditions. For instance, if black spruce is a more shallowly rooting species than white spruce (Farrar 1995, Fryer 2014, Abrahamson 2015), then black spruce may experience greater drought stress than white spruce in areas with deeper soils in dry years than in wet years, and as soils in some landscapes become drier with continued climate warming. Other indirect climate effects will also influence the future abundance and distribution of the two species. For instance, fire, which is a key driver of boreal forest landscape pattern and processes, is expected to increase in frequency, extent, and severity with continued climate warming (Balshi et al. 2009, Kasischke et al. 2010, Turetsky et al.

2011) catalyzing a shift from spruce to broadleaf dominance in interior Alaska (Johnstone et al. 2010*a*, Barrett et al. 2011). Also, future climate conditions in interior Alaska are expected to be conducive to spruce bark beetle outbreaks (Bentz et al. 2010), which target white spruce over black spruce and interact with drought stress (Anderegg et al. 2015, Csank et al. 2016), potentially leading to widespread white, but not black spruce, mortality.

Our objective in this study was to directly assess the climate–growth responses of co-occurring white and black spruce trees. Our goal in examining growth dynamics of black and white spruce trees growing in the same location was to eliminate the confounding factor of differing site conditions between these two species and thus enable a direct comparison of climate–growth responses. We sought to determine whether white and black spruce, growing in the same site conditions, respond similarly or differently to annual variations in weather conditions. Given the large overlap of the species' current distributions and the apparent lack of climate–growth differences between the two species reflected in the literature, we hypothesized the two species would respond very similarly to climate conditions. However, given paleoecological evidence of shifting species dominance with increased effective moisture, we expected black spruce to have a greater growth response to increased precipitation than white spruce. We also sought to understand the role that thaw depth of the active layer may play in these two species responses to weather conditions.

METHODS

Study area

Our study area was in interior Alaska, near the northwestern range limits of both black and white spruce. Study sites were located within three national park and/or preserves: Yukon-Charley National Preserve (YCNP), Denali National Park and Preserve (DNPP), and Wrangell-St. Elias National Park and Preserve (WNPP), which collectively make up the National Park Service's Central Alaska Network (CAKN; Fig. 1). Within these parks, we focused on areas where black and white spruce co-occur, which, not surprisingly, tended to be areas intermediate to the two species habitat preferences (Appendix S1: Fig. S1).

Plot selection

We selected study sites from the CAKN long-term vegetation monitoring plots that happened to have both black and white spruce cored. Of the nearly 900 CAKN vegetation monitoring plots with cored trees, only 101 had both black and white spruce cored together. To bolster our sample, we selected an additional 32 supplemental plots accessible from the Yukon River where both species were present (Fig. 1). Most of our plots were in YCNP (n = 115), but there were also 10 plots in DNPP and eight in WNPP (Fig. 1). The CAKN vegetation monitoring plots were established with a randomized two-stage systematic grid sampling design. A 20-km grid was established over the park study areas with an intensified 10-km grid within a 6-km buffer of access routes (park roads, Yukon River). At each grid, intersection is a mini-grid of 25 plots (five rows of five plots separated by 500 m); for further details on CAKN vegetation monitoring study design, see Roland et al. (2004, 2019).

Plot and tree sampling

Our supplemental plots were sampled in the same manner as the CAKN vegetation monitoring plots. Each plot in our study was circular and 16 m in diameter. At each plot, we recorded a suite of topographic, edaphic, and vegetation variables (Table 1). Relevant to this study, we recorded elevation, slope, and aspect. We measured plot tree basal area (m^2/ha). At four soil pits located in cardinal directions 1 m outside the plot, we recorded depth of the soil organic layer and soil temperature (at 10 cm depths) and collected soil samples for pH, carbon, and nitrogen analysis. At 16 locations within the plot, we recorded depth of thaw or depth to restrictive feature in using a 130-cm soil probe. Because our sampling occurred between 15 June and 15 August and the depth of thaw increases throughout summer, we standardized our probe depth measurements to an estimated 20 July value following Swanson (2015). We employed thaw depth standardization if the plot was determined to be underlain by shallow permafrost; otherwise, we did not adjust the probe depth measurement. Standardized thaw depth was the

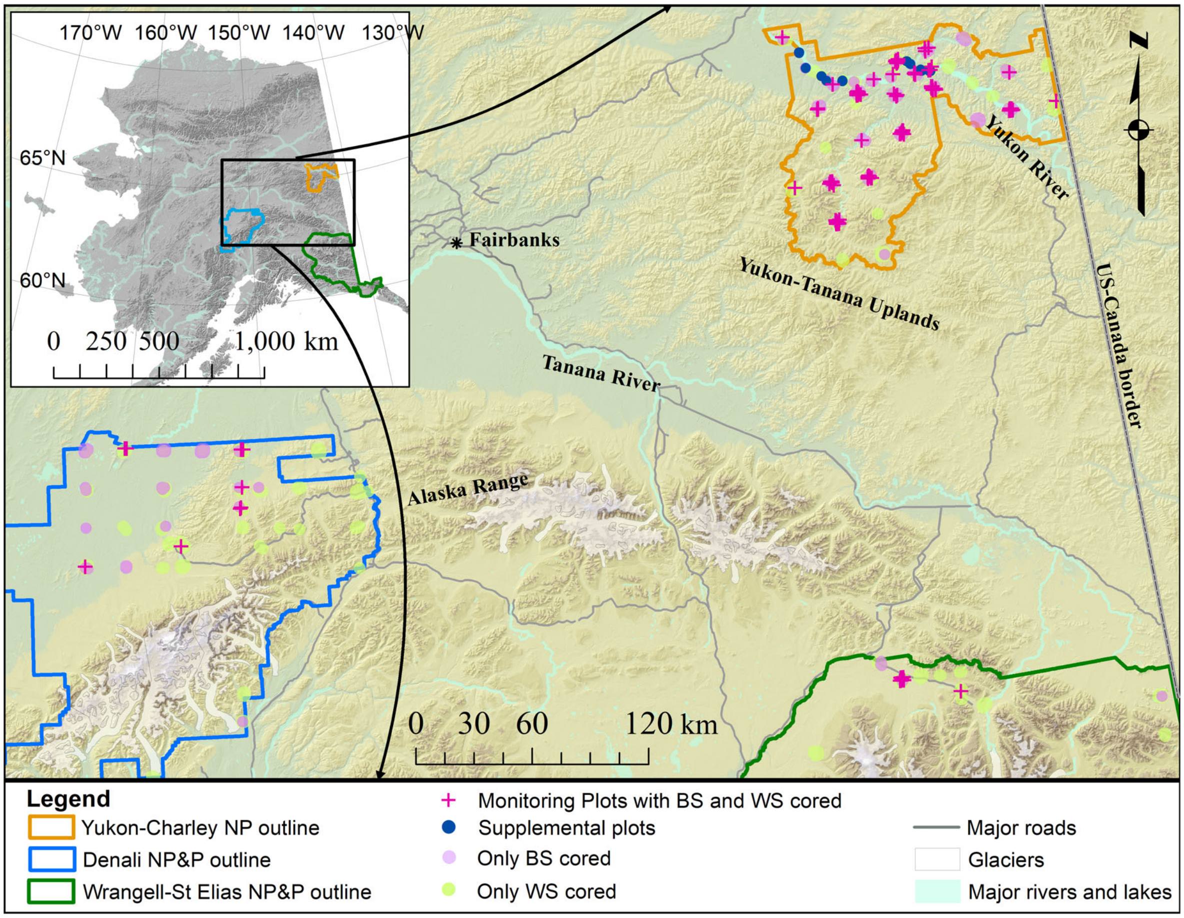


Fig. 1. Map showing the study region and locations for plots where both black (BS) and white spruce (WS) were cored, both the Central Alaska Network vegetation monitoring plots and the supplemental plots. The map additionally shows Central Alaska Network monitoring plots where only black or white spruce were cored.

