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LETTER

Warm summer nights and the growth decline of shore pine in Southeast Alaska

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Abstract

Shore pine, which is a subspecies of lodgepole pine, was a widespread and dominant tree species in Southeast Alaska during the early Holocene. At present, the distribution of shore pine in Alaska is restricted to coastal bogs and fens, likely by competition with Sitka spruce and Western hemlock. Monitoring of permanent plots as part of the United States Forest Service Forest Inventory and Analysis program identified a recent loss of shore pine biomass in Southeast Alaska. The apparent loss of shore pine is concerning, because its presence adds a vertical dimension to coastal wetlands, which are the richest plant communities of the coastal temperate rainforest in Alaska. In this study, we examined the shore pine tree-ring record from a newly established plot network throughout Southeast Alaska and explored climate-growth relationships. We found a steep decline in shore pine growth from the early 1960s to the present. Random Forest regression revealed a strong correlation between the decline in shore pine growth and the rise in growing season diurnal minimum air temperature. Warm summer nights, cool daytime temperatures and a reduced diurnal temperature range are associated with greater cloud cover in Southeast Alaska. This suite of conditions could lead to unfavorable tree carbon budgets (reduced daytime photosynthesis and greater nighttime respiration) and/or favor infection by foliar pathogens, such as Dothistroma needle blight, which has recently caused widespread tree mortality on lodgepole pine plantations in British Columbia. Further field study that includes experimental manipulation (e.g., fungicide application) will be necessary to identify the proximal cause(s) of the growth decline. In the meantime, we anticipate continuation of the shore pine growth decline in Southeast Alaska.

Introduction

The temperate rainforest of Southeast Alaska exhibits moderate temperatures for its latitude and abundant precipitation, allowing for potentially complex relationships among temperature, moisture and tree growth. Like other high latitude regions, the climate of Southeast Alaska is changing (Serreze and Barry 2011). Perhaps the best-known consequence of climate change in terrestrial ecosystems of Southeast Alaska is the yellow-cedar (*Callitropis nootkatensis* or *Cupressus nootkatensis*) forest decline. Several lines of evidence support the hypothesis that yellow-cedar decline is caused by increasingly shallow winter snowpacks and associated freezing injury to cold-intolerant fine roots, particularly in wet areas where fine roots are concentrated near the soil surface (Schaberg *et al* 2008, 2011, Hennon *et al* 2012).

Shore pine (*Pinus contorta* ssp. *contorta*) is a subspecies of lodgepole pine that occurs in peatland bogs and fens throughout Southeast Alaska. While the habitats and species distributions of shore pine and yellow-cedar overlap somewhat in Alaska, shore pine is better able to tolerate the high water tables of bogs and fens

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(Hennon *et al* 1990, Bisbing *et al* 2015). Macrofossil records indicate that shore pine was a dominant tree species throughout Southeast Alaska during the early Holocene (Heusser 1960, Peteet 1991). However, its current range is thought to have been reduced to the poorest sites through competition following colonization by Sitka spruce and Western hemlock (Carrara *et al* 2007, Bisbing *et al* 2015). Permanent plots established between 1995 and 2003 and revisited between 2004 and 2008 as part of the United States Forest Service Forest Inventory and Analysis (FIA) program revealed a statistically significant 4.6% decline in live aboveground biomass of shore pine in coastal Alaska (Barrett and Christensen 2011). The coastal bogs and fens in which shore pine grows are the richest terrestrial plant communities of the coastal rainforest (Neiland 1971, Martin *et al* 1995). The apparent loss of shore pine biomass is concerning because its presence provides a vertical dimension to these ecosystems, thereby promoting diversity.

To identify potential causes of biomass change in the Alaskan shore pine population, a permanent 46-plot network (separate from FIA) was established at five locations throughout the range of shore pine in Southeast Alaska to gather detailed information about damage agents and to track tree survival over time (Mulvey and Bisbing 2015). Increment cores were collected from dominant or co-dominant trees from plots at each of the five locations to obtain long-term shore pine growth data. We then asked if there are discernable trends in shore pine growth over time and if variability and trends in the shore pine chronology can be explained by climate variables available in the Juneau instrumental climate record (1942-present) and/or those in the Climatic Research Unit (CRU) 3.22 gridded climate dataset.

Methods

Updating trends in live aboveground tree biomass

The FIA plot network in the temperate rainforest region of coastal Alaska extends from Kodiak Island to Ketchikan. As a systematic sample from all land except National Forest wilderness and Glacier Bay National Park, the FIA plots can be used to infer whether the population of a tree species is increasing or decreasing. We updated and improved the estimates from Barrett and Christensen (2011) using additional plots from unmanaged forests, for a total of 912 permanent plots that were installed from 1995 to 2003 and re-measured from 2004 to 2010. Live tree aboveground biomass was estimated by species at both time periods using individual tree height and diameter measurements and allometric biomass equations (Barrett 2014). Statistical estimates used standard national estimation procedures (Bechtold and Patterson 2005).

