Cluster Analysis as a Means of Examining Topographically-mediated Bristlecone Pine (Pinus longaeva) Growth in the American Southwest

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Cluster analysis as a means of examining topographically-mediated bristlecone pine (Pinus longaeva) growth in the American Southwest

By

Tyler J. Tran

Accepted in Partial Completion
Of the Requirements for the Degree
Master of Science

Kathleen L. Kitto, Dean of the Graduate School

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MASTER’S THESIS

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Tyler J. Tran
12 May 2016
Cluster analysis as a means of examining topographically-mediated bristlecone pine (Pinus longaeva) growth in the American Southwest

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

By
Tyler J. Tran
May 2016
Abstract

Tree-ring analysis can provide information about the surrounding environment of trees, as ring widths often reflect the variability of the factors that limit their growth. Great Basin bristlecone pine (*Pinus longaeva* D. K. Bailey) provides crucial tree-ring data to understand paleoclimate, but the growth signals can be difficult to interpret. The bristlecone record could present a potentially confounding narrative because of its mixed growth signals; in many cases, not all trees at one site are limited by the same environmental variable. Trees that are sensitive to patterns in temperature tend to grow in the alpine upper treeline ecotone, and trees limited by moisture availability have the tendency to grow downslope. At four sites in the Great Basin region, USA, this study uses cluster analysis to find dual-signal patterns in tree growth, and uses topoclimate modeling to better understand bristlecone growth. I found two-cluster patterns at two of those sites; both of these sites included a cluster that correlated well with temperature data and one cluster that correlated with reconstructed drought data. Temperature-limited clusters contained trees growing in colder areas at higher elevations, and moisture-limited clusters contained trees at lower elevation in warmer areas. This study presents models to predict the primary limiting factor of an individual tree based on topoclimate variables in hopes of furthering understanding of mixed-signal growth patterns and improving the accuracy of climate reconstructions using bristlecone pine.
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1 Introduction

1.1 Using tree rings to understand climate variability

Tree-ring analysis can provide information about the surrounding environment of trees, as ring widths often reflect the variability of the factors that limit their growth. The field of dendroclimatology typically focuses on using variations in tree growth on a subannual to annual scale to infer interannual and longer-term variations in climate conditions (Fritts 1966; LaMarche 1974a). While there are other paleoclimate records that are often used in conjunction with tree rings as climate proxies (e.g., lake sediment cores, ice cores), tree-ring records tend to have better temporal resolution than other proxies, which typically have less-than-annual resolution (Rohling and Plike 2005; Steinhilber et al. 2012). Dendrochronology is an important tool in understanding prehistorical climate variability, allowing inferences about climate that would be impossible with the instrumental climate record alone.

Great Basin bristlecone pine (*Pinus longaeva* D. K. Bailey) provides crucial tree-ring data in understanding paleoclimate, but the growth signals can be difficult to interpret. Bristlecone pine is known for being extremely long-lived, sometimes reaching ages of nearly 5000 years (Currey 1965; LaMarche 1969), for climate sensitivity (Ferguson 1968; LaMarche and Stockton 1974), and for its use in calibrating the radiocarbon scale (Suess 1967). The overall chronology can span an even longer period than individual trees because data from dead wood can be pieced together using the concept of crossdating (Stokes and Smiley 1968) to create a multimillennial time series, potentially providing records of climate variability over much of the late Holocene. Its longevity and climate sensitivity make bristlecone pine valuable in dendroclimatology, however using bristlecone ring-width data as a climate proxy does not come without complications. The bristlecone record could present a potentially confounding narrative because of its mixed growth signals; in many cases, not all trees at one site are limited by the same environmental variable, with some trees responding more strongly to temperature, and some being limited more acutely by
moisture availability (Bunn et al. 2011; Salzer et al. 2009, 2013, 2014). Trees that are sensitive to patterns in temperature tend to grow in the alpine treeline ecotone, and my study seeks to further understanding of their growth patterns in relation to their position on the landscape.

1.2 Alpine treeline as a temperature-limited ecotone

In the semiarid high-elevation regions where bristlecone pine grows, the forest is bounded on two sides by upper and lower treelines, defining areas of the trees’ dual-signal patterns. At the lower forest border, ring-width data from bristlecone pines has long been used in reconstructing past precipitation records (e.g., Hughes and Funkhouser 1998, 2003; LaMarche 1974b). Tree-ring chronologies from the upper forest border have been used as temperature proxies (e.g., LaMarche 1974a; LaMarche and Stockton 1974; Salzer et al. 2009, 2013).

The mixed-signal structure in bristlecone pine growth is further evidenced by different frequency of growth responses between upper treeline trees and lower forest border trees. While there is positive correlation between high-frequency (one to several years) variations at all trees, there is a negative relationship in low-frequency (multidecadal to centennial) variations between upper and lower forest border trees (Hughes and Funkhouser 2003; LaMarche 1974b). LaMarche (1974b) linked these growth trends to climatic trends. He found that low-frequency fluctuations in ring width were likely driven by temperature variations and that high-frequency patterns were likely caused by moisture and precipitation patterns.

Salzer et al. (2009, 2014) found an elevational threshold between different growth signals in bristlecone pine only 60 to 80 meters below upper treeline. The authors found that growth in trees above the threshold more closely mirrors a temperature signal while trees lower in elevation were better proxies of precipitation or moisture variability. This threshold could mean that individual trees just tens of meters apart could be responding to different limiting factors.
The temperature-limited upper treeline is valuable both in studying tree growth signals, which will be discussed in-depth in this report, and in examining tree demography (Korner 2012; Wardle 1971). The presence of dead wood above current treeline allows researchers to study tree demography, and treeline elevational movement with changing temperatures (e.g., Korner 1998; Korner and Paulsen 2004; Lloyd and Graumlich 1997). Several studies suggest that increasing temperatures are driving upslope treeline movement (e.g., Elliott and Kipfmueller 2011; Elliott 2012; Harsch et al. 2009; Walther 2003), and Salzer et al. (2013) found that upward treeline advances were greater in the 20th century than at any other time in the last 4000 years. High-altitude treeline seems to be formed under very similar growing season temperature conditions worldwide (Korner 2007). These common thermal thresholds for tree presence confirm the crucial role that temperatures play in tree demography and tree growth at upper treeline.

Treeline movement must be taken into account when reconstructing past climates on a longer-scale, with the knowledge that trees growing at the upper forest border are limited by temperature while the growth signal downslope tends to be moisture limited (Salzer et al. 2009). Treeline models such as the one created by Paulsen and Korner (2014), which uses climate data to predict treeline elevation globally, could be used to study the shifting ecotonal boundary. However, Lloyd and Graumlich (1997) suggest that with warming temperatures, precipitation will play a larger role in dictating upper treeline position and structure, further complicating the larger puzzle of understanding mixed signals in bristlecone pine growth.