Table 1. Plot characteristics.

Variable	Units	Description	Mean	Min	Max
Elevation	m	Elevation at plot center	491	203	1046
Slope	degrees	Slope angle	13	0.5	45
pH	pH	Reaction of the soil sample	5.38	3.56	7.18
Soil organic layer (SOL)	cm	Depth of soil organic layer	15	2	30†
Thaw depth of the active layer (TD)	cm	Mean of four deepest soil probe depths standardized to 20 July	57	18	135†
Conifer Basal area	m^2/ha	Basal area of conifer trees	8.26	0	43.17
Broadleaf Basal area	m^2/ha	Basal area of broadleaf trees	2.58	0	34.75

† Our ruler for measuring SOL was 30 cm, and our soil probe for measuring thaw depth of the active layers was 130 cm, so there were likely deeper SOL and TD, but our measurements were limited.

mean of the four deepest standardized probe depths.

Most of our plots with shallow soil probe depth to a restrictive feature fit the definition of shallow active layer thickness and had cold soils with permafrost as the restrictive feature. Plots with deeper probe depths typically did not have permafrost or any restrictive feature within 1 m of the ground surface and were warmer. In general, shallow probe depths were associated with cold, wet, and nutrient-poor soils with low pH and low aboveground productivity, while deeper soils were associated with warmer, drier, and more nutrient-rich soils with higher aboveground productivity (Roland et al. 2013, 2019).

We used twig pubescence, cone size, and cone location to distinguish between the two species. There have been reports of hybridization between black and white spruce (Little and Pauley 1958, Larsen 1965, Roche 1969, Dugle and Bols 1971), but none have been genetically substantiated. Some of these putative hybrids, with careful morphological analysis (Parker and McLachlan 1978) and with cytological markers (Nkongolo et al. 2005), have been shown to be clearly one species or the other (Parker and McLachlan 1978). The low incidence of natural hybridization and the difficulty in producing artificial hybrids suggest there are strong barriers to introgression for these species (OECD 2010) and that our sample likely contains no hybrids.

We cored paired black and white spruce trees growing within 50 m of each other at each plot. At each long-term vegetation monitoring plot, black and white spruce trees were cored outside the plot, but typically within 15 m of the plot perimeter. At the supplemental plots, trees were cored within the plot and up to 28 m from plot center. We cored, measured, cross-dated, and calculated basal area increment (BAI) on 310 black spruce and 318 white spruce from 133 plots (Table 2). We cored between one and eight trees of both species at each of the plots. Plot sampling occurred between mid-June and mid-August from 2004 and 2016. Cores were mounted and sanded up to 2000 grit. Growth rings were measured to 0.001 mm using either CooRecorder (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden), WinDENDRO (Regent Instruments Inc., Quebec, Canada), or sliding scale. Ring widths were visually cross-dated using CDendro 8.1 (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden), and cross-dating was validated with COFECHA 12K XP (Holmes 1983).

Radial growth metrics

We calculated three metrics of growth. First, we calculated ring width indices using the signal-free regional multi-curve detrending procedure in the CRUST program (Melvin and Briffa 2014*a*, *b*). In this detrending process, tree ring series are grouped by mean ring width (>40 tree series per group) and the age-related curve for each group is fit and the ratio of the observed vs. expected as a function of age is calculated. We used four ring width-dependent groups following Sullivan et al. (2016) to account for different average growth rates of the trees (i.e., fast- and slow-growing trees). With the aim of retaining long-term climatic forcing signals within the ring width data, we used the CRUST program to produce signal-free indices, in which the raw ring widths were repeatedly divided by the detrended chronology (up to 10 times; Melvin and Briffa 2008). We conducted the RCS signal-free multi-curve detrending on the two species separately. After determining the age, curves from the three study areas were similar (Appendix S1: Fig. S2), and because most trees were from YCNP, we pooled trees from all parks by species for this procedure. Hereafter, the regional curve standardized ring width indices are referred to as RCS rwi. Second, we detrended the ring widths with a 30-yr flexible spline

Table 2. Characteristics of sampled black and white spruce trees and raw ring width series overall, and for trees on plots with shallow (<57 cm) and deep (>57 cm) midsummer thaw depths (TD).

	Black spruce			White spruce		
Tree characteristic	All	Shallow TD	Deep TD	All	Shallow TD	Deep TD
Ring count	116	122 (36, 332)	101 (30, 262)	123	133 (24, 344)	106 (28, 334)
dbh (cm)	12.2	12.2 (4.5, 25.2)	13.1 (5.2, 37.1)	16.6	17.1 (5.7, 39.0)	17.5 (5.5, 41.8)
BAI (mm^2/yr)	142	126 (0, 1481)	178 (0, 2710)	279	252 (0, 3009)	322 (0, 3198)
Ring width (mm/yr)	0.503	0.47 (0, 3.42)	0.60 (0.03, 5.87)	0.69	0.61 (0, 5.65)	0.82 (0, 4.84)
Tree count	310	208	102	318	187	131

Notes: BAI, basal area increment; dbh, diameter at breast height. Ring count is used as an age proxy. The mean or total is shown for all categories, and the minimum and maximum where possible are shown in parenthesis (min, max).

(hereafter "spline rwi") using the program dplR (Bunn et al. 2020), which eliminates most long-term trends and retains and emphasizes the inter-annual fluctuations. Finally, we used ring widths and tree radius to calculate BAI, the estimated area of wood produced by each tree in each year of growth using the outside-in approach (Biondi 1999, Johnson and Abrams 2009). We used the sum of the ring widths as the radius unless the measured tree radius ((diameter at core/2) − average bark width) was greater than ring width sum, in which case we used the measured radius as the radius. Cores with missing outer rings were not used.

Climate variables

We considered eight growing season climate variables: mean air temperature and precipitation sums from June to July and August of the previous growing season and from May and June to July of the current growing season. The Scenarios Network for Alaska and Arctic Planning (SNAP) provides these downscaled and spatially interpolated climate data (retrieved in 2019 from http://ckan.snap.uaf.edu/dataset?tags=historical-observed; from CRU TS4.0) for the years 1906–2015. 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 1-km 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, we extracted the mean monthly temperature (°C) and precipitation sum (mm). We selected these data over station data because some of our study plots were separated by hundreds of kilometers and nearby station data are limited. Further, the SNAP climate data integrate lapse rate information from PRISM, so that plots at different elevations have associated climate data that, in theory, are more like what the tree experienced than if we used distant station data. There is, however, likely unmeasurable bias in these data, particularly the precipitation data (McAfee et al. 2014), which may be exacerbated by topographically complex terrain.