Increment core sampling locations

Increment cores (1 core/tree) were collected from shore pine growing near Juneau (95 trees across 8 plots), Hoonah (23 trees across 10 plots) and on Wrangell (17 trees across 10 plots), Mitkof (15 trees across 10 plots) and Prince of Wales Islands (15 trees across 8 plots), with the goal of extending our inferences to a large portion of Southeast Alaska (figure 1). Permanent plots from which cores were collected were randomly selected from palustrine emergent and palustrine shrub–scrub wetland polygons (National Wetland Inventory classifications, Cowardin *et al* 1979), which generally contain shore pine and were at least 1.6 ha in size and within 0.8 km of a road or trail. A larger number of cores were collected from plots near Juneau, because of the high quality long-term climate record available for this location. We also collected increment cores from a wider range of tree sizes (ages) near Juneau to improve estimates of the age-related decline in growth (see below). Codominant trees cored in 2012 and 2013 throughout our plot network ranged from 7.1 to 59.7 cm dbh with estimated cambial ages from 80 to 472 years. Coring of additional smaller trees near Juneau in 2014 decreased the minimum cambial age to 45 years.

Increment core collection and processing

Increment cores (5 mm dia) were collected from the main stem of large trees at breast height during the growing seasons of 2012, 2013 and 2014. The cores were air dried, mounted and sanded to 600 grit. After visual cross-dating, ring widths were measured to the nearest 0.001 mm using a sliding bench micrometer and digital encoder (Velmex Inc., Bloomfield, NY). The resulting ring width chronologies were analyzed by location (e.g., Hoonah) and as an aggregate dataset in COFECHA (Holmes 1983) to identify and correct dating errors. A final analysis in COFECHA, after correcting dating errors, yielded a mean inter-series correlation of 0.264 and mean sensitivity of 0.198. Thus, while this dataset is useful for examining low frequency growth trends and low frequency growth-climate relationships over a large geographic area, the diffuse sampling strategy makes it less suitable for paleoclimate reconstruction.

Ring width series from each of the five locations were aligned by cambial age to examine age-related growth trends. There was clear evidence of a negative exponential decline in ring width as a function of cambial age (supplemental figure 1). Therefore, we used the regional curve standardization (RCS) method (Esper *et al* 2003) to detrend the ring width measurements as an aggregate dataset in version 45_v2b of the RCSigFree program (Cook *et al* 2014). Ring width indices were calculated as ratios, the spline stiffness was set at 10 years, no additional spline stabilization was utilized and the chronology was calculated using

