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Contrasting drivers and trends of coniferous and deciduous tree growth in interior Alaska

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Abstract. The boreal biome represents approximately one third of the world’s forested area and plays an important role in global biogeochemical and energy cycles. Numerous studies in boreal Alaska have concluded that growth of black and white spruce is declining as a result of temperature-induced drought stress. The combined evidence of declining spruce growth and changes in the fire regime that favor establishment of deciduous tree species has led some investigators to suggest the region may be transitioning from dominance by spruce to dominance by deciduous forests and/or grasslands. Although spruce growth trends have been extensively investigated, few studies have evaluated long-term radial growth trends of the dominant deciduous species (Alaska paper birch and trembling aspen) and their sensitivity to moisture availability. We used a large and spatially extensive sample of tree cores from interior Alaska to compare long-term growth trends among contrasting tree species (white and black spruce vs. birch and aspen). All species showed a growth peak in the mid-1940s, although growth following the peak varied strongly across species. Following an initial decline from the peak, growth of white spruce showed little evidence of a trend, while black spruce and birch growth showed slight growth declines from ~1970 to present. Aspen growth was much more variable than the other species and showed a steep decline from ~1970 to present. Growth of birch, black and white spruce was sensitive to moisture availability throughout most of the tree-ring chronologies, as evidenced by negative correlations with air temperature and positive correlations with precipitation. However, a positive correlation between previous July precipitation and aspen growth disappeared in recent decades, corresponding with a rise in the population of the aspen leaf miner (*Phyllocnistis populiella*), an herbivorous moth, which may have driven growth to a level not seen since the early 20th century. Our results provide important historical context for recent growth and raise questions regarding competitive interactions among the dominant tree species and exchanges of carbon and energy in the warming climate of interior Alaska.

Key words: Betula neoalaskana; *boreal forest; climate change; dendrochronology;* Phyllocnistis populiella; Picea glauca; Picea mariana; Populus tremuloides; *SPEI.*

Introduction

The boreal forest is an integral component of global terrestrial biogeochemical and energy cycles (Bonan 2008). Rising air temperature has been associated with a decline in land surface greenness since the early 1980s in some areas of the boreal forest (Verbyla 2008, Beck and Goetz 2011, Ju and Masek 2016). In addition, numerous studies have highlighted an apparent growth decline in white spruce (*Picea glauca*) and black spruce (*Picea mariana*) in recent decades, which is thought to be driven by temperature-induced drought stress (Barber et al. 2000, Lloyd and Bunn 2007, McGuire et al. 2010, Beck et al. 2011, Juday and Alix 2012, Walker and Johnstone 2014, Girardin et al. 2016, Hogg et al. 2017). The combined evidence of a changing fire regime (Kasischke et al. 2010) and declining spruce growth has led some researchers to suggest that interior Alaska may be in the early stages of a “biome shift” from a conifer-dominated region to one increasingly populated by deciduous species and/or grasslands (Beck et al. 2011, Juday et al. 2015), with important implications for wildlife and biogeochemical cycles. This hypothesized biome shift is supported by modeling efforts that predict increasing deciduous forest cover in many parts of the boreal biome in the 21st century (Rupp et al. 2000, Lucht et al. 2006).

In interior Alaska, rising air temperature in recent decades has not been accompanied by an increase in precipitation (Wendler and Shulski 2009, Bieniek et al. 2014). Deciduous species may be better adapted to a warmer and drier climate than spruce, as evidenced by the abundance of aspen in continental areas at lower latitudes (Peterson and Peterson 1992) and palynological records that show an increase in paper birch (*Betula papyrifera*) and balsam poplar (*Populus balsamifera*) during the Holocene thermal maximum (Brubaker et al. 1995). Additionally, differences in xylem anatomy, rooting depth distribution and water relations may favor deciduous species during moisture-limiting conditions. Aspen and birch are diffuse-porous species with larger diameter vessels, greater hydraulic conductance (Sperry et al. 1994) and deeper rooting depths than spruce

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(Gale and Grigal 1987). This may enable angiosperms to maintain greater stomatal conductance and transpirational water fluxes during periods of moderate moisture limitation, when compared with the tracheid anatomy of gymnosperms. However, the larger diameter vessels of aspen and birch may be more susceptible to freeze-thaw and/or drought-induced embolism (Hacke and Sperry 2001) than the narrower tracheids of black and white spruce during periods of severe moisture limitation. A complicating factor, however, is outbreaks of phytophagous insects in Alaska and Canada that may interact with moisture limitation and further constrain growth of deciduous (Hogg et al. 2002) and coniferous tree species (Berg et al. 2006). Thus, species differences in xylem anatomy, water relations and susceptibility to insect damage may influence the probability that deciduous trees will maintain dominance of the forest canopy during the later stages of boreal forest succession in a warmer climate.

There are a number of potential mechanisms by which deciduous species might rise to dominance in a warmer and drier climate. One of the most common conclusions is that increases in the frequency of severe wildfires that consume most or all of the soil organic horizon and leave exposed mineral soil, may promote the establishment of deciduous tree species, altering the successional trajectory and supporting deciduous dominance of the post-fire forest canopy (Chen et al. 2009, Johnstone et al. 2010, Shenoy et al. 2011, Gibson et al. 2016). A shift toward deciduous dominance in the boreal forest would alter biogeochemical cycling (Melvin et al. 2015), modify wildlife habitat (Kielland et al. 2006) and lead to major changes in surface energy budgets that feedback to affect climate (Euskirchen et al. 2010). However, to fully understand the consequences of changes in forest composition, direct effects of climate on tree productivity and indirect effects of climate on biotic and abiotic disturbance regimes must be considered.