Statistical analyses

We employed several methods to compare the two species' radial growth–climate responses: a paired t test at the plot level, a linear mixed-effects model at the tree level, and a comparison of growth over time. First, since our study design involved paired black and white spruce trees at each plot, our data were suited for a two-tailed paired t test to assess whether the two species showed different climate–growth correlations. We averaged the spline detrended rwi by species and year at each plot to make chronologies. We then calculated Spearman's rank correlation coefficient for the relationship between growth and climate variables for both species at each plot. We selected Spearman's correlation because of a nonlinear relationship between growth and some climate variables. We used eight growing season climate variables (Table 3) from 1902 to 2015, such that we had correlation coefficients for both species at each of the 133 plots for each climate variable of interest. We then ran a two-tailed paired t test on the Fisher r-to-z-transformed correlation values to assess whether the two species had significantly different climate–growth correlation for each of the eight climate variables. We additionally calculated the climate–growth correlations for the study area-wide black spruce and white spruce spline detrended chronologies for comparison in the R package treeclim using exact bootstrapping (Zang and Biondi 2015) and using the averaged climate data from each plot.

Second, we ran linear mixed-effects models of individual tree BAI growth that included species and their interactions with climate variables and standardized thaw depth of the active layer. Our primary interest in these models was whether the two species had different climate–growth responses. That is, did adding a species–climate interaction term improve model fit? We additionally tested whether the two species had different climate–growth responses across a gradient of thaw depths of the active layer. That is, did adding a species–climate–thaw depth interaction further improve model fit? To avoid overfitting, we limited the climate variables in the three-way interaction to only June–July climate variables, as these typically have the largest effect on BAI. We assessed model fit with second-order Akaike information criterion (AIC_c; calculated with R package MuMIn, version 1.43.15) where the

Table 3. Climate–growth correlations were assessed for both species by plot and by study area.

Climate variable	PIMA mean plot corr. coefficient (lower CI, upper CI)	PIMA chronology corr. coeff.	PIGL mean plot corr. coefficient (lower CI, upper CI)	PIGL chronology corr. coeff.	Paired *t* test *P* value
Mean prev. June–July temp.	−0.14 (−0.16, −0.12)	−0.26*	−0.12 (−0.14, −0.10)	−0.23*	0.169
Sum prev. June–July precip.	0.12 (0.10, 0.13)	0.23*	0.07 (0.05, 0.09)	0.18	<0.0001
Mean prev. August temp.	−0.09 (−0.11, −0.07)	−0.17	−0.08 (−0.10, −0.06)	−0.13	0.594
Sum prev. August precip.	0.10 (0.08, 0.12)	0.16	0.09 (0.07, 0.11)	0.16	0.525
Mean current May temp.	−0.12 (−0.14, −0.10)	−0.25*	−0.12 (−0.14, −0.10)	−0.25*	0.686
Sum current May precip.	0.00 (−0.02, 0.01)	0.02	−0.02 (−0.03, 0.00)	−0.01	0.210
Mean curr. June–July temp.	0.01 (0.00, 0.03)	0.03	0.04 (0.02, 0.06)	0.12	0.020
Sum curr. June–July precip.	0.01 (−0.01, 0.03)	−0.04	0.00 (−0.02, 0.02)	−0.06	0.451

Notes: The mean climate–growth correlation coefficients from all plots and for both species with upper and lower confidence intervals (CI) are reported (*n* = 133 plots). If the CI overlapped zero, we interpreted the correlation coefficient to be nonsignificant. Also shown are the climate–growth correlation coefficients for the overall white and black spruce chronologies; asterisks indicate significance. The paired *t* test assessed whether the correlation coefficients found at each plot for the two species were significantly different. All correlation coefficients shown and used in paired *t* tests were transformed using Fisher's Z. All climate correlations were conducted using the 30-yr spline detrended ring width indices.

selected model was the most parsimonious model with an $\mathrm{AIC_c}$ value within two points of the lowest $\mathrm{AIC_c}$ value (Burnham and Anderson 2002).

Model construction and assumption testing

We log-transformed BAI to attain a more normal distribution for the response variable. Our base model included the same eight climate variables used in the correlation analysis and *t* test, but we additionally included nonlinear (quadratic) terms for June–July temperature and precipitation as black and white spruce have been shown to have nonlinear response to climate (Lloyd et al. 2013, Nicklen et al. 2016, Sullivan et al. 2017). Each model included a cambial diameter term for each year of growth to account for the influence of size on climate–growth relationships and trends over time (Trouillier et al. 2019). We tested various age and size terms (Table 4) and found the log of estimated cambial diameter at core height to be the best covariate to account for influence of tree size on climate–growth relationship as measured by $\mathrm{AIC_c}$ and model weight (Table 4). We calculated estimated cambial diameter as 2× the running sum of ring widths for each year of growth. When estimated rings to pith were available, we used these to estimate the missing distance to pith (last ring width × number of missing rings) in cores where the pith was missed. Each model also included three random effect terms: year, minigrid, and an autoregressive term with current-year BAI dependent on previous year's BAI

Table 4. Two sets of model comparisons.

Objective	Model	$\Delta\mathrm{AIC_c}$	Akaike weight
Test age and size terms	$\mathrm{A + dbh + CLIM^2}$	136.9	0.000
	$\mathrm{A + A^2 + dbh + CLIM^2}$	52.7	0.000
	$\mathrm{log(A) + dbh + CLIM^2}$	64.7	0.000
	$\mathrm{CD + CLIM^2}$	273.5	0.000
	$\mathrm{CD + CD^2 + CLIM^2}$	62.9	0.000
	$\mathrm{logCD + CLIM^2}$	0.0	1.000
Test species–climate and species–climate–soil depth terms	$\mathrm{logCD + CLIM^2}$	145.7	0.000
	$\mathrm{logCD + CLIM^2 \times SPP}$	55.8	0.000
	$\mathrm{logCD + CLIM^2 \times SPP \times AL}$	0.0	1.000

Notes: A, estimated ring age for each year of growth for each tree; $\mathrm{AIC_c}$, Akaike's information criterion, corrected for sample sizes; CD, estimated cambial diameter for each year of growth for each tree; dbh, diameter at breast height; $\mathrm{CLIM^2}$, all climate variables including quadratic terms for June–July climate variables. The first set compares models with different age and size terms. The second set includes the best model from the first set and tests whether including species–climate interaction terms and species–climate–soil depth interaction terms improves the base climate model.

