

UNRAVELING ENVIRONMENTAL FACTORS THAT AFFECT PINUS
LONGAEEVA GROWTH IN THE WHITE MOUNTAINS, CALIFORNIA

by

Christine Lee Hallman

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As members of the Dissertation Committee, we certify that we have read the dissertation prepared by Christine Lee Hallman

entitled Unraveling Environmental Factors that Affect Pinus Longaeva Growth in the White Mountains, California

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy

Date: June 23, 2010
Paul R. Sheppard

Date: June 23, 2010
Connie Woodhouse

Date: June 23, 2010
Katie K. Hirschboeck

Date: June 23, 2010
David M. Meko

Date: June 23, 2010
Jake Weltzin

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copies of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

Date: June 23, 2010
Dissertation Co-Director: Paul R. Sheppard

Date: June 23, 2010
Dissertation Co-Director: Connie Woodhouse

STATEMENT BY AUTHOR

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SIGNED: Christine Lee Hallman

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"When research has been carried far enough in these Methuselah pines, perhaps their misshapen and battered stems will give us answers of great beauty"

Schulman, Edmund. 1958. Bristlecone pine, oldest known living thing. National Geographic Magazine. 113(3): 354-372.

DEDICATION

This dissertation is dedicated to my grandparents and all those little scientists curious about the world.

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ABSTRACT

Two of the most pressing questions involving ancient bristlecone pines are how microsite factors lead to differences in tree responses to climate at high-elevation sites, and how global change has impacted growing season events. Disparities in climate response at treeline and subalpine locations have been associated with local environmental characteristics while the increasing growth trend found at treeline has been linked to warming. In this study, environmental conditions were considered in order to identify microsite differences between trees growing at two different elevations on four aspects of a conical-shaped mountain in the White Mountains, California. Dendrochronological, environmental, correlational, and spectral methods were employed to explore differences in ring-width chronologies. Albedo, soil thickness, and percent slope led to ring-width variability. Northwestern upper site was most highly correlated with precipitation, while the Southeastern lower site showed a strong negative correlation with temperature. This work indicates that selection of climate-sensitive trees *a priori* necessitates the consideration of local environmental factors, and these microsite differences resulted in different climate responses between nearby trees. By monitoring growing season events at the historic phenology site from the 1962-64 (Fritts 1969), natural variations and responses to climate change can be identified. Morphological and physiological phenophases, dendrometer traces, and environmental data were collected throughout the summers of 2007 and 2008. Duration and timing of cambial activity (tracheid lifespan) in the present study were similar to those recorded in the Fritts (1969) investigation, while pollination onset and bud opening occurred earlier in this study. No

change was found in duration and timing of cambial activity suggesting that changes in cambial phenology are not an explanation for the increasing growth trend found at upper forest borders. On the other hand, changes in bud opening and pollination onset may be related to recent warming. To monitor diurnal and seasonal stem variability as part of phenologic studies on several trees, a point potentiometer dendrometer was designed. The newly designed point potentiometer dendrometer was tested in multiple environments and found to be versatile, cost-effective, and portable, working well in semi-arid and arid environments.

CHAPTER 1: INTRODUCTION

1.1 Explanation of the Problem

The overarching objectives of this research were to investigate how microsite factors lead to differences in tree response to climate at high-elevation arid sites, and to determine if changes in growing season have occurred in comparison to the 1960s. This was accomplished through a multi-faceted project that involved biogeography, dendrochronology, phenology, and new technology. In order to understand the effects of microsite characteristics on *Pinus longaeva* growth and phenologic relationships of *Pinus longaeva*, a two-pronged approach was taken where site selection criteria were evaluated at Blanco Mountain and a variety of phenophases were tracked at a historic observation site (Fritts 1969) in the White Mountains, California, located about 18 km northeast of Bishop, California. While designing the overall project, it became apparent that new technology would improve data collection; thus, a point potentiometer dendrometer was manufactured.

Ring widths are the result of biological and environmental factors that occur on multiple time and spatial scales. Debate is prevalent involving why bristlecone pine response to climate differs at upper forest borders, and why an increasing growth trend occurs at treeline (Salzer et al. 2009). This work investigates how both microsite characteristics and potential growing season changes impact *Pinus longaeva* (Great Basin bristlecone pine) growth at high-elevation sites in the White Mountains of California. Bristlecone pines exhibit a complex climate signal, responding to both temperature and precipitation (Fritts 1969). Specifically, trees located at upper forest borders tend to

respond differently based on their proximity to treeline and possibly local environmental factors (Kipfmüller and Salzer 2010).

To systematically evaluate the influence of microsite characteristics on bristlecone pine ring widths, a conical-shape landform, Blanco Mountain, with distinct aspects and elevations was identified. The first portion of this dissertation addresses the following questions relating to microsite differences: (1) how do microsite characteristics affect *Pinus longaeva* response to climate, and (2) how do elevation, geology, percent slope, and soil thickness influence ring width variability on Blanco Mountain. Next, a phenologic comparison study was conducted to identify any potential growing season changes between data collected in 1962-64 (Fritts 1969) and the present, providing insights into the impact of global change on bristlecone pines and potential explanations for the increasing ring-width trend found at treeline. The second part of this dissertation strives to answer these two questions: (3) what is the relationship between morphological phenophases and cambial activity?, and (4) how does present bristlecone pine phenology compare to that observed 45 years ago by Fritts (1969)? Lastly, diurnal and seasonal stem changes offer information associated with weather and growing season events (Fritts and Fritts 1955; Fritts 1969). Monitoring stem variability on multiple trees across rugged topography in the White Mountains proved problematic. Consequently, a new dendrometer was designed and tested to address the following question: (5) how can stem variability be monitored over a spatially extensive, topographically diverse landscape? Woven together, research involving these five questions provides invaluable information on bristlecone pine growth and variability in general, and specifically

addresses the pressing questions of why bristlecone pines in close proximity respond differently to climate and how global change may be affecting bristlecone pine growth.

Microsite

Pinus longaeva (Great Basin bristlecone pine) are the longest-lived, annually dated trees in the world, with the oldest at over 4700 years (Schulman 1958; Currey 1965). Remnant bristlecone pines remain on steep slopes in the White Mountains, California for millennia (Ferguson 1968; Lanner 2007). As a result, some of the longest chronologies in the world have been created from these trees in order to reconstruct past climate conditions (Fritts 1969; LaMarche 1969; LaMarche 1974b; Graumlich 1993; Hughes and Graumlich 1996; Hughes and Funkhouser 2003; Bunn et al. 2005; Salzer et al. 2009).

Tree growth is impacted by climate, disturbance, physiology, competition, microsite characteristics, and other factors (Cook 1987). In the White Mountains, *Pinus longaeva* are part of an open forest with few disturbances; therefore, the predominant influences on tree growth are climate, genetics, and microsite variables. Disentangling the complex climatic and environmental characteristics that influence *Pinus longaeva* growth would provide a more complete picture of the factors that affect ring-width variability and seasonal growth patterns.

Bristlecone pine ring growth in the White Mountains, California has been related to a mixture of prior and current growing season temperatures and precipitation characteristics (Fritts 1969). Although interannual variability associated with precipitation is found at both the upper and the lower forest borders, this variation is less

pronounced at upper locations. Low frequency variability linked to temperature dominates the upper forest border (LaMarche 1974a); thus, *Pinus longaeva* exhibit a complex climate signal. Trees growing at treeline tend to correlate positively with temperature, but may also possess a positive correlation with precipitation, suggesting that a better understanding of microsite variables would assist in the identification of temperature-sensitive trees *a priori* at treeline and subalpine locations (Salzer et al. 2009; Kipfmüller and Salzer 2010).

Few studies involving these climatically sensitive conifers have been conducted where aspect, elevation, slope, and geology have been assessed involving trees in close proximity to each other. My work begins to fill this gap in knowledge by explaining why bristlecone pines at upper forest borders respond differently to temperature. With a greater comprehension of how microsite characteristics affect tree-ring growth at high elevation sites, climate-sensitive trees can be chosen that will enable the building of climate reconstructions with a clear signal. This systematic investigation of local environmental parameters aids in the evaluation of dendrochronologic principles of site selection and provides insights into how local characteristics influence bristlecone pine growth. My work considers the impact of elevation, aspect, geology, and slope on tree-ring widths on an isolated, conical-shaped mountain in the White Mountains, California.

Phenology

Phenology, the study of periodic life cycle events, is increasingly being utilized to monitor ecological responses to climate variability and climate change (Walther et al. 2002). Identifying high-elevation conifer growing season variability is crucial for

recognizing deviations outside the normal growing season range. By tracking morphological and physiological phenophases, variability in individual phenophases as well as shifts in the overall growing season can be identified. Recently, some upper forest border bristlecone pines have shown an increasing growth trend, which has been associated with increasing temperatures, CO₂ enrichment, changes in phenology, and other environmental parameters (LaMarche et al. 1984; Cooper et al. 1986; Graybill and Idso 1993; Mann et al. 1998; Salzer et al. 2009). Data related to recent seasonal growth behavior of bristlecone pines are lacking except for investigations done by Fritts (1969) and Bailey (1970), which were over 45 years ago.

Growing season shifts and/or lengthening are associated with climate variability and change (Walter et al. 2002). With updated growing season data, the impact of climate change on bristlecone pine phenology, and growing season changes as an explanation for the recent increasing growth trend can be assessed. The current study investigates bristlecone pine morphological and physiological phenology to better understand their variability and how they are related to each other. My research provides updated phenologic information that is compared to data collected in the early 1960s. This study provides data into how global climate change may be affecting long-lived bristlecone pine and the influence of changes in cambial activity (tracheid life) on the increasing growth trend found in bristlecone pines living at treeline.

Dendrometer

Numerous tools are available for dendrochronologic use; unfortunately, many are expensive and/or problematic. This necessitates the design and implementation of new

technology. Currently dendrometers can be purchased that collect and store diurnal and seasonal growth patterns via an automated datalogger (Zweifel and Häsler 2001; Biondi et al. 2005; Intrigliolo and Castel 2005; Rossi et al. 2006; Drew et al. 2008; Pérez et al. 2009). Often these dendro-monitoring systems are expensive and restricted by cable length to the datalogger (Biondi et al. 2005). As part of this dissertation, an inexpensive and portable point potentiometer dendrometer was designed to alleviate these problems. Instruments were tested in multiple environmental settings to evaluate its accuracy. Dendrometer data collected from five *Pinus longaeva* in 2008 were also used in the phenology study mentioned earlier.

1.2 Literature Review

1.2.1 Bristlecone pines

High altitude and latitude ecosystems are some of the most sensitive to climate and therefore are important indicators of climate change (Tranquillini 1979; Lloyd and Graumlich 1997; Tessier et al. 1997; Malanson et al. 2007). High-elevation conifers in the western U.S.A., such as bristlecone pines and *Pinus balfouriana*, are sensitive to precipitation and temperature variability (LaMarche 1974b; Graumlich 1993; Hughes and Graumlich 1996; Bunn et al. 2005). Consequently, multi-millennial length chronologies have been created from these samples in order to develop paleoclimate reconstructions (Fritts 1969; LaMarche 1969).

Generally, bristlecone pines do not have a single-component climate signal, but rather they respond to both seasonal temperature and precipitation patterns. A multi-

decadal precipitation signal is present at lower forest border sites (Briffa 1996; Ni et al. 2002), while low frequency variation associated with temperature occurs at upper forest border sites (Hughes and Funkhouser 2003). Bristlecone pines located at some treeline locations appear to be positively correlated with temperature while at other treeline sites they show no significant correlation with temperature (Salzer et al. 2009; Kipfmüller and Salzer 2010).

A recent unprecedented increasing trend in bristlecone pine ring widths at upper forest borders has been identified in the western USA (LaMarche et al. 1984; Graybill and Idso 1993; Mann et al. 1998; Salzer 2009). Several hypotheses have been presented for bristlecone pine ring width increases at treeline in the last 150 years. Increasing temperatures (LaMarche and Stockton 1974; Salzer et al. 2009) and atmospheric CO₂ levels have long been associated with enhanced bristlecone pine growth (LaMarche et al. 1984; Graybill and Idso 1993) while higher levels of insolation, changes in phenology (Cooper et al. 1986) and nitrogen fertilization (Fenn et al. 2003; Brooks and Coulombe 2009) have also been offered as explanations for growth trends at treeline locations. Of these potential reasons for increased growth, warming remains a leading candidate for increasing bristlecone pine ring widths at treeline, but recent phenology studies in the area are lacking. Additionally, a pronounced sensitivity to temperature occurs within 150 m of the upper forest border at some bristlecone pine sites, which all show a distinct positive correlation with temperature while bristlecone pines a couple of hundred meters lower correlate negatively with temperature, suggesting that trees growing in extreme conditions at treeline are most sensitive to temperature (Salzer et al. 2009).

The most pressing questions involving bristlecone pines are why do trees growing in close proximity respond differently to climate, what causes the increasing growth trend found at treeline, and how has bristlecone pine growing season been affected by climate change. This work addresses these three questions by investigating how microsite factors impact tree growth and identifying changes in phenology between the present and the 1960s. Assessing the degree to which microsite differences influence ring widths enables the selection of climate-sensitive trees, resulting in climate reconstructions that incorporate a single-component climate signal. This research also provides an updated comparison to Fritts (1969) where shifts in bristlecone pine growing season events are associated with changes in climate and weather events.

1.2.2 Microsite

Trees respond to climate via complex interactions between ecological and physiological processes and microsite characteristics (Dougherty et al. 1994; Tessier et al. 1997; Girardin and Tardif 2005). Climate variability and climate change are processed at the tissue, individual tree, stand, and ecosystem scales (Smith and Hinckley 1995). Difficulties arise when attempts are made to separate the influence of temperature, precipitation, aspect, elevation, and soil characteristics on tree growth in order to reconstruct past temperatures (Tessier et al. 1997; Oberhuber and Kofler 2000; Liang et al. 2006). Disentangling these influences is problematic for tree-ring studies of living trees, not to mention paleo-environmental reconstructions using trees that lived thousands of years ago, such as *Pinus longaeva*.

The linear aggregate model uses age-size trends, climate, disturbance, and other signals to explain ring-width variability (Cook 1987). By comparing trees in close proximity, which are influenced by the same regional climate and rarely experience disturbance, impacts of local terrain on ring widths can be determined. This is the case with *Pinus longaeva* in the White Mountains, California, where trees survive for millennia in open forests where fires are uncommon. A conical-shaped mountain with upper and lower stand limits, four aspects, and only two rock types in the White Mountains provides an excellent opportunity to investigate the effects of microsite differences such as aspect, elevation, geology, and slope on tree-ring widths.

To unravel the climate-site-tree complex, the impact of microsite characteristics must be determined. Elevation, slope, and aspect affect soil and air temperatures, wind exposure, and snow accumulation (Ettl and Peterson 1995; Kirchhefer 2000; Kjallgren and Kullman 2002; Tardif et al. 2003; Li and Yang 2004; Oberhuber 2004; Case and Peterson 2005; Johnson and Miller 2006; Fan et al. 2009). Soil erosion, water availability, and nutrient supply are also altered by aspect and slope magnitude (Gutiérrez 1991; Villalba et al. 1994; Oberhuber and Kofler 2000; Sheppard et al. 2001; Li and Yang 2004; Johnson and Miller 2006). Additionally, albedo of surface materials plays an important role in temperature and soil moisture availability (Wright and Mooney 1965).

In order to delve into local landscape differences and tree-ring width, this study compares *Pinus longaeva* raw ring-width chronologies from varying aspects and

elevations on Blanco Mountain in the White Mountains of California to answer the following questions:

- How do microsite characteristics affect *Pinus longaeva* response to climate?
- How do elevation, geology, percent slope, and soil thickness influence ring width variability on Blanco Mountain?

Bristlecone pines exhibit a complex signal at upper forest border locations where not all trees have positive correlations with temperature (Salzer et al. 2009).

Investigating the influence of microsite factors on ring growth offers explanations into why ring widths differences occur at high elevation locations. With an in-depth systematic evaluation of microsite characteristics, the selection of climate-sensitive trees *a priori* is possible enabling the building of upper forest border climate reconstructions with a clear climate signal.

1.2.3 Phenology

The timing of growing season events affects a variety of environmental processes. The initiation, ending, and length of the growing season influence global biogeochemical cycling by impacting movement and storage of water, carbon, and nutrients (Ludeke et al. 1994; Chuine and Beaubien 2001; McCarty 2001; Penuelas et al. 2001; Prigent and Aires 2001; Leinonen et al. 2002; Linderholm et al. 2006; Reed 2006). Additionally, accurate and precise phenological data have been indispensable for tree growth, climate, and ecological models used to better understand vegetation changes, which is key for indentifying current tree-climate relationships and forecasting potential changes in forest growth, ecosystem productivity, and changes in carbon sequestration (Dougherty et al.

1994; Leinonen and Kramer 2002; Peltola et al. 2002; Vaganov et al. 2005; Bailey and Harrington 2006; Linkosalo et al. 2006; Cleland et al. 2007).

Observable phenophases in conifers include onset and cessation of cambial growth, bud opening, needle elongation, emergence of reproductive parts, and pollination. The timing of morphological events varies according to both genetic and environmental conditions (Dougherty et al. 1994; Chuine and Cour 1999; Chuine et al. 2003; Mutke et al. 2003; Cleland et al. 2007). Physiological phenology refers to xylogenesis, the process of ring formation, including onset and termination of cambial growth. Growth onset is driven predominantly by spring temperatures (Rossi et al. 2006; Rossi et al. 2007; Deslauriers et al. 2008). In climatically sensitive European and Canadian conifers, onset of cambial activity occurs within a narrow window of daily temperatures (Rossi et al. 2008). Cessation of growth occurs at approximately the same time annually, which suggests that photoperiod controls cambial growth termination (Dougherty et al. 1994; Rossi et al. 2006; Rossi et al. 2007).

Ring widths are determined by size of earlywood cells (Deslauriers et al. 2008) and/or rate of cell production (Fritts et al. 1999). Consequently, phenological changes may impact ring widths. For instance, lengthening of the growing season may increase the amount of wood produced by a given tree annually and lead to an increasing growth trend (Cooper et al. 1986).

***Pinus longaeva* and prior physiological studies**

Previous bristlecone pine physiological studies were conducted in the 1960s. Bailey (1970) botanically distinguished *Pinus longaeva* from *Pinus balfouriana* and

Pinus aristata using differences in needles, cones, male strobili, and other characteristics. Although no in-depth phenological study was conducted, the written descriptions and photographs aided in the identification of *Pinus longaeva* vegetative and reproductive parts. Fritts (1969) conducted an intensive study of a variety of *Pinus longaeva* characteristics in the White Mountains, California. Of particular interest to the current study is the collection of phenologic and environmental data in the summers of 1962-64, where cambial activity duration was 45-60 days in length. Phenophases varied from year to year and with elevation. Onset of growth depended on temperature while rate of growth depended on moisture regimes.

By using descriptions from Bailey (1970) and growing season data from Fritts (1969), the present study was able to identify and document *Pinus longaeva* phenophases. Growing season and environmental information collected over 45 years ago at the historic phenologic site (Fritts 1969) provides the basis for comparing data recorded in this study so that further insights on *Pinus longaeva* growth patterns and any differences in phenophases between the studies can be identified.

The objectives of this investigation were to answer the following:

- What is the relationship between morphological phenophases and cambial activity?
- How does present bristlecone pine phenology compare to that observed 45 years ago by Fritts (1969)?

Understanding the relationship between morphological phenophases and cambial activity may enable the detection of growing season shifts and/or lengthening through the use of easily observable morphological events rather than lab-intensive procedures

associated with monitoring cambial growth. Additionally, investigation of bristlecone pine physiology provides details into the growth of these ancient trees used to reconstruct past climate. This knowledge adds to previously collected growing season data collected by Fritts (1969) and enables the assessment of potential growing season changes associated with climate change. Alterations in bristlecone pine growing season may also provide a possible explanation for the increasing growth trend found in temperature-sensitive treeline locations.

1.2.4 Dendrometers

Understanding complex tree-environmental relationships on individual and stand scales requires numerous samples and long-term investigations in multiple locations. Studies of diurnal and seasonal stem changes have been conducted for decades (MacDougal 1921; Fritts and Fritts 1955; Studhalter et al. 1963; Fritts et al. 1965; Drew and Downes 2009). The daily contraction and expansion and seasonal changes of a tree bole provide insights into water-tree relationships (Abe and Nakai 1999; Zweifel and Häsler 2001; McLaughlin et al. 2003; Bucci et al. 2004), drought effects or water stress (Hinckley and Bruckerhoff 1975; Intrigliolo and Castel 2005; Drew et al. 2008; Tognetti et al. 2009), wood density (Wimmer et al. 2002; Bouriaud et al. 2005), phenology (Turcotte et al. 2009), and radial growth (Deslauriers et al. 2003; Rossi et al. 2006; Deslauriers et al. 2007; O'Brien et al. 2008).

Dendrometers are used to measure stem changes in order to identify variability among trees and between trees and their environment. Band and point are two types of dendrometers often used. Band dendrometers measure diurnal variability around the

circumference of a stem at a particular height (Reineke 1932) while point dendrometers measure stem fluctuations along a single radius (Breitsprecher and Hughes 1975).

Advantages and disadvantages are apparent for band and point dendrometers. Additional time is needed to equip the tree with a band dendrometer since bark must be scraped around entire tree circumference (Fuller et al. 1988; Keeland and Sharitz 1993), while point dendrometers require fewer installation tools and are easier to set up. Automatic band dendrometer readings are transferred from band movement to a friction wheel to a rotary potentiometer, which allows for encoding errors to occur more frequently (Pesonen et al. 2004). Alternatively, automated point dendrometers are in direct contact with the stem via a plunger resting against the trunk reducing the steps between stem movement to datalogger (Drew and Downes 2009). Although band dendrometers integrate stem variability over a circumference and provide an accurate estimation of overall radial growth, they may underestimate cambial growth (Bower and Blocker 1966). Point dendrometers are less sensitive to temperature changes (AEC 2010), but involve the measurement of relatively small movements. Point dendrometers also provide a method to monitor unusual tree growth forms or habits.

Dendrometers and associated dataloggers have advanced tremendously over the last forty years, but they remain expensive and/or cumbersome. Linear Variable Differential Transformers (LVDT) have been used in point dendrometers to record stem fluctuations in both plantation and forest settings (Gensler and Diaz-Munoz 1983, Tardif et al. 2001; Zweifel and Häsler 2001; Deslauriers et al. 2003; Mäkinen et al. 2003; Pesonen et al. 2004; Rossi et al. 2006; Drew et al. 2008; Turcotte et al. 2009). LVDT

dendrometers are accurate, but they are relatively expensive, connected to fairly large dataloggers, and limited by cable length from sensor to datalogger (Biondi et al. 2005). Another type of automated dendrometer, the rotary potentiometer band dendrometer, is durable, but requires custom fabrication at a machine shop, slightly overestimates tree growth, and requires complex calculation for data formatting (Pesonen et al. 2004).

Light-weight, cost-effective dendrometers, dataloggers, and associated installation tools improve the ease with which equipment is carried and increase the number of instruments that can be installed during a single field trip. Tree studies are often located in steep, rocky terrain and therefore are difficult to access by vehicle; thus, relatively small, inexpensive dendrometers and dataloggers enable greater numbers of trees to be investigated, which strengthens the interpretability of results.

Monitoring of stem variability on multiple trees in the White Mountains necessitated the design of a new dendrometer. The dendrometer was tested in multiple environments in order to answer the following:

- How can stem variability be monitored over a spatially extensive, topographically diverse landscape?

1.3 Organization of Dissertation

This dissertation contains three pre-publication manuscripts that appear as Appendices A, B, and C.

The first manuscript (Appendix A) is entitled, “Effects of microsite characteristics on *Pinus longaeva* ring-widths at Blanco Mountain in the Whites Mountains, California.”

For this portion of my research, I designed the project, collected and analyzed all on-site

temperature and soil moisture data, and prepared, crossdated, and analyzed all tree-ring cores collected. Over the course of two summers, I and three field assistants collected tree-ring samples. I wrote the manuscript. My co-author on this manuscript is Paul Sheppard. This paper will be submitted to *Madroño*.

The second manuscript (Appendix B) is entitled, “Morphological and physiological phenology of ancient *Pinus longaeva* in the White Mountains of California.” For this part of my research, I modified the project design of Fritts (1969), collected and analyzed phenologic, wind, soil temperature, air temperature, photosynthetically active radiation, and dendrometer data; Howard Arnott processed the cambial samples; I analyzed all of the data and wrote the manuscript. My co-author on this manuscript is Howard Arnott. This manuscript will be submitted to *Trees: Structure and Function*.