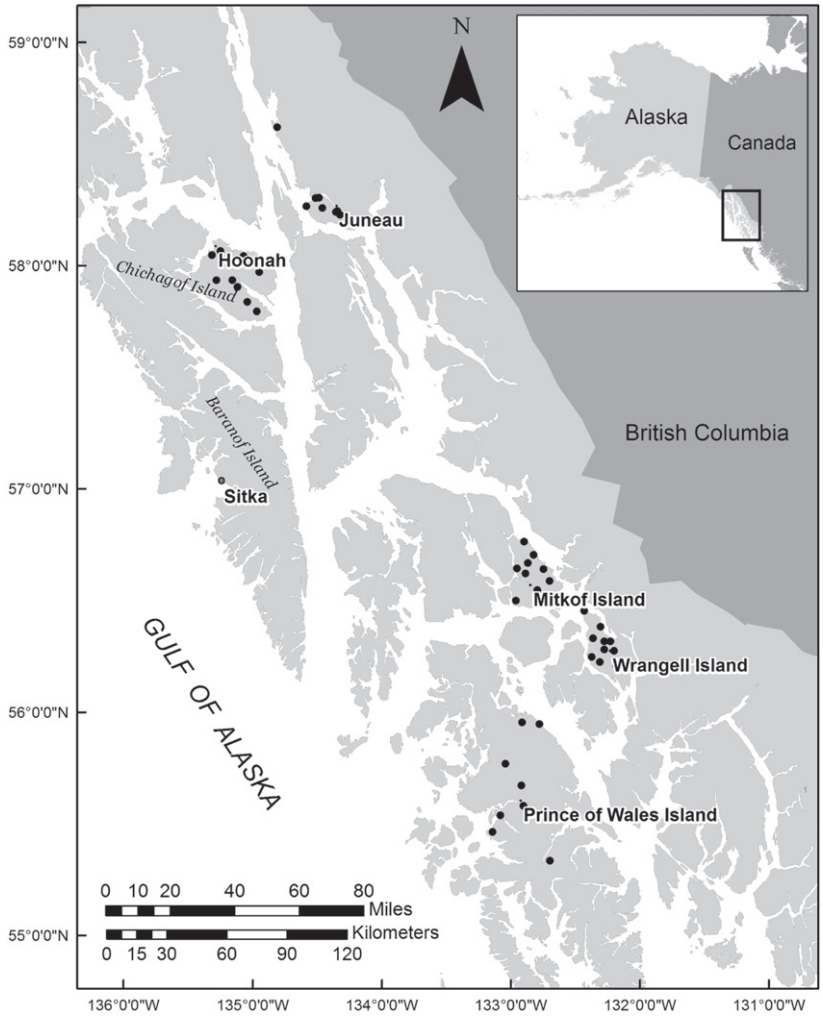

Figure 1. Map of Southeast Alaska showing the sites of shore pine increment core sampling near Juneau, Hoonah, Wrangell and on Mitkof and Prince of Wales Islands, Alaska.

Tukey's biweight robust mean. We did not attempt to adjust for increment cores that missed the pith. The expressed population signal (EPS), which is a measure of how well our overall detrended chronology represents the population mean, was calculated using a 51 year moving window to ensure that the portion of the chronology used in climate-growth analyses had EPS values above the established threshold of 0.85 (Wigley *et al* 1984). Our sample size from each of the four locations outside of Juneau was too small to produce well-constrained tree-ring chronologies. Therefore, we elected to aggregate all of our data in one high-quality chronology.

Relating the tree-ring chronology to climate

Two sources of climate data were utilized to examine growth-climate relationships. The instrumental record from Juneau (1942–2013) was acquired from the Alaska Climate Research Center at the University of Alaska Fairbanks. This dataset includes daily mean, maximum and minimum air temperature, daily precipitation, daily snowfall and daily snow depth. Gridded climate data (1901–2013, CRU TS v. 3.22, Harris *et al* 2014) were also acquired for the grid cell nearest Juneau. This dataset includes monthly mean, maximum and minimum air temperature, monthly precipitation, monthly mean atmospheric vapor pressure deficit, monthly mean potential evapotranspiration, monthly mean cloud cover and monthly ground frost days. Comparison of monthly mean air temperature between the two datasets for the common period revealed very strong agreement ($r^2 = 0.99$, instrumental $= 1.59 + 0.93^{*}$gridded). The utility of the gridded climate data was thus to extend the period of the analysis from 71 to 112 years and include some climate variables that are unavailable in the instrumental record. We used climate data for Juneau, because over half of our increment cores were collected from the Juneau area and because it is one of only two first-order climate stations in Southeast Alaska. The other (Yakutat) is >300 km North of our Northernmost site.

Potential relationships between shore pine growth and climate were investigated through Random Forest

Table 1. Estimated net change in aboveground live tree biomass in the temperate rainforest region of Alaska, using FIA plots established from 1995 to 2003 and re-measured from 2004 to 2010. The estimates exclude National Forest Wilderness, Glacier Bay National Park and areas with recorded silvicultural and/or harvest activity.

Species	# plots containing species	Initial biomass (Gg)	Decadal net change (Gg)		Decadal net change (%)
			Total	SE	
Western hemlock	663	317 300	2084	3060	0.7
Sitka spruce	676	187 455	7075	3708	3.8
Mountain hemlock	549	95 156	1901	1229	2.0
Yellow-cedar	366	74 867	1180	722	1.6
Western redcedar	182	37 774	2114	510	5.6
Shore pine	165	9634	−299	183	−3.1
All conifers	912	722 185	14 055	5137	1.9

regression, which is an ensemble regression tree approach, using the randomForest package (Liaw and Wiener 2002) in R 3.1.2 (R Core Team 2014). While Random Forest is thought to be relatively insensitive to collinearity, including predictors that contain redundant information can reduce ecological interpretability and predictive power (Murphy *et al* 2010). Therefore, we first conducted an analysis that included all of the potential predictors (supplemental table 1) to obtain initial variable importance rankings. Second, we constructed a correlation matrix that included all of the potential predictors. For each pair of predictors with a correlation coefficient greater than 0.5 or less than −0.5, only the variable with greater importance was retained in subsequent analyses. Third, we used the model selection function (rf.modelSel) in the rfUtilities package (Evans and Murphy 2014) to identify the smallest suite of predictors that minimized the mean squared error and maximized the pseudo-r^2 (Murphy *et al* 2010). Finally, we conducted a Random Forest regression comprised of 1000 trees. Three randomly selected predictor variables were tested at each node when relating the ring width indices to the gridded climate data, while two variables were tested at each node when relating the ring width indices to the instrumental record. The final models were tested for significance using the rf.significance function (Murphy *et al* 2010) in the rfUtilities package. We also produced partial dependence plots, which depict the modeled relationship between growth and a given climate variable, while holding all other predictors at their mean values. We made one exception to our collinearity rule: we retained high-ranking predictors of the same variable averaged over different time periods, even if they were correlated. For instance, in the CRU 3.22 dataset, mean diurnal minimum air temperature was correlated across consecutive growing seasons ($r = 0.65$), because there is a strong upward trend in this variable over time. Tree growth responds to climate conditions during the current and previous growing seasons because of resource storage (e.g., Richardson *et al* 2013). Thus, it makes biological sense that the same variable averaged over different time periods could be important to growth. The drawback to this approach is that the relative importance of conditions during the growth year and the previous growing season should be interpreted with caution.