(AR1) by individual tree. The year random effect was included to account for any temporal non-independence not explained by our climate variables. The mini-grid random effect addressed spatial non-independence of our plots. The AR1 term by tree addressed the non-independence of repeated measures within a tree and the strong autocorrelation found in tree radial growth. Visual inspection of residual plots did not show obvious deviations from homoskedasticity, normality, or temporal autocorrelation. Model covariates were considered interpretable if the 95% confidence intervals (estimate ± 1.96 × standard error of estimate) around the estimate did not overlap zero or were not within 0.001 of zero. We ran the models using the package lme4 1.1-14 (Bates et al. 2015) in R version 3.4.2 (R Core Team 2017).

We additionally ran the selected BAI model with the three other radial growth metrics as response variables: RCS rwi, a pre-whitened RCS rwi (RCSAR rwi), and spline rwi. Because we used BAI, RCS rwi, and spline rwi in separate analyses, we wanted to compare these metrics to assess whether their mixed-effects model results were broadly similar or whether there were differences worth considering among growth metrics. Results of this analysis are presented in Appendix S2.

Finally, we created study area-wide chronologies of the two species ring width to compare the species' growth over time. To make these chronologies, we used the RCS rwi averaged for each year for the two species. We additionally split these two species chronologies by deep and shallow standardized thaw depths. Note that while standardized thaw depth was a continuous variable in our mixed-effects model, we used the mean thaw depth of our plots (57 cm) as the break point between the shallow and deep thaw depth groups (Table 2). Caution is warranted when interpreting growth trends over time as covariation in tree age, size, and stand characteristics, as well as inherent sampling bias in tree rings, can affect growth trends (Bowman et al. 2013, Duchesne et al. 2019, Trouillier et al. 2019). Our goal in this undertaking was not to interpret trends over time, but to compare the growth of the two species that were sampled from the sample plots over time and in deep and shallow soil conditions. These comparisons are facilitated by the fact both species were cored at each of our plots and our samples of the two species had very similar age distributions (Table 2). We also used the two species chronologies to examine 30-yr running climate–growth correlations over time using the treeclim package (Zang and Biondi 2015) in R version 3.4.2 (R core team 2017). We examined the difference in climate correlation between the two species over time. We used the same climate variables as used in the *t* tests and mixed models, but because we are working with study area-wide chronologies, we averaged the climate data from all the plots in our study.

RESULTS

Paired t *test*

While the climate–growth correlation coefficients for the two species were largely very similar, our paired *t* test results showed a few differences. Specifically, black spruce growth showed a positive response to previous-year June–July precipitation sums, while white spruce growth showed little to no response (P value < 0.0001; Table 3). White spruce growth showed a marginally more positive response to mean current June–July temperature (paired *t* test P value = 0.02, Table 3). Otherwise, the two species had very similar climate–growth responses. Both species had stronger radial growth responses to the summer conditions in the year prior to ring formation than in the year of ring formation. Radial growth was negatively correlated with previous mean June–July and August temperatures and current May temperatures for both species, which were not statistically different (Table 3). Both species' radial growth was positively correlated with precipitation in August of the previous year. Neither species growth was correlated with May or June–July precipitation during the year of ring formation.

Mixed-effects growth model

The two spruce species responded differently to certain climate conditions, as evidenced by the significant improvement in model fits that included species–climate interaction terms over the climate-only models (Table 4). The largest difference in climate–growth responses between

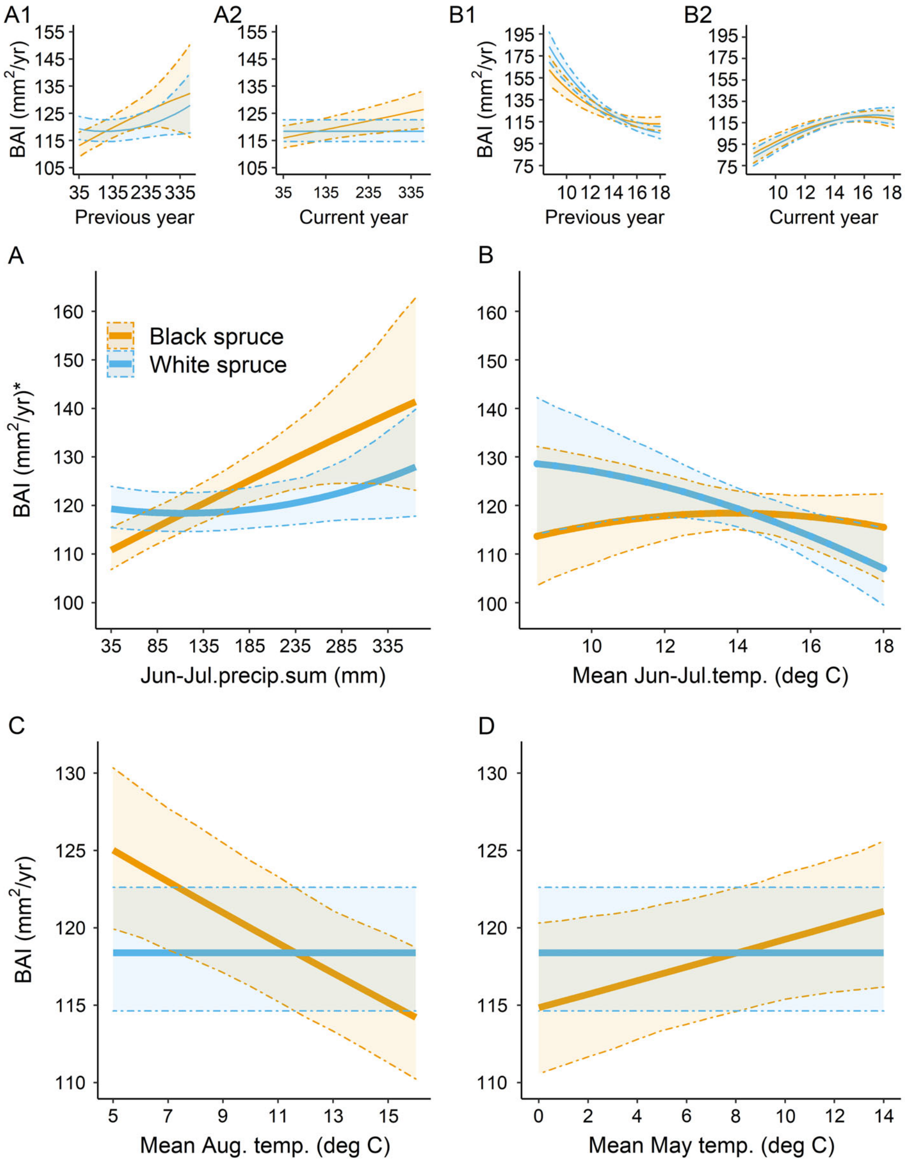


Fig. 2. Basal area increment (BAI) response of black (orange line) and white spruce (blue line) to (A) June–July precipitation sums and (B) mean June–July temperatures in the year of and prior to ring formation and to (C) mean August temperature in the year prior to ring formation and (D) mean May temperature in the year of ring formation. Shaded bands are 95% confidence intervals. *The BAI response to June–July precipitation and temperature is the response to the cumulative effect of previous-year and current-year June–July weather conditions. The BAI responses to precipitation and temperature in the year prior to (A1, B1) and concurrent with (A2, B2) growth year are shown in A1,2 and B1,2.