1.3 Using topoclimate to understand mixed growth signals

Recent research has found that complex topography can have a significant effect on local climate, and in turn, on tree growth (Adams et al. 2014; Bunn et al. 2011; Salzer et al. 2014). Many studies have examined the effects of topography on surface temperatures, or what is termed topoclimate, in mountain environments (e.g., Ashcroft et al. 2012; Dobrowski et al. 2009; Slavich et al. 2014). A better understanding of topoclimate may
help to explain different growth signals in trees at a single site. Much of the past work in
dendroclimatology has relied on site chronologies, with all trees from a single site averaged
together into a mean chronology to examine growth patterns (Fritts 1974; Hughes 2011).
The use of site chronologies in topographically complex environments might muddle the
presence of multiple growth signals.

Trees that are relatively close to each other (on the order of tens of meters apart) may
be limited by different factors because of topography (Bunn et al. 2005, 2011; Salzer et al.
2014). Across the mountainous landscapes where bristlecone pines grow, there may be
temperature inversions of several degrees Celsius on a fine vertical scale (tens of meters),
where cold air tends to pool depending on topography (Van de Ven and Weiss 2009). In
these cases, trees growing at lower elevation show growth responses similar to trees at
the upper forest border, because cold air pooling at lower elevations mimics conditions
similar to those at upper treeline. Conversely, upper treeline trees might show growth
patterns more common in downslope trees if warming trends continue. Instead of using site
chronologies to study bristlecone pine growth, the dual-signal (temperature-limited growth
versus moisture-limited growth) may be better explored with smaller, topographically-
modified chronologies that use topoclimatic conditions specific to individual trees.

1.4 Objectives

This study builds on recent bristlecone pine research (see Bunn et al. 2011; Salzer et al.
2009, 2013, 2014) and uses cluster analysis to examine growth. Several studies have used
cluster analysis as a means of identifying radial growth patterns using ring-width data
(see Fritts 1974; Kipfmueller and Salzer 2010; Koprowski and Zielski 2006; Wilmking
et al. 2004; Wilson and Hopfmueller 2001). Cluster analysis provides useful techniques
for examining multivariate ring-width data, with each year of growth used as a variable.
Using tree-ring data from four topographically complex sites in different mountain ranges,
I attempt to answer the following:
• At each site, are there multiple growth signals (multiple growth clusters)?

• If there are multiple growth signals, what are the characteristics of each in terms of topoclimate?

• How can the results of this study improve the accuracy of climate reconstructions using bristlecone pine ring-width data?

At each site, I use cluster analysis to separate different bristlecone pine growth signals. I attempt to better understand the presence of mixed signals in the bristlecone chronology by using fine-scale topoclimate modeling and by examining differences in growth of individual trees. I perform a climate-growth analysis in hopes of understanding the climate response of different growth clusters. The goal of this analysis is to help improve the accuracy of climate reconstructions using bristlecone pine ring-width data.

2 Methods

2.1 Study areas

Bristlecone pine grows at high elevation, typically in dry and cool climates in the American West. The tree cores collected in this study were added to a larger preexisting data set used by Bunn et al. (2011), Salzer et al. (2009, 2013, 2014), and other studies. Cores were collected at four sites (figure 1) in eastern California and eastern Nevada: Mount Washington, Snake Range, NV (henceforth MWA, 38.91 N, 114.31 W, treeline position approximately 3400 m.a.s.l.); the White Mountains, CA (henceforth WHT, 37.5 N, 118.2 W, treeline approx. 3500 m.a.s.l.); Chicken Spring Lake, Sierra Nevada Range, CA (henceforth CSL, 36.46 N, 118.22 W, treeline approx. 3600 m.a.s.l.); and at Pearl Peak, Ruby Range, NV (henceforth PRL, 40.23 N, 115.54 W, max elevation approx. 3300 m.a.s.l.). These four sites were chosen both for reasons of accessibility and to maintain continuity with past research in the same locations.
The Great Basin region extends from eastern California, through Nevada, and into Utah. High elevation sites in the region are known for being cold and dry, and these conditions drive growth patterns in bristlecone pine. Substrate varies by site: sites at WHT are known for their dolomite and sandstone substrate, and other sites are underlain with limestone (LaMarche and Stockton 1974). While bristlecone pine grows at MWA, WHT, and PRL, foxtail pine (*Pinus balfouriana* Grev. et Balf.) grows at CSL. Foxtail pine and bristlecone pine have very similar growth responses to climate, so I treat them similarly throughout the study (Bunn et al. 2005).

![Site map showing MWA, WHT, CSL, and PRL.](image)

**Figure 1:** Site map showing MWA, WHT, CSL, and PRL.

### 2.2 Chronology construction

Tree cores from live trees and cross sections from dead wood were collected in order to create bristlecone chronologies at each of my four sites. When sampling, an attempt was made to choose trees that were growing across the range of complex terrain. The collection included trees in the 60-80 vertical meters below treeline, in hopes of capturing a positive growth-response with temperature (Salzer et al. 2014), and trees much further downslope.

Bristlecone samples were prepared according to standard dendrochronological protocol (Stokes and Smiley 1968). For cores, this included air drying, gluing to mounting boards, and sanding with progressively finer grit to achieve a high polish. Cross sections were also
sanded for analysis. The samples were then crossdated and absolute dates (with annual resolution) were assigned to the tree rings. Accuracy of the crossdating was confirmed using COFECHA software (Holmes 1999) and dplR (Bunn 2008, 2010). The ring widths were then measured to the nearest 0.001 mm for each calendar date of the chronologies. GPS points were recorded at each tree location. The coordinates were differentially corrected, yielding a horizontal accuracy ≤ 2 meters.

Because I had multiple cores for each tree, I averaged ring widths between multiple cores for each tree. I detrended the ring-width data using a smoothing spline to create ring-width indices at the four sites. The spline uses a wavelength that is 2/3 the series length. The use of a smoothing spline seeks to remove non-climatic variability (Cook and Peters 1981). Though the ring-width data extend back in time to around 2000 BC in some cases, I only used data from the past four to five centuries in this research in order to preserve robustness of both sample size and time period.

2.3 Fine-scale temperature modeling

This research incorporates fine-scale temperature data modeled from a network of iButton temperature sensors (Maxim Integrated, San Jose, CA) at each site, along with topographic data to model topoclimate variables. In this report, I provide a relatively brief account of data collection, correction, and actual topoclimate modeling, but for further explanation of methods, see Bruening (2016).

At each of the four sites, approximately 50 iButton temperature sensors were placed across the landscape, making an effort to capture the topographic heterogeneity. The sensors recorded hourly temperatures for a period of one year. Sensors at MWA and PRL recorded from September 2013 - September 2014; sensors at WHT and CSL recorded from September 2014 - September 2015. The thermochrons were attached to trees one meter above the ground, enclosed in PVC radiation shields.

Multiple steps were taken to correct the data and ensure maximum accuracy of the resultant temperature models. At certain daytime hours, some of the radiation shields
allowed direct sunlight to strike individual temperature sensors. These anomalous maxima were removed, and neighboring hours were used to interpolate the missing data.