Despite the potential consequences of a shift in dominant vegetation type, we are not aware of a study that has directly compared long-term trends in main stem radial growth of spruce with those of birch and aspen in interior Alaska. While a change in tree species dominance may well be initiated by changes in the wildfire regime, comparison of climate-growth relationships and long-term tree growth trends provide an opportunity to examine potential changes in boreal forest productivity with increasing deciduous tree abundance and the likelihood that birch and/or aspen may be able to outcompete spruce in mixed stands during the later stages of succession. We took advantage of a large and spatially extensive collection of tree-cores from the Tanana Valley in interior Alaska to compare long-term growth trends of two coniferous (*Picea glauca* and *P. mariana*) and two deciduous (*Betula neoalaskana* and *Populus tremuloides*) tree species. Importantly, like all tree-ring studies, our inference is limited to radial growth, whereas trees are known to shift allocation in response to changes in their environment (Poorter et al. 2012). Nevertheless, given the suggestion that birch and aspen may overtake black and white spruce as the dominant tree species of interior Alaska, we sought to test the general hypothesis that birch and aspen showed more positive growth trends than black and white spruce during a period of rising air temperature in the latter half of the 20th century. Specifically, we examined the following questions:

1) How do long-term growth trends differ between white spruce, black spruce, Alaska paper birch and trembling aspen?
2) Are there differences among species in their growth responses to changes in temperature and precipitation?
3) How has aspen growth responded to the recent outbreak of the aspen leaf miner (*Phyllocnistis populiella*), an herbivorous moth, in interior Alaska?

METHODS

Increment core collection and processing

Increment cores were collected across interior Alaska during the summer months of 2013–2016 (Fig. 1) from the four dominant tree species in the region: white spruce (*Picea glauca*), black spruce (*Picea mariana*), Alaska paper birch (hereafter, birch; *Betula neoalaskana*) and trembling aspen (hereafter, aspen; *Populus tremuloides*). Collection methods have been reported previously (Sullivan et al. 2016) and can be found in greater detail in Appendix S1, while plot characteristics (aspect, elevation and slope) are summarized in Table 1. Cores were stored in paper straws and allowed to air dry for several weeks before mounting, sanding to 1,200 grit and measuring ring widths to the nearest 0.001 mm using a sliding bench micrometer and digital encoder (Velmex Inc., Bloomfield, New York, USA). Because cores were collected during the growing season, the outermost ring was only used for dating purposes and was not included in the ring width series. Several aspen and birch cores displayed latewood boundaries that were too faint to be accurately measured. In those cases, cores were stained by soaking for several minutes in a 1% solution of phloroglucinol followed by a 50% solution of hydrochloric acid (Patterson 1959). The pith was missing from 27% of the white spruce, 40% of the black spruce, 8% of the birch and 55% of the aspen cores. We estimated the number of missing rings on cores for which the innermost ring formed a complete arc using the geometric method (Duncan 1989). Potential dating errors were evaluated using COFECHA (Holmes 1983) and corrected when possible after re-examining the cores. In total, 339 white spruce, 213 black spruce, 231 birch and 111 aspen cores were suitable for dating (Table 1).

Detrending

Numerous detrending methods have been developed, each with the goal of removing age- or size-related trends in tree growth while preserving climate-driven variation in the tree-ring chronologies. Five detrending methods were compared to examine the implications for long-term growth trends and the strength of climate-growth correlations: no detrending, the negative exponential/negative linear method, the Hugershoff method, multiple curve age RCS and multiple curve diameter RCS. No detrending involves computing the average ring width for each year across trees, without fitting a detrending curve. The negative exponential/negative linear method involves fitting a negative exponential model or negative linear model to each ring width series. The Hugershoff method fits a modified negative exponential, negative linear or horizontal model to each series. Age RCS aligns ring

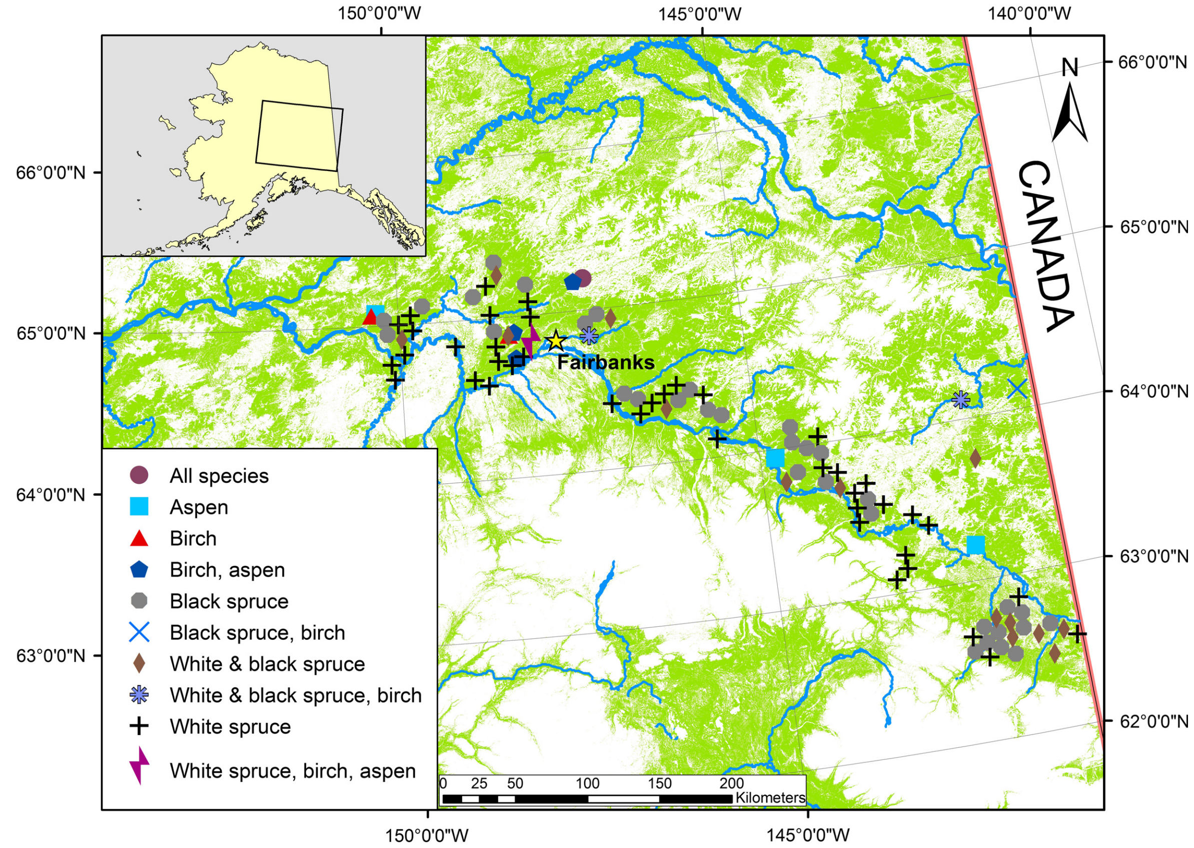

FIG. 1. Plot locations indicating where tree cores were collected throughout the Tanana Valley, Alaska. Blue features are major river systems and the green overlay represents approximate forested area. Plots are delineated based on the tree species collected at each plot. In total, 103 plots were visited between 2013 and 2016.

width data by cambial age, then fits an empirical model to estimate and subsequently remove the age-related ring width decline. Similarly, diameter RCS aligns ring width data by the radius of the stem at the time the ring was formed and fits an empirical curve to the relationship between ring width and radius. Age and diameter RCS provide the option to fit separate curves to evenly distributed subsets of tree-ring series to account for ecological variation in growth rates and/or biomass allocation patterns (Melvin and Briffa 2014). To implement multiple-curve RCS, series are sorted by mean ring width (Melvin 2004), grouped as evenly as possible (>40 series), and an age or diameter-related curve is defined separately for each group. Due to the small number of aspen cores relative to the other species in our dataset, multiple curve RCS was limited to two curves for this species.