the two species was black spruce's greater positive response to June–July precipitation as compared to white spruce, which was also shown in our plot-level paired *t* test. Black spruce BAI increased by an estimated 28 mm^2/yr, whereas white spruce BAI increased only 6 mm^2/yr with increasing June–July precipitation over the observed range (Fig. 2A). This difference was most pronounced in response to June–July precipitation sums from the year prior to ring formation (Fig. 2A1). White spruce showed a greater negative response to mean June–July temperature in the year prior to ring formation and a slightly more positive response to mean June–July temperature in the year of ring formation than black spruce (Figs. 2B1, 3B2), such that the cumulative two-year effect of the highest observed June–July temperature reduced white spruce BAI growth by an estimated 22 mm^2/yr, but had nearly no effect on black spruce BAI (Fig. 2B). Basal area increment responses to summer temperature and precipitation, however, were modified by thaw depth, particularly for white spruce (see following paragraph). Black spruce reduced BAI growth by an estimated 11 mm^2/yr in the years following the hottest August mean temperatures relative to the growth following the coolest mean August temperatures; however, white spruce showed no significant BAI response to prior-year mean August temperature. Black spruce BAI modestly increased in response to increasing mean May temperature in the year of ring formation, increasing growth by an estimated 6 mm^2/yr across the range of observed mean May temperature, while white spruce showed no response to current-year mean May temperature (Fig. 2D). Both species decreased BAI growth with increasing May precipitation (not graphed; see Appendix S2: Table S1, Fig. S3).

Species climate–growth responses were mediated by permafrost (represented by thaw depth). On deeper thaw depths, white spruce had an overall positive response to mean June–July mean temperatures, increasing an estimated 21 mm^2/yr with increasing temperature across

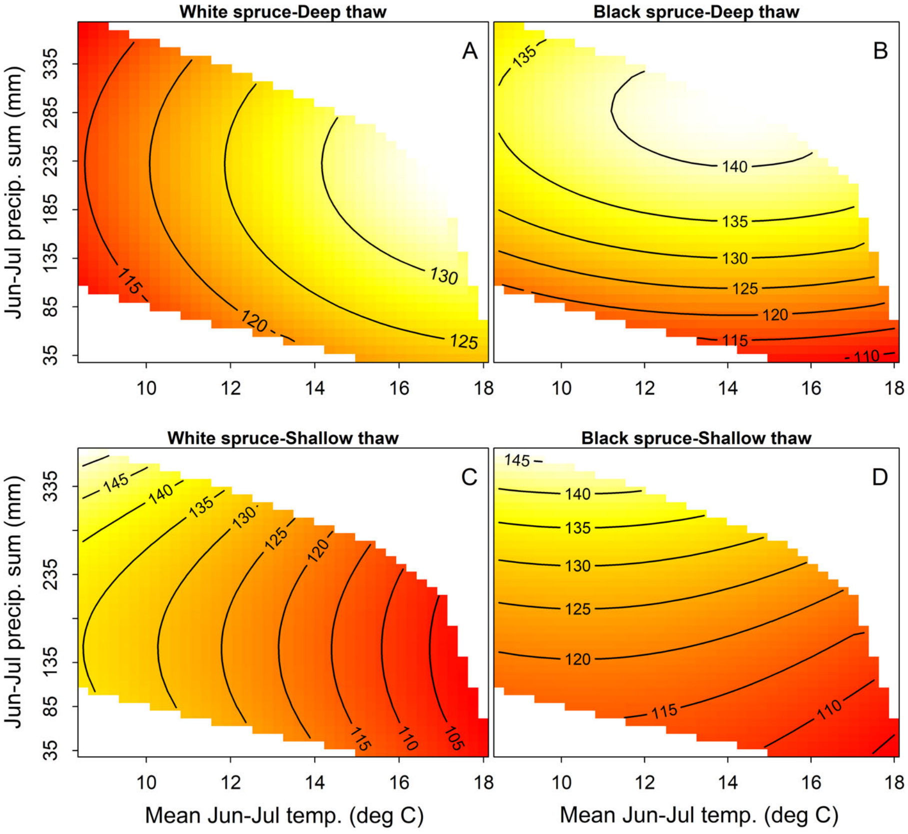


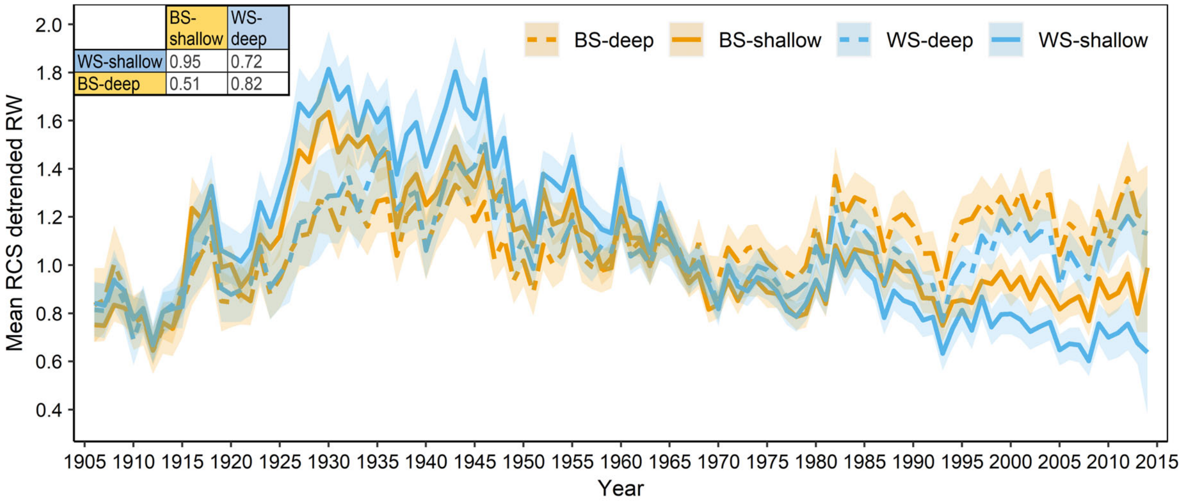
Fig. 3. Basal area increment (BAI) response to the cumulative effect of previous-year and current-year June–July mean temperature and precipitation sums for white spruce (left; A, C) and black spruce (right; B, C) on deep active layers (130-cm depth, A, B) and shallow active layers (30 cm depth, C, D). Color gradient corresponds to estimated BAI response, with deeper red representing lower BAI and lighter yellow representing higher BAI.

the observed range, but was relatively insensitive to June–July precipitation (Fig. 3A). However, on shallow thaw depths, that is, where permafrost is present close to the surface, white spruce had the opposite response to mean June–July temperatures, decreasing an estimated 41 mm^2/yr with increasing temperature across the observed range (Fig. 3C). Like white spruce, black spruce had a negative BAI growth response to June–July temperatures when growing on shallow thaw depths (Fig. 3D), but not nearly as negative a response as white spruce (estimated 10 mm^2/yr decrease for black spruce vs. 41 mm^2/yr for white spruce over the range of June–July mean temperatures). While black spruce was relatively insensitive to June–July temperatures on both deep and shallow active layers, black spruce was more sensitive to precipitation than white spruce, and this relative positive response to precipitation was consistent on both shallow and deep active layers (Fig. 3B, D).