Five climate variables were calculated for each site using data collected from temperature sensors after being corrected. Monthly minimum and maximum temperatures ($T_{\text{min}}$ and $T_{\text{max}}$) are averages of daily minimum and maximum temperatures. Monthly mean temperatures ($T_{\text{mean}}$) are averages of all hourly values recorded within the month. Diurnal temperature range (DTR) values result from averaging the range of daily temperature for all days in a month. Degree hours above 5°C (DH5C) is the sum of the number of hours that temperatures are above 5°C in a month, and 5°C is an estimate of the minimum temperature required for xylogenesis (Korner 2012). In this study, most of the temperature data that are compared to tree growth are monthly averages from months of the growing season (May to September, inclusive).

Temperatures during the period of collection (2013–2015) were anomalous from a 120-year climate normal calculated from 1895-2015. Differences between PRISM climate data unique to each site (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu/) and the climate normal were calculated, and these differences were subtracted from the aggregated monthly variables discussed above. Because a simple subtraction would not accurately correct DH5C, the corrected variable was calculated using a linear model.

Topography profoundly affects temperatures in mountainous settings such as those at my four sites. Stahl et al. (2006) proposes several different methods of spatially interpolating air temperature in complex terrain, using regression-based and weighted-average approaches, with some methods utilizing specified lapse rates. Because of the complex topography at the four sites in this study, simple lapse rate calculations would have likely been inadequate to capture patterns in surface temperature (Dobrowski 2010; Lundquist and Cayan 2007). Several topographic variables (slope, derivations of aspect, solar radiation, and two topographic indices) were calculated using a 10 meter resolution digital elevation model (DEM). Then, a lasso regression from the R package ‘caret’ (Kuhn 2008)
was used to model the temperature variables mentioned above in terms of topography. These regression models were used to calculate temperatures across the spatial range at a 10 meter resolution.

2.4 Cluster analyses

2.4.1 Choice of cluster methods

Cluster analysis is commonly used to understand patterns in multidimensional environmental data, including time-series data (Liao 2005; Shaw and King 1992). In this case, the annual ring-width measurements as ring-width index (RWI) are the variables used in clustering. Cluster analyses were performed using Euclidean distance matrices and Ward’s method (Ward 1963) for cluster linkage. To satisfy the criteria of Ward’s method, I used squared Euclidean distances as input (Murtagh and Legendre 2014; Wishart 1969). Bunn et al. (2011) and Kipfmueller and Salzer (2010) also used Euclidean distance and Ward’s method to cluster bristlecone ring-width data. I chose an agglomerative hierarchical clustering method instead of employing partitioning methods so that I could explore growth patterns without having to previously specify the number of clusters. Hierarchical methods do not require the user to specify \( k \) clusters of the \( n \) data points before analysis; instead, hierarchical methods result in a range of \( k \) clusters from \( k = 1 \) to \( k = n \) (Kaufman and Rousseeuw 1990).

The use of hierarchical methods allows the user to explore the data patterns and to subsequently decide on an appropriate value for \( k \) number of clusters. In this analysis, I attempted to identify two distinct growth signals in the ring-width data: temperature limited and moisture limited. Partitioning methods would force each tree into one of two clusters instead of first ensuring that a two-signal pattern is present. After performing the cluster analysis, the user can assign samples to clusters depending on dendrogram structure. A more supervised automated approach (\( i.e. \), automated methods to assign samples to one of \( k = 2 \) clusters in this case) would also be appropriate. Algorithms to
automatically identify $k$ and to assign each sample to a cluster (Langfelder et al. 2008) would likely ignore the intent of first identifying a mixed-signal pattern.

Some types of cluster analyses do not have strict statistical assumptions such as normally distributed data or uncorrelated variables (Milligan 1996). However, some research suggests that there are statistical assumptions to be met to calculate a Euclidean distance matrix, an input of hierarchical clustering with Ward’s method (Mooi and Sarstedt 2011). The data in my study are not multivariate normal; most, but not all variables (in this case, growth years) pass tests for univariate normality. The data in my study have correlated variables. The nature of tree growth is autocorrelative; growth is influenced by and correlated with previous growth (Kohyama et al. 2005). I proceeded using Euclidean distance and Ward’s method of hierarchical clustering for several reasons: 1) Norusis (2010) states that while clustering based on a distance matrix with normally-distributed, independent data is best, using data that do not meet these assumptions is acceptable; 2) hierarchical clustering is better suited to this research than partitioning methods, as the user does not have to choose the $k$ number of clusters \textit{a priori}, like a non-metric clustering method such as Riffle (Matthews and Hearne 1991; Matthews et al. 1994) would require; 3) using Euclidean distance and Ward’s method allows comparison with results from Bunn et al. (2011) and Kipfmueller and Salzer (2010), who use the same clustering methods; and 4) performing the same analysis using non-metric Riffle clustering produced similar, though less-defined, results.

2.4.2 Performing cluster analyses

The time periods over which I clustered the tree-ring data varied slightly between the four sites. I sought to maximize the number of years of growth data for more robust clustering while preserving the sample size of trees used in analysis. I used ring width from 98 trees from 1652-2005 at WHT, 51 trees from 1651-2002 at MWA, 41 trees from 1774-2000 at PRL, and 25 trees from 1517-2009 at CSL. The clustering methods require completely enumerated data with no NA values to properly function.
I performed cluster analysis for each of the four sites. Hierarchical cluster analysis allows the user to interpret the dendrogram with multiple numbers of clusters ($k = 1, 2, 3, \ldots, n$). For simplicity, I chose to recognize two clusters in my analysis instead of using a more refined approach with higher $k$ (i.e., recognizing more than two growth signals). If there did not appear to be multiple growth signals (if $k = 1$) through examination of dendrograms, I accepted that there was likely only one growth signal present in the data. The choice of two clusters seeks to mirror two growth scenarios: limitation either by temperature or moisture availability. I calculated correlation coefficients between the two clusters at each site (table 1). Additionally, I ran simulations with each tree randomly assigned to a cluster (1 or 2). I ran the simulations 1000 times at each site, calculating the average correlation coefficient (table 1) between clusters with a 95% confidence interval. I performed all analysis in the R scripting language and environment version 3.1.2 (R Core Team 2014).

2.4.3 Cluster topoclimate and growth differences

In order to understand what drives a two-cluster separation of the data (or a lack of multiple distinct signals) at each site, I compared the topoclimate and growth characteristics of trees in each cluster. I used multiple methods to compare tree growth in terms of topoclimate: I used classification models to find the most important topoclimate variables for determining tree growth; I used exploratory boxplots and simple comparisons of means of different topoclimate variables to visualize differences between the two clusters; and I used ordination at each site as a complementary analysis.