Detrending was performed in CRUST (Melvin and Briffa 2014). All ring width indices were calculated as ratios of observed to expected growth and chronologies were constructed using Tukey's biweight robust mean. We truncated chronologies when the sample size fell below 20 trees. Signal-free chronologies were produced with the aim of correcting for the inadvertent removal of the climate signal during detrending (Melvin and Briffa 2008). This was accomplished by repeatedly dividing the raw ring widths by the detrended chronology (≤10 iterations) to minimize the variance. A potential limitation of RCS is that insufficient variability in size and/or ages of the trees can yield a detrending curve (or curves) that contain some of the low-frequency climate-driven trend(s) in tree growth (Melvin and Briffa 2014). In our dataset, the age and size distribution of sampled trees were broad (Appendix S2) and the range of tree ages was at least half the length of each chronology (Table 1) – a criterion identified by Melvin and Briffa (2014) to avoid the aforementioned bias.

Choice of detrending method had a large effect on the tree-ring chronologies for all species (Appendix S3). In an effort to objectively select the most appropriate chronology for each species, we compared climate-growth correlations using the treeclim package (Zang and Biondi 2015) in R 3.3.2 (R Core Team 2014). The detrending method that produced the greatest number of significant correlations with climate across all species was assumed to represent the most appropriate detrending method. Among the detrending methods tested, chronologies produced using two-curve diameter RCS generally showed the strongest and/or greatest number of significant correlations with climate (Appendix S4). Furthermore, adding more than two curves during multiple RCS detrending provided limited improvements to the birch, black and white spruce chronologies (Appendix S5). Thus, to ensure comparability across species, we elected to use chronologies constructed using two-curve diameter RCS for all four tree species in the remaining analyses. Our primary goal was to compare climate-growth

Table 1. Tree and chronology statistics by species.

				Cambial age (years)			Diameter at breast height (cm)			Plot characteristics		
Species	*n* (no. trees, 1 core/tree)	Mean interseries correlation	Mean auto-correlation	Mean	Median	Range	Mean	Median	Range	Aspect	Elevation (m)	Slope
P. glauca	339	0.33	0.73	116	108	18–366	21.3	20.1	3.7–60.2	North (0–359)	455 (98–932)	8.3 (0–22)
P. mariana	213	0.38	0.73	106	93	15–238	11.0	10.5	4.2–28.9	North (3–359)	522 (123–978)	8.3 (0–22)
B. neoalaskana	231	0.54	0.68	73	72	24–186	20.0	20.1	7.5–35.3	South (119–327)	410 (155–978)	8.9 (0.5–21.6)
P. tremuloides	111	0.70	0.70	96	89	42–190	26.5	26.7	11.4–57.3	East (65–327)	346 (218–553)	11.3 (0.6–21.6)

Notes: Mean interseries correlation is the average correlation between each series and a master chronology, based on raw ring widths. Mean first-order autocorrelation was determined from raw ring widths. Descriptive statistics of cambial age and diameter at breast height exclude trees that were burned prior to data collection. Aspect is reported as the mode (range) of plots where at least one species was cored, whereas elevation and slope are the mean (range) of the same plots. Plot-specific details can be found in Appendix S1.

relationships and tree growth trends over a large area of interior Alaska. To this end, one tree-ring chronology was produced for each species. The strong interseries correlation (Table 1) and robust fit of the detrending curves to the ring width data (Appendix S6) provided confidence that a single chronology was appropriate for each species.

Climate-growth relationships among species

One of the most reliable sources of long-term climate data for interior Alaska is the record for Fairbanks, AK (1915–2015), which we obtained from the Alaska Climate Research Center. Although cores were collected throughout the 922,00 ha of forested land in the Tanana Valley State Forest and the Tetlin National Wildlife Refuge, we elected not to use data from additional locations in climate-growth analyses because (1) most stations have short and/or incomplete records, (2) gridded precipitation data for Alaska are plagued by temporal inhomogeneities associated with differences in record length across stations (McAfee et al. 2014) and (3) the Fairbanks summer air temperature record is well-correlated with records from other stations throughout interior Alaska and western Canada (Sullivan et al. 2017). Ring width indices were assessed for their correlation with mean monthly air temperature and total monthly precipitation during the growing season (May–August) for the growth year and the year prior to ring formation using the treeclim package in R. Significant correlations ($\alpha = 0.05$) between climate and tree-ring indices were determined using "stationary" bootstrap resampling (1,000 iterations). This bootstrapping method addresses the potential for temporal autocorrelation by resampling within blocks (Politis and Romano 1994). The number of observations in each block is chosen randomly and has a geometric distribution (Zang and Biondi 2015). Another method of addressing temporal autocorrelation in tree-ring and climate data is to prewhiten the time series prior to performing climate-growth analyses (Hamed 2009). Prewhitening of both the climate data and the tree-ring data made little qualitative difference to climate-growth correlations in our dataset (Appendix S7).

