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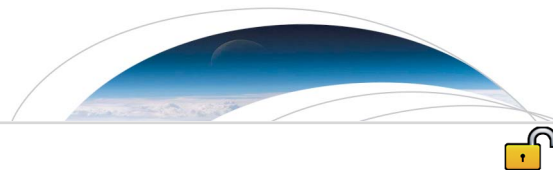*Western Washington University*

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Key Points:
- High elevation bristlecone pine growth patterns vary with small changes in topoclimate
- Growth of high elevation trees in warmer exposures is limited by moisture, rather than temperature
- The highest, coldest trees show weakened sensitivity to temperature in recent years

Spatiotemporal Variability in the Climate Growth Response of High Elevation Bristlecone Pine in the White Mountains of California

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Abstract Tree-ring chronologies from bristlecone pine (*Pinus longaeva*) are a unique proxy used to understand climate variability over the middle to late Holocene. The annual rings from trees growing toward the species' lower elevational range are sensitive to precipitation variability. Interpretation of the ring-width signal at the upper forest border has been more difficult. We evaluate differences in climate induced by topography (topoclimate) to better understand the dual signals of temperature and moisture. We unmix signals from trees growing at and near the upper forest border based on the seasonal mean temperature (SMT) experienced by each tree. We find that trees growing in exposures with SMT <7.5 °C are limited by temperature, while trees with SMT > 7.5 °C are limited by moisture. We demonstrate this independently through analysis of growth in the frequency and time domains and using a process model of xylogenesis. Furthermore, we identify increasing moisture sensitivity in trees formerly limited by temperature.

Plain Language Summary Tree rings from ancient bristlecone pines are a remarkable proxy for climate, extending back thousands of years. However, interpreting this record has been difficult because some trees record information on both past temperature and past soil moisture variability. These dual growth responses can be hard to separate. We show that differentiating trees based on relatively small differences in location, determined by their topographical setting and therefore the "local climate" individual trees have experienced, can help unravel these mixed signals and provide a better basis for understanding growth and past climate. We find that even near the alpine treeline, only trees in the coldest settings show ring-width growth that is sensitive to temperature. However, we also show that recent warming might have weakened this temperature response by causing bristlecone pine to switch to a moisture-sensitive growth response.

1. Introduction

The annual rings of climate-sensitive trees are important archives in reconstructing climate from periods before reliable instrumental records exist. Indeed, the insights gained from dendroclimatology have greatly improved our understanding of Holocene climate dynamics and the role of internal and natural variability (see recent reviews by Scott, 2014, and Anchukaitis, 2017). Dendroclimatology takes advantage of trees growing near the limits of their climate tolerance to reconstruct past temperature or moisture variability (Fritts, 1966, 1976). However, in the presence of forced trends in temperature from greenhouse gasses, many of the assumptions that tacitly underlie climate reconstructions and inferences made from paleoclimate data have to be assessed carefully (Milly et al., 2008). Even in treeline environments where temperature should be a strong control on growth variability (Körner & Paulsen, 2004; Stevens & Fox, 1991), the climate response of these trees to progressively increasing temperatures can be complex (Álvarez et al., 2015; Daniels & Veblen, 2004; Lavergne et al., 2015; Lloyd & Fastie, 2002; Wang et al., 2017). In this paper we analyze spatial patterns and temporal variability in the climate sensitivities of Great Basin bristlecone pine (*Pinus longaeva* D. K. Bailey) ring widths depending on relatively subtle differences in biophysical setting. We show that our understanding of this proxy changes in important ways due to the interaction of topoclimate and climate change.

Great Basin bristlecone pine is a valuable species for dendrochronology due to the great age the trees can reach (Ferguson, 1968), the sensitivity of their rings to variations in climate (Salzer et al., 2009), and its use in calibration of the radiocarbon scale (Pearson et al., 2018; Stuiver et al., 1986). In the White Mountains of California, bristlecone pine grows at the upper forest border at the alpine treeline ecotone, above which it is too cold for trees to establish. It also grows down to the lower forest border below which it is too dry for full grown trees. At the upper forest border, the upright trees give way to alpine plants. At the lower forest border, bristlecone pine mixes with piñon juniper shrub and woodland. The juxtaposition of these two tree-lines has been used to make inference about temperature variability at the upper forest border and moisture variability at the lower forest border. This ecological gradient was first used as leverage to better understand temperature and moisture limitations on growth by LaMarche, (1974a, 1974b) and LaMarche and Stockton (1974) who concluded that growth at the upper forest border generally increased with warmer temperatures but that soil moisture deficits could modify that response. These studies also noted that trees at the lower forest border were more strongly limited by moisture availability. Subsequent work used tree-ring chronologies from lower forest border as a proxy for moisture (Hughes & Funkhouser, 1998, 2003; Hughes & Graumlich). Indeed, Hughes and Funkhouser (2003, 2003) extended the findings of LaMarche (1974b) to four mountain ranges in the Great Basin. They showed strong common high-frequency variability between upper and lower forest border chronologies within each mountain range that they related to moisture variability. They also showed low-frequency correlation in growth between the four mountain ranges over the past millennium, consistent with a temperature signal on those time scales. Salzer et al. (2009) found that growth patterns at even the highest elevation bristlecone pine in the White Mountains correlate with both temperature and moisture at interannual scales. This mixture of temperature and precipitation signals in the bristlecone pine tree rings at the upper treeline has hindered clear reconstructions of temperature from using this species at these locations.