While black spruce in our sample clearly has smaller average diameter at breast height and BAI than white spruce (Table 2), species was not a significant factor in the mixed-effects models. We found that the random effect for tree, the AR1 term by tree, and the size term all contributed to explaining this size variation among trees, such that if these terms were removed, then the species term did not overlap zero and confirmed that the estimated black spruce BAI is less than white spruce BAI on average in our sample.

Growth over time

Examination of our study area-wide chronologies showed that the two species had very similar growth patterns over time, but that the growth patterns differed depending on thaw depth (Fig. 4). While the detrended ring width indices are standardized so size differences are not illustrated, white spruce consistently had greater BAI than black spruce (Table 2). The two species chronologies fluctuated annually in similar patterns. The long-term patterns of the two species were also similar, though after the late 1970s, there was a change in which species had higher mean RCS detrended ring widths. From the mid-1920s to mid-1940s, white spruce had a higher mean RCS detrended ring width than black spruce (though the confidence intervals largely overlap), but starting after 1980, black spruce had greater mean RCS detrended rwi



	BS-shallow	WS-deep
WS-shallow	0.95	0.72
BS-deep	0.51	0.82

Fig. 4. Four-curve RCS detrended ring width chronologies for black (BS) and white spruce (WS; orange and blue lines, respectively) growing in areas with deep or shallow thaw depths (dotted and solid lines, respectively) with 95% confidence interval. Thaw depths greater than average (57 cm) were considered deep, and depths less than average depth were considered shallow. Numbers of trees contributing to chronologies ranged from 128 to 208 black spruce and 118 to 187 white spruce on shallow active layer plots and 32–102 black spruce and 39–131 white spruce on deep active layer plots. The table insert shows a correlation matrix for the four chronologies.

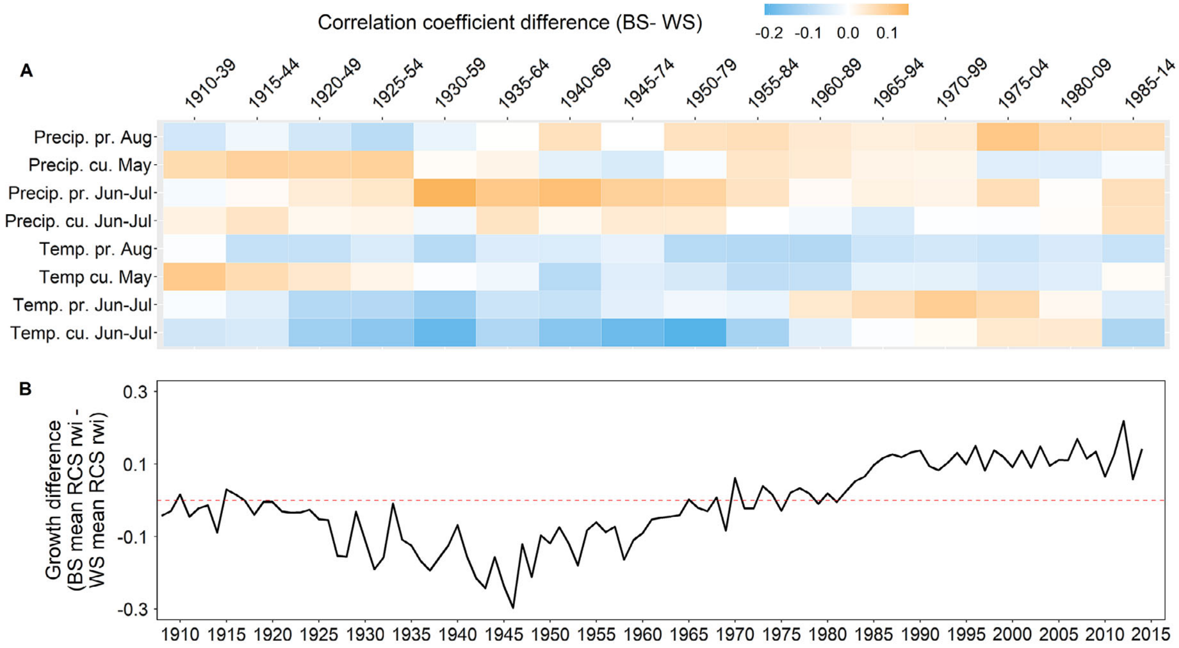


Fig. 5. (A) Heatmap showing the difference in climate correlations over time between black spruce and white spruce. We computed 30-yr running climate correlations for the black and white spruce chronologies using the program treeclim in R. We used the 30-yr flexible spline detrended ring widths and study area-wide mean climate data. This heatmap shows the difference (black spruce minus white spruce) between the two species' running climate correlations. Cells are blue (negative) if white spruce had a higher (more positive or less negative) correlation coefficient value than black spruce, and cells are orange if black spruce had a more positive or less negative correlation coefficient than white spruce. (B) Line graph showing the difference in black and white spruce RCS chronologies over time (BS − WS mean RCS rwi), with a red dashed line at $y = 0$ for visual interpretation.

than white spruce (Figs. 4, 5B). This reversal pattern was similar in both shallow and deep active layers, though the difference is greater in the trees growing on shallow active layers (Fig. 4).

Standardized thaw depth had a greater effect than species on the chronology patterns (Fig. 4). Indeed, a correlation matrix of the four chronologies showed stronger correlations between the two species growing in the same site type than within a species on different site types (Fig. 4). The chronologies of black and white spruce on shallow thaw depths both showed a distinct peak in growth between the mid-1920s and mid-1940s and steady declines in growth since the peak in the 1940s. Black and white spruce growing in areas with a deep thaw layer also showed increasing growth between the mid-1920s and mid-1940s but did not show the same declines in growth thereafter. Rather, these chronologies showed stable to potentially increasing growth in recent decades (Fig. 4). Both species showed greater RCS rwi on shallow rather than deep thaw depth during the 1925–1946 peak. This pattern was reversed after 1980, when both species had greater RCS rwi on deep rather than shallow thaw depth (Fig. 4).

In examining the difference in the climate correlations over time between the two species (Fig. 5), we found that black spruce radial growth had a more negative correlation with mean June–July temperatures than white spruce during the 1925–1955 time period (Fig. 5A), and a less negative correlation with mean June–July temperatures between 1965 and 2004. These shifts in relative correlation with June–July temperature correspond to the shifts in mean ring width size between the two species (Figs. 4, 5B).