In addition to the topoclimate variables from the fine-scale modeling discussed above (maximum, minimum, and mean temperatures, and degree-hours above 5°C (DH5C) for the growing season), I also calculated potential evapotranspiration (PET) with the Hargreaves method to get an idea of water availability, though I do not have a measure of water balance in this study (Lu et al. 2011). The Hargreaves method uses modeled minimum and maximum temperatures, as well as growing season radiation values unique to each
tree as inputs, to calculate PET (Hargreaves and Samani 1985).

Internal statistics to describe growth include first-order autocorrelation coefficient (AR1), standard deviation, and expressed population signal (EPS) (Briffa and Jones 1990).

Using recursive partitioning for classification with the R package ‘rpart’ (Therneau et al. 2014), I created classification models that describe which growth cluster trees belong to. The only input parameters of these models were topoclimate variables. For each site, the use of the package ‘rpart’ results in a single classification tree, a type of decision tree with leaves representing the two growth signals, and branches representing climate variables that most strongly drive growth patterns in bristlecone pine (Loh 2011). At the branches, the classification tree also displays thresholds between the two clusters in terms of the climate variables of importance.

To confirm the results of the cluster analysis at the sites with a two-cluster pattern, I used non-metric multidimensional scaling (Minchin 1987; Oksanen et al. 2015). I reduced the data matrix from 51 dimensions (at MWA) and 98 dimensions (at WHT) to two dimensions, then plotted the results in the two-dimensional ordination space with weighted averaging methods. I displayed topoclimate variables that I compared between clusters as vectors on the ordination plots. Variables that were significantly correlated ($p \leq 0.05$) with the ordination are displayed as black vectors, and those not significantly correlated ($p > 0.05$) are displayed as gray vectors.

2.4.4 Growth-climate analysis by cluster

To analyze tree growth in terms of climate patterns, I used ring-width index from the trees at MWA and WHT, separated by cluster, over the period 1400-2000. The record could have extended further back in time, but was truncated at 1400 to ensure robustness of the chronology in terms of sample depth. The series were standardized with a nonlinear model of biological growth with the form $y_t = ae^{bt} + k$, where $a$, $b$, and $k$ values vary by series (Fritts 1976). I used this standardization model to detrend increased juvenile
growth because I extended the chronologies back to 1400 for the growth-climate analysis.

I compared ring-width indices from both clusters at MWA and WHT to modeled temperature and Palmer Drought Severity Index (PDSI) data. The temperature model used was the Max Planck Institute ECHO-G model (ERIK2, AD 1000-1990) (Legutke and Voss 1999; Stevens et al. 2008). I used near-surface temperatures from the western United States from the ECHO-G model, as Salzer et al. (2013) did. I used reconstructed PDSI data from the North American Drought Atlas (Cook and Krusic 2004). Though the PDSI data were reconstructed from tree-ring data, none of the trees used in this study were used in the PDSI reconstructions. I calculated decadal correlations between temperature and ring-width index (RWI) and annual correlations between PDSI and RWI for clusters at both sites. I also used wavelet analysis to examine tree growth in the frequency domain (Torrence and Compo 1998).

3 Results

3.1 Two-cluster distinction

Cluster analysis of ring-width data demonstrated that trees at MWA and WHT showed two clearly distinct growth clusters (figures 2 and 3). CSL had only one growth signal (figure 4), and PRL had a more complicated structure than a dual-signal pattern (figure 5). Distinct clusters in the provided dendrograms are colored red and blue for easier distinction and for later reference as ‘red cluster’ and ‘blue cluster.’ Color choice has no significance.

The goal of cluster analysis is to identify groupings in data, with trees in a cluster being more similar to each other than to the overall collection of trees. Correlation coefficients between two clusters are a telling measure of cluster separation, along with visually examining dendrograms. The two clusters at MWA and the two clusters at WHT are less-strongly correlated with each other than the two clusters at each of CSL and PRL (table 1). The correlation coefficients between clusters for trees randomly assigned to either cluster are significantly higher than the actual between-cluster r values at MWA and
WHT (random correlation coefficients with 95% confidence interval in table 1). Random r values are similar to actual r values at CSL and are very close to actual r values at PRL.

Table 1 also displays the Euclidean distance values at which all data agglomerate into one cluster ($k = 1$) and a distance difference measure, or the difference between distances at $k = 1$ and $k = 2$ for each cluster analysis. These distance measures are indicative of similarity of trees in each cluster, with larger distances or distance differences denoting individual trees in a cluster being more similar to each other (i.e., better cluster “quality”). For the purpose of this study, I use larger distance and distance difference values as an indicator of better cluster quality and more distinct separation.

**Table 1:** Cluster distances and correlation coefficients. Distance and distance difference are measures of cluster quality in the analysis, with higher numbers denoting stronger two-cluster separation. A larger difference between r and random r suggests a stronger two-cluster separation.

<table>
<thead>
<tr>
<th>Site</th>
<th>Distance</th>
<th>Dist. difference</th>
<th>$r_{red,blue}$</th>
<th>Random r ± 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>MWA</td>
<td>13.49</td>
<td>4.41</td>
<td>0.58</td>
<td>0.90 ± 0.001</td>
</tr>
<tr>
<td>WHT</td>
<td>22.84</td>
<td>10.38</td>
<td>0.55</td>
<td>0.96 ± 0.001</td>
</tr>
<tr>
<td>CSL</td>
<td>9.95</td>
<td>0.08</td>
<td>0.73</td>
<td>0.84 ± 0.001</td>
</tr>
<tr>
<td>PRL</td>
<td>8.58</td>
<td>1.80</td>
<td>0.75</td>
<td>0.76 ± 0.003</td>
</tr>
</tbody>
</table>

**Figure 2:** MWA dendrogram of clustering from 1651-2002. There are two distinct growth signals at MWA. I will henceforth refer to these two clusters as the ‘blue cluster’ and ‘red cluster,’ appropriately colored on the dendrogram.
Figure 3: WHT dendrogram of clustering from 1652-2005. There are two distinct growth signals at WHT. I will henceforth refer to these two clusters as the ‘blue cluster’ and ‘red cluster,’ appropriately colored on the dendrogram.

Figure 4: CSL dendrogram of clustering from 1517-2009. There do not appear to be multiple distinct growth signals at this site.
Figure 5: PRL dendrogram from 1774-2000. There appear to be multiple growth signals at PRL, but the growth patterns seem much more complicated than the dual-signal structure seen at MWA and WHT. I will henceforth refer to the two dominant clusters as the ‘blue cluster’ and ‘red cluster,’ appropriately colored on the dendrogram.

3.2 Cluster topoclimate and growth differences

Trees at MWA and WHT show distinct two-cluster patterns in radial growth. Growth at CSL and PRL display patterns inconsistent with this binary temperature-limited/moisture-limited conceptual model. For this reason, I proceed with analysis only at MWA and WHT by performing a between-cluster comparison of topoclimate and growth characteristics. I use several methods to compare clusters at the two sites: I simply compare means of topoclimate variables for the two clusters at both sites; I create classification models to find the most important topoclimate variables in determining cluster membership; I present boxplots of the most important topoclimate variables and growth characteristics; I use ordination (including the most important topoclimate variables) as a complementary analysis.