The finding of nonstationary climate-tree growth relationships has becoming increasingly common in recent years (e.g., Briffa *et al* 1998, D'Arrigo *et al* 2008). To test for temporal variation in the strength (and sign) of the correlation between climate and tree growth, we conducted a moving window correlation analysis using the climate variable identified as the most important predictor of shore pine growth in the Random Forest analyses. The window was set at 31 years and the analysis was repeated with the Juneau instrumental climate record and the CRU 3.22 time series using the cor.test and running functions in R 3.1.2.

Results

Our updated estimates of trends in live aboveground tree biomass on FIA plots in the temperate rainforest region of Alaska revealed an overall increase in conifer biomass ($\alpha = 0.10$, $T = 2.7$, $P = 0.05$) that was driven in large part by increases in Western redcedar and Sitka spruce (table 1). Shore pine was the only species that showed a net loss of biomass. However, many of the plots re-measured between 2008 and 2010 showed smaller decreases in shore pine biomass than plots re-measured before 2008, diminishing the trend from a statistically significant 4.6% loss of biomass to a statistically non-significant 3.1% decline ($T = 1.6; P = 0.12$).

The Juneau instrumental and CRU 3.22 climate datasets agree well with one another and point to substantial changes in the climate of Southeast Alaska, particularly during the latter half of the 20th century (figure 2). Between 1960 and 2013, the Juneau instrumental record shows that June–August mean diurnal minimum air temperature increased ($r = 0.69$, $P < 0.01$), mean diurnal maximum air temperature was relatively stable ($r = 0.16$, $P = 0.25$) and mean winter snow depth may be declining ($r = -0.19$, $P = 0.18$). Meanwhile, the CRU 3.22 time series

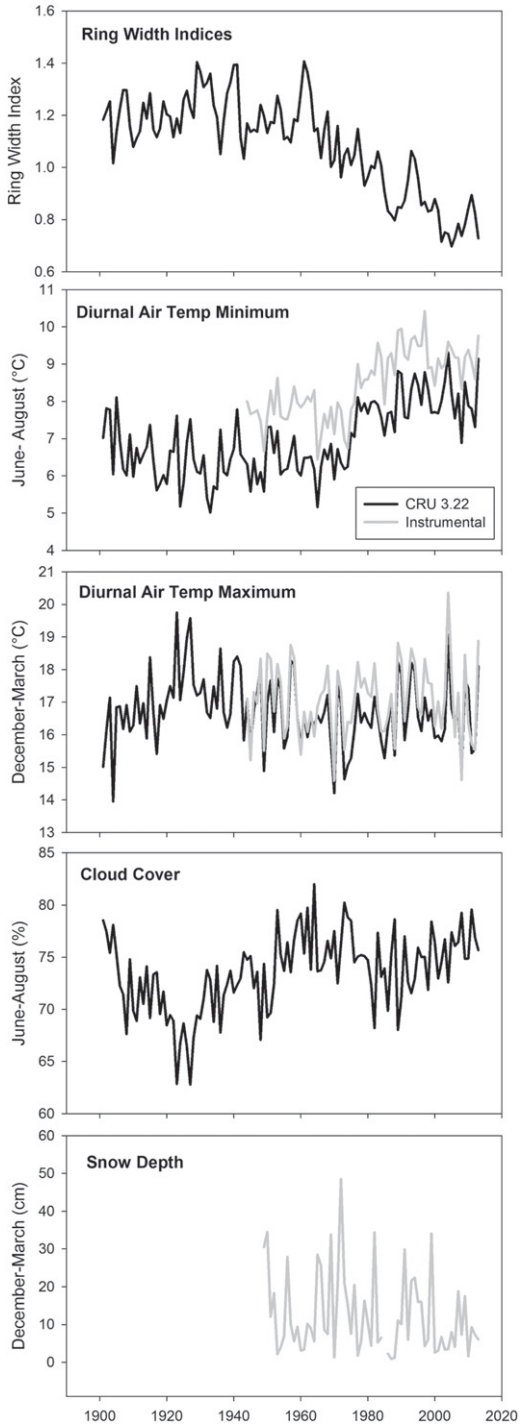

Figure 2. Temporal trends in the climate variables identified as important predictors of shore pine growth in the Random Forest analyses. Instrumental data from Juneau, AK are shown in gray, while the CRU 3.22 gridded climate data for Juneau, AK are shown in black.

suggests that, following a decline from ∼1960–1980, cloud cover may be increasing ($r = 0.47$, $P < 0.01$, 1980–2013).