The third manuscript (Appendix C) is entitled, “Monitoring stem variability over a spatially extensive, topographically diverse landscape.” For this portion of my research, I collected and analyzed all of the dendrometer data; I wrote the manuscript. Scott Parkinson and I designed the new dendrometer and he manufactured it. My co-author on this manuscript is Scott Parkinson. This paper will be submitted to *Environmental Monitoring and Assessment*.

CHAPTER 2: PRESENT STUDY

The methods, results, and conclusions of this study are presented in papers appended to this dissertation. The following is a summary of the most important findings in this document. Detailed descriptions and complete studies are located in the appendices.

2.1 Effects of microsite characteristics on *Pinus longaeva* ring widths

Unraveling tree-environment relationships provides a better understanding of how trees respond to their regional and local settings. At the same time, selecting climate-sensitive trees in a given location is vital to reconstructing past climates. With the need to build accurate paleoclimate reconstructions that represent a single-component climate signal, selecting trees from climate sensitive sites is imperative. This portion of the dissertation specifically addresses the influences of microsite characteristics on tree-ring growth in the White Mountains of California.

In order to investigate microsite effects on tree-ring growth, Blanco Mountain, an isolated, conical-shaped mountain, was investigated. The shape provided an opportunity to sample trees from two elevations and multiple aspects within a short distance of each other. Treeline is present only on the NW top site, where mobile, steep, boulder slopes inhibit bristlecone pine establishment (Lanner 2007). A minimum of twenty trees was sampled within each plot (total of 180 trees) in 2007-09. Samples were prepared (Phipps 1985), crossdated (Douglass 1941), measured (Robinson and Evans 1980), and statistically checked for quality control using COFECHA (Stokes and Smiley 1968; Fritts 1976; Holmes 1983; Grissino-Mayer 2001). To retain original ring-width values and

avoid data transformation biases, tree-ring widths were not standardized (Salzer et al. 2009). Instead, sub-plot chronologies were built by using a biweight robust mean to average trees, creating tree-ring chronologies based on averaged ring widths (Cook 1985; Briffa et al. 1996; Salzer et al. 2009). Trees younger than 300 years old were not used in the chronologies, and early portions of ring series exhibiting growth trends were removed. Tree-ring series were also combined to create elevation and aspect chronologies. Time series plots and descriptive statistics were used in comparison analysis (Macias et al. 2004; Liang et al. 2006; Fan et al. 2009). Air temperature was collected within each plot every four hours from 2007-09 in order to determine if measureable temperature differences were present. Soil moisture sensors were installed near each temperature sensor during the summer of 2008 at a depth of 15 to 20 cm, where the majority of *Pinus longaeva* roots are located (Fritts 1969; Lanner 2007). Daily and monthly median temperatures were calculated for each sub-site and then compared. Using Nevada Division 3 climate data (<http://www1.ncdc.noaa.gov>), correlations (Blasing et al. 1984) between each chronology and monthly temperature and precipitation were determined for 1896-2007. Low-frequency similarities and differences between sites were investigated using spectral analysis (Ise and Moorcroft 2008).

Results

Similarities and differences between chronologies were identified using dendrochronological, environmental, correlational, and spectral techniques. Sub-site chronologies correlate significantly with each other at $P < 0.001$. In the relatively short time span of 1800 to 2007, no significant series-length trend is present in any of the sub-

sites. The bottom chronologies show noticeably higher radial growth than top chronologies.

For tree growth and temperature, standard seasonal correlations (prior summer, prior fall, prior winter, spring, summer) generally show negative correlations with all seasons except prior winter temperatures, while seasonal correlations are positive with all but current summer precipitation. The strongest correlations with precipitation are found in the top chronology while the bottom is more negatively correlated with temperature.

Of the sub-plot chronologies, SE Bottom has the highest low-frequency spectral value at 80 years while NE Top and NW Top exhibit the lowest. Amplitudes are high for bottom sub-site and SW Top chronologies, which indicate they have more decadal variability than the other chronologies.

Results from this investigation indicate that microsite characteristics play an important role in how trees respond to climate. In particular, albedo, soil characteristics, and percent slope produce ring width variability between sub-sites in close proximity. This work confirms the hypothesis offered by Kipfmüller and Salzer (2010) that local environmental factors may lead to noticeable differences in bristlecone pine response to climate at upper forest borders. As a result, identifying trees *a priori* that are likely to respond positively to temperature is possible if microsite characteristics are evaluated prior to sampling. Consequently, temperature-sensitive trees can be selected to build temperature reconstructions producing chronologies with a clear climate signal.

2.2 Morphological and physiological phenology of *Pinus longaeva*

Tracking phenology, periodic growing season events, is an excellent method for monitoring both climate variability and climate change (Walther et al. 2002).

Understanding the relationship between phenophases enables in-depth comprehension of tree growth and tree response to its environment. Delineating natural growing season variability aids in the identification of unusual trends and long-term patterns of climate-sensitive species (i.e., *Pinus longaeva*).

Additionally, debate involving the cause(s) of the unprecedented increasing trend in *Pinus longaeva* ring widths at upper forest borders began over 30 years ago and continues today. The most widely accepted reason for the unusual growth is increasing temperatures, but CO₂ enrichment, nitrogen fertilization, and changes in phenology have been offered as causes as well (LaMarche et al. 1984; Cooper et al. 1986; Graybill and Idso 1993; Mann et al. 1998; Fenn et al. 2003; Brooks and Coulombe 2009; Salzer et al. 2009). This part of the dissertation focuses on understanding relationships between morphological and physiological phenophases and comparing the timing and duration of growing season events today with those observed in the 1960s by Fritts (1969).

The historic Fritts (1969) study site was re-identified in 2006 using the study map provided in the publication. The present phenological study included 16 trees in 2007 and 2008 and five additional trees in 2008. Morphological phenophases based on reconstructed Fritts (1969) descriptions were identified and documented during the summers of 2007 and 2008. These phenophases were recorded via photographs and

measurements taken every 3 to 4 days from four branches per tree. Terminal bud diameter and length and needle length were measured using digital calipers.

Cambial samples were collected weekly in the summers of 2007 and 2008 from five trees each summer. The five trees punched in 2008 were also equipped with point dendrometers. Cambial samples were stored in Formalin-Acetic Acid-Alcohol (FAA) solution, 70% alcohol, (Arnott 1958) in the field and were processed by Dr. Howard Arnott. Samples were thin-sectioned using razor blades and living tracheids were counted (Bonar et al. 1925; Foster 1942; Sass 1951; Berlyn and Miksche 1976). Morphological phenophases were compiled and dates were determined for each tree based on the average of four observation branches. Morphological and cambial phenology dates for 1962-64 were compared statistically with those collected in this study. In order to identify any relationships between phenophases, weekly rates for bud swelling and elongation, needle elongation, and tracheid formation were calculated and analyzed. Air and soil temperature, photosynthetically active radiation, wind, and precipitation data were also collected. Daily averages for minimum and maximum air and soil temperatures were calculated.

Results

Phenological observations indicate that growing seasons in 2007 and 2008 were similar in length and that phenophases progressed in the same sequence. However, variability in the timing of phenophases was observed. Cambial onset initiated during bud swelling and elongation, whereas bud opening occurred soon after cambial activity began. Generally, pollination ceased before cambial activity ended. Length of cambial

activity was virtually the same while the timing of growing season onset was shifted 12 days later in 2008. The majority of morphological phenology occurred earlier in 2007 than 2008. Differences in the timing of phenophases between years are associated with weather variability. A slight decrease in bud length growth coincided with cambial onset. A decrease in needle length growth occurred simultaneously with pollination end. A peak in needle length rate occurred with cessation of cambial growth.

A comparison of results from this study and Fritts (1969) show that cambial activity during the 1960s study varied from 46 to 54 days in duration which is similar to both 2007 and 2008. Bud opening and pollination onset was earlier in 2007 and 2008 when comparing data from this study and data collected in 1962-64.

This research indicates that present cambial activity (tracheid lifespan) is not different from the 1960s Fritts landmark study, potentially leaving warming as a leading candidate for the increasing growth trend found at treeline. Further phenologic studies at treeline are necessary to confirm this hypothesis. Also, earlier bud opening and pollination onset suggest that these phenophases may be sensitive to increasing temperatures and potentially provide evidence for climate change on bristlecone pines in the White Mountains, California. Continuous tracking of phenophases in the White Mountains will enable the detection of growing season trends.

2.3 Newly designed point potentiometer dendrometer

Monitoring diurnal and seasonal stem variation provides information on stem-water relationships (Abe and Nakai 1999; McLaughlin et al. 2003), drought stress

(Hinckley and Bruckerhoff; Drew et al. 2008), wood properties (Wimmer et al. 2002; Bouriaud et al. 2005), radial growth (Deslauriers et al. 2003; Rossi et al. 2006) and phenology (Turcotte et al. 2009). The ability to monitor numerous stems in rugged isolated landscapes permits the collection of stand-level stem changes. With more trees observed, tree-environment connections can be better understood. The creation of a portable, cost-effective point dendrometer enables the observation of more stems. This portion of my dissertation involved the manufacture and testing of a newly designed Point Potentiometer Dendrometer (PPD).

Point Potentiometer Dendrometer assessment was conducted on several *Pinus longaeva* growing in valley and steep, rugged settings in the White Mountains of California during the summers of 2007 and 2008. Of those, two were installed with both the Linear Variable Differential Transformer (LVDT) system (AEC 2010) and the PPD. Tree A was installed with PPD and LVDT dendrometers and evaluated for 50 days while Tree B was observed for 82 days. Daily temperatures ranged from 7 to 20° C in 2007 and 8 to 21° C in 2008. Total precipitation in the summer of 2007 was 1 to 2 cm while 3 to 4 cm fell in 2008.

In order to test the PPD on different species and in different environments, trees inside and outside Biosphere 2, an environmentally controlled facility near Tucson, Arizona, were equipped with dendrometers in 2009. Tree C, an *Acacia nilotica* growing in the tropical savanna biome of Biosphere 2 was selected based on its diameter (greater than 30 cm) and ease of access, and it was equipped for 47 days. Tropical savanna temperatures and relative humidity varied from 18-32° C and 31-94%, respectively

(Schronk 2010). Two *Platanus wrightii* tested outside of Biosphere 2 are located in a low-lying area near an irrigated field. Temperatures collected *in situ* ranged from 3 to 29° C with no measureable precipitation recorded during this period (National Weather Service 2010). Stem readings for Tree D were collected for 20 days while readings for Tree E were recorded for seven days. Stem variations were recorded for 16 days on the *Eucalyptus* spp. in January 2010 located in central Tucson. Temperature varied from 1-22° C and 5.3 cm of precipitation was recorded (National Weather Service 2010). Daily minimum, maximum, and median values were calculated and used for correlation analysis.

Results

Point Potentiometer Dendrometers recorded both diurnal and seasonal stem changes on multiple trees under several environmental conditions. Using time series comparisons, PPD matched the automated LVDT point dendrometer (AEC 2010) fairly consistently. Expansion of stems during early morning and contraction in afternoon and long-term seasonal fluctuation of stems were evident. All median dendrometer values are significantly correlated between the LVDT and PPD. In the instances where daily minimum and maximum values are not highly correlated between instruments, diurnal fluctuations may be minimal and/or differences result from relative heights of dendrometers on stem.

2.4 Major conclusions

2.4.1 Effects of microsite characteristics on *Pinus longaeva* ring widths

In the present study, chronologies within 1200 m of each other share interannual variation, but show differences in dendrochronologic, correlation, and spectral values. Differences in geology, steepness, soil thickness on Blanco Mountain impact moisture availability, and thereby, influence ring-width variability. Dendroclimatic sites are chosen based on their aspect, elevation, and slope. A problem occurs when microsite characteristics are more influential than assumed, warranting evaluation of local environmental factors. This dataset from Blanco Mountain allows for a systematic investigation into how microsite landscape characteristics impact ring widths and suggests that these factors be considered in site selection of climatically sensitive trees for paleoclimate reconstructions.

This study begins to fill the gap between what is known about *Pinus longaeva* response to climate components and how microsite parameters influence tree response to the environment. Rock type and percent slope led to a prominent drought signal at NE and SE Bottom sites. Percent slope and soil thickness influence the frequency of locally absent rings on the NW Bottom. Shading from nearby topographic features influences temperature and moisture retention at the SW Bottom. On Blanco Mountain, the NW Top emerges as the best site for reconstructing precipitation as ring widths are significantly correlated with precipitation. SE and NE Bottom locations are negatively correlated with temperature and would be likely locations for reconstructing drought

signals. As a result of this work, microsite characteristics appear to be the reason for differences in temperature response of high-elevation *Pinus longaeva*.

At this particular mountain in the White Mountains, a more instrumentally intensive study would provide additional data on the overall influence of local factors on ring-width. With the use of more temperature sensors, soil moisture sensors, and numerous anemometers, a more resolved picture of microsite factors could be discovered. Incorporating all spatial data, including satellite imagery and snow information, into a GIS would aid in the identification of spatial differences between sites (Bunn et al. 2005b).

Investigating how the importance of a given microsite factor may change over time would assist in creating more accurate paleoclimate reconstructions. This could be accomplished by acquiring samples from remnant wood and snags on Blanco Mountain. Collecting samples in swaths from top to bottom would shed light on transitions in elevation. In order to better understand the influence of microsite factors on ring widths and paleoclimate reconstructions, additional conical mountains with a wider elevation range should be analyzed as well.

2.4.2 Morphological and physiological phenology of *Pinus longaeva*

This research provides an updated and detailed examination of *Pinus longaeva* growing season in the White Mountains, California. As in Fritts (1969), phenophases occur in a predictable sequential pattern driven by genetics. Cambial onset was twelve days later in 2008 as opposed to 2007 while the duration of cambial activity was nearly the same for both years. The later onset was the result of a late season snow storm.

Cambial growth occurred at warmer temperatures than those observed in Canadian and European conifers studied by Rossi et al. (2008). The duration of cambial activity for this study and Fritts (1969) were similar except for in 1964, which was slightly shorter. This study suggests that changes in the duration and timing of *Pinus longaeva* cambial activity are probably not responsible for the increasing growth trend at treeline. Bud opening and pollination onset occurred earlier in the present study, indicating that these phenophases may be influenced by increasing temperatures. Both Fritts (1969) and this investigation found that earlier growing season onsets tend to take place in dry, warm springs, indicating that during extended dry, warm periods, shifts to earlier growing season onsets may occur.

Two short periods of time, 1962-64 and 2007-08, do not provide adequate data to identify long-term phenologic patterns, but rather they simply present data on the possible natural range of growing season variability. Frequent monitoring of phenology would reveal long-term growing season trends in these and other climatically sensitive trees.

2.4.3 Monitoring stem variability over a spatially extensive, topographically diverse landscape

The Point Potentiometer Dendrometer is an inexpensive and convenient option for monitoring tree stem fluctuations simultaneously on numerous trees. The PPD recorded data on multiple species in temperatures ranging from 1 to 32° C and relative humidity ranging from 31-94%, suggesting that it is a versatile instrument. LVDT and PPD stem data are most highly correlated in arid to semi-arid environments. An advantage of the

PPD is that it resists oxidation, while the main disadvantage is that it appears to be less sensitive to stem changes than the LVDT. Durability of Point Potentiometer

Dendrometers in cold environments and its lifetime of usability remain unknown.

Further testing and calibration of the PPD on more trees in other environments would provide additional information on its utility and reliability.

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APPENDIX A

**EFFECTS OF MICROSITE CHARACTERISTICS ON *PINUS LONGAEEVA* RING
WIDTHS AT BLANCO MOUNTAIN IN THE WHITE MOUNTAINS,
CALIFORNIA**

Christine Hallman and Paul Sheppard

RH: Effects of microsite factors on *Pinus longaeva*

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Effects of microsite characteristics on *Pinus longaeva* ring widths at Blanco Mountain in
the White Mountains, California

Christine Hallman^{1*}, Paul Sheppard¹

¹ *The University of Arizona, Laboratory of Tree-Ring Research, Tucson, AZ 85721*

*Corresponding author: Laboratory of Tree-Ring Research, The University of Arizona,
105 West Stadium, Tucson, AZ 85721, USA. Tel: +520-621-5391, fax: +520-621-8229,
email: hallman@ltrr.arizona.edu

A.1 Abstract

Millennial-length reconstructions built from high-elevation *Pinus longaeva* in the western USA provide a remarkable record into past precipitation and temperature patterns. Tree response to climate is modified by local-scale conditions where individual trees grow. These high-elevation conifers respond to temperature and precipitation variability, which often leads to a complex climate signal recorded in their ring widths. Microsite investigations involving *Pinus longaeva* are rare and this study would begin to bridge the gap between what is known about their response to climate and the mechanisms that lead to different growth responses to temperature at upper forest borders. To analyze microsite differences, eight sub-sites on a conical shaped mountain in the White Mountains, California were investigated. Air temperature, soil moisture, geology, aspect, percent slope, and elevation were considered in order to identify differences between sub-sites, aspect, and elevation. Dendrochronological, environmental, correlational, and spectral analysis methods were employed to explore differences in raw ring-width chronologies. Results indicate that microsite characteristics play an influential role in ring width variability between trees in close proximity to one another. Low albedo strata and gentle slopes produce a prominent drought signal on NE and SE Bottom sites. A gentle slope and thick soil influence the frequency of locally absent rings on the NW Bottom. Shading from nearby topographic feature influences temperature and moisture retention at the SW Bottom. Microsite characteristics appear to be the reason for differences in temperature response of high-elevation *Pinus longaeva*.

Keywords: bristlecone pine, microsite

A2. Introduction

Trees respond to climate via complex interactions between ecological and physiological processes and microsite characteristics (Dougherty et al. 1994; Tessier et al. 1997; Girardin and Tardif 2005). Climate variability and climate change are processed at the tissue, individual tree, stand, and ecosystem scales (Smith and Hinckley 1995). Understanding how local landscape characteristics, such as aspect, elevation, percent slope, and soil characteristics, affect tree-ring growth allows the building of accurate paleoclimate reconstructions (Tessier et al. 1997; Oberhuber and Kofler 2000; Liang et al. 2006). Disentangling these microsite influences is especially difficult for tree-ring studies involving species that have a complex climate signal. For example, *Pinus longaeva* are relatively high elevation species, which may suggest a dependence on temperature, but their growth is associated with temperature *and* precipitation (Fritts 1969; LaMarche 1974a). Trees growing at or very near treeline are positively correlated to temperature however trees growing at slightly lower elevations are negatively correlated with temperature (Salzer et al. 2009). Upper forest border *Pinus longaeva* growth also contains a precipitation component. These subtle differences in elevation and temperature/precipitation sensitivity suggest microsite variables may influence observed differences in ring widths at treeline. Mechanisms for the differences in trees response to regional climate are thought to be related to microsite characteristics, but such comprehensive local scale *Pinus longaeva* studies are rare (Kipfmüller and Salzer 2010). This study presents the first detailed analysis attempting to unravel the climate-site-tree complex by systematically identifying the influence of microsite characteristics.

Microsite

Elevation, slope, and aspect affect soil and air temperatures, wind exposure, and snow accumulation (Ettl and Peterson 1995; Kirchhefer 2000; Kjallgren and Kullman 2002; Tardif et al. 2003; Li and Yang 2004; Oberhuber 2004; Case and Peterson 2005; Johnson and Miller 2006; Fan et al. 2009). Soil erosion, water availability, and nutrient supply are also altered by aspect and slope magnitude (Gutiérrez 1991; Villalba et al. 1994; Oberhuber and Kofler 2000; Sheppard et al. 2001; Li and Yang 2004; Johnson and Miller 2006). Additionally, albedo of surface materials plays an important role in temperature and soil moisture availability (Wright and Mooney 1965).

A linear aggregate model can employ age-size trends, climate, disturbance, and other signals to explain ring-width variability (Cook 1987). By comparing trees in close proximity influenced by the same regional climate that rarely experience disturbance, the impacts of local terrain on ring widths can be identified. This is the case with *Pinus longaeva* in the White Mountains, California where trees survive for millennia in open forests where fires are uncommon.

In general, it has been shown that trees growing at the upper forest border tend to be temperature sensitive while lower forest border trees are limited by precipitation. However, subsequent studies have emphasized that the climate signal recorded by five-needle pines in Western North America is complex, and that tree growth is influenced by temperature and precipitation *and* microsite factors (Kipfmueller and Salzer 2010). Although *Pinus longaeva* is a high elevation conifer, its ring widths correlate with seasonal temperature and precipitation parameters producing a complex signal (Fritts

1969). At the lower forest margin in the White Mountains, *Pinus longaeva* have been utilized to reconstruct past droughts (Hughes and Graumlich 1996) while upper treeline chronologies exhibit a mixed climate signal where growth is positively correlated with precipitation and temperature (Salzer et al. 2009). In order to maximize the temperature signal found in these conifers and build millennial-length temperature reconstructions, *Pinus longaeva* growing within 150 m of treeline that are positively correlated with temperature, have been sampled with the caveat that these trees may have a precipitation component relating to microsite characteristics (Kipfmueller and Salzer 2010). With the need to build accurate paleoclimate reconstructions that represent a clear climate signal, selecting trees from the most climate sensitive sites is imperative. To accomplish this, identifying the degree to which microsite characteristics affect tree-ring widths is essential.

Bristlecone pines

Pinus longaeva (Great Basin bristlecone pine) are the longest-lived, annually dated trees in the world, with the oldest at over 4700 years (Schulman 1958). Remnant bristlecone pines remain on steep slopes in the White Mountains, California for millennia (Ferguson 1968; Lanner 2007). As a result, some of the longest chronologies in the world have been created from these trees in order to reconstruct past climate conditions in California (Fritts 1969; LaMarche 1969; LaMarche 1974b; Graumlich 1993; Hughes and Graumlich 1996; Hughes and Funkhouser 2003; Bunn et al. 2005a; Salzer et al. 2009).

Identifying the sensitivity of bristlecone pine upper and lower forest borders to temperature and precipitation has been the focus of early studies conducted in the 1960s

and 1970s. *Pinus longaeva* ring growth in the White Mountains, California was shown to be related to a mixture of prior and current growing season temperatures and precipitation characteristics and not solely related to summer temperatures (Fritts 1969). Interannual ring width variability associated with precipitation is present at upper and lower forest borders, but it is less pronounced at the upper forest border, where low frequency variability (i.e., decadal or longer) related to temperature dominates (LaMarche 1974a; Hughes and Funkhouser 2003). Bristlecone pines in the San Francisco Peaks, AZ are significantly associated with monthly mean-maximum temperatures (Salzer and Kipfmüller 2005). *Pinus longaeva* at treeline on Sheep Mt., CA and Pearl Peak and Mt. Washington, NV show a distinct positive correlation with temperature while *Pinus longaeva* growth less than 200 m lower correlate negatively with temperature (Salzer et al. 2009) (Fig. A1). The explanation(s) for the change from positive to negative temperature correlation and differing sensitivities of some five-needle pines to precipitation remains unknown, but local characteristics may play a role in this change in climate sensitivity.

The purpose of this study is to systematically examine the importance of microsite factors on ring widths. To accomplish this, a relatively small landform, which provides differences in aspect, elevation, and slope while consisting of similar geologic strata was located. Blanco Mountain in the White Mountains of California, a relatively small conical-shaped mountain with four distinct aspects and two prominent elevations, provides an excellent location for unraveling the effects of microsite parameters on tree-ring growth (Fig. A2). The mountain covers an area of 2 km²; hence, trees are within

about 1200 m of one another and respond to the same regional climate. Therefore, any site to site variations can be attributed to microsite characteristics. Elevation range of *Pinus longaeva* in the White Mountains is ~2800 to 3500 m, and Blanco Mountain varies from ~3100 to 3450 m providing mid- to upper- elevation range *Pinus longaeva* for sampling. Treeline is present only on the northwest top of Blanco Mountain and appears to be a geomorphic-induced treeline formed by steep boulder slopes that are fairly mobile (Fig. A3). Blanco Mountain consists predominantly of Reed Dolomite with outcrops of the Wyman Formation (quartzitic sandstone, siltstone, and dolomite) on its lower eastern side (Nelson 1966). This limits ring width differences resulting from geology to two rock units where in other parts of the White Mountains the geology is more complex. Given that Blanco Mountain, in the White Mountains has several different microsite environments available, this location provides an excellent opportunity to investigate the effects of differences in aspect, elevation, geology, and slope on tree-ring widths.