At both MWA and WHT, trees in the blue clusters grow in colder areas for most temperature variables (Tmax, Tmean, DH5C) than trees in the red clusters (table 2). There are no discernible differences in PET between clusters at MWA, and the red cluster has slightly higher PET at WHT, though the difference might not be significant.
Table 2: Topoclimate differences between two clusters at MWA and WHT. Means of all trees in a cluster along with standard deviation in parentheses. All temperature values are in units °C except DH5C, which is in degree-hours. PET is presented in mm. **I believe that the red cluster Tmin and DTR values at WHT may be untrustworthy.

<table>
<thead>
<tr>
<th>Variable</th>
<th>MWA Blue cluster</th>
<th>MWA Red cluster</th>
<th>WHT Blue cluster</th>
<th>WHT Red cluster</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tmin</td>
<td>2.96 (0.22)</td>
<td>3.47 (0.41)</td>
<td>2.60 (0.66)</td>
<td>1.00 (1.19)**</td>
</tr>
<tr>
<td>Tmax</td>
<td>14.77 (0.70)</td>
<td>16.09 (1.59)</td>
<td>13.70 (1.43)</td>
<td>17.42 (3.02)</td>
</tr>
<tr>
<td>Tmean</td>
<td>8.55 (0.28)</td>
<td>9.42 (0.63)</td>
<td>5.28 (0.37)</td>
<td>5.67 (0.82)</td>
</tr>
<tr>
<td>DH5C</td>
<td>2829 (133)</td>
<td>3206 (292)</td>
<td>2831 (235)</td>
<td>3198 (453)</td>
</tr>
<tr>
<td>DTR</td>
<td>11.83 (0.71)</td>
<td>12.59 (1.63)</td>
<td>10.98 (2.06)</td>
<td>17.05 (4.31)**</td>
</tr>
<tr>
<td>PET</td>
<td>2.30 (0.09)</td>
<td>2.29 (0.18)</td>
<td>2.16 (0.23)</td>
<td>2.52 (0.43)</td>
</tr>
</tbody>
</table>

The second method of comparing growth signals/clusters by topoclimate used R package ‘rpart’ to create models that predict tree cluster membership based on topoclimate variables. Figures 6 and 7 display the classification trees from MWA and WHT, respectively. At MWA, Tmin is the variable that best predicts the cluster that trees are members of; minimum growing season temperatures above 3.1°C tend to yield trees in the red cluster, while a growing season Tmin < 3.1°C tends to result in blue cluster trees. At WHT, Tmax is the primary driving factor in the model. However, I excluded Tmin from the model. I will address this exclusion further in the discussion section of this report. Trees in areas with a growing season Tmax warmer than 17°C tend to be in the red cluster. Trees in colder areas may belong to the blue cluster or the red cluster; there is confusion in this branch of the classification. I used Cohen’s kappa statistic as a measure of the quality of the classification. A kappa value of zero would mean that the results of the classification are the same as would be expected with random data. The kappa value at MWA ($\kappa = 0.71$) was quite high, suggesting substantial agreement between predicted class and actual class in the classification models. The kappa value at WHT ($\kappa = 0.44$) was lower, suggesting moderate agreement between predicted and actual classes.
**Figure 6:** Classification tree at MWA shows that Tmin is the most important topoclimate variable in predicting growth signal at this site. Trees growing in areas with Tmin colder than 3.1°C during the growing season tend to be in the blue cluster, while trees in warmer areas tend to be in the red cluster.

**Figure 7:** Classification tree at WHT shows that Tmax is the most important topoclimate variable in predicting growth signal at this site. Trees growing in areas with Tmax warmer than 17°C during the growing season tend to be in the red cluster.

According to the classification models, growing season minimum temperature is the topoclimate variable that best predicts growth at MWA, and growing season maximum temperature is important at WHT. I display these driving topoclimate variables along with PET, first order autocorrelation, and ring width standard deviation by cluster in figures 8 and 9 as boxplots. Expressed population signal is not displayed because all clusters had high EPS (> 0.9). At MWA, trees in the blue cluster grow in areas of lower Tmin, higher AR1, and higher standard deviation than red cluster trees. There are no discernible differences in PET between clusters. At WHT, blue cluster trees grow in areas with lower Tmax. Blue cluster trees may have lower PET and higher AR1 and ring width standard deviation than red trees, though the differences are not as distinct.
As a complementary analysis, I used non-metric multidimensional scaling to explore topoclimate differences in the trees. The results of the ordination (figure 10) confirm the results shown as boxplots in figures 8 and 9. The data were reduced to two dimensions, with topoclimate variables and growth characteristics displayed as vectors in the ordination space. At both sites, higher temperature values are associated with trees in the red clusters. Higher values of AR1 are associated with trees in the blue clusters. At MWA, blue trees are associated with higher standard deviation; SD is not significantly correlated.
at WHT. Trees in the red cluster have higher PET at WHT, and PET is not significantly correlated with the ordination at MWA.

3.3 Climate-growth analysis by cluster

LaMarche (1974a) found that climate responses in tree-ring data are frequency dependent. Temperature signals are observed most prominently in decadal to multidecadal frequencies; whereas, moisture signals are more apparent on an annual to sub-decadal scale. With this knowledge, I calculated correlations between ring-width index (RWI) and climate data both as annual data and with 20-year smoothing splines of those data. Table 3 presents the correlation coefficients between RWI and climate data. At both sites, relationships between 20-year splines of RWI and temperature have the highest coefficients for the blue clusters. For red clusters, the most notable correlations are between RWI and annual PDSI data. Henceforth, I refer to blue clusters as temperature-limited clusters and red clusters as moisture-limited clusters.

Wavelet analysis plots are displayed in figures 11-14. At both sites, low-frequency variation is more evident in temperature-limited clusters, and high-frequency variation is more evident in moisture-limited clusters. In the temperature-limited clusters, variation is most apparent with multidecadal frequencies. In moisture-limited clusters, more
sub-decadal variation is present. Additionally, temperature-limited clusters at both sites (figures 11 and 13) show increased growth in recent years, as displayed by increases in RWI.

Table 3: Correlations between RWI of clusters and climate variables. Most notable coefficients are in bold. MWA is above, WHT is below. I did not perform significance testing, because the large sample size would likely result in finding meaningless statistical significance (Sullivan and Feinn 2012).