Radial growth in the main stem of mature shore pine trees was very limited. For a cambial age of 100 years, the average ring width was ∼0.5 mm (supplemental figure 1). Our shore pine chronology shows a prolonged period of slowly increasing annual growth from 1700 through the middle of the 20th century (figure 3). Growth decreased briefly between 1875 and 1890, after which the increasing growth trend resumed, reaching distinct peaks in 1929, 1941 and 1961. After 1961, shore pine growth began a steep and declining trend that has continued through the present.

Random Forest analysis, using the Juneau instrumental climate record, explained 53% of the variation in the shore pine ring width indices (MSE = 0.014, $P < 0.01$) using only three predictor variables: mean diurnal minimum air temperature during the previous growing season (June–August), mean diurnal minimum air temperature during the growth year (June–August) and mean snow depth during the previous winter (December–March). Mean diurnal minimum temperature during the previous growing season was the most important predictor of shore pine growth (table 2). Examination of the partial dependence plot revealed a negative relationship between shore pine growth and the mean diurnal minimum temperature (figure 4(a)). The same relationship was observed regardless of whether the ring width indices were related to mean diurnal minimum temperature during the growth year or during the previous growing season (figure 4(b)). There was weak evidence that a shallow winter snowpack may be unfavorable for shore pine growth, but snow depth ranked much lower in importance and there were numerous years in which shallow snow coincided with above average shore pine growth (e.g., the 1961 growth peak).

Random Forest analysis, using the CRU 3.22 gridded climate data, explained 51% of the variation in the shore pine ring width indices (MSE = 0.016, $P < 0.01$) using five predictor variables: mean diurnal minimum air temperature during the previous growing season (June–August), mean diurnal minimum air temperature during the growth year (June–August), mean diurnal maximum air temperature during the growth year (June–August), mean cloud cover during the growth year (June–August) and the number of ground frost days during the previous winter (December–March). Again, mean diurnal minimum temperature was the most important predictor of shore pine growth. The analysis using CRU data revealed several other climate variables that contributed modestly to the model's overall explanatory power. There was evidence that a greater number of winter ground frost days was associated with greater shore pine growth, up to a point that was just short of continuous ground frost from December through March (∼121 days, figure 4(f)). The CRU analysis also revealed a positive relationship between shore pine growth and growing season diurnal temperature maxima (figure 4(g)). This contrasts with the (more important) relationship between growth and diurnal temperature minima. Finally, the CRU analysis also revealed a negative relationship between shore pine growth and growing season mean cloud cover (figure 4(h)).

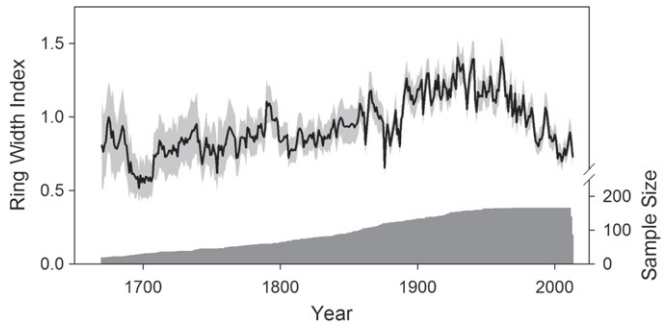

Figure 3. Shore pine chronology for the period with an EPS > 0.85. The gray shading indicates the 95% confidence limits, while the number of trees contributing data is indicated at the bottom of the panel.

Table 2. Variable importance rankings from Random Forest analyses relating the Juneau instrumental climate record (1942–2013) and the CRU 3.22 gridded climate data for Juneau (1902–2013) to our overall shore pine chronology (5 locations, 165 trees). A greater increase in node purity indicates a more important predictor of shore pine growth.

	Juneau instrumental	CRU 3.22
Variable	Increase in node purity	
Previous June–August mean diurnal minimum air temperature	0.879	1.476
June–August mean diurnal minimum air temperature	0.793	1.031
Previous December–March snow depth	0.316	NA
June–August mean diurnal maximum air temperature	NA	0.351
Previous December–March ground frost days	NA	0.344
June–August cloud cover	NA	0.342

Growing season mean diurnal minimum temperature was identified by both analyses as the most important predictor of shore pine growth. Examination of strength and sign of the correlation between this variable and the shore pine ring width indices over time revealed a case of nonstationarity (figure 5). Prior to ∼1960, there was no evidence of a significant correlation between growth and growing season mean diurnal minimum temperature. However, during the latter half of the 20th century, a strong and statistically significant negative correlation emerged, regardless of the climate dataset utilized. Interestingly, in recent years, the lack of a correlation between growth and growing season mean diurnal minimum temperature appears to have reemerged.