This study compares *Pinus longaeva* raw ring-width chronologies from varying aspects, elevations, slopes, and rock types on Blanco Mountain in the White Mountains of California in order to answer the following questions: (1) How do microsite characteristics affect *Pinus longaeva* response to climate?, and (2) How do elevation, geology, percent slope, and soil thickness influence ring width variability on Blanco Mountain?

A.3 Methods and Materials

Study Area

Bristlecone pines (*Pinus longaeva*) located in the White Mountains, California (37°N, 118°W) receive only 20 cm of precipitation on average a year, experience temperatures ranging from -22 to 30° C annually (unpublished data, Harlan 2007), and maintain a relatively short growing season of 45 to 60 days (Fritts 1969; Appendix B). Blanco Mountain ranges in height from 3100 to 3450 m, where the mountain top consists of dolomite boulders and cobbles and thin soil (less than 15 cm) (Fig. A4). The eastern base of Blanco Mountain is composed predominantly of sandstone while dolomite makes up the majority of the western base. All bottom sites, except the southwest, have lower percent slopes than the top sites, and consequently the northeast, northwest, and southeast bottom locations have thicker soils. Areas of moderate soil thickness retain more moisture than locations where soil is thin (Thompson and Turk 1991). Snow tends to accumulate on gentle slopes near the bottom where it infiltrates into the soil, whereas less snow accumulates on the steep upper slopes (Selby 1993). Snowmelt and precipitation moves downhill toward the bottom sites (Finlayson and Statham 1980). For a portion of the day, a nearby hill shades the SW Bottom.

Data Collection and Analysis

After examining the topography and using natural ridgelines, eight sub-plots were delineated to provide the greatest possibility of determining the effects of elevation and aspect variation in tree growth (Fig. A2). Trees were sampled on each aspect at upper and lower extents of *Pinus longaeva* distribution on Blanco Mountain so that a wide

elevation range could be investigated. One i-button temperature sensor (Maxim, California) was installed within each plot to collect temperature data every four hours from 2007-09. In order to identify anomalous temperature readings, additional sensors were suspended inside ventilated 4-inch diameter PVC tubes in 2008. Granular Matrix Gypsum soil moisture sensors (Spectrum Technologies, Inc., Illinois) were installed near each temperature sensor during the summer of 2008 at a depth of 15 to 20 cm, where the majority of *Pinus longaeva* roots are located (Fritts 1969; Lanner 2007). Daily and monthly temperatures were averaged for each sub-site and then compared. After identifying anomalous temperature fluctuations from the sensor at the NET when compared to the sensor located inside the PVC tube, median temperatures were calculated for each site. The median is a conservative indicator of central tendency because it reduces the effects of outliers (Sokal and Rohlf 1987).

At least twenty trees with a minimum diameter of 50 cm were sampled within each plot (total of 180 trees) in 2007-09. Full bark trees were sampled where available. Of the 180 trees sampled, ~25% are strip bark trees. Samples were prepared (Phipps 1985), crossdated (Douglass 1941), measured (Robinson and Evans 1980), and statistically checked for quality control using COFECHA (Stokes and Smiley 1968; Fritts 1976; Holmes 1983; Grissino-Mayer 2001). In order to retain original ring-width values and avoid data transformation biases, tree-ring widths were not standardized (Salzer et al. 2009). Instead, sub-plot chronologies were built by using a biweight robust mean to average trees creating tree-ring chronologies based on raw averaged ring-widths (Cook 1985; Briffa et al. 1996; Salzer et al. 2009). Trees younger than 300 years old were not

used in the chronologies and early portions of ring series exhibiting growth trends were removed. This determination was done visually, resulting in the removal of 50-200 rings in the remaining cores. In order to obtain an Expressed Population Signal (EPS) > 0.85 (Wigley et al. 1984), chronologies span AD 1800 to 2007. Tree-ring series were also combined to create elevation (bottom with a range of 3100-3220 m and top with a range of 3380-3440 m), and aspect (northeast, northwest, southeast, and southwest) chronologies. Time series plots and descriptive statistics were used in comparison analysis (Macias et al. 2004; Liang et al. 2006; Fan et al. 2009).

Using Nevada Division 3 climate data (<http://www1.ncdc.noaa.gov>), correlations (Blasing et al. 1984) between each chronology and monthly temperature and precipitation were determined for 1896-2007. This dataset was chosen based on its length of record and completeness. The nearest climate station, White Mountain Research at Crooked Creek, has about 30 years of data, but the record is discontinuous and contains many missing values. Although PRISM (Daly et al. 2008) temperature data matched fairly well with those recorded at Crook Creek, precipitation values did not; thus, Nevada Division 3 data were chosen. Bristlecone pine studies have utilized Nevada Division 3 data as part of their correlation analysis (Hughes and Funkhouser 1998; Hughes and Funkhouser 2003). The use of Nevada Division 3 data are also problematic as it is average monthly climate data derived from multiple stations across a large area.

Spectral frequency decomposes the complex interannual signal found in a time series to highlight low frequency variability. In this case, spectral signatures from each sub-plot were assessed in order to identify low-frequency similarities or differences

between sites (Ise and Moorcroft 2008) using the smoothed periodogram method (Bloomfield 2000). *Pinus longaeva* have long been associated with low frequency variation (LaMarche 1974a; Hughes and Funkhouser 2003).

A.4 Results

Dendrochronological comparisons

All sub-plots are in fairly close proximity to each other and experience the same regional climate. Consequently, the chronologies crossdate with each other and correlate significantly with each other at $P < 0.001$. However, the strength of the correlation varies by sub-site. NE Top and NW Bottom have the lowest between sub-site correlations while NE Bottom versus SE Bottom and NW Bottom versus NW Top have the highest (Table A1). Correlations between aspect chronologies vary from $r = 0.83$ to $r = 0.91$, NW versus SE and NE versus SE, respectively. Bottom versus top chronologies correlate at $r = 0.94$.

In the relatively short time span of 1800 to 2007, no significant series-length trend is present in any of the sub-sites (Fig. A5). The bottom chronologies show noticeably wider radial growth than top chronologies. Aspect means are similar with the lowest mean found on the NE aspect (Fig. A6). Of particular interest are 1867-1872, 1902-20, and 1977-86 when a pronounced separation between SE bottom and top chronologies and to a lesser extent NE bottom and top chronologies (Fig. A6b and A6d). During these years, trees growing in these locations may be able to take advantage of relatively cooler temperatures and/or as a result of soil properties retain moisture more efficiently than other locations.

Mean sensitivity reflects the between-year variation in ring widths (Strackee and Jansma 1992). Through this statistic, trees that are potentially the most climatically sensitive can be identified. SW Top and SE Bottom exhibit the highest mean sensitivity with SW Bottom the lowest (Figure A7a). The site with the highest R-bar is SE Bottom while the lowest is SW Bottom. When comparing R-bar, which is the average correlation between tree-ring series and an expression of chronology signal strength (Cook and Kairiukstis 1990), and mean sensitivity, a positive relationship is present ($R^2=0.50$) where sub-sites with higher signal strength also exhibit higher interannual variability. NW Bottom has the lowest percent of locally absent rings, which may be the result of a gentle slope and relatively thick soil. The top sites exhibit the lowest first-order autocorrelation. The lowest mean sensitivity, percent locally absent rings, and first-order autocorrelation are found on the NW aspect (Fig. A8). When grouped in top and bottom chronologies, the top chronology has the higher percent of locally absent rings while both top and bottom chronologies have similar mean sensitivity. Steep, rocky slopes on the top of Blanco Mountain lead to stressed conditions and more frequent locally absent rings.

Microsite environmental comparison

Environmental data were collected in order to identify possible microsite temperature and soil moisture differences between sub-sites. Median monthly temperature varies similarly throughout the year with minor disparities among sites. Soil moisture information was only collected for one summer, but indicates sub-site

differences. These *in situ* data provide preliminary insights into observable differences and potential hypotheses for why ring-widths may vary between sub-sites.

Temperature

To determine whether sub-sites exhibited measurable differences in temperature, i-button data were compared. Monthly median temperatures for Blanco Mountain ranged from 17° C to -9° C during the June 2007 to December 2008. The maximum i-button median temperature difference between upper and lower sites in the winter was about 1.5° C; the difference in the summer was 1.5-4° C with bottom sites were warmer than their corresponding top sites, except SW Bottom. Daily median summer temperatures calculated for 2007 and 2008 coincide with cambial activity (Fritts 1969; Appendix B), and provide insights into between sub-site variability (Fig A9A and A9B). During summer 2007, SW Top, NE Bottom, and SE Bottom had the warmest i-button temperatures while SW Bottom had the coolest. In the summer of 2008, NW Bottom, NE Bottom, and SE Bottom tended to be the warmest while NW Top, SW Bottom and SE Top were the coolest.

Rock type is one reason NE and SE Bottom locations exhibit warm temperatures. The low albedo Wyman Formation is exposed at NE Bottom and SE Bottom sites where temperatures tend to be warm. In the White Mountains, sandstone reflects 15-25% less energy than dolomite, which leads to soil temperatures that are 2 to 4° C warmer (Wright and Mooney 1965). In the same study, they suggest that the soil weathered from sandstone may be capable of retaining more moisture than soil from dolomite.

Although the drainage located near SW Bottom does not contain surface water, moisture present in the soil may provide a cooling effect via evaporation. Several cold air drainages exist in the White Mountains and the drainage located near the SW Bottom may very well be one, but its influence on temperature may be minimal since SW Bottom is located at the head of the drainage. SW Bottom sub-site is also partially shaded by a nearby hill, which tends to cool this location.

Soil Moisture

Microsite differences in soil moisture availability can potentially lead to ring width variability between trees in close proximity; therefore, soil moisture data collected at each sub-site provides insights into soil moisture patterns (Fig. A9C). The top sub-sites tend to have the lowest relative soil moisture, steep slopes, and thin soil. Specifically, NW Top and SW Top are the driest sites until the 12 July 2008 rain event, when NE Top became the driest. On the other hand, the sites with the highest soil moisture are bottom sites. SE Bottom and NE Bottom are the wettest until 12 July; afterward, NE Bottom is the wettest. Collection of soil moisture data at SE Bottom ceased due to animal interference; hence, soil moisture is unknown. The eastern bottom sites are located on sandstone substrate that retains more moisture (Wright and Mooney 1965).

Tree growth response to seasonal climate

For tree growth and temperature, standard seasonal correlations (prior summer, prior fall, prior winter, spring, summer) generally show negative correlations with all seasons except prior winter temperatures, while seasonal correlations are positive with all

but current summer precipitation (Fig. A10). SE Bottom and NE Bottom exhibit stronger negative correlations with temperature in prior summer and fall than other bottom sites. NW Top and NE Top are less negatively correlated with temperatures than their corresponding bottom sites. NW aspect shows a less negative correlation with temperature than other aspects (Fig. A11). The bottom chronology is less correlated with precipitation while the top chronology is less correlated with temperature.

All sub-site, aspect, and elevation chronologies exhibit strong positive correlations with prior July through current July precipitation and negative correlations with prior July through prior October average monthly temperature. NW aspect shows the weakest negative correlation with temperature (Fig. A12). The SW aspect exhibits the lowest correlation with precipitation while the NE and NW aspects have the highest, which are counter to dendrochronologic principles where SW aspects are assumed to have the highest correlations with precipitation (Fritts 1976). There is a tendency for sub-sites more negatively correlated with prior July through prior October temperature to show lower positive correlations with prior July through current July precipitation (i.e. NW Top and NE Top) (Fig. A13). A similar relationship occurs when sub-sites are less negatively correlated with temperature then they also show a higher positive correlation with precipitation (i.e. NE Bottom and SE Bottom). This is somewhat counter to the dendrochronologic principles that indicate moisture sensitive sites are located at low elevations (Fritts 1976). Results from the current study indicate that microsite characteristics, specifically percent slope, size of sediment particles, and soil presence, on Blanco Mountain may have a more influential role in ring growth than elevation.

Spectral Analysis

A noticeably high spectral power was located at ~80 years for sub-site chronologies. Of the sub-plot chronologies, SE Bottom has the highest low-frequency spectral value at 80 years while NE Top and NW Top exhibit the lowest (Fig. A14A). The SE aspect chronology shows the highest spectral power while NE and NW aspects have the lowest (Fig. A14B). The high elevation chronology has a lower spectral value than the low elevation chronology. Based on the spectral analysis, the series were smoothed using a spline that expresses 75% of the 80-year period (Cook and Peters 1981) (Fig. A15). Amplitudes are high for bottom sub-site and SW Top chronologies, which indicate they have more decadal variability than the other chronologies. Also, the north-facing sub-sites diverge after 1900.

A.5 Discussion

When considering site selection for dendroclimatic reconstructions, microsite characteristics play an influential role in tree-ring variations. Blanco Mountain provides an excellent location for this type of investigation since it allows for the study of multiple factors in a small area. In this arid location, some of the temperature variability between higher and lower elevation sites can be explained by the environmental lapse rate (1° C/100m) (Barry and Chorley 2003) while other temperature differences are a result of aspect, geology, percent slope, and influence of nearby topographic features. Diurnal shifts in mountain and valley winds may also play a role in temperature differences on Blanco Mountain where upslope winds in the afternoon move warm air toward the mountain top and increasing temperatures. Downslope winds during the night have the

opposite impact. Although wind readings were collected by a hand-held anemometer on Blanco Mountain, they were sporadic. Hence, continuous wind patterns on remain unknown. Cold air drainages are also present in the White Mountains, which can affect temperatures along the drainage.

With the highest mean sensitivity, SW Top experiences more year-to-year ring-width variability than other locations. Of the top sub-sites, SW Top has the warmest summer temperatures and the most stressed trees growing out of rock outcrops in very steep locations with little soil; thus, soil moisture availability is potentially low.

SE Bottom and NE Bottom have the strongest negative correlation with prior July through prior October temperatures while NW Top the least. This implies that SE Bottom and NE Bottom show a more pronounced drought signal than other sites, which is related to the dark sandstone and possibly their lower percent slope. The opposite is true for the NW Top, which is located on dolomite, and maintains relatively cool temperatures and probably experience less water loss as a result of evapo-transpiration than other locations. Additionally, top sub-sites are potentially exposed to high winds, very steep, and rocky with little or no soil, which is not conducive to moisture retention (Thompson and Turk 1991; Selby 1993).

On Blanco Mountain, moisture availability is influenced by percent slope. Steepness of the top sites leads to less snow and/or moisture retention as compared to the more gently sloping bottom sites (Selby 1993) and those upper sites are also exposed to severe winds. For example, NW Bottom shows the lowest percentage of locally absent rings, which is the result of greater snow retention on its gentler slope, thicker soils

(Thompson and Turk 1991) and possibly more efficient subsurface water draining from the NW Top than on other slopes (Finlayson and Statham 1980).

All of the bottom sub-plots are warm except the SW Bottom, which is partially shaded by a nearby hill and in close proximity to a drainage. SW Bottom is not as highly correlated with precipitation as other sub-sites, has the lowest \bar{R} , and the lowest mean sensitivity. Cooler temperatures and proximity to a drainage at the SW Bottom may lead to less evapo-transpiration and slightly more access to moisture than other sub-sites.

An increasing trend in ring-widths has been discovered in high altitude conifers located at treeline (LaMarche and Stockton 1974; LaMarche et al. 1984; Salzer et al. 2009). From 1800 to present, no significant trends were identified at any of the sub-sites. Treeline is present only on NW Top, where the slope is very steep, composed of unconsolidated cobble- and boulder-size dolomite, and is mobile; all of which makes *Pinus longaeva* germination and survival difficult (Lanner 2007). The lack of climatic treeline and slightly lower elevation on Blanco Mountain seem to be the reason for the absence of a trend at the upper sub-sites (Kipfmüller and Salzer 2010). NE Top and NW Top with less negative correlations with temperature than their corresponding bottom sites may be transitions between Sheep Mountain, which is positively correlated with temperature and Patriarch Lower, which is negatively correlated with temperature (Salzer et al. 2009). Results from this study indicate that microsite differences lead to temperature and precipitation response discrepancies in high-elevation trees, thus providing evidence for why not all treeline conifers respond to temperature in the same manner.

A.6 Conclusions

In the present study, chronologies 300-1200 m from each other share high frequency variation, but show differences in dendrochronologic, correlation, and spectral values. Dendroclimatic sites are chosen based on their aspect, elevation, and slope; often steep slopes at upper or lower forest borders. A problem arises when microsite characteristics are more influential than assumed, warranting evaluation of local environmental factors. This dataset from Blanco Mountain allows for in-depth investigation into how microsite characteristics affect ring widths and provide insights into why trees in close proximity respond differently to their environment. This study begins to fill the gap between what is known about *Pinus longaeva* response to climate components and how microsite parameters influence tree response to the environment.

Specific conclusions from this study include the following:

- Rock type and percent slope lead to a prominent drought signal at NE and SE Bottom sites.
- Percent slope and soil thickness influence the frequency of locally absent rings on the NW Bottom site.
- Shading from nearby topographic features influence temperature and moisture retention at the SW Bottom site.
- Microsite characteristics appear to be the reason for differences in temperature response of high-elevation *Pinus longaeva*.

At this particular mountain in the White Mountains, a more instrumentally intensive study would provide additional data on the overall influence of local factors on

ring-width. With the use of more temperature sensors, soil moisture sensors, and numerous anemometers, a more resolved picture of microsite factors could be discovered. Incorporating all spatial data, including satellite imagery and snow information, into a GIS would aid in the identification of spatial differences between sites (Bunn et al. 2005b).

Investigating how the importance of a given microsite factor may change over time would assist in creating more accurate paleoclimate reconstructions. This could be accomplished by acquiring samples from remnant wood and snags on Blanco Mountain. Collecting samples in swaths from top to bottom would shed light on transitions in elevation. In order to better understand the influence of microsite factors on ring widths and paleoclimate reconstructions, additional conical mountains with a wider elevation range should be analyzed as well.

A.7 Acknowledgements:

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Table A1. Sub-site correlation matrix. Correlations between sub-site chronologies. All values are positive and significant. Largest values in bold.

	NEB	NET	NWB	NWT	SEB	SET	SWB
NET	0.85						
NWB	0.83	0.71					
NWT	0.83	0.79	0.89				
SEB	0.89	0.81	0.82	0.78			
SET	0.80	0.85	0.73	0.75	0.86		
SWB	0.82	0.77	0.73	0.74	0.81	0.80	
SWT	0.81	0.74	0.84	0.84	0.81	0.81	0.79

A.9 Figure Captions

Figure A1. Bristlecone pine sites of interest.

Figure A2. Blanco Mountain in White Mountains, CA.

Figure A3. Northwest and Southwest aspect photos. Note treeline on Northwest aspect.

Figure A4. Photographs of all sub-sites. Grouped by aspect.

Figure A5. Average raw ring-width chronologies. Sub-sites grouped by aspect.

Figure A6. Average raw ring-width chronologies. Combined by aspect and elevation.

Figure A7. Dendrochronologic statistics for sub-site chronologies.  = bottom chronologies and  = top chronologies.

Figure A8. Dendrochronologic statistics for aspect and elevation chronologies. Circle with dot represents geographic location of aspect chronology.

Figure A9. Temperature and soil moisture data. A and B = Daily median 2007 summer temperatures by sub-site, grouped by aspect. C and D = Daily median 2008 summer temperatures by sub-site, grouped by aspect. Break in data late August result of data collection. E = Summer 2008 relative soil moisture in mVolts for sub-sites. Note no data for SEB after 12 July and NEB after 28 July as a result of wire destruction.

Figure A10. Sub-sites and Nevada Division 3 climate correlations by traditional seasons.

● = $P < 0.05$, ▲ = $P < 0.001$. Notice scale of temperature correlations is reversed.

Figure A11. Aspect and elevation chronologies and Nevada Division 3 climate

correlations by traditional seasons. ● = $P < 0.05$, ▲ = $P < 0.001$. Notice scale of temperature correlations is reversed.

Figure A12. Correlations between chronologies and Nevada Climate Division 3 data.

All correlations are significant at $p < 0.01$. Notice scale of temperature correlations is reversed.

Figure A13. Relationship between prior July through October temperature correlations and prior July through July precipitation correlations.

Figure A14. Low Frequency Spectral Power Estimate for each sub-plot, aspect, and elevation chronology. Time series denoted with * have spectral estimates significantly greater than null continuum at 95% CI at ~80 years. A = Sub-sites, insets are spectral curves for SE Bottom and NW Top. B = Aspect and Elevation chronologies.

Figure A15. Average raw ring-width chronologies smoothed with spline. Grouped by north sub-sites, south sub-sites, aspect, and elevation chronologies.

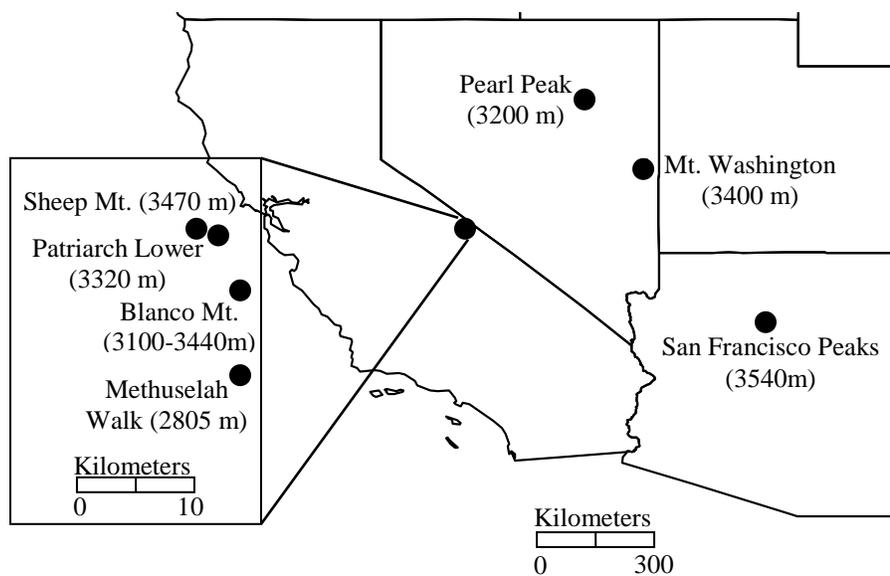
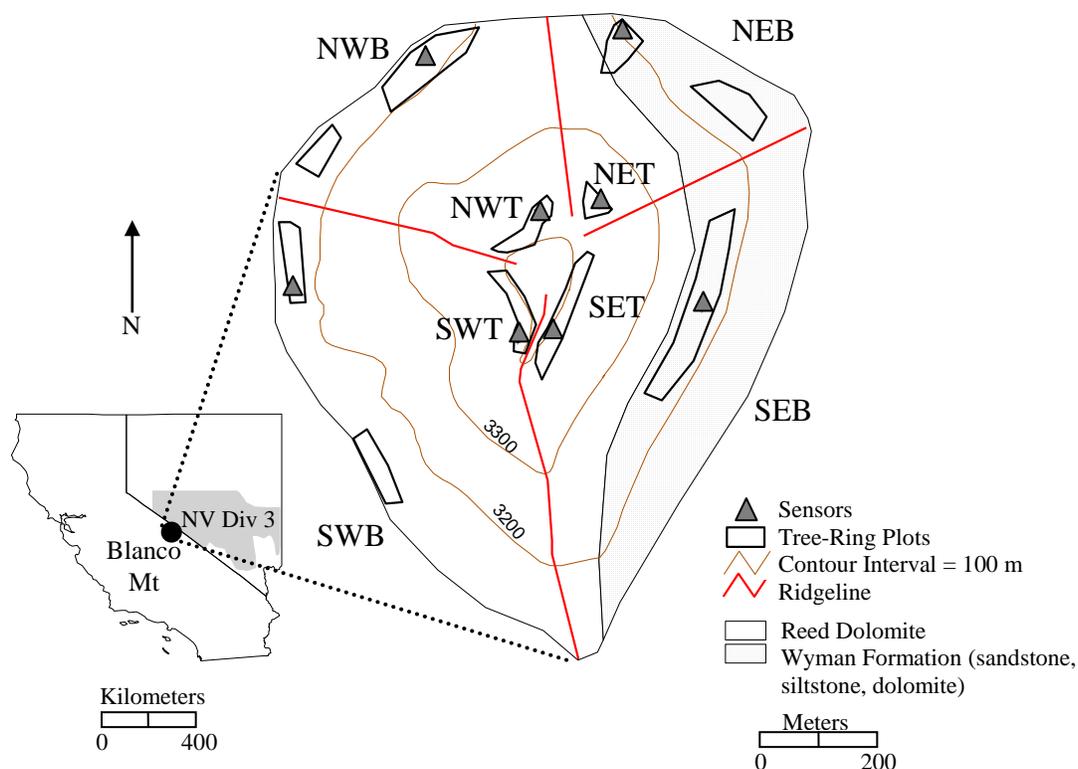


Figure A1. Bristlecone pine sites of interest with elevations in parentheses. Sheep Mt., Patriarch Lower, Methuselah Walk, Pearl Peak, and Mt. Washington elevation from Kipfmüller and Salzer 2010. San Francisco Peaks elevation from Salzer and Kipfmüller 2005.