In prior work, we extracted low-frequency temperature signals from high elevation bristlecone pine over the last five millennia (Salzer et al., 2013) and noted a sharp elevational threshold where the positive correlations between temperature and growth invert and become negative at short distances below the upper treeline (Salzer et al., 2009). In order to further understand this phenomenon, we evaluated temperature sensitivity using topographic indices (Bunn et al., 2011; Salzer et al., 2014; Tran et al., 2017), which suggested the interaction of topography and climate as an explanation for the threshold response between growth and temperature near treeline. We hypothesized that complex topography could affect localized maximum and minimum temperatures beyond what one would expect from an elevational lapse rate and synoptic-scale anomalies. We used an array of temperature sensors to model variations of temperature with topography ("topoclimate") and found that temperatures during the warm season vary several times more than predicted by the dry adiabatic lapse rate alone. These observations help explain variations in the position of the alpine treeline on the landscape (Bruening et al., 2017, 2018). The fundamental finding from these papers was that seasonal mean temperature (SMT) and the length of the growing season were critical in determining the location of the treeline and that very small differences in climate at the scale of individual trees might allow us to select trees that were sensitive to temperature versus those trees limited by moisture.

Our previous work used unsupervised classification (cluster analysis) to find natural groupings of growth patterns that we later linked to topoclimate. This work did not, however, explore dynamic changes in the climate response nor demonstrate changes in the limiting factors of growth. Here we show that high elevation bristlecone pine show different limitations on growth based on topoclimate. We quantify growth patterns in the time and frequency domains based on spatial variations in topoclimate. We validate this empirical, statistical finding using a process model to better understand physiological limits on ring formation. Finally, we provide the first evidence that even the highest elevation bristlecone may not remain recorders of temperature variability in a warming climate.

2. Methods

2.1. Study Site and Topoclimate Data

The study site is located in the Ancient Bristlecone Pine Forest which is part of the Inyo National Forest in Inyo County California, United States (Figure 1). This area has seen sharp increases in both annual and warm-season temperature over the past two decades without a corresponding change in precipitation (PRISM, 2017; Salzer et al., 2009).
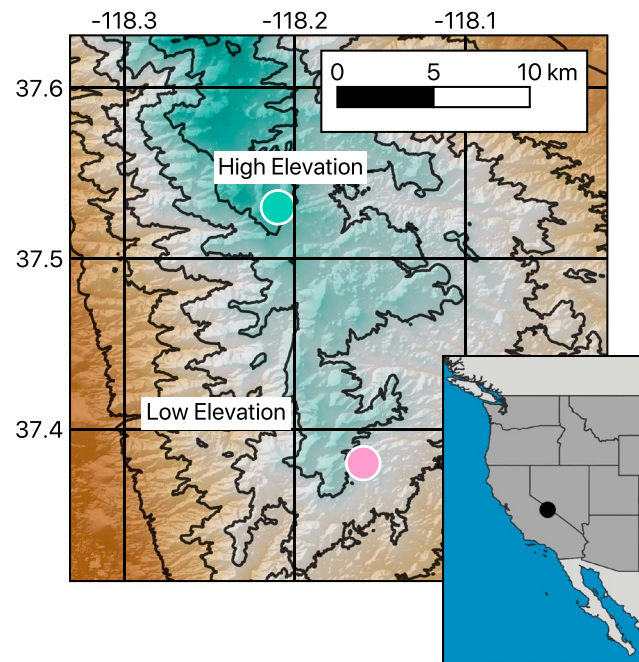
Figure 1. Location of bristlecone pine sites in the Inyo National Forest, California, United States. The high elevation bristlecone pine sites at Sheep Mountain (Figures 2a–2c) are shown along with the low elevation site at Methuselah Walk (Figure 2d). The contour lines show 500-m intervals.

The area is an open-canopy forest of bristlecone pine growing on rocky and sandy permeable dolomite substrate. We use interpolated surfaces of topoclimate developed at this location by Bruening et al. (2017). The surfaces were created as a way of exploring the effects of topography on temperature variability at the scale of tens of meters. They were built using 50 thermochron loggers (Maxim Integrated, San Jose CA model DS1922L-F5) arrayed across the approximately 1-km^2 landscape. Seasonal and monthly temperatures were then modeled using topographic indices including seasonal radiation, aspect derivatives, topographic position, and topographic convergence. The topoclimate surfaces show spatiotemporal temperature variability over this landscape is several times larger than what the lapse rate alone would suggest. Further details on topoclimate modeling are described by Bruening et al. (2017).

An important variable we extract from these surfaces is SMT, which is the average daily temperature on days where the minimum daily temperature is above 0.9 °C (Paulsen & Körner, 2014). The mean SMT is 7.3 °C for the trees we used in this study, and the average annual temperature (calculated using monthly average temperatures over the 1981–2010 climate normal) is approximately 1.6 °C . Our topoclimate analysis does not include measures of precipitation, but data from the PRISM (2017) model informed by long-standing weather stations near the site and maintained by the White Mountain Research Station indicate total average annual precipitation of 494 mm, with most of that (74%) falling outside of the growing season.