<table>
<thead>
<tr>
<th></th>
<th>Blue (Annual)</th>
<th>Blue (20 yr)</th>
<th>Red (Annual)</th>
<th>Red (20 yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MWA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PDSI</td>
<td>0.06</td>
<td>-0.03</td>
<td>0.39</td>
<td>0.10</td>
</tr>
<tr>
<td>Temp</td>
<td>0.42</td>
<td>0.48</td>
<td>0.30</td>
<td>0.47</td>
</tr>
<tr>
<td>PDSI (20 yr)</td>
<td>-0.06</td>
<td>-0.07</td>
<td>0.17</td>
<td>0.23</td>
</tr>
<tr>
<td>Temp (20 yr)</td>
<td>0.54</td>
<td>0.66</td>
<td>0.40</td>
<td>0.64</td>
</tr>
<tr>
<td>WHT</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PDSI</td>
<td>0.11</td>
<td>0.001</td>
<td>0.52</td>
<td>0.20</td>
</tr>
<tr>
<td>Temp</td>
<td>0.47</td>
<td>0.54</td>
<td>0.26</td>
<td>0.39</td>
</tr>
<tr>
<td>PDSI (20 yr)</td>
<td>0.01</td>
<td>-0.02</td>
<td>0.40</td>
<td>0.51</td>
</tr>
<tr>
<td>Temp (20 yr)</td>
<td>0.63</td>
<td>0.74</td>
<td>0.33</td>
<td>0.53</td>
</tr>
</tbody>
</table>

Figure 11: MWA blue cluster wavelet analysis. Most variability is low-frequency (decadal to multidecadal).
Figure 12: MWA red cluster wavelet analysis. Most variability is high-frequency (annual to sub-decadal).

Figure 13: WHT blue cluster wavelet analysis. Most variability is low-frequency (decadal to multidecadal).
4 Discussion

4.1 Two-cluster distinction

Dendrograms from the hierarchical cluster analysis show that there are two distinct growth clusters at MWA and WHT (figures 2 and 3). Dendrograms from CSL and PRL (figures 4 and 5) do not show the same two-cluster patterns. The presence of a two-signal growth structure is potentially significant, as it would justify the need for analysis based on growth signal (likely related to limiting factor) rather than overall site chronologies in dendroclimatological studies (Fritts 1976).

The dual-signal structure evident both at MWA and WHT confirms findings by Bunn et al. (2011) and Salzer et al. (2014). While one tree may be responding to low temperatures (in the temperature-limited cluster) a tree growing just tens of meters away might be a member of the moisture-limited cluster, and therefore not an accurate recorder
of past temperatures. These different growth signals for individual trees could have potentially significant implications in terms of climate reconstruction. For example, when reconstructing past temperatures, if one assumes that all trees at a site are temperature-limited, the moisture-limited trees that get mixed in will likely present noise and further mask the temperature signal in the chronology.

The lack of a clear two-signal growth structure at CSL and PRL could be a result of sampling techniques when collecting wood or a true growth pattern at the site. The dendrogram structures of trees at CSL and PRL (figures 4 and 5) suggest that only one growth pattern is present at CSL, while trees at PRL display more of a three-cluster pattern. Table 4 provides an idea of sampling heterogeneity at both sites in terms of elevation range of trees and range of growing season degree hours above 5°C at tree locations. Trees sampled at MWA, WHT, and PRL grow in a relatively wide range of elevations and DH5C conditions, while at CSL there are only 85 meters between the highest and lowest trees sampled (and similarly low DH5C range). I conclude that the single-signal data structure at CSL is at least partially a product of sampling techniques, while at PRL, a more complicated growth structure is unlike the dual-signal patterns at MWA and WHT. The single-signal pattern at CSL contains mostly temperature-limited trees (see appendix), while the signals at PRL are difficult to unravel.

The dendrogram structure at PRL (figure 5) shows more than two clusters, but one of the distinct clusters only contains four trees, smaller than any of the clusters at the other three sites. Though there is no valid reason to remove these four trees, excluding them

Table 4: Differences in site characteristics. DH5C was chosen as a topoclimate parameter because it is more consistent in pattern among clusters than Tmin.

<table>
<thead>
<tr>
<th>Site</th>
<th>n trees</th>
<th>Elevation range (m)</th>
<th>Growing season DH5C range</th>
</tr>
</thead>
<tbody>
<tr>
<td>MWA</td>
<td>51</td>
<td>234</td>
<td>1326.28</td>
</tr>
<tr>
<td>WHT</td>
<td>98</td>
<td>375</td>
<td>1739.08</td>
</tr>
<tr>
<td>CSL</td>
<td>25</td>
<td>85</td>
<td>280.97</td>
</tr>
<tr>
<td>PRL</td>
<td>41</td>
<td>292</td>
<td>1266.95</td>
</tr>
</tbody>
</table>

24
produces the dendrogram shown in figure 15. After removal of the four trees that made up the blue cluster in figure 5, the new dendrogram (figure 15) shows more resemblance to the structures of dendrograms for MWA and WHT, with a clearer dual-signal pattern, though there is still separation in the larger blue cluster. Additionally, updated correlations between the two clusters at PRL are more similar to the patterns of MWA and WHT previously displayed in table 1. The correlation between the two clusters had a coefficient $r = 0.50$, compared to the randomized $r = 0.83 \pm 0.002$. Though the removal of four trees caused trees at PRL to cluster into more of a dual-cluster pattern like at MWA and WHT, I will not continue with analysis in this fashion, lacking a valid reason to do so other than a results-driven motive.

4.1.1 Cluster quality and validity

Though hierarchical cluster analyses always result in some type of cluster separation, the clusters are not always meaningful to the context of study. Numerous studies have focused on measuring cluster validity and stability (Bezdek and Pal 1998; Halkidi et al. 2001;
Hennig 2007). I used the clValid package in R (Brock et al. 2008) to assess the validity of cluster analysis at each site, including both internal measures (e.g., connectivity, Dunn Index) and stability measures (e.g., average distance, figure of merit, etc.). There were not obvious inter-site differences in the cluster validity and stability measures calculated, as hierarchical clustering consistently does well with these measures (Brock et al. 2008).

I make use of distance measures from the cluster analysis (table 1), simpler metrics of cluster “quality” than those described above. These distance measures are derived from the Euclidean distance matrix and error sum of squares (ESS) employed with Ward’s method (displayed as ‘height’ on dendrogram in many statistical softwares). Clusters at MWA and WHT are more separated, as shown by larger distance measures in table 1, and the correlations between clusters at these two sites are quite low compared to CSL and PRL. A low inter-cluster correlation suggests that there is truly a two-signal structure in the data, because the clusters are dissimilar. Further, correlation coefficients at MWA and WHT are significantly different than r values of randomly-created clusters, while inter-cluster correlation coefficients for the true clusters and randomly-created clusters are quite similar at CSL and PRL.

4.2 Cluster topoclimate and growth differences

Past research shows that trees that grow at upper treeline tend to be temperature limited, while trees growing at lower elevations tend to be moisture limited (Bunn et al. 2011; Salzer et al. 2014). The results from MWA and WHT are largely in agreement with this idea. In this section, I discuss differences in topoclimate variables and growth statistics by cluster, as presented in classification trees, boxplots, and ordinations above, along with possible reasons for these differences.