Discussion

In this study, we compared black and white spruce climate–growth responses and growth trends for a set of trees that were growing together to eliminate the confounding factor of site conditions. Additionally, we included thaw depth of the active layer as a representation of permafrost, as a factor in our analyses. We examined the climate–growth responses of co-occurring black and white spruce at the individual (mixed-effects models), plot (paired *t* test), and species level (chronology comparison). At each level, the two species showed very similar patterns with a few key differences. Specifically, black spruce showed a more positive radial growth response to June–July precipitation than white spruce. Both species showed different responses to June–July temperature across a gradient thaw depth. This difference was minimal for black spruce, but strong for white spruce, which showed a positive response to June–July temperatures on deep thaw depths and a strong negative response on shallow thaw depths. Indeed, the chronologies of the two species also differed more by thaw depth than by species, highlighting the importance of this factor in mediating how trees respond to climate in interior Alaska (Fig. 4).

Overall, and at the plot level in particular, we found low and weak climate–growth correlations for both species (Table 3). The apparent weak climatic drivers are likely the result of methodical choices. Our study was born out of a broad-visioned vegetation monitoring program; consequently, we have fewer sampled trees per plot than a traditional dendroecological study. Our plots were extracted from a set of monitoring plots placed in a systematic random design across the landscape (Roland et al. 2019) and, thus, fall in a wide spectrum of site conditions contributing to considerable climate–growth variability (Nicklen et al. 2016). Further, our study area covers a large spatial extent (Fig. 1) including varying climatic conditions. These factors combined with possible inaccuracies and biases in spatially interpolated climate data based on sparse station data, often with short time series, likely contributed to the low plot-level climate–growth correlations. It is worth noting that while our plot level and overall chronology–climate correlation are weaker than those found in more targeted dendroecological studies (treeline or drought-sensitive areas), they apply to a wide range of conditions and geography.

Differences in black and white spruce climate–growth responses

We found that black spruce had greater positive radial growth response to increasing June–July precipitation than white spruce. We also found that black spruce was less sensitive to June–July temperature than white spruce (Figs. 2, 3), which showed positive growth responses to June–July temperature in deeply thawed areas, but negative responses in shallowly thawed areas. There are multiple potential explanations for these observations. First, there is some evidence that black spruce is a more shallowly rooting species than white spruce (Farrar 1995, Fryer 2014, Abrahamson 2015). If this is true, then during dry summers when surface soil layers may be more quickly depleted of moisture due to evapotranspiration than the deeper soil layer, black spruce may have less access to soil moisture than white spruce. Second, because our sample includes plots with both species present, we cannot rule out the possibility the two species are directly competing for water. White spruce is generally the faster growing species (Chapin 1986; Table 2); thus, it is possible that white spruce may out-compete black spruce for soil water in our study area.

Based on the mixed-effects model of BAI, we suspect different mechanisms are at play on deep vs. shallow thaw depths that may explain the greater June–July temperature sensitivity of white spruce compared with black spruce in these areas (Fig. 3). For deeply thawed sites, we hypothesize that because deeper-rooted white spruce trees potentially have better access to soil moisture (for reasons given above), warm summers do not adversely affect white spruce growth in these areas but are positively associated with growth. Also, because of its higher potential growth rate, white spruce may simply have a greater radial growth response to good growing conditions than black spruce. However, in shallowly thawed areas, we hypothesize that black spruce's tolerance of low-nutrient availability, a condition common in areas with shallow thaw depths, conveys an advantage in maintaining steady leaf nitrogen levels and associated photosynthetic activity over white spruce during adverse growing conditions. For example, white spruce has a relatively short needle life span, higher needle nitrogen, higher photosynthetic capacity, and a lower photosynthetic nitrogen use efficiency compared with black spruce (Kayama et al. 2007). During (or following) a particularly hot summer, neither species may have the ability to produce many high-quality needles, but this would more adversely affect white spruce growth as this species is more reliant on new needles, while black spruce has a larger reserve of older and more efficient needles (Kayama et al. 2007).

The role of thaw depth of the active layer on climate–growth responses and growth trends

Our results demonstrate a distinct discrepancy in the growth responses of white and black spruce to summer warmth that is contingent upon edaphic conditions related to permafrost, which is likely a primary mechanism causing differences in the distribution of these two coniferous tree species throughout landscapes in boreal interior Alaska. Specifically, in lowland areas with the warmest summer temperatures, white spruce responds more negatively to June–July warmth than black spruce, negating the potential competitive advantage conferred on this species by its faster intrinsic rate of growth. It is likely that areas with shallow thaw depths that occupy large parts of interior basin lowlands represent poor-quality white spruce habitat, leaving these areas available for colonization by its more cold, waterlogged, nutrient-poor soil-tolerant congener, black spruce.

Our results point to site conditions as having an important impact on a tree species climate–growth responses and growth patterns over time. Our model results showed both species had greater radial growth when growing on deeper thaw depths (Appendix S2: Table S1, Fig. S3), an expected result that agrees with other studies of forest productivity in interior Alaska (Van Cleve et al. 1983, Viereck et al. 1993, Roland et al. 2013, 2019). The chronologies of black and white spruce growing on deep and shallow thaw depths (Fig. 4) reinforce the significance of thaw depth on growth patterns as there was strong synchrony between black and white spruce growing in the same locations and considerably less synchrony within species growing in different locations. This finding highlights the need to compare species growing in the same site conditions and, like other studies (Lloyd and Fastie 2002, Wilmking et al. 2006, Wilmking and Myers-Smith 2008, Johnstone et al. 2010*b*, Nicklen et al. 2016, Wolken et al. 2016), points to the important role that local site characteristics play in shaping tree species responses to climate conditions.

We found that thaw depth played a pivotal role in the two species climate–growth responses, suggesting that the effect of climate warming on the two species radial growth hinges on the degree of thaw depth. One important implication of this finding is that widespread thawing of permafrost (Osterkamp and Romanovsky 1999, Osterkamp 2003, Romanovsky et al. 2010, Panda et al. 2014) may ultimately foster expansion of white spruce in this region at the expense of black spruce as has been suggested (Wirth et al. 2008, Roland et al. 2013) due to a relaxing of the growth constraints on white spruce imposed by conditions associated with a shallow thaw depth. At first, this transition may be complicated by expansion of very wet areas as thermokarst results in subsidence and formation of ponds and bogs (Jorgenson et al. 2001). Over time, it seems likely that a widespread process of permafrost degradation will result in improved drainage and warmer soils (Lloyd et al. 2003) regionwide.