2.2. Tree-Ring Data

We use 176 previously collected tree-ring samples from 96 adult bristlecone pine trees growing in the Sheep Mountain/Patriarch Grove area at and near the upper forest border (mean elevation 3407 m above sea level). We prepared these increment cores according to standard methods (Stokes & Smiley, 1968), the samples were crossdated (Bunn, 2010; Holmes, 1999), and the rings measured to the nearest 0.001 mm. We treated the tree-ring data in the most conservative way possible, using raw ring widths in order to avoid any effects from standardization. We truncated the series to start at the year 1500 CE to ensure robust sample depth. All of the trees in this study are from mature trees which do not show any age-related growth that might bias the early part of the record. The location of each tree was measured with differential GPS to within 2-m horizontal accuracy. Analysis was done in the version 3.5 of R programming environment (Core Team, 2018) relying on the dplR package (Bunn, 2008).
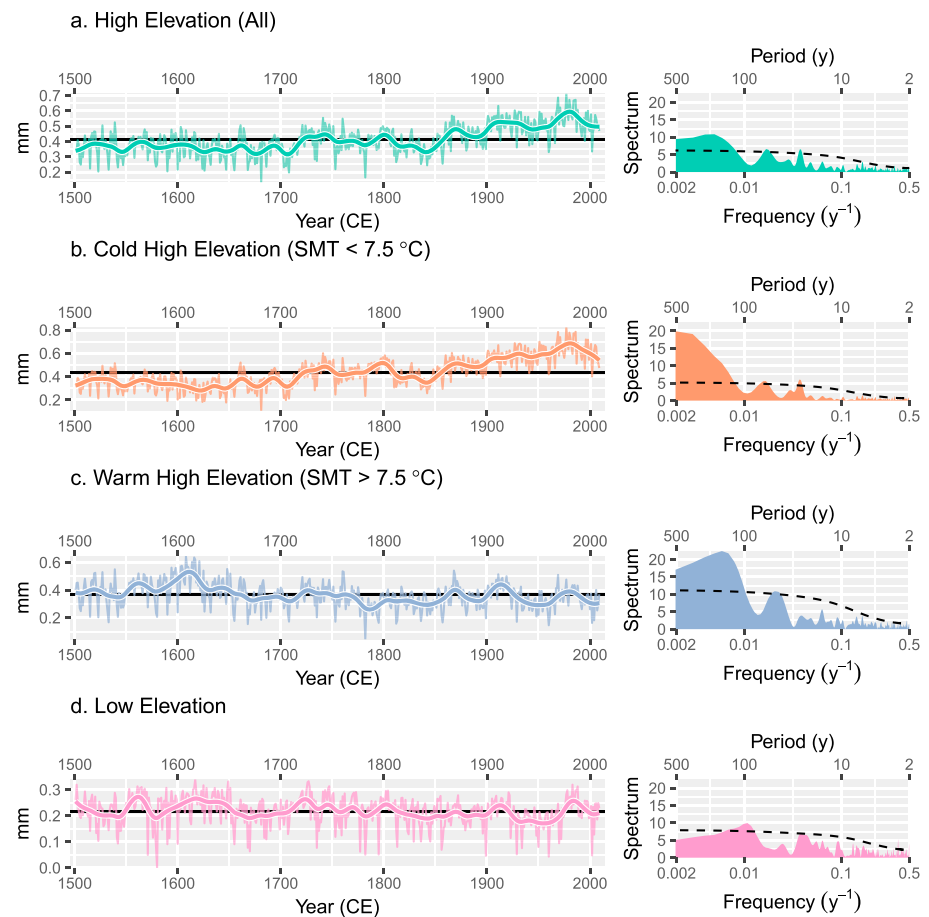
Figure 2. Raw ring-width chronologies (left) and their power spectra (right) are shown for four chronologies of bristlecone pine. Each chronology is smoothed with a 30-year spline (thick line). (a), (b), and (c) are from trees from at or near the upper forest border, while the (d) is from trees growing at the lower forest border. The middle two chronologies (b and c) are comprised from trees used in the high elevation chronology (a) but subset according to the seasonal mean temperature of the individual tree with (b) being trees in colder topoclimate sites than trees in (c). Power spectra are from scaled ring widths. The black-dashed line indicates the 95% confidence interval from 5,000 Monte Carlo simulations using red noise (ϕ_1) estimated from the data. SMT = seasonal mean temperature.

An unsupervised cluster analysis by Tran et al. (2017) using bristlecone pine trees at this site over a larger elevation gradient found two distinct patterns of growth. An analysis of environmental correlates showed that topoclimate variables associated with growing season length and temperature could explain this difference. The most parsimonious model from Tran et al. (2017) suggests that generally a SMT of 7.5 °C separates temperature-limited from moisture-limited trees. In this work, we take this statistical finding and test this threshold temperature by building three separate tree-ring chronologies: The first uses all 176 of our samples taken from 96 trees. The second uses 123 samples from 68 high elevation trees situated in colder topoclimates with SMT < 7.5 °C. The third uses 53 samples from 28 high elevation trees situated in warmer topoclimates with SMT > 7.5 °C. We also compare these upper treeline chronologies to a chronology built from 147 samples from 117 moisture-sensitive adult bristlecone pine trees growing at the lower forest border (approximately 2,800 m above sea level) about 15 km to the south and east. All chronologies were constructed with the annual growth across trees averaged by year using Tukey's biweight robust mean to reduce the impact of outliers (Cook et al., 1990). The record for all four chronologies spans the years 1500 to 2009 CE. All four of these chronologies have excellent statistical quality with long segment lengths, high interseries correlations, and high values of expressed population signal (supporting information Table S1).