Multiple lines of evidence support the hypothesis that low temperatures limit bristlecone pine growth at upper treeline, and that moisture availability is of a secondary concern to those trees (Korner 2012; LaMarche and Stockton 1974; Salzer et al. 2009, 2014). The classification models in this study suggest that growing season minimum temperature is a
Figure 16: A comparison of Tmax and Tmin at MWA (left) and WHT (right) with boxplots comparing diurnal temperature range by cluster above. Each dot represents an individual tree, with blue dots being members of the temperature-limited cluster and red dots in the moisture-limited cluster. The Tmin model for red-cluster trees at WHT is likely inaccurate, resulting in low predictions of Tmin values.

A stronger predictor than other topoclimate variables (e.g., Tmax, Tmean, DH5C) concerning a tree’s growth signal (or its limiting factor) at MWA and that Tmax is strongest at WHT. Tmin might be important at WHT also, but it was excluded from WHT classification modeling because of concerns about model accuracy at lower elevations (near many red-cluster trees). Those models give Tmax or Tmin thresholds between temperature limitation and moisture limitation at the two sites (figures 6 and 7). Like Korner and Paulsen (2004) defined thresholds for the alpine treeline limit, I estimate thresholds for a different forest limit: the limit between temperature- and moisture-limited trees, alluded to in terms of elevation by Salzer et al. (2014). These thresholds allow a better understanding of bristlecone pine physiology. For example, at MWA I am able to infer that trees growing in
areas with growing season Tmin > 3.1°C will be limited by temperature. As temperature is more meaningful than elevation as a driver of growth, temperature thresholds from the classification models allow better biological understanding than the elevational threshold 60-80 meters below upper treeline that Salzer et al. (2014) propose.

Minimum temperature was excluded from classification modeling at WHT because of concerns regarding the accuracy of the temperature model. At WHT, the Tmin model was heavily influenced by topographic convergence index (TCI). In some low elevation areas, the Tmin model predicted large-scale cold air pooling because of a large upslope area and the strong influence of TCI in the model. The model predicted low temperatures in those low elevation areas where many moisture-limited trees grow. To give an idea of anomalous minimum temperature modeling at WHT, figure 16 displays a side-by-side comparison of Tmin and Tmax at MWA versus at WHT, along with diurnal temperature range.

It is possible that cold air pools at lower elevations (Katurji and Zhong 2012; Lundquist and Cayan 2007), though likely not at the scale predicted by the Tmin model at WHT. Cold air pooling could lead to trees at lower elevations (i.e., in valleys) experiencing lower minimum temperatures. Multiple studies have found that cold air drainage primarily occurs during clear nights (Goulden et al. 2006; Smith et al. 2010), and Tmin is typically a nighttime occurrence. The Tmin model at WHT likely exaggerates cold air pooling. There is no apparent biological mechanism that would drive trees in areas with very low minimum temperatures (with some growing season Tmin values < 0) to have a “moisture-limited growth signal.” I conclude that the Tmin model at WHT has been extrapolated too far outside of the area of thermochron placement, leading to inaccuracies in the model.

Though temperature and water availability are the two main limiting factors of bristlecone pine growth, potential evapotranspiration (PET) as a proxy for water balance is not at all as accurate as topoclimate modeling for temperatures in this study. PET is correlated with several other climate and topographic variables, as it was calculated from Tmax, Tmin, and radiation values (Hargreaves and Samani 1985), therefore cluster separation for PET depends on leverage in the other variables. At MWA, where there are no
discernible differences in radiation between the temperature-limited and moisture-limited clusters, there are also no clear differences in PET. Though the moisture-limited cluster at WHT has higher PET values than the temperature-limited cluster, using PET as a proxy for plant-available water may be flawed. PET would be more meaningful in the context of aridity and drought with fine-scale precipitation data, which were not available (Paulo et al. 2012). Incorporating fine-scale hydrologic modeling similar to the temperature modeling in the study or like the California Basin Characterization Model (Flint et al. 2013) could allow for a clearer understanding of moisture limitations on bristlecone growth. I discuss the need for this in the Future Work section below.

Internal tree-ring statistics such as standard deviation and first order autocorrelation coefficient (AR1) are sometimes indicative of different limiting factors of a tree-ring chronology. AR1 describes the relationship between growth in any year \(t\) and the year previous \(t-1\), showing persistence, likely of a biological mechanism, in the trees’ growth (Fritts 1976). Standard deviation, or a measure of variation in ring width, serves as an indicator of the magnitude of environmental ‘signal’ in a chronology (LaMarche and Stockton 1974). LaMarche and Stockton (1974) found that trees at the upper forest border (i.e., temperature-limited trees at highest elevations) had lower standard deviation and higher AR1 than the mean chronology. Similar to the results of LaMarche and Stockton (1974), ring-width data from MWA and WHT in this study demonstrated higher AR1 for temperature-limited trees. But, the data in this study showed that temperature-limited trees had higher standard deviation, unlike the findings of LaMarche and Stockton (1974). Conversely, Wilson and Luckman (2003) found that upper treeline Engelmann spruce chronologies had both high AR1 and high standard deviation, like the temperature-limited clusters in this study. The separation between clusters for standard deviation and AR1 was not as defined as cluster separation for temperature variables (figures 8 and 9).

In this study, I modeled temperatures to study mixed signals in tree growth, while Bunn et al. (2011) used unitless topographic indices like topographic convergence index and topographic position index (De Reu et al. 2013; Van de Ven et al. 2007) to compare
different modes of growth. Finding potential temperature thresholds between a tree being
temperature limited or moisture limited might aid in understanding biological mechanisms
controlling growth. However, the trees are complicated organisms, and several factors
contribute to their success or limitation. The topoclimate modeling in this study takes
several different topographic variables into account, but studying topoclimate in complex
landscapes is complicated, and many factors work together and are correlated in the
natural system.

4.3 Climate-growth analysis by cluster

Several lines of evidence suggest that low-frequency signals are associated with temper-
ature variability and that high-frequency signals are related to moisture variability in
tree-ring chronologies (Esper et al. 2002; Hughes and Funkhouser 2003; LaMarche 1974b).
Low-frequency temperature signals are often visible on multidecadal and multicentennial
terms, while high-frequency moisture signals have one to several year variations (Hughes
and Funkhouser 2003). Temperature-limited clusters at MWA and WHT show most power
around 32-years and greater periods (figures 11 and 13). Moisture-limited clusters show
higher power in higher frequencies, though there are some low-frequency signals mixed in
(figures 12 and 14).

At both sites, what I term ‘temperature-limited clusters’ seem to be composed of
almost exclusively trees that are indeed temperature limited. Temperature models and
RWI (with 20-year smoothing splines) correlate very well (r = 0.66 and r = 0.74 at MWA
and WHT, respectively) for the temperature-limited clusters (table 3). These clusters also
have negligible correlation with PDSI, suggesting that trees in the temperature-limited
clusters were properly clustered. Because the temperature-limited cluster does not have
a mixed signal like the overall site chronologies, mean chronologies from the temperature-
limited clusters in this study would be appropriate for temperature reconstructions.