Discussion

The climate of Juneau has changed over the past 50 years. Growing season mean diurnal minimum air temperature has increased, while mean diurnal maximum air temperature shows no evidence of a trend, leading to a reduced diurnal temperature range (DTR). Meanwhile, shore pine growth, which is inherently limited by wetland site conditions, has declined steeply since the early 1960s throughout much of Southeast Alaska. This trend is mirrored by the recent decrease in shore pine biomass on FIA plots, suggesting that changes in climate and/or site factors may be stressing shore pine, constraining growth and causing mortality.

Tree-ring studies are limited in their ability to identify mechanisms responsible for observed growth trends. They are, however, excellent tools to develop informed hypotheses. Mean diurnal minimum air temperature during the growing season was identified as the most important variable in explaining shore pine growth in all of our analyses. Warm nighttime temperatures were associated with much lower growth. Meanwhile, mean diurnal maximum air temperature was either unimportant in explaining shore pine growth (instrumental record) or had a positive effect on growth (gridded climate data). Declining growth of shore pine has been coincident with a declining trend in the growing season DTR. This observation agrees well with our finding that greater growing season cloud cover may be associated with limited shore pine growth, as greater cloud cover is commonly associated with a reduced DTR. Cloud cover is, however, a highly synthetic variable in the CRU 3.22 dataset. Therefore, this result should be viewed with caution. Together, this suite of climate-growth relationships suggests that relatively clear skies, warm days and cold nights are favorable for shore pine growth, while cloudy conditions with warm nights are associated with declining growth.

There are two potential mechanisms by which cool, cloudy days and warm nights could adversely affect shore pine growth: one that involves tree carbon budgets and another that relates to pathogens. While