Site	Elevation (most trees)	Geology	Slope
Northeast bottom (NEB)	3145 to 3230 m (3170 m)	Sandstone, Dolomite gravels, soil	20°
Northeast top (NET)	3353 to 3377 m (3353 m)	Dolomite, thin soil	35 – 40°
Northwest bottom (NWB)	3157 to 3218 m (3182 m)	Dolomite, minor amounts of granite, soil	15 - 20°
Northwest top (NWT)	3365 to 3414 m (3365 m)	Dolomite, patchy thin soil	30°
Southeast bottom (SEB)	3218 to 3243 m (3231 m)	Sandstone, Dolomite gravels, soil	25°
Southeast top (SET)	3365 to 3426 m (3414 m)	Dolomite, thin soil	30 - 35°
Southwest bottom (SWB)	3096 to 3182 m (3158 m)	Dolomite, thin soil	30°
Southwest top (SWT)	3389 to 3438 m (3426 m)	Dolomite, thin soil	30 - 45°

Figure A2. Blanco Mountain in White Mountains, CA.



A. Northwest Aspect



B. Southwest Aspect

Figure A3. Northwest and Southwest aspect photos. Note treeline on Northwest aspect.



A. Northwest High



B. Northeast High



C. Northwest Low



D. Northeast Low



E. Southwest High



F. Southeast High



G. Southwest Low



H. Southeast Low

Figure A4. Photographs of sub-sites. North aspect A-D and South aspect E-H.

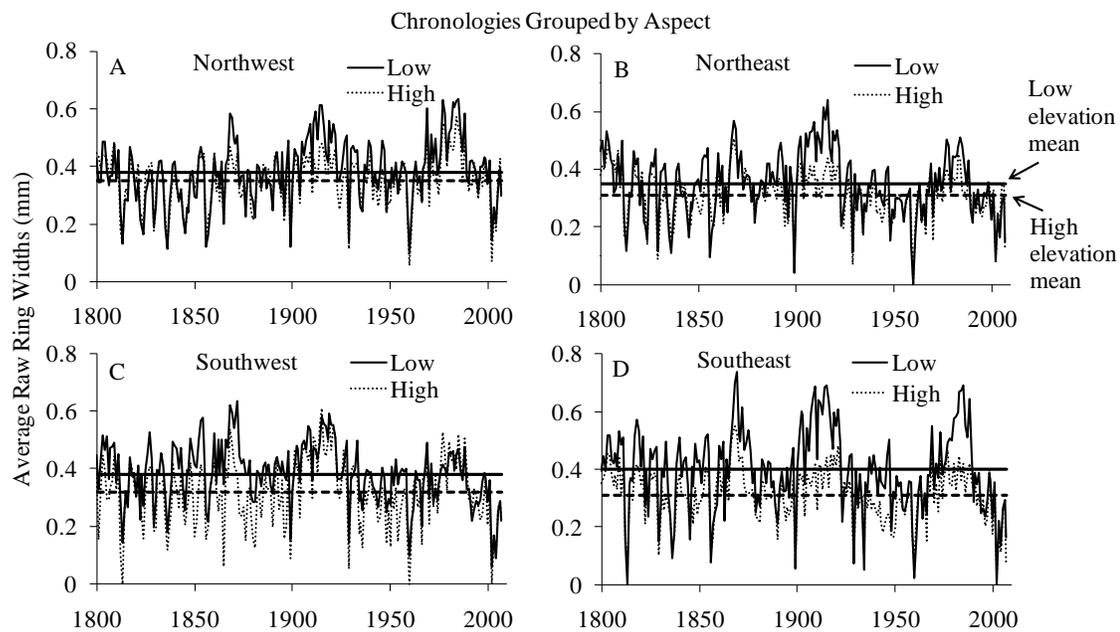


Figure A5. Average raw ring-width chronologies. Sub-sites grouped by aspect.

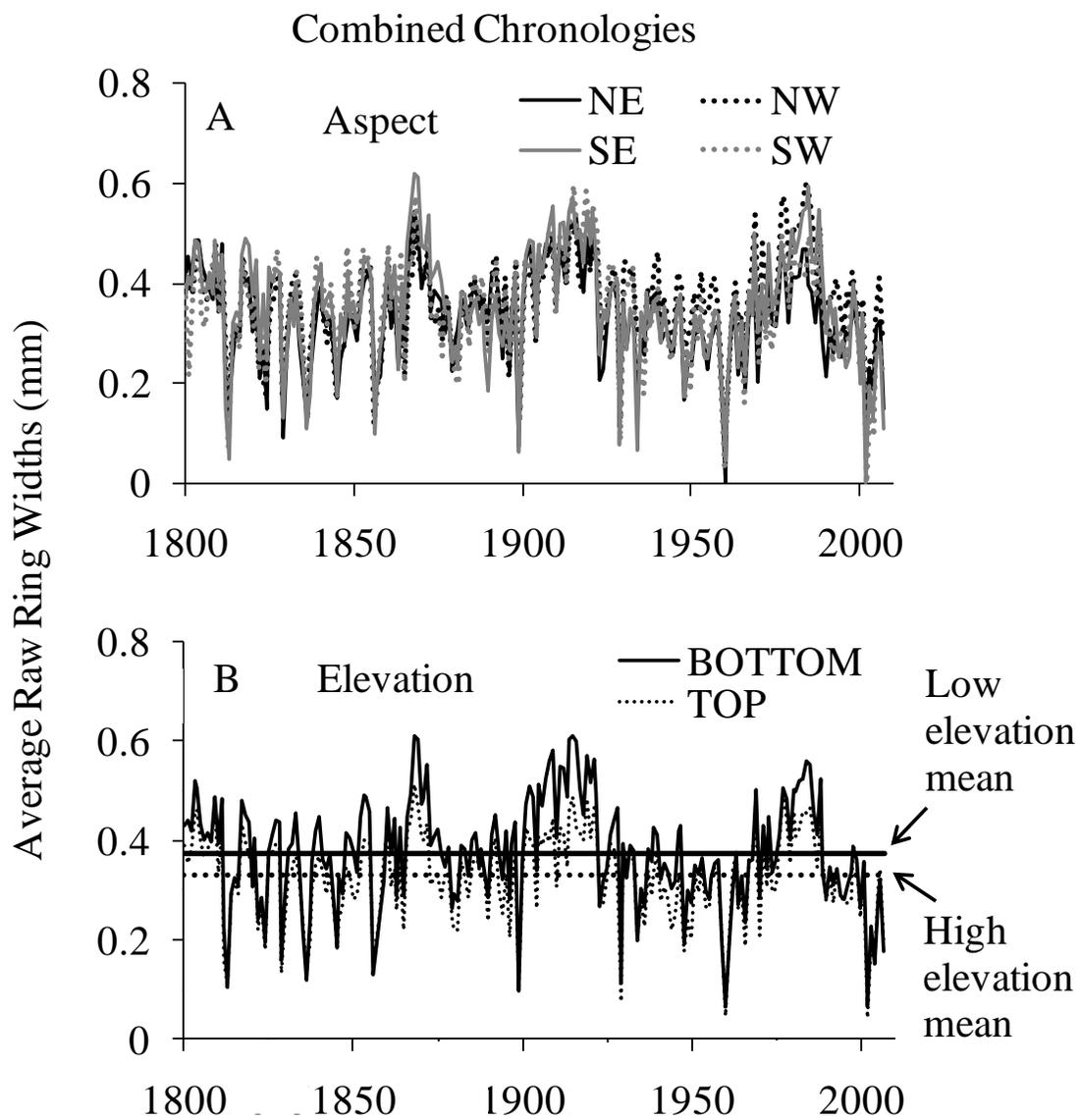


Figure A6. Average raw ring-width chronologies. Combined by aspect and elevation.

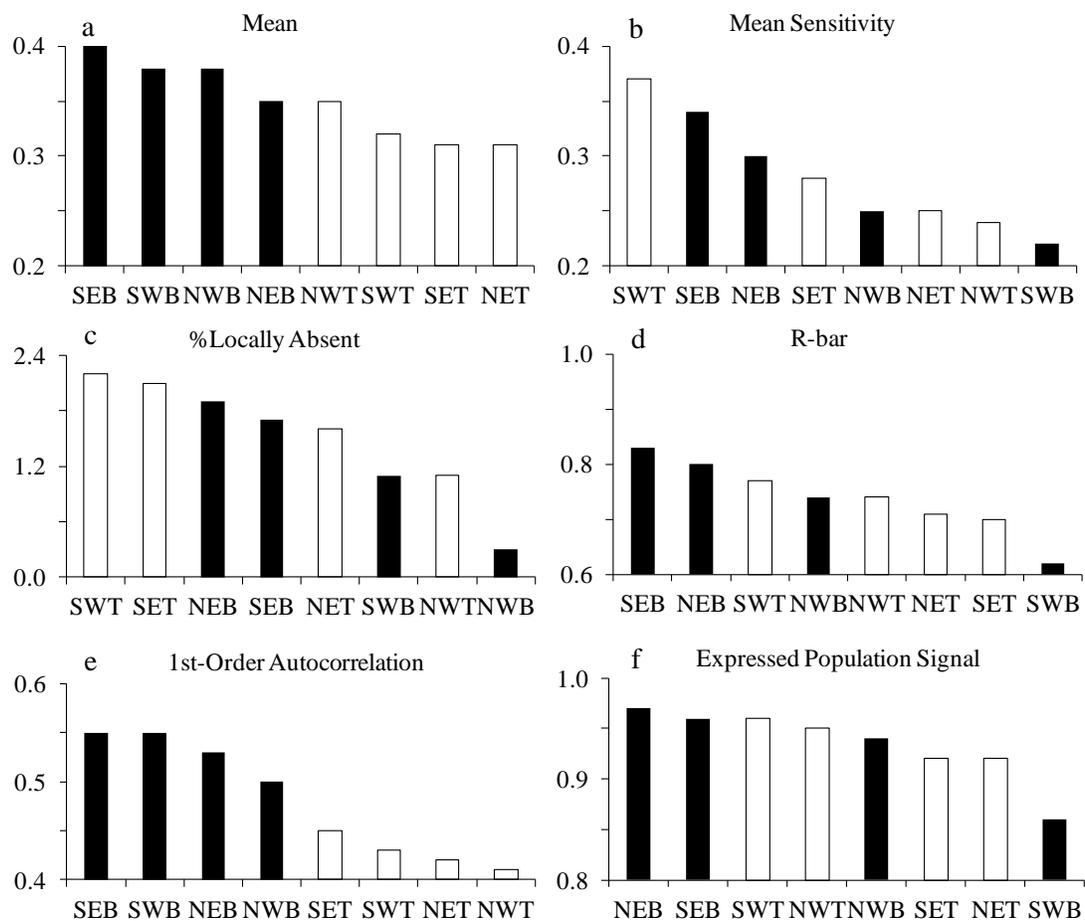


Figure A7. Dendrochronologic statistics for sub-site chronologies. **■** = bottom chronologies and **□** = top chronologies.

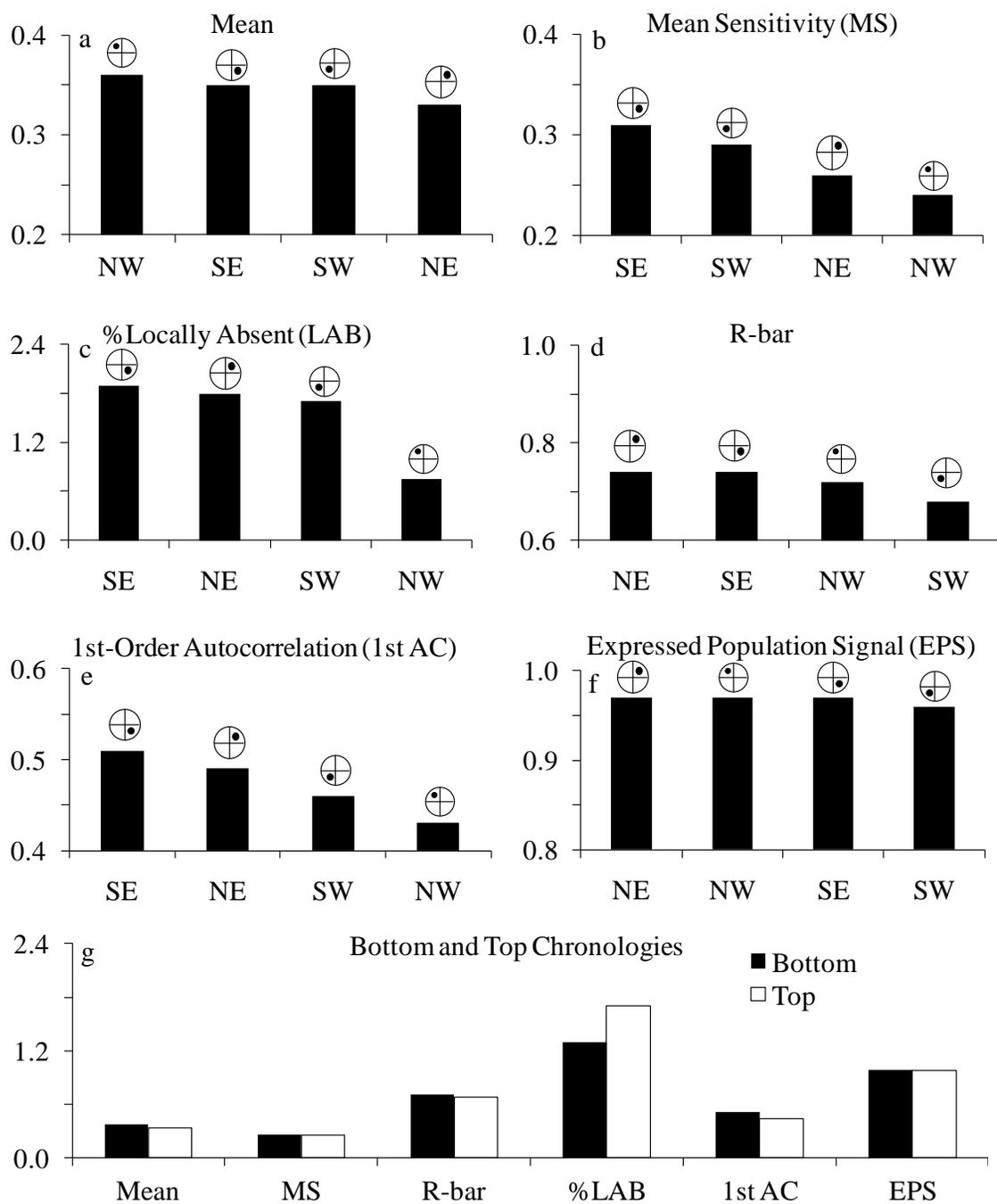


Figure A8. Dendrochronologic statistics for aspect and elevation chronologies. Circle with dot represents geographic location of aspect chronology.

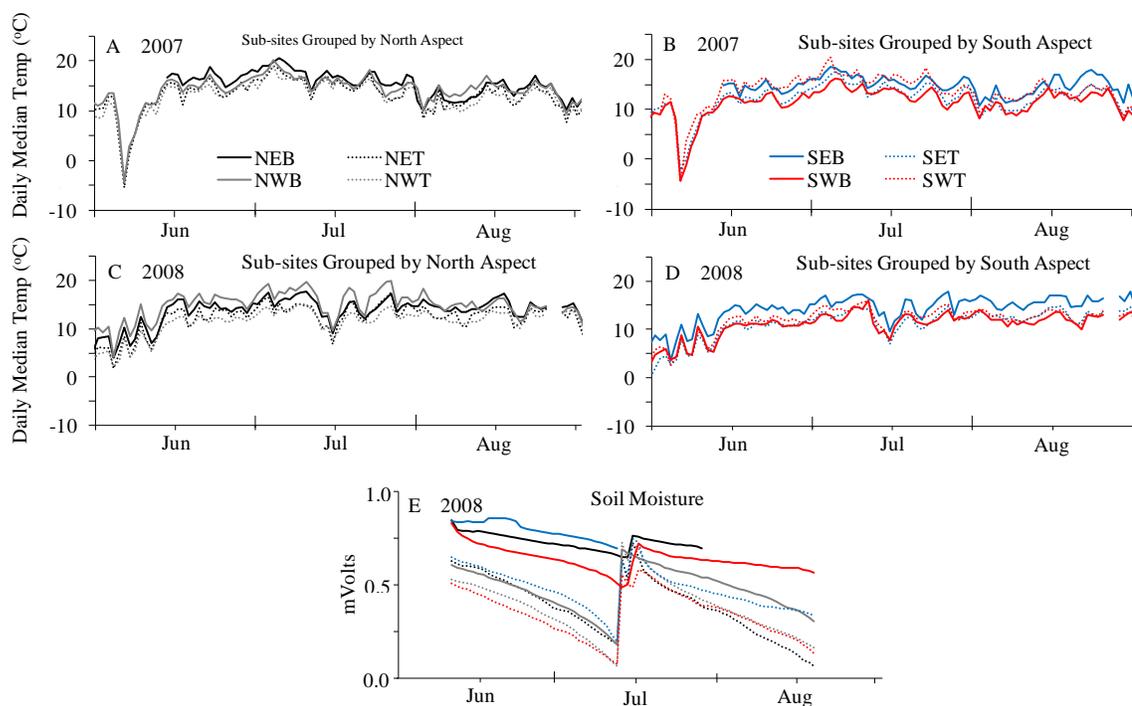


Figure A9. Temperature and soil moisture data. A and B = Daily median 2007 summer temperatures by sub-site, grouped by aspect. C and D = Daily median 2008 summer temperatures by sub-site, grouped by aspect. Break in data late August result of data collection. E = Summer 2008 relative soil moisture in mVolts for sub-sites. Note no data for SEB after 12 July and NEB after 28 July as a result of wire destruction.

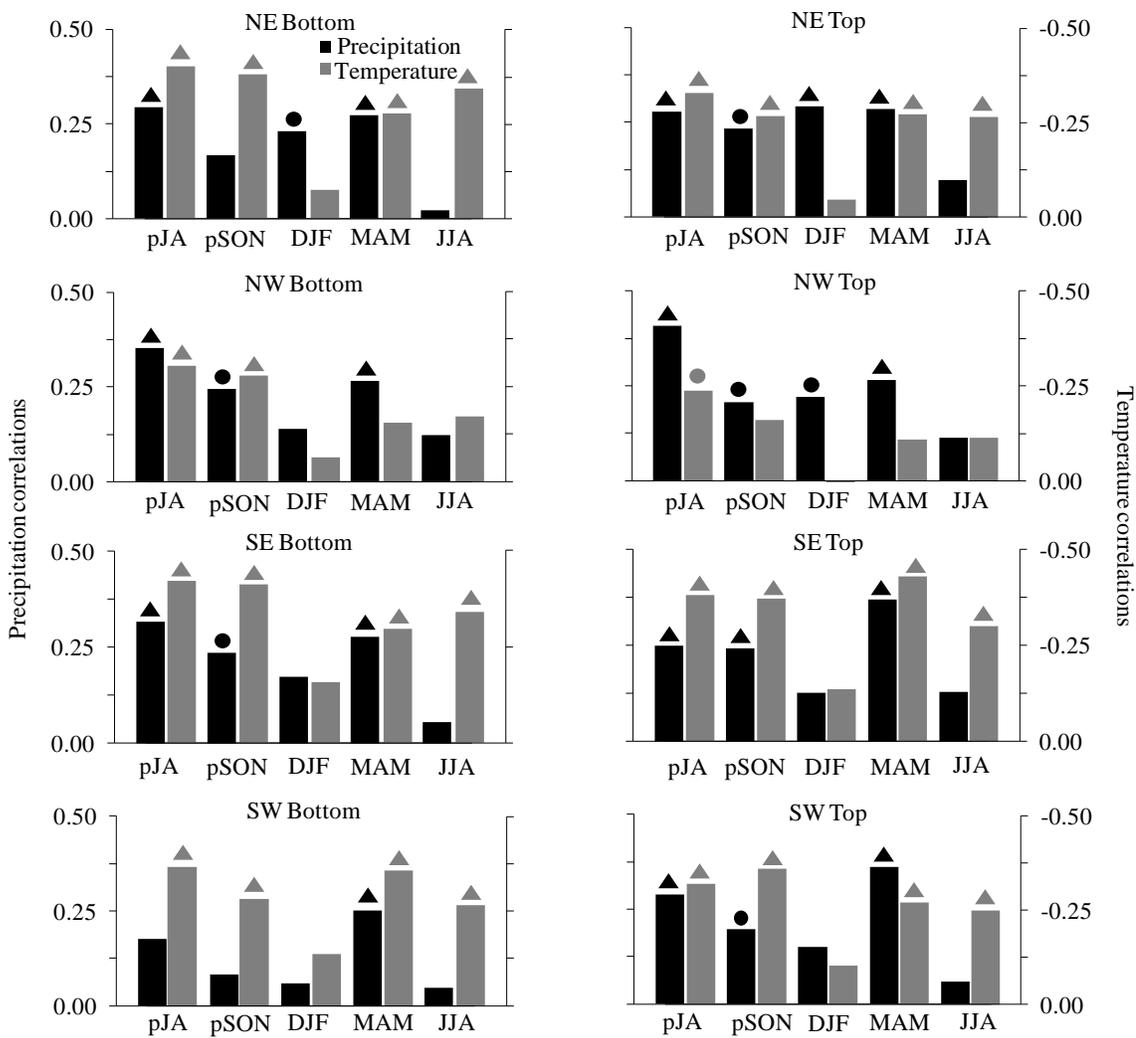


Figure A10. Sub-sites and Nevada Division 3 climate correlations by traditional seasons.

● = $P < 0.05$, ▲ = $P < 0.001$. Notice scale of temperature correlations is reversed.

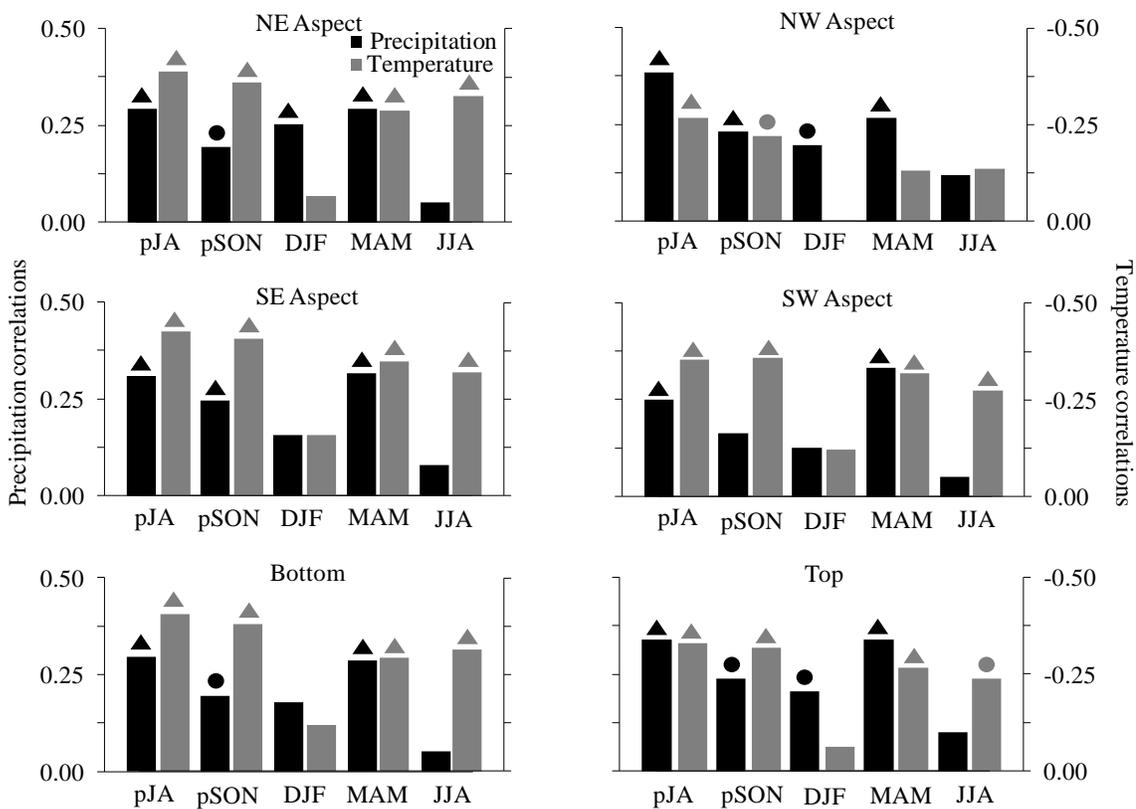


Figure A11. Aspect and elevation chronologies and Nevada Division 3 climate correlations by traditional seasons. ● = $P < 0.05$, ▲ = $P < 0.001$. Notice scale of temperature correlations is reversed.