To improve our understanding of tree growth responses to moisture limitation, we performed an additional climate-growth analysis using the standardized precipitation evapotranspiration index (SPEI; Vicente-Serrano et al. 2010). Although numerous drought indices are available, SPEI accounts for fluctuations in temperature as a driver of warming-induced moisture limitation, while considering climatic water balance at various temporal scales. Water balance was determined as the difference between precipitation and potential evapotranspiration (PET), calculated using the simplified Thornwaite equation (Thornwaite 1948). The Thornwaite model was chosen over more complex calculations of PET (e.g., Penman-Monteith) because it is based upon mean air temperature, which is arguably the most reliable long-term climate variable available in interior Alaska. In contrast, the Penman-Monteith method requires estimates of solar radiation, relative humidity and wind speed, variables that are not available throughout the Fairbanks climate record. A less commonly used method of calculating PET that also relies upon air temperature is the Hargreaves equation, which uses air temperature minima and maxima, rather than the mean (Droogers and Allen 2002). The Hargreaves equation produced monthly SPEI values that were strongly correlated with those derived from the Thornwaite estimates ($r = 0.92$ $P < 0.05$) with very similar patterns in growth-climate correlations (Appendix S8). SPEI was standardized using a log-logistic distribution in the SPEI package (Beguería and Vicente-Serrano 2013) in R. Correlation between ring width indices and mean monthly SPEI for May-August for the growth year and the year prior to ring formation was again assessed using the treeclim package with significance ($\alpha = 0.05$) determined using "stationary" bootstrapping (1,000 iterations).

Tree growth responses to biotic agents

To gain insights into biotic drivers of tree growth, we examined the relationship between aspen leaf miner (*Phyllocnistis populiella*) and aspen ring width indices at two spatial scales. First, population estimates of defoliating insects were monitored twice per summer between 1976 and 2012 at Bonanza Creek LTER (Werner et al. 2012). During each sampling campaign, individuals were counted from two branches collected at five sites. At a broader scale, we compared aspen growth with damage estimates from the aspen leaf miner (ALM) collected during annual aerial surveys by the U.S. Forest Service, Forest Health Protection Program. We focused our analysis on ALM because it: (1) is a leading defoliator in interior Alaska compared with other pests (Dubois and Burr 2015), (2) has reduced aspen photosynthesis and growth in experimental studies (Wagner et al. 2008) and (3) has recently been observed as a leading cause of mortality among inventory plots in the Tanana Valley (Trugman et al. 2017). We examined the relationship between growth and ALM population (insects/m^2 of foliage) using ring width indices for cores collected from Bonanza Creek LTER in 2015 (n = 18). At the landscape scale, ring width indices from the entire dataset were compared with aerial estimates of ALM damage. We assessed the influence of ALM on aspen radial growth using Pearson's correlation coefficient in R for the growth year and the previous year. In an attempt to disentangle the effects of climate and ALM on aspen growth, we examined climate-growth correlations before and after the ALM outbreak. The post-ALM outbreak years were 2000–2015 and pre-ALM outbreak years were divided into the 15 yr prior to widespread herbivory for symmetry (1984–1999) and the remainder of the chronology that aligned with the climate record (1916–1984).

RESULTS

Climate trends in interior Alaska

Growing season (May–August) air temperature near Fairbanks, AK has risen considerably since the middle of the 20th century, while precipitation has remained relatively stable over the instrumental record (Fig. 2a). The combination of rising temperature and stable precipitation has presumably resulted in greater evaporation and reduced moisture availability in interior Alaska, as suggested by more frequent negative departures in the standardized precipitation evapotranspiration index (SPEI) since the late 1960s (Fig. 2b).

Long-term growth trends among interior trees

Tree-ring chronologies for the dominant coniferous and deciduous species in interior Alaska contrasted in length, variation and modern growth rates (Fig. 3). Chronologies for the coniferous species were much longer and displayed substantially less variation in growth over time than the deciduous species. Birch, white spruce and black spruce showed a pronounced growth peak in the 1940s, followed by a return to growth rates similar to the early decades of the 20th century. Aspen growth was much more variable than the other species. Following several decades of greater growth beginning around 1915, aspen growth showed a decline from the 1950s to present, with a very sharp growth reduction beginning in the 1980s. Overall, recent growth (last 20 yr) of white spruce and black spruce was 3% and 16% lower, respectively, than the 20th century mean (a time period common to all species). Meanwhile, recent birch and aspen growth was 16% and 48% lower, respectively, than the 20th century mean for each species. When considering the entire chronology for each species, recent growth for white and black spruce was *greater* than the overall average (11% and 8%, respectively), while recent birch and aspen growth was *lower* (17% and 43%, respectively) than the long-term mean.

Climatic and biotic drivers of tree growth

For the tree-ring chronologies as a whole, growth of white spruce, black spruce and birch showed significant positive correlations with monthly precipitation in August of the year prior to growth and August of the growth year for both spruce species (Fig. 4). Growth of all three species was negatively correlated with air temperature in the same months. All four species displayed significant positive correlations with mean SPEI in August of the year prior to growth, while SPEI in August of the current year was also significant for black and white spruce. When considering the entire chronology, aspen growth was not significantly correlated with precipitation, but showed significant negative correlations with air temperature in June, July and August of the year prior to growth and May through July of the growth year.

To explore additional factors related to changes in aspen radial growth, we investigated the potential role of ALM outbreaks. Results indicated a strong and significant negative correlation ($r = -0.78$, $P < 0.01$) between aspen growth and ALM damage estimated through annual aerial surveys throughout interior Alaska. (Fig. 5). Damage by ALM increased rapidly in the late 1990s, peaking in 2007. Meanwhile, aspen growth was reduced to very low levels during the same period, particularly between 2005 and 2007. At a finer scale, ALM showed a similar increase in population at the Bonanza Creek LTER (Fig. 6) and a significant negative relationship with the ring width indices of the 18 aspen trees sampled within the LTER site ($r = -0.70$, $P < 0.01$).

We examined the possibility that the recent ALM outbreak may have affected climate-growth analyses for aspen by comparing correlations separately for the periods before and during the ALM outbreak. Aspen growth showed significant, but weak positive correlation with previous July precipitation and negative correlation temperature during the period 1916–1983, prior to the documented major ALM outbreak (Table 2). Aspen growth appears to have developed increasing sensitivity to summer air temperature during the 15 yr prior to the ALM outbreak (1984–1999). We detected a significant negative correlation with current May temperature and, although not significant, strong negative correlations with previous July, previous August and current July air temperature. During the 15 yr of the ALM outbreak (2000–2015), aspen growth showed very strong significant negative correlation with air temperature in May and July of the year prior to growth and May of the growth year.