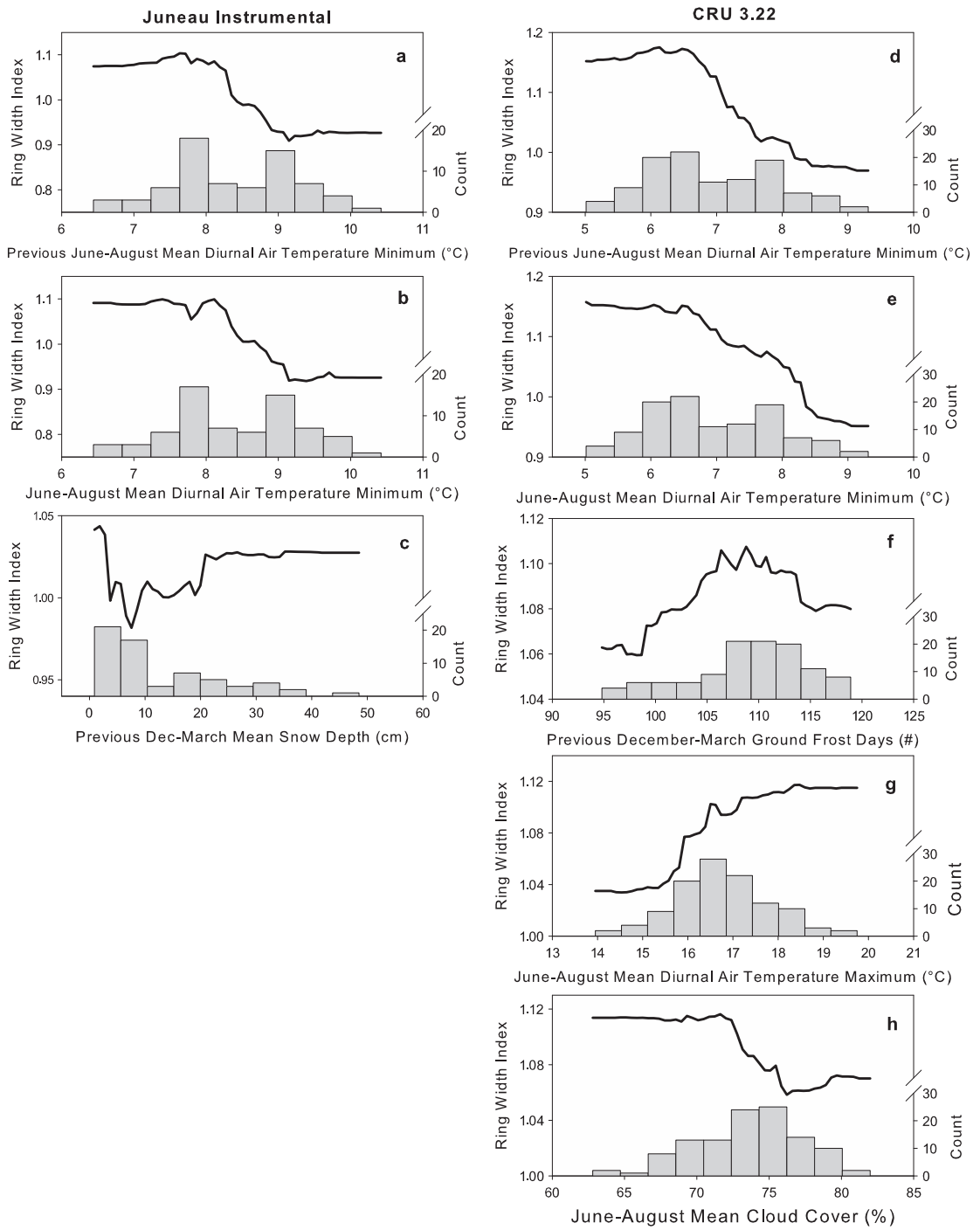

Figure 4. Partial dependence plots, which show the modeled effect of a given climate variable on the shore pine ring width indices, while holding all other climate variables at their mean values. Histograms at the bottom of the panels depict the distributions of the climate data.

physiological data for shore pine are rare, its conspecific lodgepole pine (*Pinus contorta* ssp. *latifolia*) has been heavily studied. Lodgepole pine typically grows in dry montane forests of Western North America that exhibit high irradiance and large DTRs. In a study of growth responses to contrasting light environments for eleven boreal tree species in British Columbia, Wright *et al* (1998) showed that lodgepole pine was the least shade tolerant of all the species examined, exhibiting the greatest growth reduction under low light. It is well known that diffuse light under cloudy conditions can enhance canopy-scale photosynthesis in tree species or forests with dense foliage, where self-shading can limit light penetration (e.g., Hollinger *et al* 1994). However, shore pine canopies are sparse and self-shading probably does not limit light availability at the level of individual needles. It is possible that increasing cloud cover and declining light availability may be limiting photosynthesis in shore pine. Reduced daytime carbon uptake could

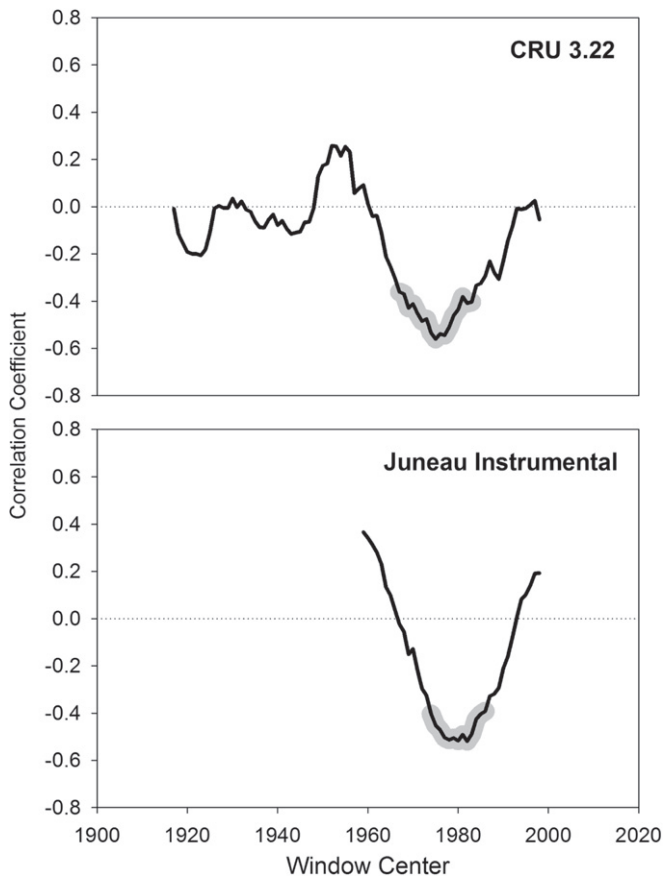

Figure 5. Moving window correlation of June–August mean diurnal minimum air temperature with the shore pine ring width indices, using both the CRU 3.22 and Juneau instrumental climate data. Width of the window was 31 years. Gray shading indicates correlations that were statistically significant ($P < 0.05$).

potentially be exacerbated by greater nighttime respiration under warmer diurnal minimum temperatures. Trees are well known to show respiratory acclimation to changing temperature regimes and it is generally expected that climate warming will lead to an increase in respiration that is less than predicted by a typical Q_{10} response (e.g., Atkin *et al* 2008). However, a case where diurnal minimum temperature is increasing at a greater rate than diurnal mean and maximum temperature, as observed in Juneau, may inhibit acclimation. Thus, the combination of reduced daytime carbon uptake and greater nighttime carbon loss may be leading to unfavorable tree carbon budgets and reduced growth. Given the paucity of physiological data available for shore pine and the possibility that unfavorable tree carbon budgets may be contributing to the growth decline, we argue that a comparative study of the carbon and water relations of lodgepole and shore pine would be a useful contribution.