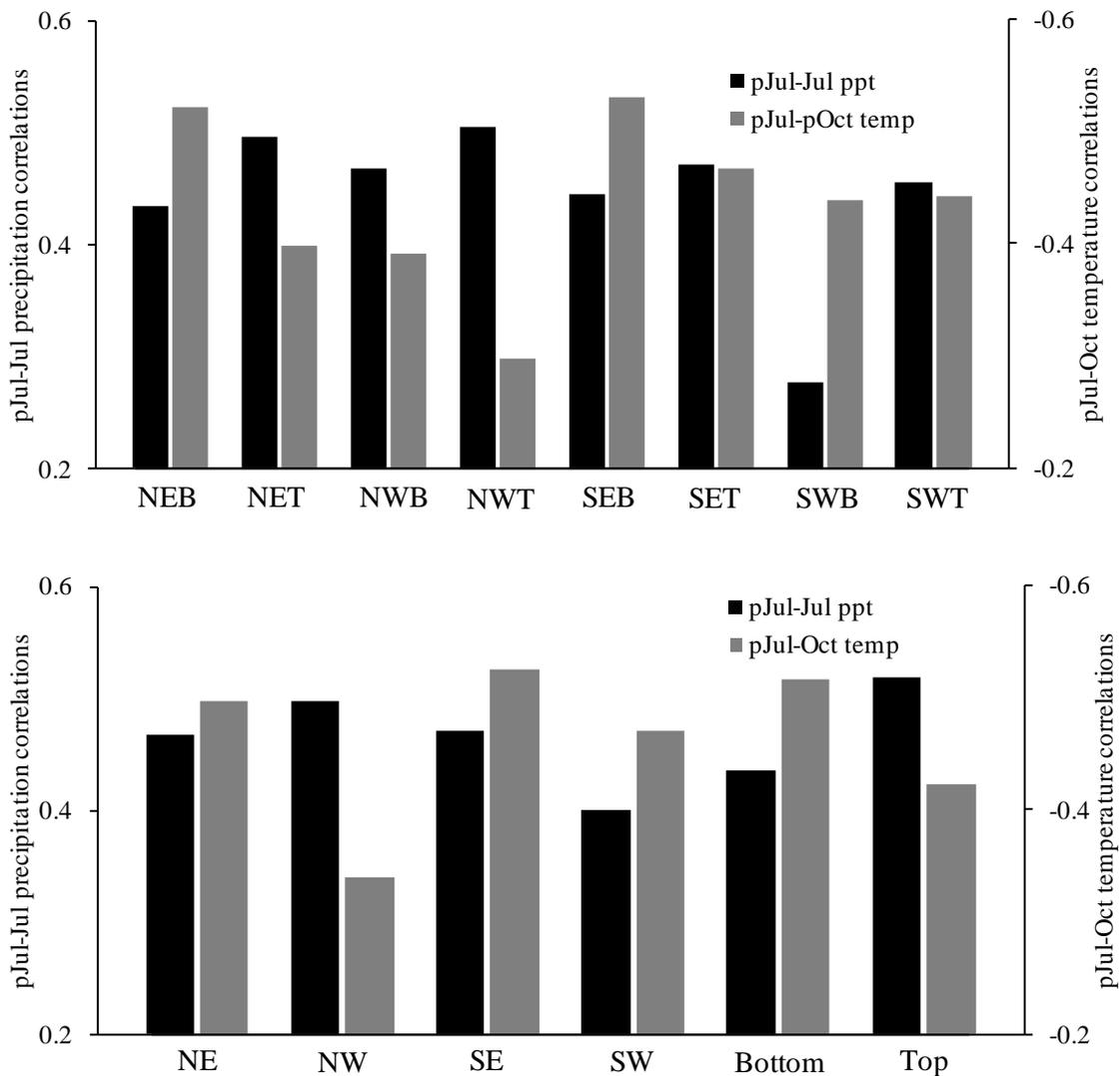


Figure A12. Correlations between chronologies and Nevada Climate Division 3 data. All correlations are significant at $p < 0.01$. Notice scale of temperature correlations is reversed.

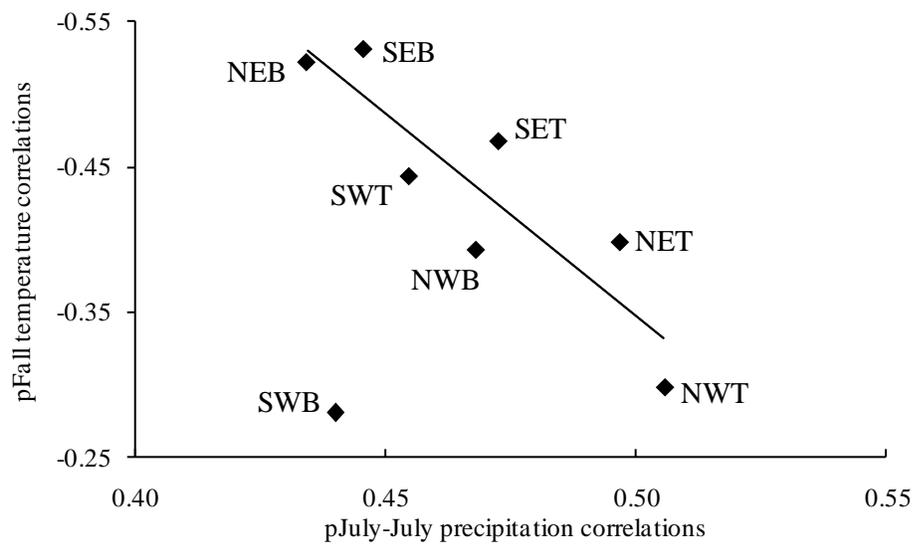


Figure A13. Relationship between prior July through October temperature correlations and prior July through July precipitation correlations.

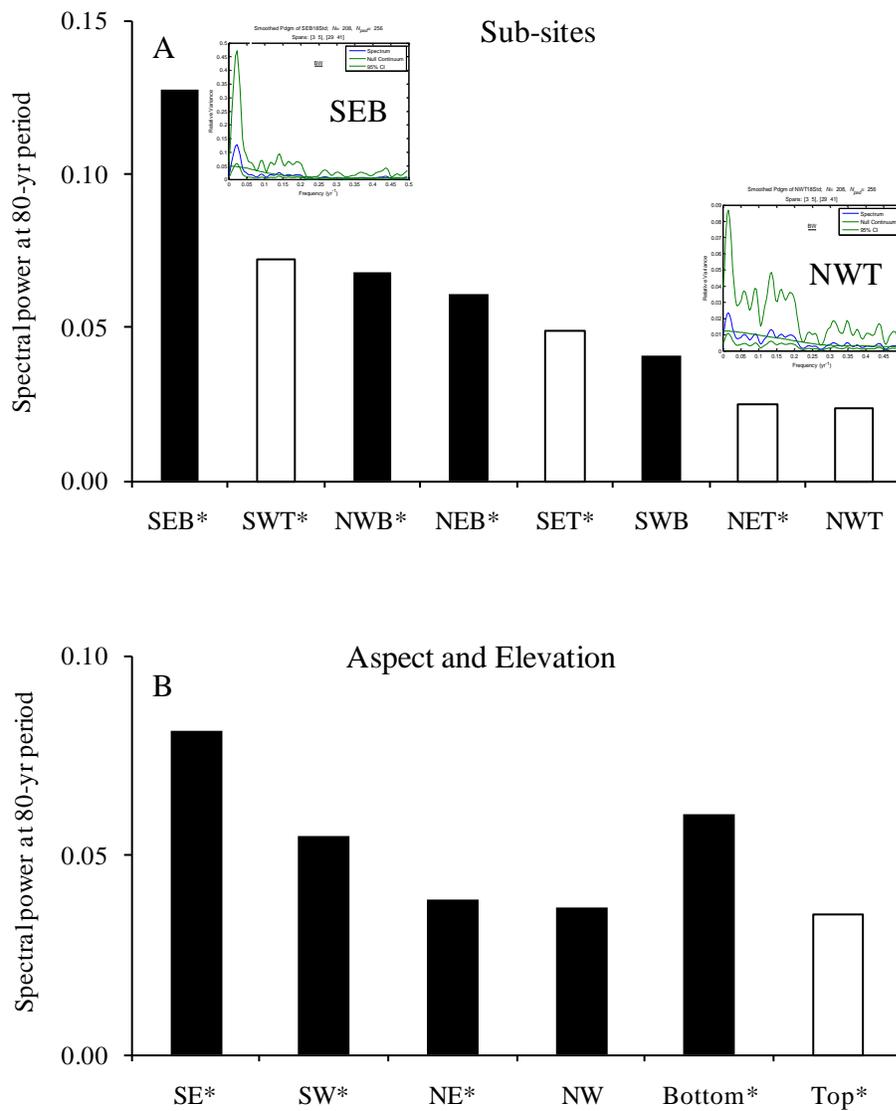


Figure A14. Low Frequency Spectral Power Estimate for each sub-plot, aspect, and elevation chronology. Time series denoted with * have spectral estimates significantly greater than null continuum at 95% CI at ~80 years. A = Sub-sites, insets are spectral curves for SE Bottom and NW Top. B = Combined Aspect and Elevation chronologies.

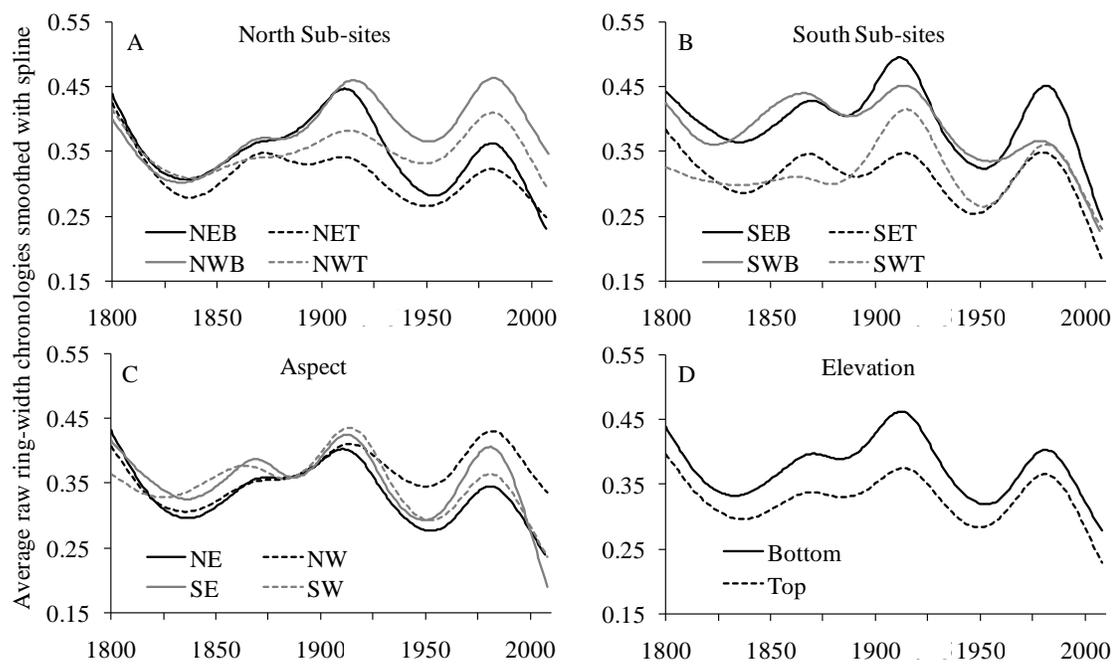


Figure A15. Average raw ring-width chronologies smoothed with spline. Grouped by north sub-sites, south sub-sites, aspect, and elevation chronologies.

APPENDIX B

MORPHOLOGICAL AND PHYSIOLOGICAL PHENOLOGY OF ANCIENT

***PINUS LONGAeva* IN THE WHITE MOUNTAINS OF CALIFORNIA**

Christine Hallman and Howard Arnott

Running Head: *Pinus longaeva* phenology

Journal: *Trees*

Morphological and physiological phenology of ancient *Pinus longaeva* in the White Mountains of California

Christine Hallman^{1*}, Howard Arnott²

¹ *The University of Arizona, Laboratory of Tree-Ring Research, Tucson, AZ 85721*

² *Department of Biology, University of Texas – Arlington, 501 Nedderman St., Arlington, TX 76019*

*Corresponding author: Laboratory of Tree-Ring Research, The University of Arizona, 105 West Stadium, Tucson, AZ 85721, USA. Tel: +520-621-5391, fax: +520-621-8229, *email: hallman@ltrr.arizona.edu*

B.1 Abstract

By monitoring growing season events, natural variations and responses to climate change can be identified within climatically sensitive ecosystems. From 1962-64, H.C. Fritts undertook a pioneering phenologic study on *Pinus longaeva* in the White Mountains of California. Growing season events, a variety of environmental data, and dendrometer readings were collected during these summers. In this study morphological and physiological phenophases, dendrometer traces, and environmental data were collected throughout the summers of 2007 and 2008 in the White Mountains of California to better understand variability in *Pinus longaeva* phenology and identify any shifts in the growing season since the 1962-64 study (Fritts 1969). Duration and timing of cambial activity in the present study was similar to that recorded in the Fritts (1969) investigation despite a median summer temperature increase of at least 2°C. The consistency of duration and timing of cambial activity suggests that changes in tracheid formation (cambial growing season) are not responsible for the recent increasing growth trend in treeline bristlecone pine forests. Bud opening and pollination onset were slightly earlier than in the 1962-64, which may indicate that accumulated heat or a combination of environmental factors influence these phenophases. Specifically, onset of pollination in this study was significantly different from data collected 45 years ago by H.C. Fritts. This may be related to increasing temperatures, but additional data are needed for confirmation.

Keywords: bristlecone pine, growing season, cambial growth, phenology variability

B.2 Introduction

Tree species are unique in that their response to environmental conditions and can be used as a fingerprint of recent climate change (Parmesan and Yohe 2003; Root et al. 2003) and a natural archive of past climate (Fritts 1976). Phenology, the study of periodic life cycle events that are influenced by seasonal variations in temperature and precipitation, is used to track ecological responses to climate variability and climate change (Walther et al. 2002). Identifying high-elevation conifer growing season variability is crucial for recognizing deviations outside the normal growing season range. This allows the recognition of any growing season shifts or changes that are unprecedented and may be related to changing climate.

From 1962-64, H.C. Fritts undertook a pioneering phenologic study on *Pinus longaeva* in the White Mountains of California. Growing season events, a variety of environmental data, and dendrometer readings were collected during these summers. This provided both methodological standards, and comparison phenological data for future studies. With modern technology and photography, 45 years later the this investigation reconstructs and extends the Fritts (1969) study to understand both the potential impacts of increasing temperatures on these ancient trees and the connection between morphological and physiological phenophases. The present study investigates *Pinus longaeva* morphological and physiological phenology to better understand their variability and how they are related to each other.

The objectives of this investigation were to answer the following: (1) what is the relationship between morphological phenophases, such as bud opening, pollination, and

cambial activity? and (2) how does present bristlecone pine phenology compare to that observed 45 years ago by Fritts (1969)?

Phenology

The timing of growing season events affects a variety of environmental processes. The initiation, ending, and length of the growing season influence global biogeochemical cycling by impacting movement and storage of water, carbon, and nutrients (Ludeke et al. 1994; Chuine and Beaubien 2001; McCarty 2001; Penuelas et al. 2001; Prigent and Aires 2001; Leinonen et al. 2002; Linderholm et al. 2006; Reed 2006). Additionally, accurate and precise phenological data have been indispensable for tree growth, climate, and ecological models used to better understand vegetation changes, which is key for indentifying current tree-climate relationships and forecasting potential changes in forest growth, ecosystem productivity, and changes in carbon sequestration (Dougherty et al. 1994; Leinonen and Kramer 2002; Peltola et al. 2002; Vaganov et al. 2005; Bailey and Harrington 2006; Linkosalo et al. 2006; Cleland et al. 2007).

Observable phenophases in conifers include onset and cessation of cambial growth, bud opening, needle elongation, emergence of reproductive parts, and pollination. The timing of morphological events (i.e. budburst, needle emergence) varies according to both genetic and environmental conditions (Dougherty et al. 1994; Chuine and Cour 1999; Chuine et al. 2003; Mutke et al. 2003; Cleland et al. 2007). Shoot emergence is associated with temperature variables, particularly spring air temperature (Chuine and Beaubien 2001) while rate of shoot elongation varies with temperature and moisture availability (Mutke et al. 2003). In some conifer species, needle elongation

takes place at the same time as branch elongation and appears to be influenced by temperature, water stress, and genetics (Dougherty et al. 1994).

Physiological phenology refers to xylogenesis or the process of ring formation, including onset and termination of cambial growth. Growth onset is driven predominantly by spring temperatures (Rossi et al. 2006; Rossi et al. 2007; Deslauriers et al. 2008). Rossi et al. (2008) found that regardless of geographic location, onset of cambial activity occurs within a narrow window of minimum, average, and maximum daily temperatures for seven species of temperature-sensitive conifers located in Europe and Canada (Rossi et al. 2008). Cessation of growth occurs at approximately the same time annually, which suggests that photoperiod controls cambial growth termination (Dougherty et al. 1994; Rossi et al. 2006; Rossi et al. 2007).

Ring widths are determined primarily by size of earlywood cells in trees with narrow latewood (Deslauriers et al. 2008) and/or rate of cell production (Fritts et al. 1999). Consequently, phenological changes may impact ring widths. For instance, lengthening of the growing season may increase the amount of wood produced by a given tree annually as a result of a longer growing season for cell production, which may lead to wider ring widths (Cooper et al. 1986). While an increasing trend in winter precipitation in sub-arctic regions delays snowmelt, and hence postpones onset of cambial activity. In this case, when the growing season shifted later, a tree spent less time in its window of maximum growth sensitivity to temperature, which led to less overall growth (i.e. a narrower ring) (Vaganov et al. 1999).

Climate sensitivity of high-elevation conifers

High altitude and latitude ecosystems are some of the most sensitive to climate and therefore are important indicators of climate change (Tranquillini 1979; Lloyd and Graumlich 1997; Tessier et al. 1997; Malanson et al. 2007). High-elevation conifers in the western U.S.A., such as *Pinus aristata*, *Pinus longaeva* and *Pinus balfouriana*, are sensitive to precipitation and temperature variability (LaMarche 1974; Graumlich 1993; Hughes and Graumlich 1996; Bunn et al. 2005). As a result, some of the longest chronologies (thousands of years long) in the world have been created from these samples in order to reconstruct past climate conditions in California (Fritts 1969; LaMarche 1969).

A recent unprecedented increasing trend in bristlecone pine ring widths at upper forest borders has been identified (Mann et al. 1998; Salzer et al. 2009). Multiple hypotheses for this increase at treeline in the last 150 years have been presented. Warming (LaMarche and Stockton 1974; Mann et al. 1998; Salzer et al. 2009) and increasing atmospheric CO₂ levels have long been associated with enhanced bristlecone pine growth (LaMarche et al. 1984; Graybill and Idso 1993). Higher levels of insolation, changes in phenology (Cooper et al. 1986), and nitrogen fertilization (Fenn et al. 2003; Brooks and Coulombe 2009) have also been offered as explanations for increasing growth trends at upper forest border bristlecone sites. Of these possible reasons for increased growth, warming currently remains a leading candidate for increasing bristlecone pine ring widths at treeline (Salzer et al. 2009), but recent phenology studies

in the area are lacking. Without recent growing season studies, phenologic changes remain a possibility for the increasing growth trend found at some treeline sites.

Pinus longaeva and prior physiological studies

Pinus longaeva (Great Basin bristlecone pine) are the longest-lived, annually dated trees in the world with the oldest at 4700+ years (Schulman 1958). Remnant bristlecone pine specimens remain on steep slopes in the White Mountains, California for thousands of years (Ferguson 1968). As a result, multi-millennial length chronologies have been constructed from these samples in order to investigate past climate conditions (LaMarche 1969; Hughes and Funkhouser 1998; Salzer et al. 2009). Growing season changes might lead to a reduction in wood density that may affect the life span of living trees or the preservation of dead wood on the landscape (Louth 2007).

Data related to recent seasonal growth behavior of bristlecone pines is lacking except for investigations done by Bailey (1970) and Fritts (1969), which were over 45 years ago. Bailey (1970) botanically distinguished *Pinus longaeva* from *Pinus balfouriana* and *Pinus aristata* using differences in needles, cones, male strobili, and other characteristics. Although no in-depth phenological study was conducted, the written descriptions and photographs aided in the identification of *Pinus longaeva* vegetative and reproductive parts.

Fritts (1969) conducted an intensive study of a variety of *Pinus longaeva* characteristics in the White Mts., CA. Of particular interest to the current study is the collection of phenologic and environmental data in the summers of 1962-64. Growing season observations were recorded on several *Pinus longaeva* in Cardis Valley, which is

located north of the Schulman Grove Visitor Center and hidden from public view.

According to the 1962-64 study, bud swelling occurred in late June-early July and growth ceased after 45-56 days for young trees (100-300 years) and 35-43 days for old trees (>600 years). Phenophases varied from year to year and with elevation. *Pinus longaeva* growing at high elevations began growing 10-12 days later than at low elevations. Onset of growth depended on temperature while rate of growth depended on moisture regimes.

Descriptions from Bailey (1970) and growing season data from Fritts (1969), the present study was able to identify and document *Pinus longaeva* phenophases for two years, as a rough assessment of changes over the past decades since Fritts' work (1969). Growing season and environmental information collected over 45 years ago in Cardis Valley (Fritts 1969) were compared with data recorded in this study to gain insights on *Pinus longaeva* growth patterns.

The approach taken to address these two questions involved tracking *Pinus longaeva* phenology at Fritts' historic field site in the White Mountains of California to document morphological and physiological phenophases.

B.3 Methods and Materials

Study Area

The historic Fritts (1969) study site in Cardis Valley was re-identified in 2006 using the study map provided in the publication. Cardis Valley, located in the White Mountains, California (37°N, 118°W) approximately 18 km northeast of Bishop, California, runs east-west, has an elevation of 3200 m, and is 1.8 km north of the Schulman Grove Visitor Center. The valley floor contains 15 to 30 cm of sandy soil

while adjacent valley walls consist of Reed Dolomite gravel and cobbles with 10-30° slopes (Fig. B2). The site receives only 20 cm of precipitation on average a year and experiences temperatures ranging from -22 to 30° C annually (Hall 1991; Harlan 2007). Valley winds are highly variable with no predominate wind direction noted in summers 1962-64 or 2007-08. As observed in May 2008, Cardis Valley accumulates snow during the winter and spring. Field observations of damaged, bent, and leaning small-diameter trees in Cardis Valley indicate snow levels have reached 70 cm. The forest valley is open with no understory and the majority of trees are *Pinus longaeva* with minor amounts of *Pinus flexilis*. The site contains a few strip-bark trees, but most are full-bark straight-bole trees. The remaining vegetation consists of annual herbaceous dicots and *Cercocarpus*. Char on trees and fire scars indicate the area has been burned in the past, but no fire history studies have been conducted in this area. The nearest climate station is White Mountain Research Station at Crooked Creek located 11 km north of Cardis Valley. The location of this study limits visitor interference, is relatively accessible, and enables the study of several *Pinus longaeva* in close proximity to each other (Fritts 1969).

Data Collection and Methods

The original Fritts (1969) site was pinpointed based on the map published in the 1969 article. A photograph in the same article and identification of screws and putty on three trees verified that the location was the one utilized in Fritts (1969). Those same three trees were utilized in the present study along with trees in close proximity where lower branches were accessible for measurement.

The present phenological study included 16 trees in 2007 and 2008 and five additional trees in 2008. All but three of the study trees grow on the valley floor; two are located on the south facing slope and the other on the north facing slope of adjacent valley sides. North and south-facing branches were chosen where available to examine terminal bud diameter and length and needle length.

Morphological phenophases based on reconstructed Fritts (1969) descriptions were identified and documented during the summers of 2007 and 2008 (Fig. B3). These phenophases were recorded via photographs and measurements taken every 3 to 4 days from four branches per tree. Bud diameter and length were measured so that more precise data could be collected to describe bud swelling and elongation. Additionally, in 2008, USA-National Phenology Network protocols (<http://www.usanpn.org/>) for needle emergence and first pollen shedding were utilized.