DISCUSSION

To our knowledge, this study is the first to compare long-term growth trends among the dominant coniferous and deciduous species in the boreal forest of interior Alaska – a region undergoing rapid changes in climate. Our results highlight the importance of both climatic and biotic drivers of tree growth in interior Alaska. Climate change is expected to increase the frequency and severity of fires in interior Alaska (Balshi et al. 2009), which may

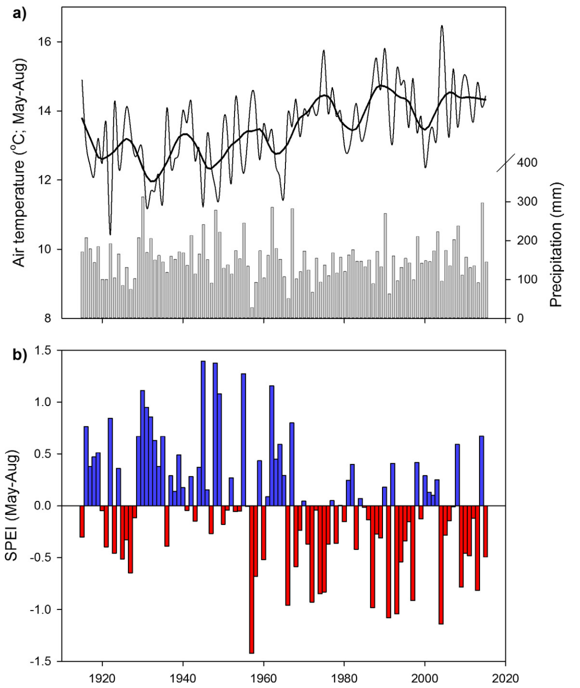

Fig. 2. Long-term trends in growing season (May–August) air temperature (solid line) fitted with a loess smoothing spline (bold) and total precipitation expressed as vertical bars (a) for Fairbanks, Alaska. Standardized precipitation evapotranspiration index (SPEI; b) averaged over the growing season. Negative values indicate more limited moisture availability. Since 1960 there has been a consistent trend of more prolonged and severe periods of negative SPEI than prior to 1960.

favor deciduous species that tend to have greater seed dispersal distance and benefit from exposed mineral soil during germination and establishment (Chen et al. 2009, Johnstone et al. 2010, Shenoy et al. 2011, Gibson et al. 2016). While warm and dry conditions may lead to more severe wildfires that favor germination and establishment of deciduous tree species, our results indicate that the same climate conditions, and potentially associated biotic conditions, may not be favorable for growth of mature birch and aspen. Although tree-ring analyses may not necessarily reflect demographic changes, trees often display reduced ring widths or greater sensitivity to climate prior to mortality events (Ogle et al. 2000, Suarez et al. 2004). Of the species in our study, only aspen appears to be experiencing a rapid decline in growth, likely driven by a recent outbreak of the aspen leaf miner. All four species exhibited some level of sensitivity to precipitation and/or temperature and aspen showed the greatest evidence of a recent growth decline. These findings raise questions about the likelihood that deciduous species will outcompete spruce during the late stages of succession in mixed stands and about the future productivity of the boreal forest of interior Alaska, if deciduous tree species do indeed increase in abundance at the expense of spruce.

Differences and similarities in tree growth among species

Comparison of growth trends revealed several key similarities and differences among species. All species showed a distinct growth peak in the 1940s. Growing season air temperature was cooler and precipitation was greater during the 15 yr prior to the growth peak than in the 15 yr following the peak, likely favoring growth of all four species. Following the peak, growth declined among all species, then appeared to stabilize during the latter half of the 20th century for white and black spruce to a point near the long-term mean. The white and black spruce chronologies were much longer than those of birch and aspen, reflecting their longer lifespans. There was also notably more inter-annual variability among the deciduous species, with several very sharp reductions in aspen growth in the early 1900s, late 1960s and since the late 1990s. Overall, birch and aspen showed fewer significant correlations with precipitation and weaker correlations with SPEI, which may partially support our hypothesis that the deciduous species would be less sensitive to moisture limitation than the spruce species.

Variation in climate-growth relationships among white spruce, black spruce and birch

Numerous studies have shown a negative growth response to temperature and a positive correlation with precipitation in white and black spruce in interior Alaska and western Canada (Barber et al. 2000, Lloyd and Bunn 2007, McGuire et al. 2010, Beck et al. 2011, Juday and Alix 2012, Juday et al. 2015, Sullivan et al. 2016, Hogg et al. 2017). The positive correlation between SPEI and growth found in our study provides further evidence that the warming trend in interior Alaska may, in part, be contributing to slight growth declines of black spruce and birch. The strong correlation between growth and SPEI in May and August of the growing season for white and black spruce suggests cool temperatures at the margins of the growing season may reduce evaporative demand during periods when soil water is either frozen (i.e., May) or at a seasonal low (i.e., August). August precipitation (significant for both spruce species and birch in the year prior to growth) likely has the important role of replenishing soil moisture at a time when it would otherwise reach a seasonal low, thereby enabling trees to maintain foliar gas exchange when evaporative demand is high. Yarie (2008) suggested that snowpack meltwater may provide an essential subsidy to upland and floodplain white spruce that were subjected to experimental reductions in summer precipitation. However, we found no evidence of positive correlations between winter precipitation and growth, nor between April 1 snow depth and growth, regardless of species (Appendix S9).

Climatic and biotic drivers of aspen growth

One of the most notable results from our study is the decline in aspen growth since the 1950s, followed by a dramatic growth reduction in the 1990s, which is likely driven largely by a widespread ALM outbreak. Climate-growth correlations pre- and post-ALM outbreak provide some insight into the relative influence of biotic and abiotic drivers of aspen growth (Table 2). Aspen growth appears to have been mildly sensitive to moisture limitation throughout most of the 20th century as we detected a significant positive