Another possibility is that changes in climate have improved conditions for foliar pathogens of shore pine. A strong candidate is the native foliage disease, Dothistroma needle blight (Woods *et al* 2015). The presence of this disease has been documented throughout our plot network but, at the time of survey, it was not severe enough to cause tree mortality. Assessing severity has been challenging, because fruiting bodies are not always present and the other symptoms (needle discoloration and premature loss) could be caused by weak pathogens, saprophytes, insects or nutrient deficiency. There is a documented severe *Dothistroma* epidemic that has been ongoing since at least 2010 on 1800 ha near Gustavus, AK and adjacent Glacier Bay National Park (FS-R10-FHP 2015). Ground-based plots established in 2013 to assess shore pine survival in severely-impacted areas revealed that, one year later, 46% of severely-diseased pines tagged for monitoring (25% of all shore pine in the plots) had died and 56% of all shore pine in the plots were dead. *Dothistroma* outbreaks have also caused extensive lodgepole pine mortality on plantations in Northwestern British Columbia (Woods *et al* 2005). A tree-ring study conducted on the plantations identified August minimum air temperature as the variable most closely correlated with the occurrence of historical outbreaks (Welsh *et al* 2014). Our results agree with this finding. Welsh *et al* (2014) also argued that periods of above normal precipitation are coincident with historical outbreaks. Precipitation was not identified among the most important predictors of shore pine growth in our study, but precipitation in

Southeast Alaska may already be sufficient for *Dothistroma*, leaving temperature as the primary limiting factor (Karadzić 1989). Our finding that precipitation was not closely correlated with shore pine growth also suggests that drought-stress and climate-induced soil waterlogging are not important growth constraints. However, shore pine growth is undoubtedly influenced by soil hydrology, as it occupies sites with high water tables through a strategy of tolerance and avoidance of competition (Bisbing *et al* 2015).

Our partial dependence plots and moving window correlation analyses point to a complex relationship between shore pine growth and mean growing season diurnal temperature minima. Both results suggest there is a specific range of growing season diurnal temperature minima (~8–9 °C in the Juneau record) that is associated with the shore pine growth decline. When diurnal temperature minima were consistently below that range, there was no evidence of a correlation between growth and diurnal temperature minima. Now that diurnal temperature minima are consistently above that range, the strong negative correlation that was apparent when temperature minima were between 8 and 9 °C has apparently diminished. Thus, it appears that, while rising growing season diurnal temperature minima were associated with the initiation of the shore pine growth decline, other variables are likely sustaining the decline. Increasing cloud cover and declining winter snowpack are possibilities in this regard. It is also possible that, as growing season diurnal temperature minima have continued to rise, the severity of the *Dothistroma* disease has reached a point where it has begun to decouple shore pine growth from climate variability. Gadgil (1974) showed that a daytime temperature of 20 °C, combined with a nighttime temperature of 12 °C, led to significantly greater *Dothistroma* infection than other temperature regimes. Thus, the climate of Southeast Alaska is almost certainly still well within, if not slightly below, the optimum temperature range for *Dothistroma*.

The well-publicized yellow-cedar forest decline in Southeast Alaska has largely been attributed to freezing injury to shallow fine roots, as a result of a diminished winter snowpack. Shore pine occupies even wetter habitats than yellow-cedar and likely maintains a shallow fine root network, but the sensitivity of shore pine roots to freezing injury is unknown. We found some evidence that warm winters with a shallow and/or ephemeral snowpack were associated with reduced shore pine growth, but these variables ranked much lower in importance than mean growing season diurnal minimum air temperature. Further, there is no evidence from our plot network nor the FIA plot network that shore pine dieback or mortality are concentrated at lower elevations or farther South, where the winter snowpack is more ephemeral (Mulvey and Bisbing 2015). While we cannot exclude the possibility that freezing injury to fine roots may be contributing to mortality and declining growth of shore pine, our results suggest the shore pine growth decline may be driven by a different suite of mechanisms than yellow-cedar decline. Further field study will be necessary to identify the proximal cause(s) of the shore pine growth decline. In the meantime, we anticipate continuation of this concerning trend.

Acknowledgments

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