2.3. Process Modeling
We use the Vaganov-Shashkin forward model (VSM) of tree-ring formation to interpret the tree-ring records (Evans et al., 2006; Vaganov, 1996; Vaganov et al., 2011). The model is fully described by Vaganov et al. (2006),
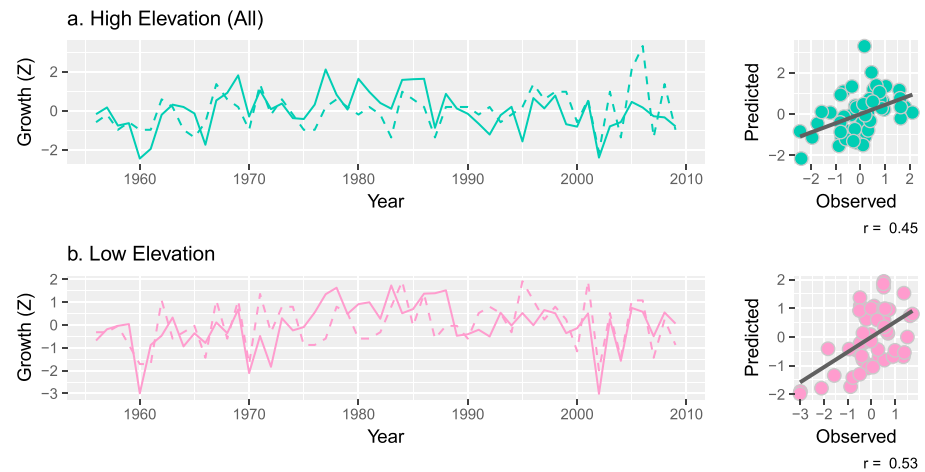
Figure 3. Observed (solid) versus predicted (dashed) growth from the Vaganov-Shashkin model is shown for the high elevation trees (a) and the low elevation trees (b) on the left from 1956 to 2009 where daily climate data that overlap the tree-ring record are available to drive the model. The correlations are shown in the scatter plots on the right.

Evans et al. (2006), and Vaganov et al. (2011). Vaganov-Shashkin is a mechanistic model that uses piecewise linear functions of light, temperature, and soil moisture to estimate daily growth rates due to the most limiting climatic factor and to form annual tree rings in response to climate. The model has been used in a variety of settings and is able to reproduce tree-ring patterns across a wide range of species with different limiting factors (Anchukaitis et al., 2006; Evans et al., 2006; Shi et al., 2008; Vaganov et al., 2006, 2011). We forced the model with daily temperature and precipitation data over the period 1956 to 2009. These climate data are a composite built from of a long station record from the Barcroft Research Facility, White Mountain Research Station (1956 to 1980) and daily data from the PRISM model (1981 to 2009). The Barcroft station (3,783 m) is about 10 km north of the high elevation trees, and the PRISM model is an interpolated surface. The VSM generates estimates of climate-mediated annual growth as well as information on the most limiting factor for that growth on a daily time step. Please see the Supporting Information S1 for details.

3. Results

The chronology composed of all 176 high elevation samples shows increased growth post 1900 CE and variability at time scales from interannual to secular (Figure 2a). The other two high elevation chronologies (Figures 2b and 2c) also show secular, centennial, and multidecadal variability and do so at higher power than the composite chronology. However, in the time domain, they are quite different from one another with the colder high elevation chronology (Figure 2b) showing increased growth post 1900 CE and the warmer high elevation chronology (Figure 2c) showing near average growth over that time period. Similarly, many of the features in the warmer high elevation chronology (Figure 2c) such as the increase in growth around 1600 CE are not present in the chronology built from colder topoclimates trees. Indeed, the high elevation chronology from the warmer topoclimates contains many of the same decadal features as the moisture-sensitive chronology from the lower forest border (Figure 2d), which shows decadal and multidecadal power but lacks lower-frequency variability.

The correlations between these four chronologies vary in sign and magnitude depending on frequency (Table S2). While all four of the chronologies correlate positively at the interannual scale, the correlations between the cold and warm high elevation chronologies diverge at lower frequencies. When compared at the 30- and 100-year frequency bands, they become negatively correlated ($r_{Cold|Warm}$ = −0.34 and −0.55, respectively). Interestingly, while the warmer high elevation chronology shows positive correlation with the low-elevation chronology at those same periodicities ($r_{Warm|Low}$ = 0.67 for both bands), the colder high elevation chronology correlates negatively with the low elevation chronology ($r_{Cold|Low}$ = −0.25 and −0.56, respectively). These results are supported by cross-spectral analysis showing the cold and warm high elevation chronologies out of phase and with low squared-coherency at these frequencies (Figure S1).

When driven with lapse-rate adjusted daily climate data, VSM is able to capture interannual variation between the high and low elevation chronologies with reasonable skill (Figure 3). For the mixed high-elevation
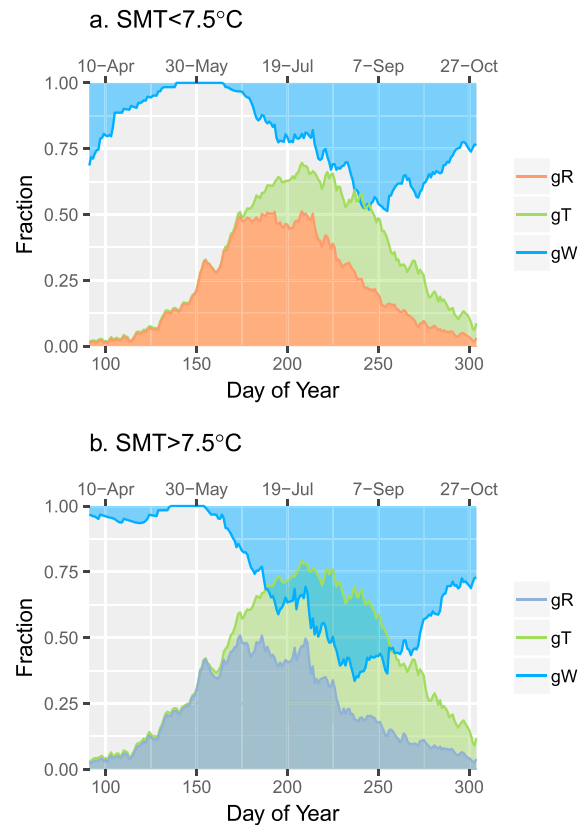
Figure 4. Average limiting factors on growth (gR) from the Vaganov-Shashkin model simulated from 1956 to 2009. (a) simulates the conditions experienced by the high elevation trees in the cold topoclimate exposures (SMT < 7.5 °C), and (b) simulates the conditions experienced by the warm high elevation trees (SMT > 7.5 °C). Growth on a given day (x axis) is limited by the minimum of either moisture (gW) or temperature (gT). The simulated growth in the colder biophysical settings is consistently limited by temperature, while conditions in the warmer settings is limited by moisture during July, August, and early September. SMT = seasonal mean temperature.