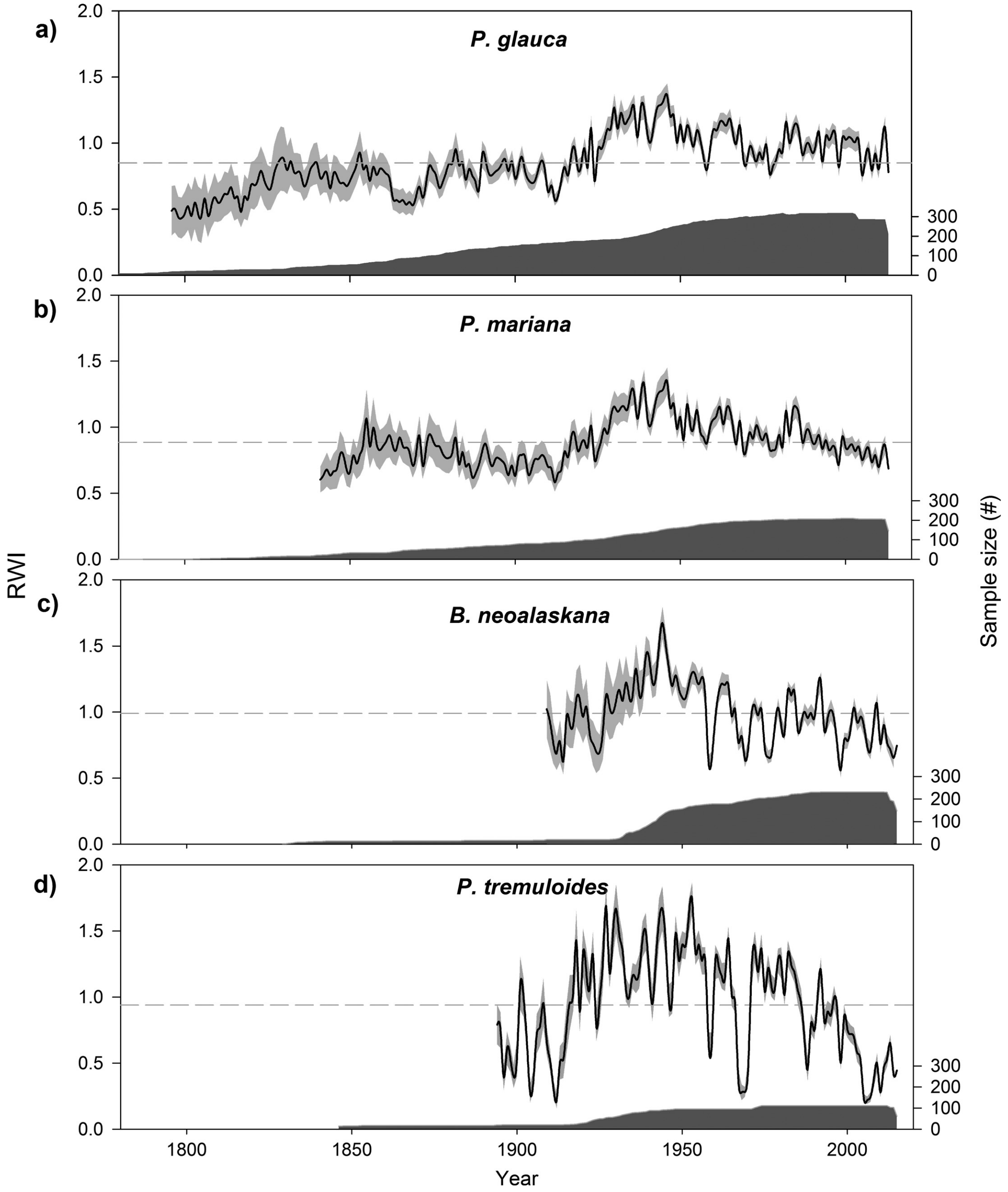

FIG. 3. Two-curve diameter RCS chronologies for white (a) and black spruce (b), birch (c) and aspen (d) sampled throughout the Tanana Valley of interior Alaska. The solid line represents the mean ring width index (RWI), the gray shading shows the 95% confidence interval, the solid fill at the bottom of each panel represents the sample size for each species and the dashed line is the mean for the length of the chronology. Both deciduous chronologies are shorter and show greater variability in growth.

correlation with precipitation and significant negative correlation with temperature for the 1916–1983 period; however the strength of the relationship was quite weak when compared with the very strong negative correlations between aspen growth and air temperature in the 15 yr prior to and during the ALM outbreak. The lack of significant correlations with precipitation immediately prior to the ALM outbreak appears to counter the possibility that the drying trend in the latter portion of the 20th century predisposed aspen to ALM infestation. However, warm early growing seasons can lead to moisture limitation by creating conditions where atmospheric demand is high but soils remain frozen, limiting soil moisture availability and may partially explain the strong negative correlation with May air temperature. Moisture limited plants may be more susceptible to herbivory because C uptake is reduced through stomatal closure, limiting the investment in C-based defensive compounds (Herms and Mattson 1992). In an experimental study of aspen saplings from the Tanana Valley, moisture limitation reduced defensive compound production in only one of four aspen genotypes (Newman and Wagner 2013). However, water relations and the connection between water relations and defense may differ in mature trees. While our dendroecological analysis hints at the possibility that