Cambial samples were collected weekly in the summers of 2007 and 2008 from five trees each summer using an increment borer. Cambial plugs contain the bark, cambial zone, and the outside 3-7 rings; thereby, allowing the identification of active tracheids and cambial activity. In this case, cambial activity refers to formation and life span of tracheids. Cambial punches were taken on various sides of the tree in order to lessen damage to one particular location on the tree stem (Fritts 1969). The five trees punched in 2008 were also equipped with point dendrometers (Appendix C). This 11-cm long instrument used a linear potentiometer with an internal spring to record stem variability every 30 minutes on a HOBO® datalogger (Onset, Massachusetts). Dendrometers were placed near the base of the tree and cambial samples were taken 1-

1.5 m above the ground to reduce the likelihood of increased growth resulting from cambial injury caused by dendrometer installation (Fritts 1969). Cambial samples were stored in Formalin-Acetic Acid-Alcohol (FAA) solution, 70% alcohol, (Arnott 1958) in the field and were processed by Dr. Howard Arnott. Samples were thin-sectioned using razor blades, and active tracheids were counted (Bonar et al. 1925; Foster 1942; Sass 1951; Berlyn and Miksche 1976). The progressive pattern of *Pinus longaeva* ring formation is documented in Figure B4.

Morphological phenophases were compiled and dates were determined for each tree based on the average of four observation branches. Morphological and cambial phenology dates for 1962-64 were compared statistically with those collected in this study: where observations from multiple trees existed from Fritts (1969), paired two-sided t-tests were used to identify any significant differences between the 1962-64 study and this investigation (Kleinbaum et al. 1988). In cases when only a mean was given in Fritts (1969), the means were compared using a one-sided t-test. To identify any relationships between phenophases, weekly rates for bud swelling and elongation, needle elongation, and tracheid formation were calculated and analyzed.

A variety of environmental data were also collected at Cardis Valley. Two DS1921G thermochron sensors (Maxim, California) were installed on two trees at heights of 1.5 – 3 m above the ground within the site reading temperature every 4 hours. A weather station was set up during the observation period with a S-LIA-M003 photosynthetically active radiation sensor, a S-WCA-M003 anemometer, and a TMC20-HD soil temperature sensor at a depth of 15 cm recording every 30 minutes on a HOBO®

datalogger (Onset, Massachusetts). An analog rain gauge at a height of 1.4 m was installed and checked every 3 to 4 days throughout the summers of 2007 and 2008. Daily averages for minimum and maximum air and soil temperatures were calculated.

B.4 Phenology Observations and Results

Phenological observations indicate that growing seasons in 2007 and 2008 were of similar length and that phenophases progressed in the same sequence. However, variability in the timing of phenophases was observed. Bud swelling, elongation, opening, and pollination were more variable in 2008 than 2007. The majority of physiological and morphological phenology occurred earlier in 2007 than 2008 (Fig. B5 and Table B2). Dates associated with the first appearance of reproductive parts were similar in both years. Pollen shedding was longer in 2008, probably related to higher number of pollen sacs in that year.

Cambial growth data show some similarities and some differences between the two years. In 2007 and 2008, cambial onset initiated during bud swelling and elongation whereas bud opening occurred soon after cambial activity began (Fig. B5). Generally, pollination ceased before cambial activity ended. The length of cambial activity was virtually the same in 2007 and 2008 while the timing of growing season onset was shifted 12 days later in 2008.

A comparison of results from this study and Fritts (1969) show that cambial activity during the 1962-64 study varied from 46 to 54 days in length, which is similar to both 2007 and 2008. Bud opening in 2007 was earlier than 1963 and 1964 while 2008 bud swelling, elongation, and opening were earlier than 1963 data ($p < 0.01$) (Table B3).

Bud swelling and elongation in 2007 was noticeably earlier than 1963. Pollination onset was earlier in 2007 and 2008 than in 1962-64. 1962 cambial onset was 11 days earlier than 2008 while cambial end was much later in 1963 as opposed to 2007. Differences in the timing of cambial activity between years are associated with weather variability (Figs. B6, B7, B8).

Relationships between cambial growth and phenophases were examined based on the weekly phenological observations and cambial activity determined from the punches. Mean weekly rates were calculated for bud diameter and length, needle length, and cambial activity so that relationships between phenophases could be identified (Fig. B9). A slight decrease in rate of bud length growth coincided with cambial onset. A decrease in needle length occurred simultaneously with pollination end. A peak in needle length growth occurred with cessation of cambial growth. In this case, cambial end represents the end of new tracheid formation.

Not surprisingly, rain events and cloud cover play a key role in stem variability, as indicated by dendrometer measurements over the two summers. Two rain events of more than 0.2 cm were recorded in the summer of 2007 while four were recorded in 2008 (Fig. B6). Abrupt increases in the dendrometer trace coincide fairly well with rain events (Fig. B10). Bud swelling corresponds to a small temporary increase in stem width, which does not coincide with a precipitation event. This may represent hydration of the stem after the dormant season (Kozłowski and Winget 1964; Winget and Kozłowski 1964; Turcutte et al. 2009).

B.5 Discussion

Phenophase and cambial observations carried out over the summers of 2007 and 2008 indicate that growing season events progress in a predictable sequence while timing of events vary as a consequence intra-annual differences in weather. In comparison with those observations made by Fritts (1969), growing season length is similar (~50 days) while bud opening and pollination onset are earlier in the current study.

Overall 2007 and 2008 cambial activity duration and timing are similar to Fritts (1969) and appear to be within normal documented variation; suggesting that slight differences are a result of natural variability. Phenological development documented in 1963 suggests that duration of cambial activity is similar from 3100 to 3350 m while onset of cambial activity is 10-12 days later at higher elevations (Fritts 1969). Since the duration and timing of cambial activity is similar in the 1962-64 and 2007-08 and duration of cambial activity is similar over a 300 m range, a dramatic shift or lengthening in the cambial growing season is not be a likely explanation for upper treeline *Pinus longaeva* showing increased growth in the last 50 years (Cooper et al. 1986). This study potentially eliminates growing season changes as a possible cause for the recent increasing growth trend found in treeline bristlecone pines, substantiating the hypothesis stated by Salzer and Kipfmueller (2005) and Salzer et al. (2009) that increasing temperature is a likely mechanism. Further phenological investigations at treeline are necessary to confirm this hypothesis since cambial activity at upper forest borders tend to be more sensitive to temperature than at lower elevations.

Another notable finding concerns the temperatures recorded during cambial activity at this site. For seven conifer species growing in latitudes from 39 to 68° N, cambial activity occurs when minimum, average, and maximum air temperatures are 4-5° C, 8-9° C, and 13-14° C, respectively. Covering a wide geographic and environmental range, conifers in the study are located at elevations of 150-2156 m, and grow in treeline, timberline, boreal, subalpine, and lowland plantation environmental settings. Rossi et al. (2008) found that minimum temperature was the factor that most constrained growth and controlled growing season length. In this study, *Pinus longaeva* cambial activity occurred during summer maximum temperatures of 21.3 - 23.7° C and minimum temperatures of 7.9-8.6° C; all of which are warmer than Rossi et al. (2008). This disparity may be the result of comparing different conifer species or may suggest that *Pinus longaeva* xylogenesis is influenced by more than threshold temperatures. Since the end of xylogenesis varied, photoperiod may not be the only factor influencing growing season cessation.

This study indicates that the duration of cambial activity did not differ between the 1962-64 and 2007-08 studies while bud opening and pollination onset were earlier (Fritts 1969). Cambial activity for *Pinus longaeva* lasts 50 to 54 days with the exception of 1964 when it was 46 days. The shortening of cambial activity in 1964 may be associated with cooler springtime temperatures (Fritts 1969). Onset of pollen shedding in this investigation was statistically earlier than the Fritts study. Bud opening was earlier in 2007-08, but was not significantly different from data collected in the 1960s. Earlier bud opening and pollination onset may be related to the impact of accumulated heat or

more complex environmental factors that are influenced by increasing temperatures and do not affect cambial activity in the same way.

In some high-elevation locations, the timing and length of growing season is changing. Several studies show growing season shifts and/or elongation in some regions associated with climate change (Menzel et al. 2001; Fitter and Fitter 2002; Sparks and Menzel 2002; Walther et al. 2002; Schwartz et al. 2006; Cleland et al. 2007). The entire *Pinus longaeva* growing season does not appear to be shifting or lengthening, but particular phenophases occurred earlier in the present study. This suggests that increasing temperatures may be affecting specific *Pinus longaeva* growing season events, particularly pollination onset. In order to eliminate the possibility that differences in observation frequency led to a discrepancy in bud opening and pollination onset dates between the 1962-64 investigation and this work, further study is necessary.

According to data collected at the Fritts site in the 1962-64, maximum air temperatures rarely reached 20° C with average maximum and minimum temperatures of ~13–17° C and 8-10° C, respectively (Fig. B6). On the other hand, average maximum temperatures for 2007 and 2008 ranged from 21.3 to 23.7° C with average minimums reaching 8.6 to 7.9° C, respectively. In order to confirm average temperatures during the summers of 1962-64 and 2007-08, data from a nearby weather station, Crooked Creek, was utilized for comparison (WMRS, accessed March 2010). Consistent with the present study, average June-August temperatures are at least 2° C warmer in 2007 and 2008 than 1962-64. In spite of the warmer temperatures, the timing and duration of cambial activity were fairly constant in the 2007-08, suggesting that in regards to xylogenesis, *Pinus*

longaeva has not changed in response to increasing temperature. On the other hand, onset of pollination may be occurring earlier, and potentially altering reproductive cycles of these ancient trees. Only continuous data collection can reveal long-term trends in phenologic changes.

Data recorded in the early 1962-64 and 2007-08 imply that onset of cambial growth and bud opening occur earlier in warmer, drier springs (Figs. B6, B7, B8). This is substantiated by conifer studies indicating that earlier onset of cell production is associated with warm springs (Deslauriers et al. 2008). Observations involving high-elevation *Pinus monticola* and *Abies magnifica* found in the Sierra Nevada, California suggest that snowmelt and no-snow dates influence onset of stem growth (Royce and Barbour 2001). With early snow melt, warm spring temperatures, and/or no late spring snowfall, onset of cambial activity and bud opening tend to occur early as opposed to years when spring temperatures are cool and snow cover is present. Therefore, if springs in the White Mountains are warm and dry over an extended period of time, changes in the timing of phenophases may occur.

B.6 Conclusions

This research provides an updated and detailed examination into the growing season of *Pinus longaeva* in the White Mts., California. As in Fritts (1969), phenophases occur in a sequential pattern driven by genetics. Cambial onset varied by twelve days in 2007 and 2008 while the duration of cambial activity was nearly the same for both years. The duration of cambial activity for this study and Fritts (1969) are similar except for the 1964, which was slightly shorter. This indicates that phenologic shifts in cambial growth

are not an explanation for the increasing growth trend found in high elevation bristlecone pines. Onset of pollination was significantly earlier in 2007-08, which may be a response to increasing temperatures.

Conclusions for this research include the following:

- Cambial activity (tracheid formation) for 2008 was 12 days later than in 2007 as a result of a late season snow storm.
- Cambial growth occurs at warmer temperatures than those observed in Rossi et al. (2008).
- Timing and duration of cambial activity are virtually the same in 1962-64 and 2007-08 suggesting that changes in cambial growth are probably not an explanation for the increasing growth trend at treeline, but further studies at treeline are needed to confirm this.
- Bud opening and pollination onset are earlier in 2007-08 than in the 1960s indicating that these phenophases may be responding to temperature changes.
- This study and Fritts (1969) found that earlier growing season onsets tend to occur in dry, warm springs, suggesting that during extended dry, warm periods, shifts to earlier growing season onsets may occur.

Monitoring phenophases and collecting environmental information as frequently as possible *in situ* would provide the much needed data to identify natural variability and unusual growing season trends in *Pinus longaeva*. Realistically, data on such a scale is time-consuming and expensive. An alternate way to monitor growing season changes

would be link *in situ* observations and high spatial resolution satellite-derived NDVI allowing observations to be taken less frequently but more inexpensively.

Two short periods of time, 1962-64 and 2007-08, do not provide adequate data to identify long-term phenologic patterns, but rather they simply present data on the possible natural range of growing season variability. Frequent monitoring of phenology will reveal long-term growing season trends in these and other climatically sensitive trees.

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Table B1. Environmental data for June-July-August of 2007 and 2008. No soil moisture data collected in 2007 after day 206.

Environmental Sensor	Summer 2007	Summer 2008	Comments
Peak photosynthetically active radiation ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	1960 to 2510	1750 to 2540	Peak virtually the same for both summers
Average daily maximum soil temperature	$12.8^{\circ}\text{C} \pm 0.9^{\circ}\text{C}$, range 14.1 to 11.1 $^{\circ}\text{C}$ (DOY 167 to 227)	$14.3^{\circ}\text{C} \pm 1.9^{\circ}\text{C}$, range 17.7 to 8.0 $^{\circ}\text{C}$ (DOY 164 to 237)	Patterns similar to air temperature
Average daily minimum soil temperatures	$9.0^{\circ}\text{C} \pm 1.2^{\circ}\text{C}$, range 11.3 to 6.9 $^{\circ}\text{C}$ (DOY 167 to 227)	$7.9^{\circ}\text{C} \pm 1.7^{\circ}\text{C}$, range 10.6 to 2.0 $^{\circ}\text{C}$ (DOY 164 to 237)	Patterns similar to air temperature
Winds	Variable	Variable	No pattern, no recognizable affect on growing season
Total precipitation, Model Acu-Rite Rain Gauge	1.35 cm	3.35 cm	More precipitation in summer 2008

Table B2. Phenological activity for 1962-64 and 2007-08. Cambial activity is an average. Mode given in parenthesis for bud opening, appearance of reproductive parts, onset of pollen shedding, and pollination duration. Bud swelling and elongation not included because they are difficult to reconstruct based on Fritts (1969).

Year	Cambial Activity (total length in days)	Bud Opening	Appearance of Reproductive Parts	Onset of Pollination	Pollination Duration
1962	168 to 222 (54)	189 to 200 (190)	---	214 to 219 (216)	---
1963	182 to 232 (50)	207	---	218 to 222 (222)	---
1964	177 to 223 (46)	191 to 196 (195)	---	210	---
2007	167 to 221 (54)	173 to 190 (183)	186 to 197 (186)	197 to 200 (200)	197 to 211 (200 to 207)
2008	179 to 231 (52)	179 to 193 (186)	186 to 200 (189)	203 to 210 (207)	203 to 225 (207 to 224)

Table B3. Significance values for mean comparison between present study and Fritts (1969). * = one sided t-test. Paired two-sided t-test used for all others. Values shaded are significant at $p < 0.01$, meaning for a given phenophase the two years are significantly different. No data for 1962-64 are available for first appearance of reproductive parts or pollination end.

Phenophase	Fritts (1969)	2007	2008
Bud Swelling	1962	0.01	0.51
	1963	< 0.00	< 0.00
	1964	0.61	<u>0.01</u>
Bud Elongation	1962	<u>0.01</u>	0.90
	1963	< 0.00	< 0.00
	1964	0.12	0.05
Bud Opening	1962	0.01	0.39
	1963*	< 0.00	< 0.00
	1964	< 0.00	0.01
Pollen Shedding Onset	1962	< 0.00	< 0.00
	1963	< 0.00	< 0.00
	1964*	< 0.00	< 0.00
Cambial Onset	1962*	0.70	< 0.00
	1963*	0.02	0.25
	1964*	0.09	0.42
Cambial Cessation	1962*	0.04	0.01
	1963*	< 0.00	1.00
	1964*	0.02	0.02

B.9 Figure Captions

Figure B1. Bristlecone pine sites of interest with elevations in parentheses. Sheep Mt., Pearl Peak, and Mt. Washington elevation from Kipfmueller and Salzer 2010.

Figure B2. Historic Fritts (1969) phenology site.

Figure B3. Phenologic Photographic Diary. Pictures taken summer 2007 and 2008. Sequence begins with an overwintering bud (a), then progresses to bud swelling (b) where bud scales pull away from bud (measured diameter). Next, the bud elongates (c) with a pronounced lengthening (measured length). Initial bud opening is defined as the opening at the tip of bud where tips of needles are visible (d). This phenophase is the same as the USA-National Phenology Network emerging needles stage. After four days, tips of needles separate, and the bud for next year is visible (e). Needles continue to emerge and separate throughout the growing season (measured length) (f). Beginning to emerge from the bud is a megastrobilus and a fully emerged female cone is seen about a week later (g). Megastrobili vary from blue to purple. Microstrobili or pollen sacs appear at the base of the bud and vary from yellow to red (h). Reproductive parts tend to appear simultaneously on a tree. Pollination onset (i) occurs when pollen first sheds from a shaken branch while pollination end (j) occurs when pollen does not fall when a branch is shaken. *Pinus longaeva* sheds yellow pollen except for one known instance where pollen is white. Pollination onset is the same as the first pollen shedding stage in USA-NPN standards. Note in this and the Fritts studies measurements were obtained using

four designated branches per tree while USA-NPN standards use three locations on a tree for phenophase determinations.

Figure B4. Cambial growth in 2007 and 2008.

Figure B5. Box plots for 1962-64 and 2007-08 phenophases. Appearance of reproductive parts and pollination end were only available for 2007-08 seasons. Cambial onset and end for 1962-64 were measured by Fritts (1969), but only available as an average.

Figure B6. Temperature and precipitation data collected in Cardis Valley during 1962-64 and 2007-08. 2007-08 temperature given as daily average.

Figure B7. June-August 2007 (A) and 2008 (B) temperature, precipitation, and phenophases. Horizontal scale in Day of Year.

Figure B8. Nevada Division 3 climate data for 1962-64 and 2007-08. Data from National Climatic Data Center, NOAA. Crooked Creek data not used because of missing values. Horizontal dashed line represents 9° C cambial initiation from Rossi et al. 2008.

Figure B9. Comparison of growth rates.

Figure B10. Median Point Potentiometer Dendrometer summer 2008. Precipitation in vertical bars.

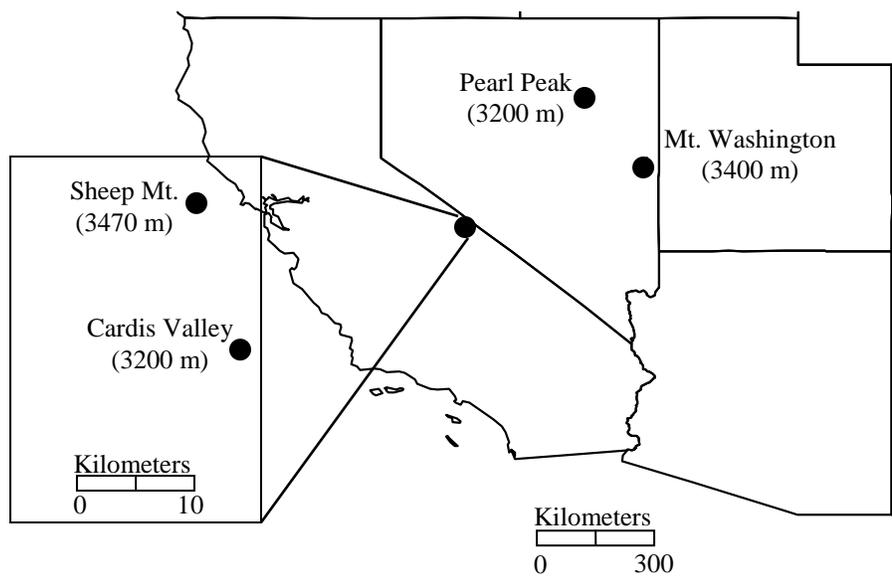


Figure B1. Bristlecone pine sites of interest with elevations in parentheses. Sheep Mt., Pearl Peak, and Mt. Washington elevation from Kipfmüller and Salzer 2010.



Figure B2. Historic Fritts (1969) phenology site.

Figure B3. Phenologic Photographic Diary. Pictures taken summer 2007 and 2008. Sequence begins with an overwintering bud (a), then progresses to bud swelling (b) where bud scales pull away from bud (measured diameter). Next, the bud elongates (c) with a pronounced lengthening (measured length). Initial bud opening is defined as the opening at the tip of bud where tips of needles are visible (d). This phenophase is the same as the USA-National Phenology Network emerging needles stage. After four days, tips of needles separate, and the bud for next year is visible (e). Needles continue to emerge and separate throughout the growing season (measured length) (f). Beginning to emerge from the bud is a megastrobilus and a fully emerged female cone is seen about a week later (g). Megastrobili vary from blue to purple. Microstrobili or pollen sacs appear at the base of the bud and vary from yellow to red (h). Reproductive parts tend to appear simultaneously on a tree. Pollination onset (i) occurs when pollen first sheds from a shaken branch while pollination end (j) occurs when pollen does not fall when a branch is shaken. *Pinus longaeva* sheds yellow pollen except for one known instance where pollen is white. Pollination onset is the same as the first pollen shedding stage in USA-NPN standards. Note in this and the Fritts studies measurements were obtained using four designated branches per tree while USA-NPN standards use three locations on a tree for phenophase determinations.



a. Overwintering bud



b. Bud swelling



c. Bud elongation



d. Initial bud opening



e. Bud opening after 4 days



f. Needle emergence



g. Emergence of megastrobili (female)
(early)



(full)



h. Emergence of microstrobili (pollen sacs)
(early)



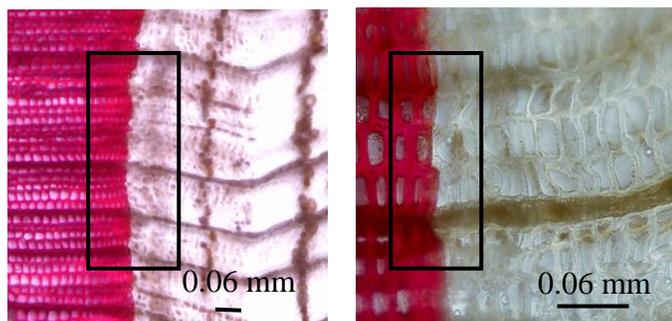
(full)



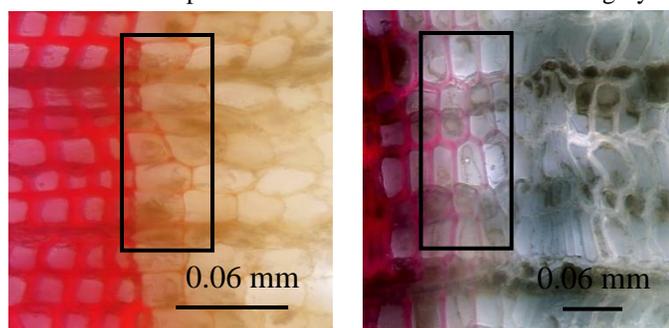
i. Pollination onset



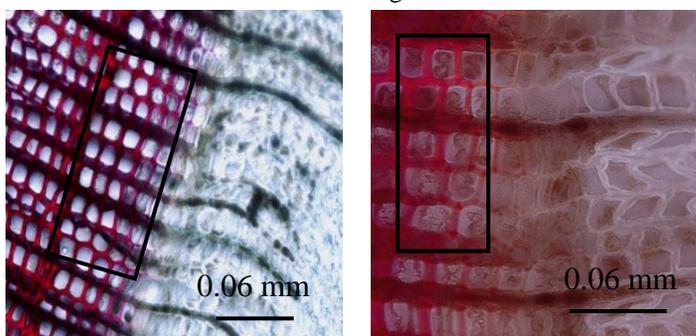
j. Pollination end



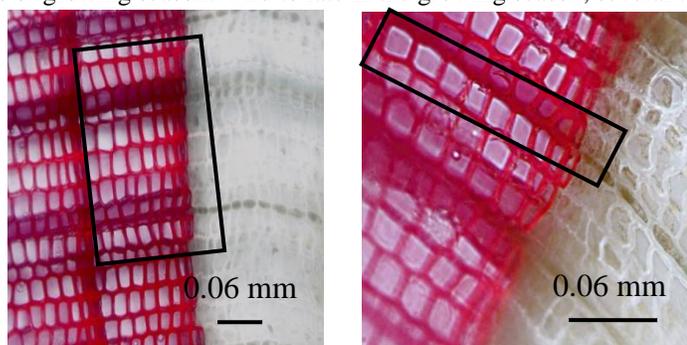
- a. Before cambial growth begins, a distinct boundary exists between prior year's lignified tracheids shown in pink to red and bark shown in white to gray.