Fire is a key driver of ecosystem processes and function in the boreal forest. While our study does not directly address this disturbance, fire is tied to climate (Balshi et al. 2009, Kasischke et al. 2010, Turetsky et al. 2011, Hoecker et al. 2020), thaw depth (Brown et al. 2016, Michaelides et al. 2019), and the flammability of vegetation cover (Rupp et al. 2002) and, thus, intimately tied to the future abundance and distribution of boreal forest tree species (Johnstone et al. 2010*a*, Barrett et al. 2011, Roland et al. 2019). How the interactive effect of fire, a warming climate, permafrost, and current forest cover will influence the growth and future abundance of white and black spruce is not clear. Black spruce is a fire-adapted species, often requiring fire for sexual reproductions; thus, increasing fire frequency associated with climate warming may benefit black spruce at the landscape scale (Roland et al. 2019). However, our results, along with others (Wirth et al. 2008, Roland et al. 2013), suggest that the synergistic negative effects of fire and a warming climate on shallow permafrost (Gibson et al. 2018) may create site conditions more suitable for white spruce or deciduous species establishment and growth. Further, increased fire severity is associated with greater deciduous-dominated successional trajectories and may lead to more deciduous trees on the landscape (Johnstone and Chapin 2006, Johnstone et al. 2010*a*, 2016, Barrett et al. 2011), though not necessarily at the expense of white and black spruce prevalence at the landscape scale (Roland et al. 2019). Also at play is the influence of species composition on fire, with black spruce-dominated landscapes promoting more frequent and widespread fires than other forest types (Rupp et al. 2002), which in turn may encourage black spruce regeneration, but not if the fires are too severe, which promotes both permafrost degradation (Gibson et al. 2018) and deciduous species establishment and persistence (Johnstone et al. 2010*a*, Shenoy et al. 2011).

Species differences in growth over time

The chronology patterns of the two species show that black spruce has had greater relative growth than white spruce in recent decades (Figs. 4, 5), while white spruce had greater growth than black spruce during a 1920s–1940s growth peak. The modest shift in relative growth rates of the two species could have multiple explanations. First, incremental changes in site conditions over time may explain the flip in species growth rates. Over time, successional changes such as deepening moss layers and increasing needle litterfall relative to herbaceous litter lead to thicker organic mats and reduced evapotranspiration and cooler soils, which slow mineralization rates and reduce available soil nutrients (Van Cleve et al. 1983). These conditions would generally depress white spruce growth relative to black spruce growth. Thus, successional changes alone may account for the flip in species relative growth. This accords with proposed successional pathways of the dominant interior Alaska forest types (Viereck et al. 1993), but not with long-term monitoring of succession in interior Alaska, which has not documented white spruce stands transitioning into black spruce (Hollingsworth et al. 2010). Indeed, under the successional change scenario we would expect a more gradual shift in divergent growth trends than observed. The more sudden shift observed around 1980 suggests a climatic influence on growth, rather than a purely successional influence, and indeed, this shift coincides with a well-documented increase in Alaska mean annual temperature in the late 1970s (Bieniek et al. 2014, Markon et al. 2018). Second, the two species growth responses to changing climate conditions may be at play and likely interact with the changing site conditions. Our model results show white spruce trees had a more negative response to June–July temperatures than black spruce when growing on shallow thaw depths (Fig. 3). Thus, with warming summer temperatures and potentially thinning thaw depths with successional processes, our model predicts greater relative radial growth for black spruce. In accordance with model results, our temporal analysis of climate–growth correlations showed a shift starting around 1965 in which white spruce shows a more negative response to mean June–July temperatures than black spruce (Fig. 5A). Following this shift in relative climate correlations, the relative growth of the black spruce chronology equals and then exceeds white spruce relative growth (Fig. 5B). Given that summer temperatures and potentially precipitation have risen throughout the study period (Wendler et al. 2017), it is possible that white spruce growth was more negatively affected by the increasing summer temperatures during this period than black spruce and black spruce growth was potentially positively affected by increasing June–July rainfall during this period (Fig. 5), contributing to the flip species growth rates.

The other time period where the chronologies show modestly diverging patterns also coincides with a relatively warm time frame in Alaska, the 1920s to mid-1940s (Bieniek et al. 2014, Markon et al. 2018). This mid- to early-century growth peak has been noted in other interior Alaska tree ring studies (Sullivan et al. 2016, Cahoon et al. 2018). Surprisingly, we found the trees on shallow thaw depths, particularly white spruce, showed relatively greater growth during this period compared with trees on deeply thawed sites. One explanation for this is that the synergistic effect of both early-successional soil conditions in the 1920s-early 1940s (i.e., warmer and more deeply thawed soils associated with an earlier successional stage relative to current conditions) and a warmer climate resulted in a growth release in this time period in the shallow TD sites and for the faster growing white spruce.

Hindering our interpretations of growth and climate–growth correlations over time is that we do not know how thaw depth has changed over time in our plots. Successional processes likely have acted to thin thaw depths (Van Cleve et al. 1993), but climate warming has likely contributed to deepening (Åkerman and Johansson 2008, Panda et al. 2014). Increases in precipitation also deepen thaw depths (Douglas et al. 2020). We also do not know how documented climatic shifts, which have been linked with non-stationarity in spruce climate–growth responses (Ohse et al. 2012), may have interactively affected climate, tree growth, and thaw depth.

The differences in climate–growth responses that we found between black and white spruce at least partly accord with pollen and fossil evidence from the Holocene. We found black spruce grows better with increased summer precipitation, just as the expansion and dominance of black spruce in the mid-Holocene was associated with increased effective moisture (Hu et al. 1998, 2006, Lynch et al. 2004, Lloyd et al. 2006, Tinner et al. 2006). The current distribution of the two species also accords with our findings. Black spruce extends further south on the east coast of North America where summers are wetter, and white spruce extends further south than black spruce in western North America where summers are more arid. These observations suggest how precipitation changes in tandem with temperature may have important consequences for future trajectories of forest change in Alaska. Looking forward, in a much warmer and potentially wetter climate (Sun et al. 2015, Wendler et al. 2017), it is possible that black spruce may show greater relative radial growth than white spruce in certain landscape positions.

Study limitations

The primary goal and contribution of our study is the direct comparison between black and white spruce growing together across a gradient of site conditions and wide geographic area. The limitation to this approach is that we exclude areas where only black or only white spruce occurs. It is likely the climate–growth responses of the species differ in these areas relative to areas where both co-occur, at least in part, due to the role of site conditions in mediating climate–growth responses of both spruce species in interior Alaska (Nicklen et al. 2016). Areas where the two species did not co-occur, and thus where we cannot draw inference, were primarily white spruce habitat at higher elevations or on productive floodplains—areas with high soil temperature and pH, and thin organic mats (Appendix S1: Fig. S1). Site conditions where only black spruce occurred were much rarer than the site conditions where only white spruce occurred (Appendix S1: Fig. S1).

Conclusions

Our most important finding was that climate–growth responses of the two dominant conifers in interior Alaska, but especially white spruce, hinge on thaw depth, which is deepening as the climate warms. This finding points to a primary mechanism behind the major differences in the distribution of these two coniferous tree species across landscapes in interior Alaska and implies that widespread thawing of permafrost may foster some expansion of white spruce in this region at the expense of black spruce. However, black spruce had a more positive radial growth response to increased summer precipitation than white spruce, and white spruce radial growth was more sensitive to warmer June–July temperature. Thus, future changes in precipitation patterns will likely exert important influences on relative rates of growth in these two species, and in some landscape positions, black spruce may gain competitive advantage over white spruce in a wetter climate. Our findings highlight the need for greater understanding of how projected climate changes will impact precipitation and deepening of the active layer across interior Alaska.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3622/full