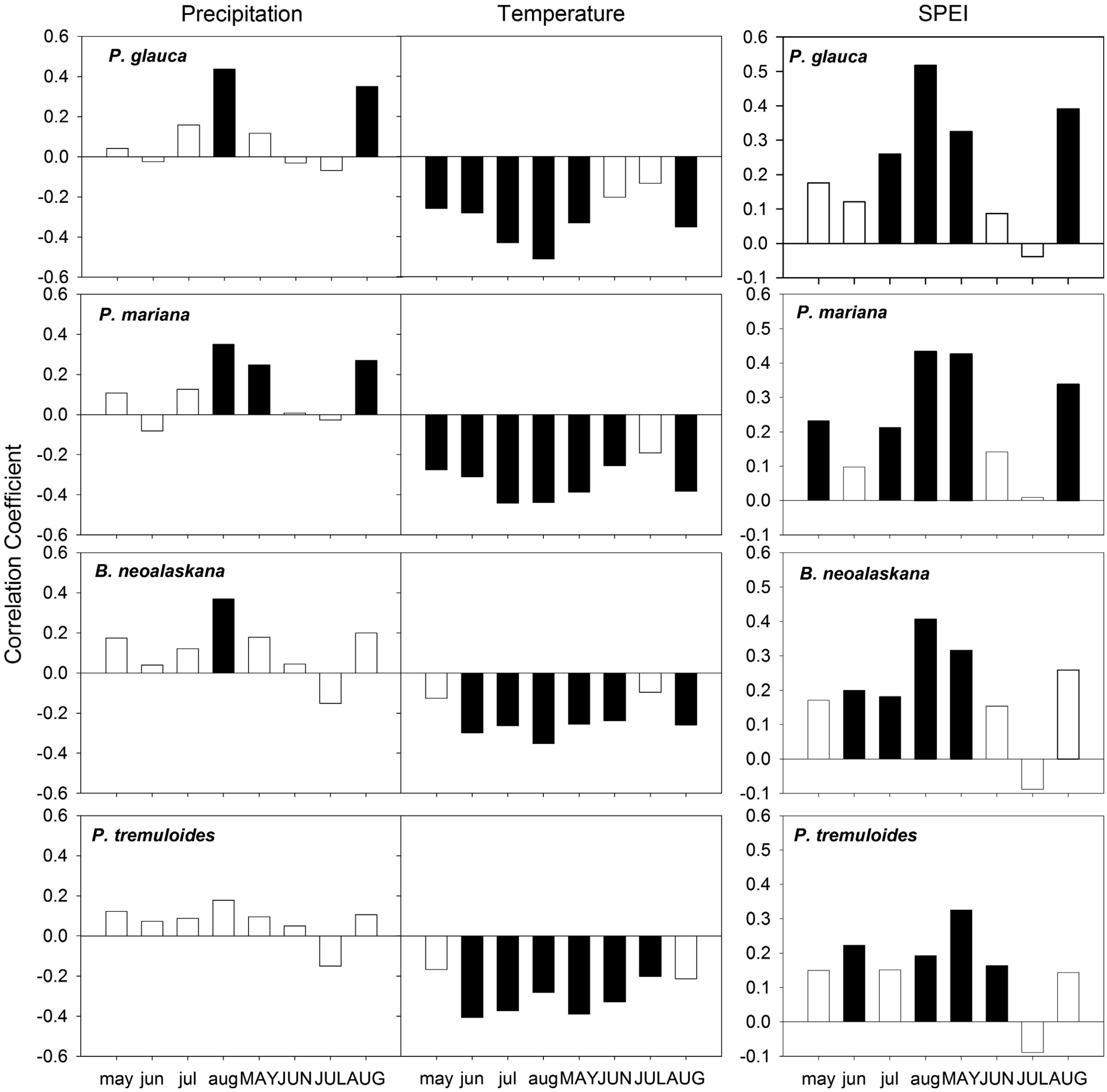

FIG. 4. Climate-growth correlation coefficients using monthly precipitation, air temperature and Standardized Precipitation Evapor-transportation Index (SPEI) as independent variables. Filled bars represent significant correlations with growth after stationary bootstrap resampling ($P < 0.05$). For clarity, error bars are not shown but can be found in Appendix S7. Lowercase text represents months in the year prior to growth and uppercase are the growth year.

moisture limitation may have predisposed aspen to ALM attack, the complexities of this interaction would benefit from further study throughout the region.

The direct mechanism by which ALM reduces aspen growth appears to be through the destruction of the guard cells, leading to stomatal closure, eventually causing the tree to deplete carbohydrate reserves (Wagner et al. 2008). The ALM outbreak appears to be the primary driver of the dramatic aspen growth decline in the late 1990s. The lack of significant correlations with precipitation after the outbreak suggests ALM herbivory either masks a coherent climate signal and/or stomatal closure associated with guard cell damage reduces canopy transpiration to the point where moisture availability is no longer limiting. In addition to reduced C-uptake as a result of stomatal closure, mined leaves tend to abscise up to 4 weeks prior to undamaged leaves, which may further reduce water use, exacerbate the loss of C-uptake potential and further limit C resources available for defensive compounds and growth (Wagner et al. 2008). The reduction in C stores and radial growth associated with ALM has been noted previously (Wagner and Doak 2013). However, our results may be the first to demonstrate these effects on such a broad scale in interior Alaska. It is also worth noting that our aspen tree-ring chronology revealed a large growth reduction in 1966–1969, which may have been driven by a major outbreak of the large aspen tortrix (*Choristoneura conflictana* Wlkr), a defoliator that affected approximately 2.5 million hectares in interior Alaska in the late 1960s (Torgersen and Beckwith 1974).

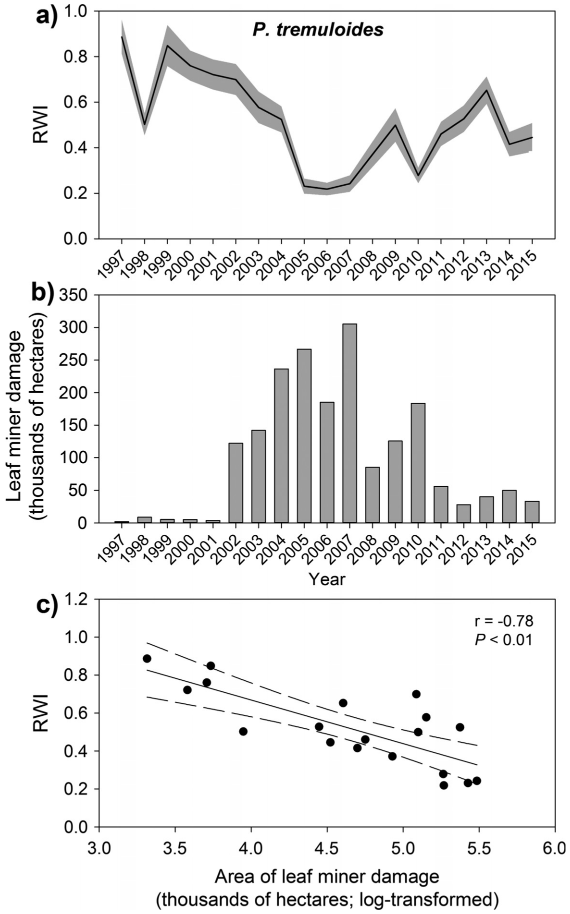

FIG. 5. Two-curve diameter RCS aspen chronology for the portion representing the period for which aerial surveys of aspen leaf miner (ALM) damage are available (a). Annual ALM damage estimates determined through aerial surveys (b). Pearson's correlation coefficient and best-fit linear model (c) for the relationship between the estimated ALM damage and aspen growth (RWI). Dashed lines represent the 95% confidence interval. Results indicate a strong negative correlation between growth and ALM damage.