chronology (Figure 2a), the model indicates both temperature and soil moisture as limiting factors to growth, while the low elevation chronology (Figure 2d) is limited by soil moisture (Figure S2). However, when the cold (Figure 2b) and warm (Figure 2c) chronologies from the high elevation are modeled using the high-elevation climate data, two very different understandings of the limiting factors on growth emerge. The simulated colder chronology shows growth limited by temperature throughout the growing season (Figure 4a), while the warmer chronology simulation shows moisture limitation as the primary control on growth after approximately 1 June (Figure 4b).

The data presented in Figure 4 are the average limiting factors over the entire model run (1956–2009). When we subset the data into three equal 18-year periods (1956–1973, 1974–1991, and 1992–2009), the simulated growth limitation on the low elevation moisture sensitive remains moisture limited in each time period (not shown), while the cold chronology switches from temperature limitation in the first two time periods to moisture limitation in the last period (Figure 5). This corresponds to a significant increase in median growing degree days (base 1.65 °C) in the 1992–2009 period (1,014) as compared to the earlier two periods (822 and 814, respectively; Figure S3 and Table S3).

4. Discussion and Conclusions

Given the complex flow of air masses in mountainous topography, elevation is not a sufficient variable for describing the position or growth of trees at the upper forest border. That the topographic position of individual bristlecone pine trees could determine their limiting growth factor was first hinted at by LaMarche (1974b) who theorized that "knowledge of the 'apparent altitude' or 'apparent location' … could yield paleo-climatic estimates." Our results support this early speculation as we are now able to better understand which
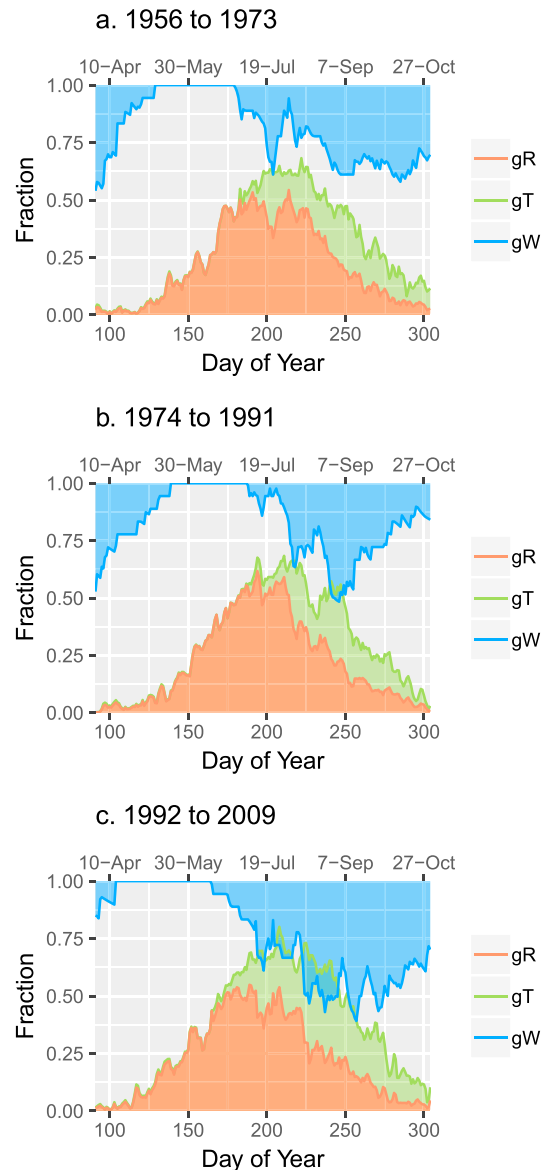
Figure 5. The average growth from Figure 4a broken into three 18-year time periods. As above, growth on a given day (*x* axis) is limited by the minimum of either moisture (gW) or temperature (gT). In the early part of the record (a), growth is limited by temperature only. In the second period of the record (b), growth is limited by moisture availability on about 7% of days in the summer months. By the last period of the record (c), moisture is limiting growth on 23% of days during the summer months.

trees are limited by temperature and which trees are limited by moisture over very short distances using small differences in the SMT at the scale of tens of meters.