Cluster analysis did not produce as clean of results for moisture-limited clusters, as
there appear to be some temperature-limited trees within the moisture-limited clusters at
both sites. The fact that the moisture-limited clusters have mixed-signals is also apparent in the dendrogram structure of the red clusters. It is likely that the signals in the red clusters are more complicated, but for the purposes of this analysis, the dual-cluster pattern creates a clean temperature-limited cluster. In the future, a more complicated cluster analysis (i.e., three or more clusters in the analysis like in Bunn et al. (2011)) could lead to a clearer understanding of the moisture-limited cluster. However, one of the strengths of this study is the use of fine-scale temperature data, so a clean temperature-limited cluster allows use of those data; the same data are not currently available to me for moisture.

Tree growth response to climate can change over the lifespan of a tree, both in magnitude of correlation coefficient with climate variables, and in changing from positive to negative relationship or vice versa (Biondi 2000; Jacoby and D’Arrigo 1995; Sullivan et al. 2015; Zang and Biondi 2015). Nonstationary climate-tree growth relationships could be especially applicable with bristlecone pine because of its extreme longevity. The use of wavelet analysis allows frequency analysis over a multicentennial time period. The wavelet plots show rather steady signals in terms of their frequencies, so it is likely that the growth-climate responses are somewhat stable. It is possible that nonstationary climate-growth relationships would become more evident over longer time periods (i.e., multimillennial time periods). In order to avoid mixing the dual modes of growth in bristlecone pine, consideration of stable relationships between growth and climate is important in ensuring accuracy of climate reconstructions.

Salzer et al. (2009) found unprecedented increases in bristlecone radial growth in the second half of the 20th century in the highest elevation trees, likely caused by increases in temperature. Plots of the RWI chronologies from temperature-limited clusters at MWA and WHT (figures 11 and 13) also show increased growth during the same time period, confirming their findings. This increased growth further points to the strong growth-climate relationship of the temperature-limited clusters and will hopefully aid in improving accuracy of temperature reconstructions over the late Holocene.
5 Conclusions

5.1 Summary

This research expands on work by Bunn et al. (2011) and Salzer et al. (2009, 2014) to examine multiple growth signals in bristlecone pines in the Great Basin of the American west. Cluster analysis is a strong tool for identifying patterns in multivariate data, and in this study, it was used to find groups of trees with similar limiting factors of growth. A central goal of this study was to more easily identify trees that are sensitive to a certain limiting factor to improve climate reconstructions of that factor. The objectives section of this report identified three main questions to be answered by this research. The body of the report served to answer these questions in detail, but I will provide an abridged version.

There are not two growth signals (clusters) at each site, according to the subset of trees used in this study, though these conclusions could be biased by sampling methods or a more complicated structure than a two-cluster system. However, at MWA and WHT, there are two growth clusters, with one likely being temperature limited and the other moisture limited. At CSL, there appeared to be only one growth signal, possibly affected by the low range of topographic and environmental conditions sampled from. At PRL, there appeared to be more than two growth clusters. I proceeded with further analysis only at MWA and WHT.

At sites with two-cluster growth structures, I compared the two clusters based on different topoclimate variables. My findings largely coincided with the results of past research (LaMarche and Stockton 1974): temperature-limited trees had the tendency to grow at higher-elevations and in colder temperatures than moisture-limited trees. Given the modeled fine-scale temperature data, I was able to take these conclusions one step further, and examine growth based on real temperature values in degrees Celsius. This allowed for estimation of thresholds between temperature-limited clusters and moisture-limited clusters for multiple environmental variables, and the creation of models to classify trees’ limiting
factors based on the most important topoclimate variables (minimum temperature at both MWA and WHT).

The results of this study will hopefully be able to aid in improving the accuracy of climate reconstructions that use bristlecone pines. Detailed descriptions of different growth signals in terms of topoclimate could help researchers better target trees for sampling and more selectively choose samples for inclusion in reconstructions.

5.2 Future work

Though the fields of dendrochronology and dendroclimatology have made significant progress in recent decades, there is much work remaining to better understand tree physiology and to create better climate reconstructions using tree-ring data. This research is a stepping stone in a larger effort to improve reconstruction accuracy and to better understand patterns in bristlecone pine radial growth.

A central aspect of this research is the use of modeled temperatures to help guide understanding of tree growth, as temperature and moisture availability are the most influential variables on bristlecone pine growth. One drawback of this study is that I used potential evapotranspiration (PET) as a proxy for moisture availability. Deploying moisture sensors across the landscape as I did with temperature sensors would have been costly. Future studies could use hydrologic modeling to better understand moisture limitations on bristlecone pine growth. A prime candidate for an appropriate hydrologic model is the California Basin Characterization Model (Flint et al. 2013).

This study uses cluster analysis to identify growth signals in tree growth. However, I approach growth through a binary lens. Literature on the topic has defined temperature and moisture availability as the two factors most commonly limiting bristlecone growth, but there are more than two signals at some sites. The use of fuzzy logic and fuzzy analysis could possibly suit complicated growth patterns; as climate correlations are often nonstationary, fuzzy analysis would not restrict a tree to a cluster as concretely as methods used in this study (Chen and Wang 1999; Yang 1993).
Milligan (1996) discusses the importance of variable selection in cluster analysis. The inclusion of variables (in this case, growth years) that are not important in finding differences/similarity between samples (in this case, trees) could be detrimental to finding the clearest clusters (Milligan 1980). Future studies could more selectively choose variables; with this data, that would require removing growth years where all trees are similar in ring width to better highlight differences between trees. Though some might view this as a form of cherry-picking, it could highlight differences in growth between individual trees.

While the estimated thresholds between temperature- and moisture-limited tree clusters in this study shed light on bristlecone pine physiology, they are site-specific and species-specific and would likely be difficult to apply to other regions. In the way that Korner and Paulsen (2004) found global thresholds for alpine treeline and that Korner (2012) discusses temperature limits for growth, similar global limits between temperature- and moisture-limited trees would be fascinating. The plausibility of expanding to other spatial areas remains to be seen. However, the thresholds between temperature- and moisture-limited clusters created from the classification models could be applied to trees at MWA and WHT growing outside of the time period in this study. Thresholds in temperature between temperature-limitation and moisture-limitation allow for a more refined understanding of tree biology and physiology, and continue a long history of progressive research on patterns in bristlecone pine growth.
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Appendix

Figure 17: CSL wavelet analysis. The data used in this figure are from the 25 trees previously mentioned in the study. Because trees at CSL did not separate into a two-cluster/dual-signal pattern, the climate and wavelet analysis was performed on all 25 trees. Most variability is low-frequency (decadal to multidecadal). The correlation coefficient between 20-year smoothed ring-width index (RWI) and temperature is 0.83, with a negligible correlation with PDSI. These trees are likely temperature-limited.