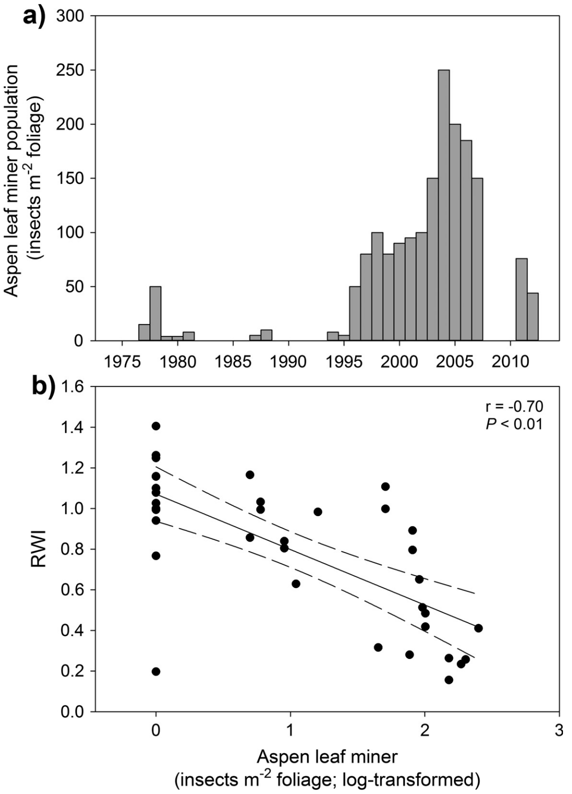

FIG. 6. Population estimates of aspen leaf miner (ALM) at the Bonanza Creek LTER, collected twice per summer (a). Pearson's correlation coefficient and best-fit linear model for the relationship between ALM population and mean RWI for trees (n = 18) cored at Bonanza Creek (b). Note that population estimates were not made in 2008 and 2009. There is a strong negative correlation between aspen growth and ALM population estimates at this finer spatial scale.

The initial causes of the ALM outbreak are uncertain, but the ongoing occurrence in interior Alaska may be sustained by ALM population dynamics and aspen host availability. During the ALM life cycle, eggs are deposited on aspen leaves when bud break begins in May, after which, larvae emerge directly into the epidermal layer and begin consuming cell contents until mid-June when they pupate and emerge as adults. ALM larvae appear to be influenced by strong intraspecific competition during the feeding stage. Negative density-dependent survival among lavae likely limits the ALM population while simultaneously restricting aspen leaf damage to a level capable of sustaining prolonged outbreaks (Doak and Wagner 2015). Additionally, our finding that aspen growth was negatively correlated with current and previous May air temperature during the ALM outbreak may reflect synchronized timing between aspen leaf bud burst and the emergence of ALM larvae which then begin consuming newly produced leaf material.

Consistent with our findings, defoliating insects and drought have been described as the most important inciting factors in aspen dieback throughout western Canada (Frey et al. 2004)—processes that appear to be important drivers of aspen growth in interior Alaska. Although climate appears to have more limited *direct* effects on aspen radial growth than the other species investigated, a warmer and drier climate in recent decades may have had a stronger *indirect* effect on aspen growth by increasing this species vulnerability to herbivory and by initiating or exacerbating the severity of the ALM outbreak. The interaction between defoliators and moisture limitation in aspen stands could have major implications for forest productivity (Hogg et al. 2008), mortality (Hogg et al. 2002, Trugman et al. 2017) and feedbacks to climate (Michaelian et al. 2011) in the form of altered biogeochemical cycles and surface energy budgets.

Our results provide important historical context for modern growth rates among the dominant coniferous and deciduous tree species in boreal Alaska. While a widespread shift toward deciduous dominance may initially be triggered by changes in the fire regime, our analysis indicates that the recent suite of climate and biotic drivers of tree growth have not been more favorable for deciduous species than for spruce. Although model uncertainty is considerable, much of interior Alaska is expected to experience rising temperatures and greater precipitation over the next century (SNAP, 2017). However, more precipitation may not alleviate moisture

Table 2. Climate-growth correlations for aspen after dividing the chronology into pre- and post-ALM outbreak years.

	Pre-ALM		Post-ALM
Variable and month	1916–1983	1984–1999	2000–2015
Precipitation			
Previous May	0.02	−0.01	−0.26
Previous Jun	0.11	−0.22	−0.10
Previous Jul	**0.23**	0.13	0.02
Previous Aug	0.03	0.36	0.43
Current May	0.01	−0.03	−0.02
Current Jun	0.08	−0.25	−0.44
Current Jul	−0.05	−0.08	−0.31
Current Aug	0.12	−0.37	0.43
Temperature			
Previous May	0.08	0.17	**−0.65**
Previous Jun	−0.27	−0.01	−0.16
Previous Jul	**−0.23**	−0.46	**−0.65**
Previous Aug	−0.18	−0.41	−0.32
Current May	−0.16	**−0.60**	**−0.70**
Current Jun	−0.19	−0.11	0.26
Current Jul	0.03	−0.44	−0.23
Current Aug	−0.10	−0.28	−0.29

Notes: Years 1916–1983 were selected to gain long-term insight into pre-ALM climate-growth relationships. For symmetry with the outbreak years (2000–2015), the 15 yr prior to the ALM outbreak were also selected for analysis. Bold values are significant ($P < 0.05$) after bootstrap resampling 1,000 times. Because the window of pre- and post-ALM was smaller than that required for stationary bootstrapping (minimum 18 yr), "exact" bootstrapping method was used to assess significance.

limitation if longer and warmer growing seasons result in greater cumulative evapotranspiration and soil drying.

Importantly, our study is limited to just one aspect of tree growth (radial growth), while trees tend to shift resource allocation in response to changing environmental conditions (Poorter et al. 2012). For example, white and black spruce tend to have shallower roots than birch and aspen (Gale and Grigal 1987) and may therefore respond to soil drying before deeper rooted deciduous species by allocating biomass belowground during dry years. Thus, it is possible that changes in allocation could result in simultaneous declines in landscape greenness (e.g., Verbyla 2008, Beck and Goetz 2011) and stable radial growth. Additionally, the relationships among productivity, mortality and reproduction vary among species and in response to climate (McDowell et al. 2008). Therefore, radial growth may not necessarily reflect demographic processes that contribute to changes in forest composition. Nevertheless, our findings raise important questions regarding competitive interactions among the dominant tree species and potential changes in forest-atmosphere fluxes of C, energy and water in the warming climate of interior Alaska.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2223/suppinfo

DATA AVAILABILITY

Data associated with this study are available from the International Tree-Ring Data Bank; see files ak159 and ak160 at http://www1.ncdc.noaa.gov/pub/data/paleo/treering/updates/.