- b. 2 – 4 weeks of growing season. Tracheids lack or show early signs of lignification as xylogenesis begins.



- c. 4 – 7 weeks of growing season. Mid to late in the growing season, several tracheids are lignified.



- d. Cambial growth ceased, end of growing season with all tracheids lignified.

Figure B4. Cambial growth in 2007 and 2008.

Phenophases 1962-64 and 2007-08

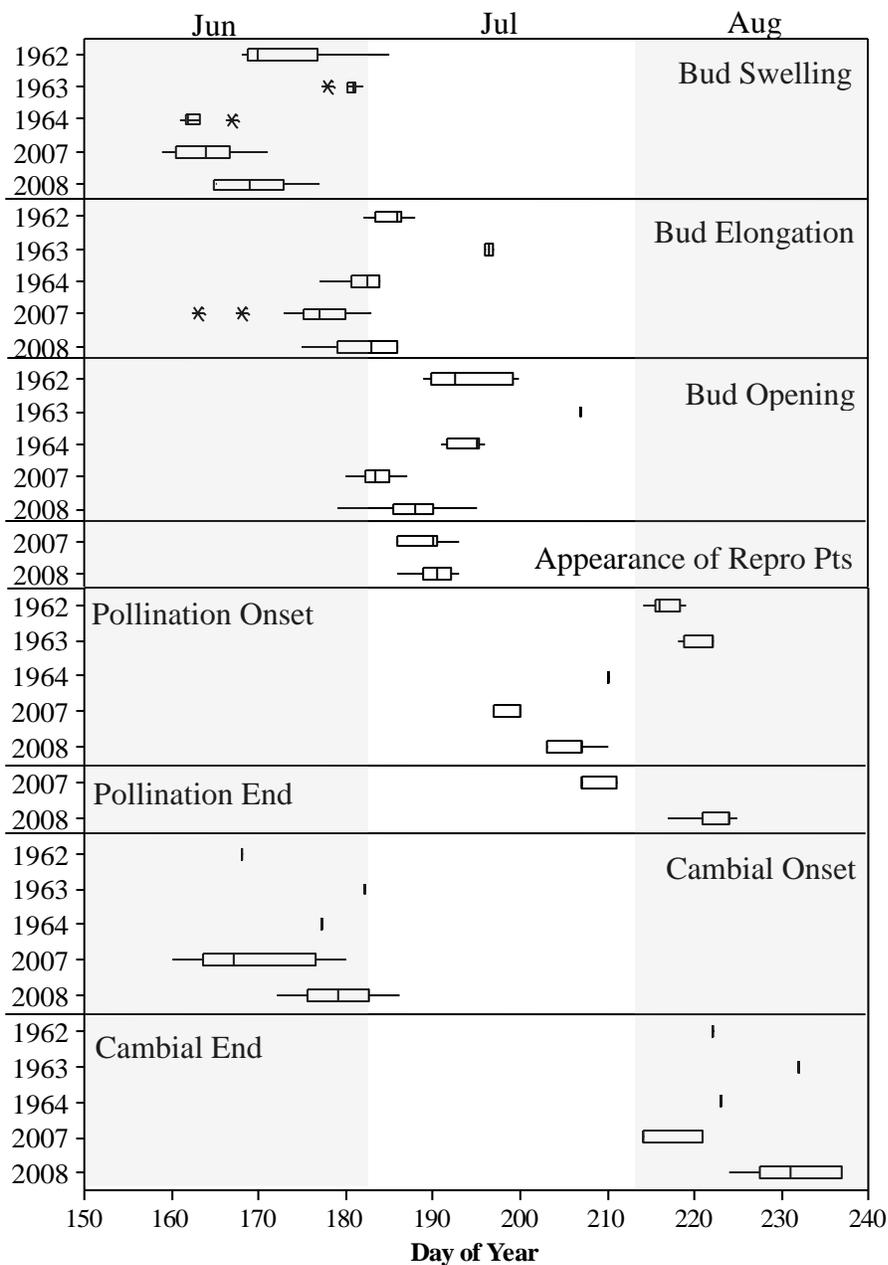
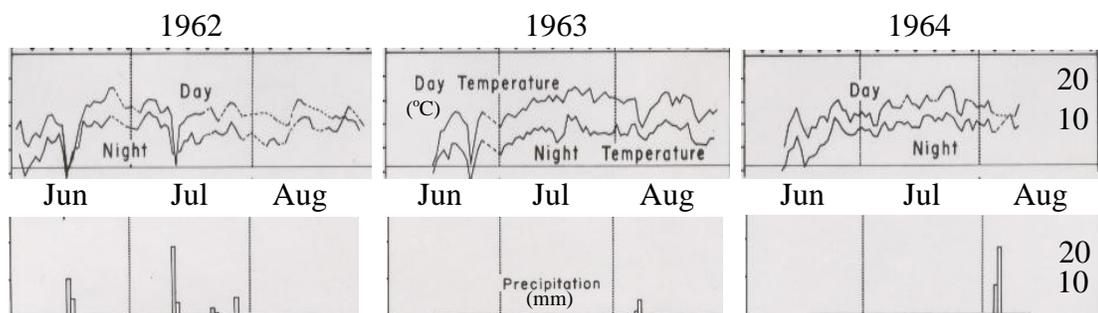


Figure B5. Box plots for 1962-64 and 2007-08 phenophases. Appearance of reproductive parts and pollination end were only available for 2007-08 seasons. Cambial onset and end for 1962-64 given as an average. Star represents outlier.

1962-64 Temperature and Precipitation (Fritts 1969)



Tabular data are unavailable.

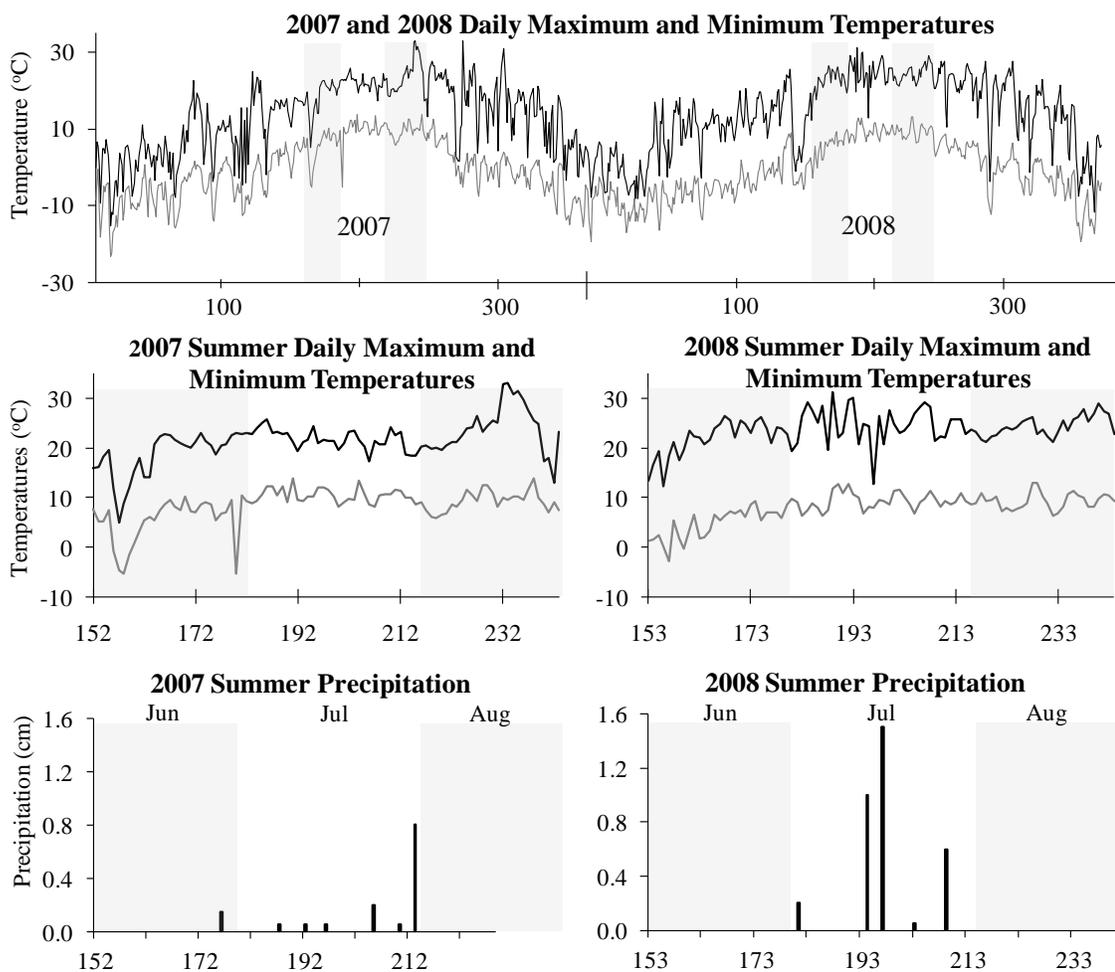


Figure B6. Temperature and precipitation data collected in Cardis Valley during 1962-64 and 2007-08. 2007-08 temperature given as daily average.

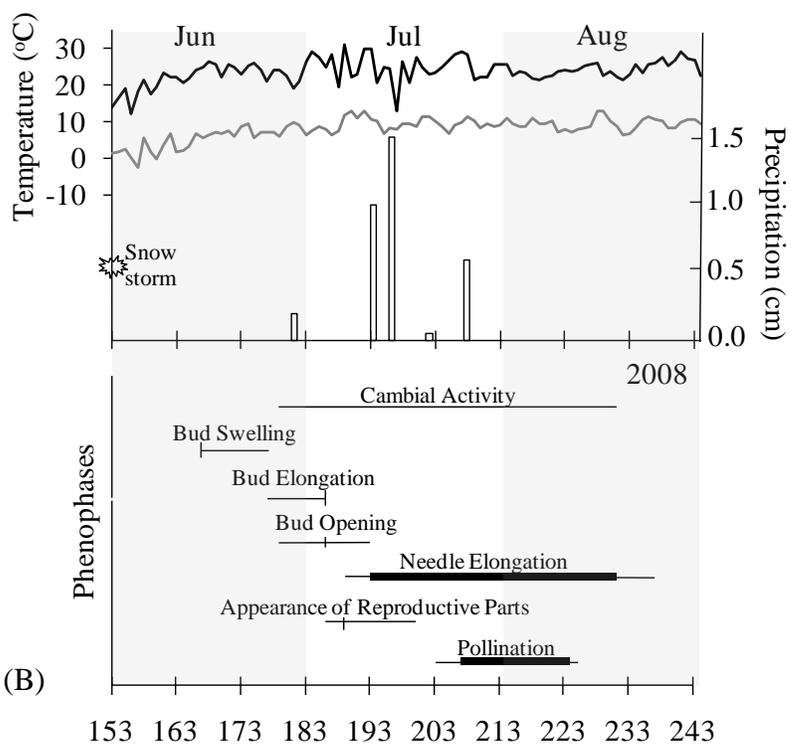
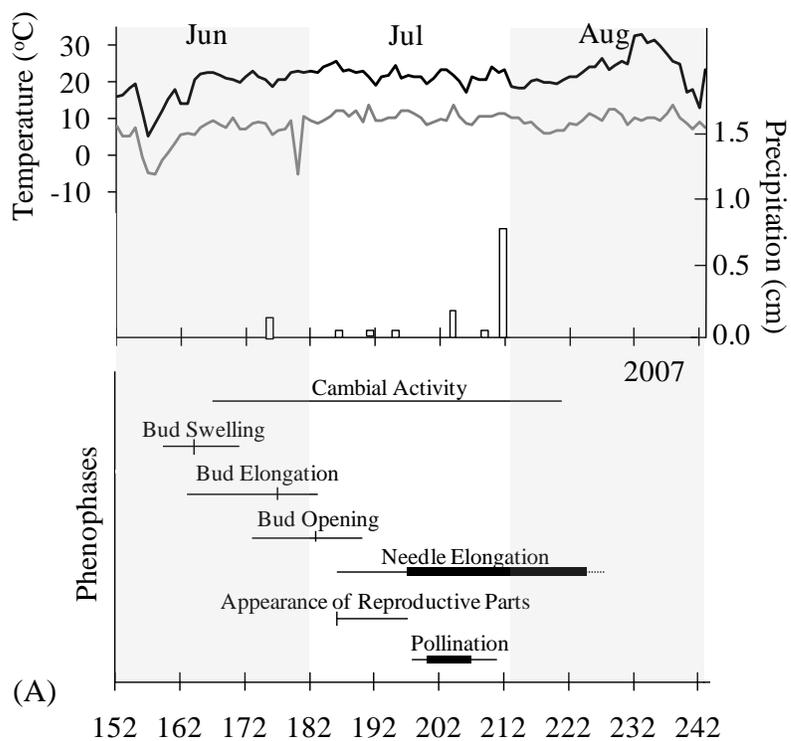


Figure B7. June-August 2007 (A) and 2008 (B) temperature, precipitation, and phenophases. Horizontal scale in Day of Year.

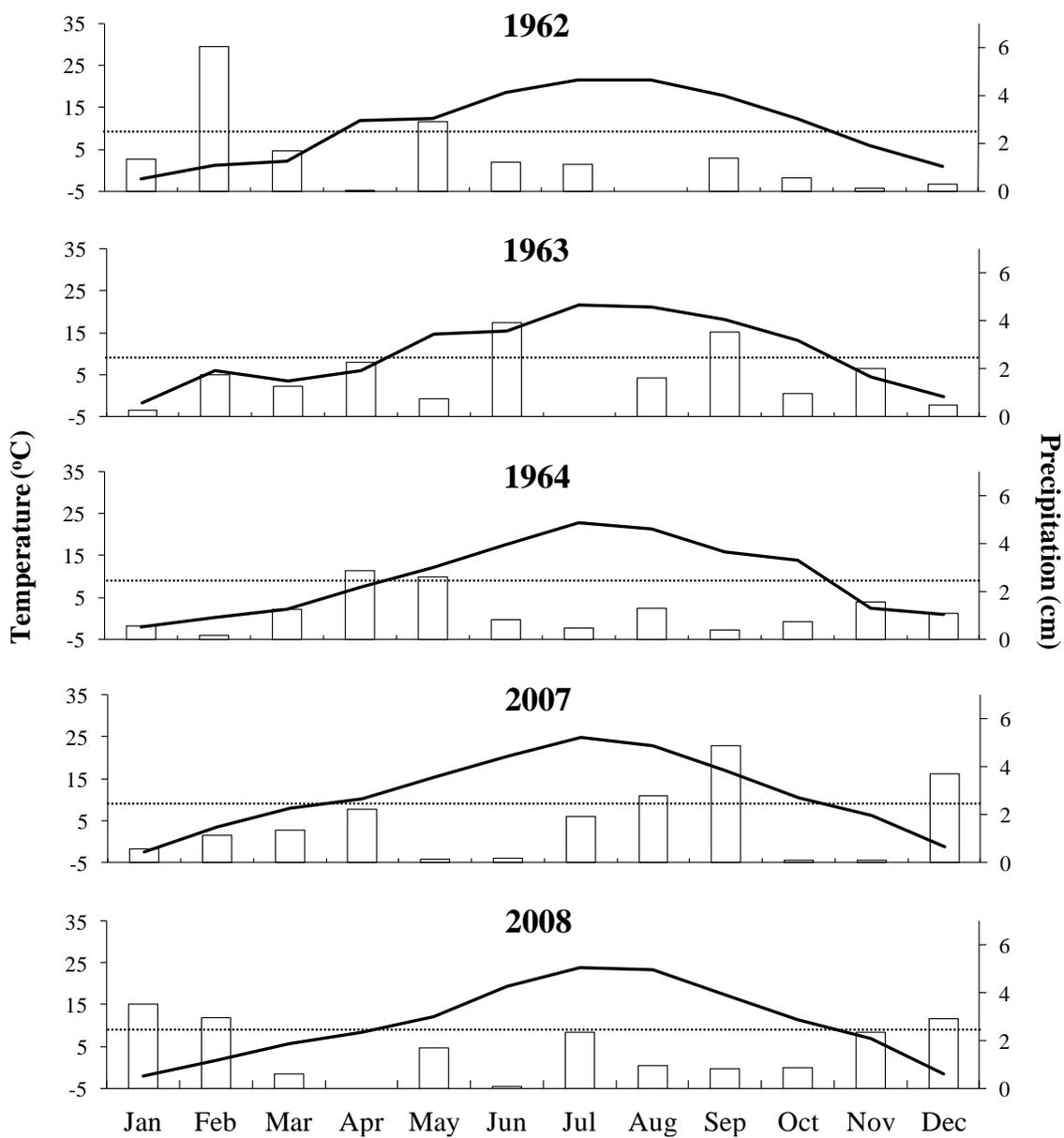


Figure B8. Nevada Division 3 climate data for 1962-64 and 2007-08. Data from National Climatic Data Center, NOAA. Crooked Creek data not used because of missing values. Horizontal dashed line represents 9°C cambial initiation from Rossi et al. 2008.

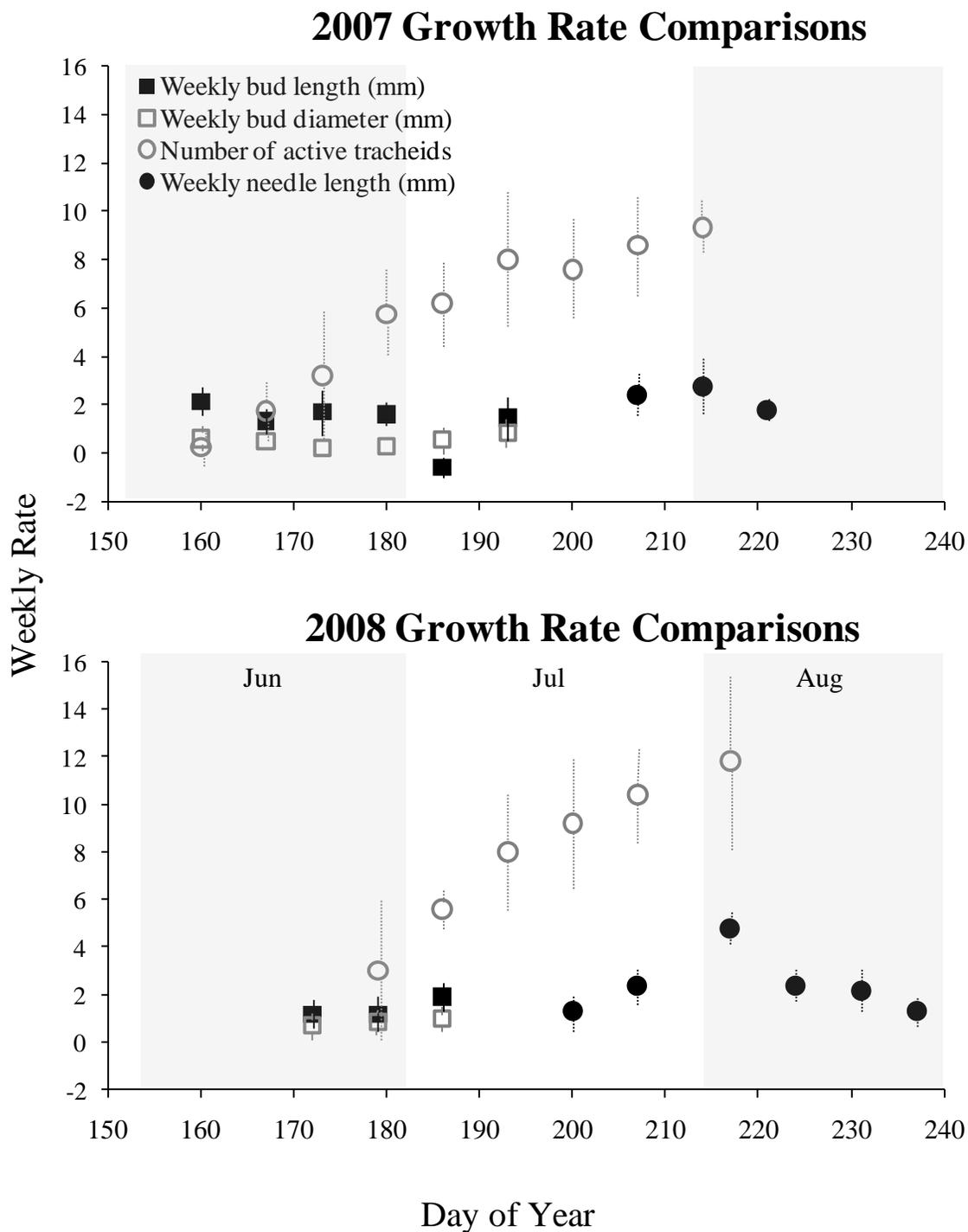


Figure B9. Comparison of growth rates.

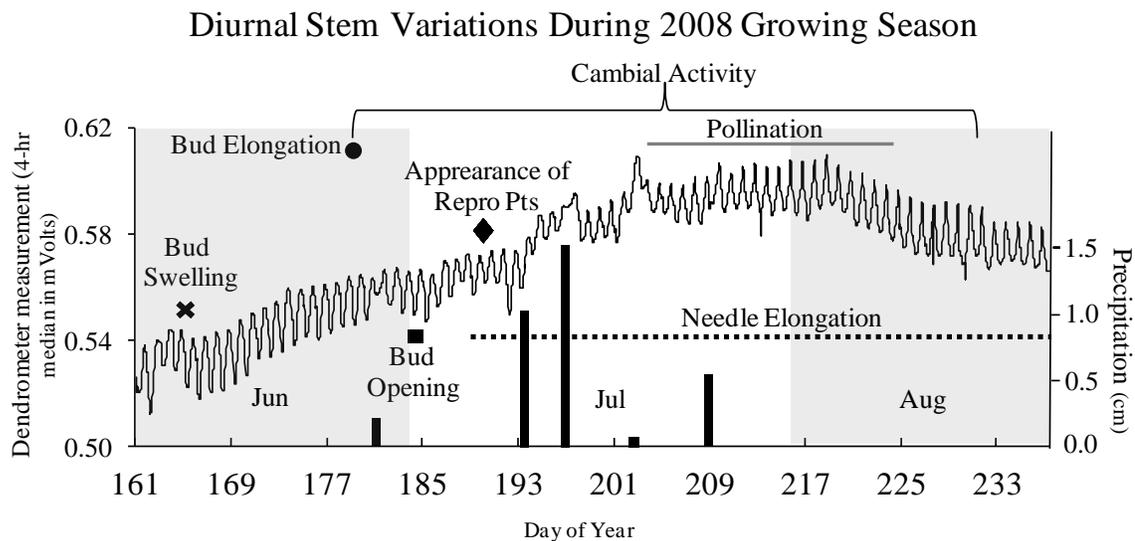


Figure B10. Median Point Potentiometer Dendrometer summer 2008. Precipitation in vertical bars.

APPENDIX C

**MONITORING STEM VARIABILITY OVER A SPATIALLY EXTENSIVE,
TOPOGRAPHICALLY DIVERSE LANDSCAPE**

Christine Hallman and Scott Parkinson

Running Head: Cost effective portable point dendrometer

Journal: *Environmental Monitoring and Assessment*

Monitoring stem variability over a spatially extensive, topographically diverse landscape

Christine Hallman^{1*}, Scott Parkinson²

¹ *The University of Arizona, Laboratory of Tree-Ring Research, Tucson, AZ 85721*

² *Roto Rooter®, 811 South Santa Rita, Tucson, AZ 85719*

*Corresponding author: Laboratory of Tree-Ring Research, The University of Arizona,
105 West Stadium, Tucson, AZ 85721, USA. Tel: +520-621-5391, fax: +520-621-8229,
email: hallman@ltrr.arizona.edu

C.1 Abstract

Collecting a representative sample from a population of interest has always been extremely important statistically and in reliably extrapolating particular properties to a large group. In this case, monitoring diurnal and seasonal stem variability with dendrometers to more accurately understand tree changes and environmental impacts on forest stands or plantations can only be accomplished via large sample sizes over large areas. Currently, automated point and band dendrometers are widely used to monitor water status, wood formation, phenology, and tree-environment relationships. Most dendrometers and associated dataloggers are expensive, cumbersome, and restricted by sensor-to-logger cable length. This newly designed point potentiometer dendrometer combines the concepts of Linear Variable Differential Transformer and rotary potentiometer dendrometers in order to create a more cost-effective, portable instrument that can be used in arid to humid environments.

Key words: point dendrometer, potentiometer

C.2 Introduction

When studying the environment, representative samples are collected and analyzed in an attempt to deduce generalized properties of a given study subject (Triola 2004). Steps must be taken to ensure findings cannot be regarded as incomplete or inadequate on statistical grounds. This is especially true when studying complex tree growth and tree-environment relationships.