Our data show that the trees from the highest elevation are not monolithic in their behavior but rather separate into two distinct modes of growth depending on SMT, which is influenced by topography. These differences in topographically mediated climate otherwise appear minor, with only a 0.5 °C difference in median SMT (Table S4). Furthermore, we show that the trees from the warmer topoclimates (SMT > 7.5 °C) grow more similarly to moisture-sensitive trees growing about 700 vertical meters further downslope at the low-elevation limit for this species at this site. All of the high elevation chronologies show significant low-frequency variability ($f < 0.01$, Figures 2a–2c). Interestingly, this centennial variability is at different frequencies and has greater power in the high elevation chronologies separated by SMT (Figures 2b and 2c) than that in the composite high elevation chronology (Figure 2a). This supports prior work by Tran et al. (2017) who found that high

elevation bristlecone pine formed two clusters of growth at this site with one cluster correlating strongly with temperature and the other with the Palmer Drought Severity Index.

The chronology of the high elevation trees (Figure 2a) is visually different than the low elevation chronology (Figure 2d). However, when the cold high elevation trees (Figure 2b) are removed, the patterns at lower frequencies are more similar to the low elevation chronology. There are several reasons, beyond this visual comparison, that we interpret these trees as more similar to the low elevation trees with regard to limiting factors on growth. First, the summary statistics (mean ring width and first-order autocorrelation) move closer to the values for the low elevation chronology (Table S1). Second, at multidecadal and centennial bands, the warm high elevation trees correlate positively and more strongly with the low elevation trees than with the trees at high elevation to which they become negatively correlated. (Table S2). Third, results from the process model indicate moisture limitation as opposed to temperature limitation for the high elevation trees in warm topoclimates (Figure 4b), which is similar to the growth response in trees growing at lower forest border (Figure S2).

Based on our analyses, we conclude that the trees at high elevation growing in topoclimate with SMT > 7.5 °C are primarily moisture limited and more similar to lower elevation trees despite their elevation and proximity to the upper forest border. Conversely, we also find that by removing the diluting effect of the moisture-limited trees, we are able to unmix the growth response of the high elevation trees and isolate the most temperature sensitive trees (those with SMT < 7.5 °C, Figure 2b). We see this again in the summary statistics for the chronologies (Table S1), the correlations between the chronologies (Table S3), and through the results of the process model which reveals temperature limitation on growth simulations for the cold, high elevation trees (Figure 4a). Meko et al. (1993) described a similar diluting effect when chronologies with differing climate sensitivity from the same region were combined without accounting for spatial variability in their climate response. We find a similar effect but at a substantially finer spatial scale as in Salzer et al. (2014).

In reference to an application of VSM to bristlecone pine growth at the lower forest border, Vaganov et al. (2006) noted, "in every year, the growth in the second part of the season is limited by low moisture, but the starting dates and growth rate at the beginning of the season are completely defined by temperature." We see the same pattern at the lower forest border (Figure S2) but see this pattern as well in the warm high elevation trees (Figure 4b) and partially in the cold high elevation trees during the more recent time period (Figure 4c). Similar findings on seasonal variations in the climate controls on xylogenesis have come from studies using dendrometers, microcoring, and wood anatomy across a range of species and sites elsewhere in the world (e.g., Cocozza et al., 2016; Deslauriers et al., 2008; Zhang et al., 2018).

A pressing issue in dendroclimatology has been the "divergence effect" whereby trees that faithfully tracked temperature variability in the instrumental record for many decades can lose that sensitivity (Barichivich et al., 2014; Briffa, Schweingruber, Jones, Osborn, Harris, et al., 1998; Briffa, Schweingruber, Jones, Osborn, Shiyatov, et al., 1998; D'Arrigo et al., 2008). This has been a controversial topic in the field with various mechanisms proposed to explain the phenomenon (Briffa, Schweingruber, Jones, Osborn, Harris, et al., 1998; D'Arrigo et al., 2008; Stine & Huybers, 2014). For the higher elevation bristlecone pines studied here, we find evidence for a change in the limiting factor of growth depending on small changes in SMT (Figure 4). Disturbingly, we also find evidence for a recent loss of temperature sensitivity even in the cold high elevation trees (Figure 5). An increase in growing degree days without a change in precipitation appears to be causing temperature-induced drought stress and changes in the climate response despite their cold topoclimate setting (Figure S3 and Table S3).

This latter finding suggests that despite our progress in improving our understanding of limiting factors in high elevation bristlecone pine, the trees are now extremely close to, or past, a threshold where their growth response switches from temperature to moisture limitation with small changes in energy and water balance even on short time scales. If this finding is real and persistent, a robust method for developing multimillennial Great Basin temperature reconstructions from high-elevation bristlecone pine will rely on mapping the spatial window of temperature sensitivity that moves across the landscape driven changes in regional climate over millennia (Bruening et al., 2018). Given the current trajectory of climate in the western United States, the long lags between growth and demographic processes in these slow growing conifers, and the age trees must reach before being ideal for dendroclimatology, it might be many centuries before newly formed high elevation bristlecone pine ring widths will be reliable and suitable recorders of temperature variability at this site.

In the broader sense, this work emphasizes that care must be given to potential spatial and temporal variability in the climate response of paleoclimate proxy data in general and to putative temperature-sensitive tree-ring data in particular, even over short time-space scales. Developing methods that explicitly incorporate a mechanistic understanding of these patterns and processes should be paramount.

References

Álvarez, C., Veblen, T. T., Christie, D. A., & Álvaro G.-R. (2015). Relationships between climate variability and radial growth of Nothofagus pumilio near altitudinal treeline in the Andes of northern Patagonia, Chile. *Forest Ecology and Management*, *342*, 112–121.

Anchukaitis, K. J. (2017). Tree rings reveal climate change past, present, and future. *Proceedings of the American Philosophical Society*, *161*, 244–263.

Anchukaitis, K. J., Evans, M. N., Kaplan, A., Vaganov, E. A., Hughes, M. K., Grissino-Mayer, H. D., & Cane, M. A. (2006). Forward modeling of regional scale tree-ring patterns in the southeastern United States and the recent influence of summer drought. *Geophysical Research Letters*, *33*, L04705. https://doi.org/10.1029/2005GL025050

Barichivich, J., Briffa, K. R., Myneni, R., van der S. G., Dorigo, W., Tucker, C. J., et al. (2014). Temperature and snow-mediated moisture controls of summer photosynthetic activity in northern terrestrial ecosystems between 1982 and 2011. *Remote Sensing*, *6* (2), 1390–1431.

Briffa, K. R., Schweingruber, F. H, Jones, P. D., Osborn, T. J., Harris, I. C., Shiyatov, S. G., et al. (1998). Trees tell of past climates: But are they speaking less clearly today? *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *353* (1365), 65–73.

Briffa, K. R., Schweingruber, F. H., Jones, P. D., Osborn, T. J., Shiyatov, S. G., & Vaganov, E. A. (1998). Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature*, *391*, 678–682.

Bruening, J. M., Bunn, A. G.– & Salzer, M. W. (2018). A climate–driven tree line position model in the White Mountains of California over the past six millennia. *Journal of Biogeography*, *45* (5), 1067–1076.

Bruening, J. M., Tran, T. J., Bunn, A. G., Weiss, S. B., & Salzer, M. W. (2017). Fine-scale modeling of bristlecone pine treeline position in the Great Basin, USA. *Environmental Research Letters*, *12* (1), 14008.

Bunn, A. G. (2008). A dendrochronology program library in R (dplR). *Dendrochronologia*, *26* (2), 115–124.

Bunn, A. G. (2010). Statistical and visual crossdating in R using the dplR library. *Dendrochronologia*, *26*, 115–124.

Bunn, A. G., Hughes, M. K., & Salzer, M. W. (2011). Topographically modified tree-ring chronologies as a potential means to improve paleoclimate inference. *Climatic Change*, *8*, 627–634.

Cocozza, C., Palombo, C., Tognetti, R., La Porta, N., Anichini, M., Giovannelli, A., & Emiliani, G. (2016). Monitoring intra-annual dynamics of wood formation with microcores and dendrometers in Picea abies at two different altitudes. *Tree Physiology*, *36* (7), 832–846. https://doi.org/10.1093/treephys/tpw009

Cook, E. R., Briffa, K. R., Shiyatov, S. G., & Mazepa, V. (1990). Tree-ring standardization and growth-trend estimation. In E. R. Cook & L. A. Kairiukstis (Eds.), *Methods of dendrochronology: Applications in the environmental sciences* (pp. 104–123). Dordrecht: Kluwer.

Core Team, R. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

D'Arrigo, Rosanne, Wilson, Rob, Liepert, Beate, & Cherubini, Paolo (2008). On the 'divergence problem' in northern forests: A review of the tree-ring evidence and possible causes. *Global and Planetary Change*, *60* (3), 289–305.

Daniels, L. D., & Veblen, T. T. (2004). Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. *Ecology*, *85* (5), 1284–1296.

Deslauriers, A., Rossi, S., Anfodillo, T., & Saracino, A. (2008). Cambial phenology, wood formation and temperature thresholds in two contrasting years at high altitude in southern Italy. *Tree Physiology*, *28* (6), 863–871. https://doi.org/10.1093/treephys/28.6.863

Evans, M. N., Reichert, B. K., Kaplan, A., Anchukaitis, K. J., Vaganov, E. A., Hughes, M. K., & Cane, M. A. (2006). A forward modeling approach to paleoclimatic interpretation of tree-ring data. *Journal of Geophysical Research*, *111*, G03008. https://doi.org/10.1029/2006JG000166

Ferguson, C. W. (1968). Bristlecone pine: Science and esthetics. *Science*, *159* (3817), 839–846.

Fritts, H. C. (1966). Growth-rings of trees: Their correlation with climate. *Science*, *154* (3752), 973–979.

Fritts, H. C. (1976). *Tree rings and climate*. Caldlwell NJ: Academic Press.

Holmes, R. L. (1999). *Users manual for program COFECHA 11*. Tucson, AZ: Laboratory of Tree-Ring Research, University of Arizona.

Hughes, M. K., & Funkhouser, G. (1998). Extremes of moisture availability reconstructed from tree rings for recent millennia in the Great Basin of western North America. In M. Beniston, & J. Innes (Eds.), *The impacts of climate variability on forests*. Berlin: Springer-Verlag.

Hughes, M. K., & Funkhouser, G. (2003). Frequency-dependent climate signal in upper and lower forest border tree rings in the mountains of the Great Basin. *Climatic Change*, *59*, 233–244.

Hughes, M. K., & Graumlich, L. J. (1996). Multimillennial dendroclimatic studies from the western United States. In Jones, P. D., etal. (Eds.), *Climatic variations and forcing mechanisms of the last 2000 years* (pp.109–124). Berlin, Heidelberg: Springer Berlin Heidelberg.

Körner, C., & Paulsen, Jens (2004). Aworld-wide study of high altitude tree line temperatures. *Journal of Biogeography*, *31* (5), 713–732.

LaMarche, V. C. (1974a). Frequency-dependent relationships between tree-ring series along an ecological gradient and some dendro climatic implications. *Tree-Ring Bulletin*, *34*, 1–20.

LaMarche, V. C. (1974b). Paleo climatic inferences from long tree-ring records intersite comparison shows climatic anomalies that maybe linked to features of the general circulation. *Science*, *183* (4129), 1043–1048.

LaMarche, V. C., & Stockton, C. W. (1974). Chronologies from temperature-sensitive bristle cone pines at upper treeline in western United States. *Tree-Ring Bullet in*, *34*, 21–45.

Lavergne, A., Daux, V., Villalba, R., & Barichivich, J. (2015). Temporal changes in climatic limitation of tree- grow that upper treeline forests: Contrasted responses along the west-to-east humidity gradient in northern Patagonia. *Dendrochronologia*, *36*, 49–59.

Lloyd, A. H., & Fastie, C. L. (2002). Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change*, *52* (4), 481–509.

Meko, D., Cook, E. R., Stahle, D. W., Stockton, C. W., & Hughes, M. K. (1993). Spatial patterns of tree-growth anomalies in the United States and Southeastern Canada. *Journal of Climate*, *6* (9), 1773–1786.

Milly, P. C. D., Betancourt, J., Falkenmark, M., Hirsch, R. M., Kundzewicz, Z. W., Lettenmaier, D. P., & Stouffer, R. J. (2008). Stationarity is dead: Whither water management? *Science*, *319* (5863), 573–574.

PRISM (2017). Oregon State University. Retrieved from http://prism.oregonstate.edu (Online; accessed October 2018).

Paulsen, J., & Körner, C. (2014). Aclimate-based model to predict potential treeline position around the globe. *Alpine Botany*, *124* (1), 1–12.

Pearson, C. L., Brewer, P. W., Brown, D., Heaton, T. J., Hodgins, Gregory W. L., Jull, A. J. T., et al. (2018). Annual radiocarbon record indicates 16th century BCE date for the Thera eruption. *Science Advances*, *4* (8), eaar8241. https://doi.org/10.1126/sciadv.aar8241

Salzer, M. W., Bunn, A. G., Graham, N. E., & Hughes, M. K. (2013). Five millennia of paleo temperature from tree–rings in the Great Basin, USA. *Climate Dynamics*, *42* (5–6), 1517–1526.

Salzer, M. W., Hughes, M. K., Bunn, A. G., & Kipfmueller, K. F. (2009). Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proceedings of the National Academy of Sciences*, *106* (48), 20,348–20,353.

Salzer, M. W., Larson, E. R., Bunn, A. G., & Hughes, M. K. (2014). Changing climate response in near-treeline bristle cone pine with elevation and aspect. *Environmental Research Letters*, *9* (11), 114007. https://doi.org/10.1088/1748-9326/9/11/114007

Scott, S. G. (2014). An overview of tree-ring width records across the Northern Hemisphere. *Quaternary Science Reviews*, *95*, 132–150.

Shi, J., Liu, Y., Vaganov, E. A., Li, J., & Cai, Q. (2008). Statistical and process-based modeling analyses of tree growth response to climate in semi-arid area of north central China: A case study of *Pinus tabulaeformis*. *Journal of Geophysical Research*, *113*, G01026. https://doi.org/10.1029/2007JG000547

Stevens, G. C., & Fox, J. F. (1991). The causes of treeline. *Annual Review of Ecology and Systematics*, *22* (1), 177–191. https://doi.org/10.1146/annurev.es.22.110191.001141

Stine, A. R., & Huybers, P. (2014). Arctic tree rings as recorders of variations in light availability. *Nature Communications*, *5*, 3836.

Stokes, M. A., & Smiley, T. L. (1968). *An introduction to tree-ring dating*. Tucson,AZ: University of Arizona Press.

Stuiver, M., Kromer, B., Becker, B., & Ferguson, C. W. (1986). Radio carbon age calibration back to 13,300 years BP and the ^{14}C age matching of the German oak and US bristlecone pine chronologies. *Radiocarbon*, *28* (2B), 969–979.

Tran, T. J., Bruening, J. M., Bunn, A. G, Salzer, M. W., & Weiss, S. B. (2017). Cluster analysis and topoclimate modeling to examine bristlecone pine tree-ring growth signals in the Great Basin, USA. *Environmental Research Letters*, *12* (1), 14007. https://doi.org/10.1088/1748-9326/aa5388

Vaganov, E. A. (1996). Analysis of a seasonal growth patterns of trees and modelling in dendrochronology. In J. Dean,etal. (Eds.), *Tree Rings, Environment and Humanity* (pp. 73–87). Tucson, AZ: Radiocarbon.

Vaganov, E. A., Anchukaitis, K. J., & Evans, M. N. (2011). How well understood are the processes that create dendroclimatic records? A mechanistic model of the climatic control on conifer tree-ring growth dynamics. In M. K. Hughes, etal. (Eds.), *Dendroclimatology* (pp. 37–75). Netherlands: Springer.

Vaganov, E. A., Hughes, M. K., & Shashkin, A. V. (2006). Environmental control of xylem differentiation, *Growth dynamics of conifer tree rings: Images of past and future environments* (pp.151–187). Berlin, Heidelberg: Springer Berlin Heidelberg.

Wang, X., Zhang, M., Ji, Y., Li, Z., Li, M., & Zhang, Y. (2017). Temperature signals in tree-ring width and divergent growth of Korean pine response to recent climate warming in northeast Asia. *Trees*, *31* (2), 415–427.

Zhang, J., Gou, X., Manzanedo, R. D., Zhang, F., & Pederson, N. (2018). Cambial phenology and xylogenesis of *Juniperus przewalskii* over a climatic gradient is influenced by both temperature and drought. *Agricultural and Forest Meteorology*, *260–261*, 165–175. https://doi.org/10.1016/j.agrformet.2018.06.011