Understanding complex tree physiology on individual and stand scales requires numerous samples and long-term investigations in multiple locations. Studies of diurnal and seasonal stem changes have been conducted for decades (MacDougal 1921; Fritts and Fritts 1955; Studhalter et al. 1963; Fritts et al. 1965; Drew and Downes 2009). The daily contraction and expansion and seasonal changes of a tree bole provide insights into water-tree relationships, such as stem hydration and transpiration (Abe and Nakai 1999; Zweifel and Häslner 2001; McLaughlin et al. 2003; Bucci et al. 2004), drought effects or water stress (Hinckley and Bruckerhoff 1975; Intrigliolo and Castel 2005; Drew et al. 2008; Tognetti et al. 2009), wood density (Wimmer et al. 2002; Bouriaud et al. 2005), phenology (Turcotte et al. 2009), and radial growth (Deslauriers et al. 2003; Rossi et al. 2006; Deslauriers et al. 2007; O'Brien et al. 2008). Additionally, stem fluctuation on multiple species enables the investigation of forest-wide water use synchrony between trees (Tardif et al. 2001).

Other research of stem variability enables a better understanding of tree-environmental interactions. By investigating relationships between weather and stem changes, the rate at which a given tree utilizes precipitation water and how temperature

impacts stem variation can be analyzed (Tardif et al. 2001; Steppe and Lemeur 2004; Pérez et al. 2009). This enables more connections among complex climate-wood properties to be identified on longer time scales (Drew and Downes 2009).

Sample size affects the ability to identify significant differences or relationships within a population (Peers 1996; Triola 2004). As always, there is a fine balance between monetary constraints and number of samples needed. With the use of affordable and portable technology, a larger number of samples can be investigated, leading to statistically valid results.

Dendrometers

Dendrometers are used to measure stem changes in order to identify variability among trees and between trees and their environment. Band and point are two types of dendrometers often used. Band dendrometers measure diurnal variability around the circumference of a stem at a particular height (Reineke 1932). Point dendrometers measure stem fluctuations along a single radius (Breitsprecher and Hughes 1975). At first, measurements were collected by comparing two points and measuring change by hand (Drew and Downes 2009). Later, paper chart recorders were utilized, allowing the collection of continuous data (Fritts and Fritts 1955). More recently, electronic dendrometers have been developed that transmit data to loggers that record and store information for a year or more at a time (Zweifel and Häsler 2001; Biondi et al. 2005; Intrigliolo and Castel 2005; Rossi et al. 2006; Drew et al. 2008; Pérez et al. 2009).

Evaluation of existing equipment and limiting factors

Stand-level monitoring of stem variation permits the study of tree-environment relationships over a large area. In order to obtain widespread stem observations from many trees, data need to be collected frequently, often in landscapes that are difficult to access, in rugged, terrain. Some trees may also have problematic growth forms.

Tree studies are often located in steep, rocky terrain and therefore are difficult to access by vehicle; thus, relatively small, inexpensive dendrometers and dataloggers enable greater numbers of trees to be investigated, which strengthens the interpretability of results. Reliable investigations require replication of samples (Triola 2004), but lack of funding hinders stem variability studies. Light-weight, cost-effective portable dendrometers, dataloggers, and associated installation tools improve the ease with which equipment is carried and increase the number of instruments that can be installed during a single field trip.

Automated or electronic dendrometers attached to computerized dataloggers allow multiple stems to be monitored in isolated areas, require less maintenance, and are easier to install than manual dendrometers (Phipps and Yater 1974; Phipps and Gilbert 1960). Readings can be collected at intervals of hours to minutes and can be utilized easily for statistical analysis. Another advantage of a datalogger lies in its ability to record other environmental conditions (e.g. temperature and soil moisture) simultaneously.

Use of one datalogger to record and store all data at a given study site risks catastrophic loss of information for a whole project. Some research locations are in

mountainous areas where weather phenomena, such as lightning or floods, damage equipment (Fritts 1997; Biondi et al. 2005) and where destruction of instruments by wildlife occurs (Fritts 1997; Baisan 2008). A solution would be to utilize multiple light-weight dendrometers and dataloggers instead of relying on a handful of dendrometers or one large datalogger.

Installation of band and point dendrometers proves to be challenging depending on species. Bark must be scraped around the circumference of the tree in order to properly install a band dendrometer; consequently, additional time is needed to equip the tree with a band dendrometer (Fuller et al. 1988; Keeland and Sharitz 1993). While point dendrometers require fewer installation tools and are easier to set up, inserting the necessary threaded rods for point dendrometer installation into small diameter trees and cacti is problematic (Table C2).

Measuring mechanisms for electronic point and band dendrometers record stem variability differently. Automatic band dendrometer readings are transferred from band movement to rotary potentiometer movement by way of a friction wheel touching the band. This wheel turns the potentiometer changing the resistance, which is measured by the logger. The transfer of data from band to rotary potentiometer to datalogger allows for coding errors to occur more frequently. A complex formula is needed to compute the movement distance due to many contact points (Pesonen et al. 2004). Alternatively, automated point dendrometers are in direct contact with the stem via a plunger resting against the trunk. Dendrometer plungers move and change resistance readings based on

stem movement, and these readings are directly recorded by the datalogger (Drew and Downes 2009).

Accuracy of stem measurements is impacted by dendrometer type. Although band dendrometers integrate stem variability over a circumference and provide an accurate estimation of overall radial growth, they may underestimate xylogenesis as a result of lag time before the band fits tightly around the trunk (Bower and Blocker 1966). Point dendrometers are less sensitive to temperature changes than band dendrometers, which is affected by thermal expansion of metal band (AEC 2010). Drawbacks of point dendrometers involve the relatively small movement recorded compared to a band dendrometer and the use of threaded rods for installation. A band dendrometer integrates stem movement for the entire tree circumference while the point dendrometer documents movement along a radius making detecting changes slightly more difficult.

Point dendrometers provide a method to monitor unusual tree growth forms or habits. Trees with strip bark (i.e., *Pinus longaeva*), lobate growth (i.e. *Juniperus sp.*), and bark shedding (i.e., *Eucalyptus spp.*) prove to be problematic for band dendrometers, since these instruments are designed to monitor cylindrical forms that do not frequently shed bark while point dendrometers record along a radius and do not encircle a tree stem.

Dendrometers and associated dataloggers have advanced tremendously over the last forty years, but they remain expensive and/or cumbersome. Linear Variable Differential Transformers (LVDT) have been used in point dendrometers to record stem fluctuations in both plantation and forest settings (Gensler and Diaz-Munoz 1983, Tardif et al. 2001; Zweifel and Häsler 2001; Deslauriers et al. 2003; Mäkinen et al. 2003;

Pesonen et al. 2004; Rossi et al. 2006; Drew et al. 2008; Turcotte et al. 2009). LVDT dendrometers are accurate, but they are relatively expensive, connected to fairly large dataloggers, and limited by cable length from sensor to datalogger (Biondi et al. 2005) (Table C3). Another type of automated dendrometer, the rotary potentiometer band dendrometer, is durable, but requires custom fabrication at a machine shop, slightly overestimates tree growth, and requires complex calculation for data formatting (Pesonen et al. 2004).

Based on the existing equipment and limiting factors discussed, point dendrometers that are portable, cost effective, and useable in conjunction with small automated dataloggers are an excellent choice for field investigations in remote, harsh topography. The LVDT system and rotary potentiometer band dendrometer are inadequate for collecting data on numerous, widespread trees growing on isolated steep slopes; therefore, concepts from both instruments were combined into a newly designed point potentiometer dendrometer that records digital data onto a HOBO® datalogger (Onset, Massachusetts). The purpose of this study is to test the usability and versatility of the newly designed point potentiometer dendrometer in multiple locations. Preliminary testing in several environments was conducted to evaluate the accuracy of the new design. Results of this testing are presented in this paper.

C.3 Design and Testing Strategy

Instrument design utilized off-the-shelf materials, a linear potentiometer, and a HOBO® datalogger. For details on materials, manufacture, and installation of the point potentiometer dendrometer (PPD), see Supplemental Materials, Fig. C1, and Fig. C2.

The newly designed Point Potentiometer Dendrometer was tested on trees growing in the White Mountains, California, inside and outside of Biosphere 2 located north of Tucson, and in central Tucson. In order to evaluate the versatility of the PPD, each location represents a different environment, arid, humid tropical, semi-desert grassland, and semi-arid urban, respectively. Species on which both LVDT and PPD were installed include *Pinus longaeva*, *Acacia nilotica*, *Platanus wrightii*, and *Eucalyptus* spp. Numerous PPD were tested, but only six were installed with both LVDT and PPD. LVDT dendrometers were installed above the Point Potentiometer Dendrometers.

Assessment of the Point Potentiometer Dendrometer (PPD) began in the White Mountains of California during the summers of 2007 and 2008. Trees were sampled both in valley and steep slopes with elevations ranging from 3100 to 3400 m on north, south, northeast, northwest, southeast, and southwest facing slopes. Valley trees grow in 15 to 30 cm of sandy soil while slope soils consisted of dolomite or sandstone cobbles and thin soils. Daily temperatures recorded using i-button thermochron sensors (Maxim, California) during dendrometer testing ranged from 7 to 20° C in 2007 and 8 to 21° C in 2008. Total precipitation in the summer of 2007 was 1 to 2 cm while 3 to 4 cm fell in 2008. Eighteen *Pinus longaeva* in 2007 were installed with PPD in both valley and steep, rugged slopes. The following year 23 trees were equipped with PPD, the same 18 as in 2007 and five additional trees. All readings were recorded every 30 minutes. In order to verify stem variability, two trees were installed simultaneously with the PPD and automatic LVDT point dendrometers (AEC 2010). Tree A was installed with PPD and LVDT dendrometers and evaluated for 50 days while Tree B was observed for 82 days.

Daily minimum, maximum, and median values were calculated and used for correlation analysis.

The second PPD test environment was Biosphere 2, an environmentally controlled facility located 56 km north of Tucson, Arizona where a variety of biomes are represented. Three trees in the tropical savanna biome (*Acacia nilotica*) were selected based on their diameter (greater than 30 cm) and ease of access. Trees are growing in flat locations, irrigated, relatively close to a surface water canal, and grow in 3-m-thick nutrient-rich soil. Tropical savanna temperatures and relative humidity varied from 18-32° C and 31-94%, respectively (Schronk 2010). Of these 3 trees, a Tree C was selected and equipped with both types of dendrometers and observed for 47 days.

Outside of Biosphere 2, in a semi-desert grassland environment (Brown 1982), four *Platanus wrightii* were equipped with dendrometers in 2009. These were located in a low-lying area near an irrigated, grassy field in rocky, clay soil over 60 cm deep. Temperature data collected from an i-button thermochron (Maxim, California) ranged from 3 to 29° C, and no measureable precipitation was recorded during this period (National Weather Service 2010). Two of the four trees were equipped with both types of dendrometers. Comparative stem readings for Tree D were collected for 20 days while readings for Tree E were recorded for seven days.

Lastly, in January 2010 a *Eucalyptus* spp. located in a central Tucson urban environment was equipped with both types of dendrometers. The *Eucalyptus* spp. grows in a non-irrigated setting in over 120 cm of sandy soil with a 15- to 20-cm-thick layer of caliche about 15 to 30 cm deep. Temperature varied from 1-22° C and 5.3 cm of

precipitation was recorded (National Weather Service 2010). Stem variations on this tree were recorded for 16 days.

C.4 Results

Thirty-two trees were used for testing the newly designed Point Potentiometer Dendrometer (PPD), but only the six installed with both automated LVDT point dendrometers and PPD were compared. These trees represent four tree species from four different environmental settings were used as the basis for correlation analysis (Table C1).

Time Series Comparisons

Point Potentiometer Dendrometers recorded both diurnal and seasonal stem changes on multiple trees under several environmental conditions. Using visual comparisons, PPD matched the automated LVDT point dendrometer (AEC 2010) fairly consistently (Figure C3). Expansion of stems during early morning and contraction in afternoon and long-term seasonal fluctuation of stems were evident.

Dendrometer traces for both instruments recorded diurnal and seasonal rhythms for Tree A located in the White Mountains, California (Fig. C3A). A substantial increase in trunk diameter occurred from day 10 to 15, which corresponded to two rain events during that time period. After day 15, both instruments document an increasing trend in tree diameter, which corresponds to cambial activity (Appendix B).

Three pronounced increases in stem diameter on Tree B occurred during the summer of 2007 (Fig. C3B). The latter two stem increases coincide with rainstorms, while the noticeable peak at the beginning is probably springtime hydration of stem

immediately before cambial growth begins (Turcotte et al. 2009). After day 40, the PPD trace decreases more rapidly than the LVDT dendrometer. The LVDT was installed about 50 cm higher than the PPD, possibly leading to this difference (Bormann and Kozlowski 1962).

Tree C monitored in the tropical savanna of Biosphere 2 shows similar diurnal patterns, but the LVDT records dramatic drops in single values when stem diameters are at a minimum (Fig. C3C). While the PPD records similar daily decreases, its range of stem variation is less than the LVDT. This tree grows in a very humid environment; therefore, it does not readily lose water to evapo-transpiration.

Dendrometer readings from trees D and E located outside of Biosphere 2 exhibit comparable daily patterns, but the LVDT dendrometers show pronounced drops in single value minimums (Figs. C3D-E). These trees are located in a semi-desert environment, but grow in a low-lying ditch with 6 to 8 cm of fallen leaves covering the ground (Fig. C2). The leaf cover tends to prevent moisture loss near the ground surface. Increased moisture availability may have led to discrepancies in dendrometer readings.

Differences in long-term trend between dendrometers were most evident in the *Eucalyptus* spp. monitored in central Tucson (Fig. C3F). The PPD recorded an increase in diameter on day 5, which corresponds to a rain event. The LVDT dendrometer also records an increase, but it is not as pronounced. The difference is possibly due to instrument location on the stem, differences in sensitivity to movement of the dendrometers, effects of cool temperatures on instruments.

The newly designed Point Potentiometer Dendrometer matched trends and events recorded by the LVDT dendrometers in multiple environments, but the magnitude of stem variation observed was less for the PPD. This implies that although the PPD and LVDT dendrometers document similar fluctuations, the LVDT may be more sensitive to stem variation.

Correlation analysis

To evaluate how well the LVDT and PPD readings matched, time series for each of the six trees equipped with both types of dendrometers were utilized in correlation analysis. Since stem variation was recorded every 30 minutes and series length varied from 7 to 82 days, the number of values for comparison was large, 336 to 3936, respectively. Consequently, data were reduced to daily median, minimum, and maximum values and all daily data were used in correlation analysis.

All median dendrometer values are significantly correlated between the LVDT and PPD (Table C1). Dendrometer readings are more highly correlated during times of precipitation events and overall trunk swelling than during dry periods. In the instances where daily minimum and maximum values are not highly correlated between instruments, diurnal fluctuations may be minimal and/or differences result from relative heights of dendrometers on stem.

Dendrometers installed on the two *Pinus longaeva* during the summers of 2007 and 2008 exhibit highly correlated daily minimum, maximum, and median values. In this arid environment during the growing season (Appendix B), stem changes recorded by the LVDT and PPD are similar.

The *Acacia nilotica* growing inside Biosphere 2 tree did not appear to show much stem expansion and contraction. Although minimum and median LVDT and PPD values are significantly correlated at $p < 0.01$, maximum values are correlated at $p < 0.05$. Again, this environment is very humid and evapo-transpiration may be reduced. This tree was fairly close to surface water and was periodically irrigated.

On the two trees outside Biosphere 2 growing in the semi-desert low-lying area, the LVDT and PPD median values are significantly correlated. Minimum values are not significantly correlated on either tree, and Tree E maximum values between the dendrometers are not correlated. Since these trees were in a low area covered in leaves, which holds moisture, and potentially benefited from irrigation runoff, they proved to be problematic in general with limited diurnal changes occurring. Also, the trees were at the end of their growing season and seasonal stem variation was minimal.

Finally, dendrometer minimum, maximum, and median values recorded on the *Eucalyptus* spp. in central Tucson were highly correlated. Several precipitation events occurred separated by days of relative warmth; therefore, enhancing diurnal changes leading to high correlation values.

C.5 Discussion

By using LVDT point dendrometers as a comparison for the Point Potentiometer Dendrometer, verification of stem patterns is possible. This type of assessment provides a higher confidence in data collected from the newly designed PPD. Readings collected from LVDT and PPD match best in arid and semi-arid, urban environments. This is a consequence of daily and seasonal loss of water via evapo-transpiration, which produces

noticeable changes in stem diameter. Discrepancies between the LVDT dendrometer and PPD recordings in tropical savanna and semi-desert, low-lying settings may be a consequence of position of equipment on stem (i.e., one was higher than the other), lack of diameter change, tree proximity to water, and/or relative sensitivity of instruments to stem variation.

At the same time, the PPD did not record dramatic drops in minimum values for Trees C-E. This substantial drop of LVDT values may indicate some sort of threshold where the LVDT does not accurately record data below a given value. An added benefit of the PPD is that its covering consists of plastic and does not rust while the LVDT dendrometer covering is metal. This was problematic in the tropical savanna environment where relative humidity was high. The main advantage of the LVDT system over the PPD is that the LVDT sensors appear to be more sensitive to stem changes, but additional testing is needed to verify this hypothesis. A caveat involving time series lengths for correlation analysis should be taken since the testing periods vary from 7 to 82 days. On longer times scales correlation values may increase.

The Point Potentiometer Dendrometer is more cost effective and portable than the LVDT system (Table C3). Since the PPD is constructed from off-the-shelf materials, total production cost remains low, under \$100 per dendrometer and \$100-200 per datalogger. By using an Onset HOBO® datalogger, which is widely used and affordable, the PPD becomes portable and more versatile than automated dendrometers that are restricted by length of cable to a relatively large datalogger. Catastrophic data loss is less likely with a PPD since several dataloggers can be utilized at one site. Also, data

recorded can be quickly viewed graphically by HOBO® software in the field where other dendrometer data must first be formatted.

C.6 Conclusions

The Point Potentiometer Dendrometer is an inexpensive and convenient option for monitoring tree stem fluctuations simultaneously on numerous trees. The PPD recorded data on multiple species in temperatures ranging from 1 to 32° C and relative humidity ranging from 31-94%, suggesting that it is a versatile instrument. LVDT and PPD stem data are most highly correlated in arid to semi-arid environments. An advantage of the PPD is that it resists oxidation, while the main disadvantage is that it appears to be less sensitive to stem changes than the LVDT. Durability of Point Potentiometer Dendrometers in cold environments and its lifetime of usability remain unknown. Further testing and calibration of the PPD on more trees in other environments would provide additional information on its utility and reliability.

C.7 Acknowledgements

We would like to thank Bill Gensler (Agricultural Electronics Corporation) and Chris Baisan for guidance and advice and Biosphere 2 for the use of their facilities and climate data. Without assistance from Dr. Paul Sheppard, Ben Parcell, Rex and Karen Adams, Alex McCord, Howard Arnott, BCP project, Sue Clark, Dave and Shane Smith, John Louth, Tom and Annita Harlan, Hal Fritts, Bob and Debbie Buecher, and many others, this project would not have been possible. The manuscript was improved by reviews from Paul Sheppard, Connie Woodhouse, Katie Hirschboeck, Dave Meko, and Jake Weltzin.

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Table C1. Trees utilized in correlation comparisons. Correlations are between the newly designed PPD and the LVDT system. Bold correlation values are significant at $p < 0.01$.

Underlined values are significant at $p < 0.05$.

Tree Id	Location	Species	Time Period	Environmental Setting	Correlations		
					Min	Max	Med
A	White Mts., CA	<i>Pinus longaeva</i>	6 July-24 Aug, 2008	Arid, open forest	0.89	0.90	0.93
B	White Mts., CA	<i>Pinus longaeva</i>	23 May-14 Aug, 2007	Arid, open forest	0.55	0.67	0.70
C	Tropical Savanna, B2	<i>Acacia nilotica</i>	22 June-7 Aug, 2009	Humid, controlled	0.93	<u>0.34</u>	0.97
D	Outside B2	<i>Platanus wrightii</i>	10 Oct-16 Oct and 31 Oct-11 Nov, 2009	Semi-desert, grassland	0.38	0.65	0.76
E	Outside B2	<i>Platanus wrightii</i>	10 Oct-16 Oct, 2009	Semi-desert, grassland	0.69	0.67	0.88
F	Central Tucson, AZ	<i>Eucalyptus</i> spp.	16 Jan-31 Jan 2010	Semi-arid, urban, non-irrigated	0.85	0.95	0.94

Table C2. Comparison of band and point dendrometer characteristics.

	Band	Point
Installation	Bark scrapped over entire circumference, which takes additional time	Fewer tools for set up and installation, but insertion of threaded rods into small diameter trees and cacti problematic
Measuring Mechanisms	Measurement coding errors may occur more frequently	Measurement coding errors tend to occur less frequently
Accuracy of Stem Measurements	Provides accurate overall growth around a circumference, but underestimates xylogenesis	Less sensitive to temperature changes, but record relatively small amount of movement making the detection of small movements difficult
Measurement of Unusual Growth Forms and Habits	Problematic as band needs to be installed around a circular stem	Works well on usual growth forms and habits as it records stem variability along a radius

Table C3. Comparison of automated point dendrometer characteristics.

	LVDT manufactured by AEC	PPD
Cost	\$650	\$80 (parts)
Datalogger Cost	\$2900	Indoor = \$108 + housing, Outdoor - \$215
Distance Restrictions	Length of cable (40 m)	NA
Dendrometer Capacity of Datalogger	16	4
Graphic Viewing of Data	DOS program to covert to text file then to EXCEL file	View on-screen in field with HOBO software
Portability (datalogger)	~10 lb (4536 g), 10 x 8 x 6 in (25.4 x 20.3 x 12.7 cm)	Indoor = 1.6 oz (46 g), 2.3 x 2.9 x 0.9 in (58 x 74 x 22 mm) Outdoor = 7 oz (200 g), 5.5 x 5.38 x 1.25 in (140 x 137 x 32 mm)

C.9 Figure Captions

Figure C1. Schematic of Point Potentiometer Dendrometer. A = plunger, B = MMR 10-8 potentiometer, C = front flat PVC cap, D = #2 bolt, E = #2 nut, F = 1-inch PVC body, G = butt splice connectors in heat shrink tubing, H = rear flat PVC cap, I = 3x18 gauge insulated wire, and J = 2.5-inch stereo jack.

Figure C2. (A) PPD installed on a *Platanus wrightii* outside of Biosphere 2. HOBO® datalogger located inside black ABS housing. (B) Potentiometer resting against the bark.

Figure C3. Visual seasonal comparison of both point dendrometer types. Graphs with negative integers have been inverted to resolve wiring issues.

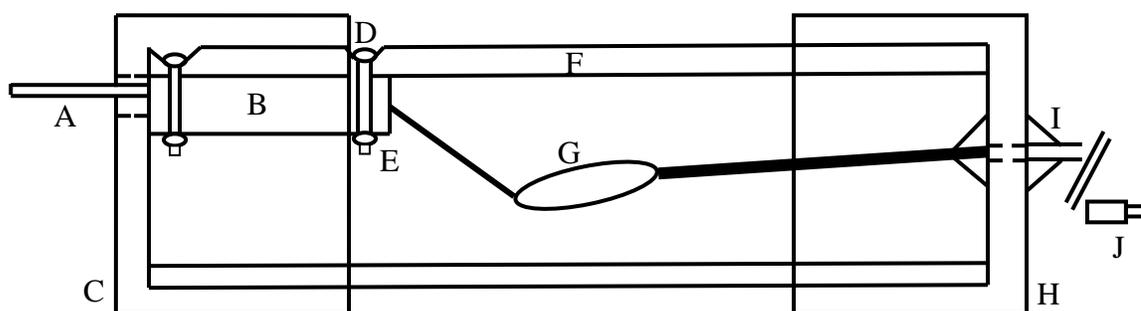


Figure C1. Schematic of Point Potentiometer Dendrometer. A = plunger, B = MMR 10-8 potentiometer, C = front flat PVC cap, D = #2 bolt, E = #2 nut, F = 1-inch PVC body, G = butt splice connectors in heat shrink tubing, H = rear flat PVC cap, I = 3x18 gauge insulated wire, and J = 2.5-inch stereo jack.



Figure C2. (A) PPD installed on a *Platanus wrightii* outside of Biosphere 2. HOBO® datalogger located inside black ABS housing. (B) Potentiometer resting against the bark.

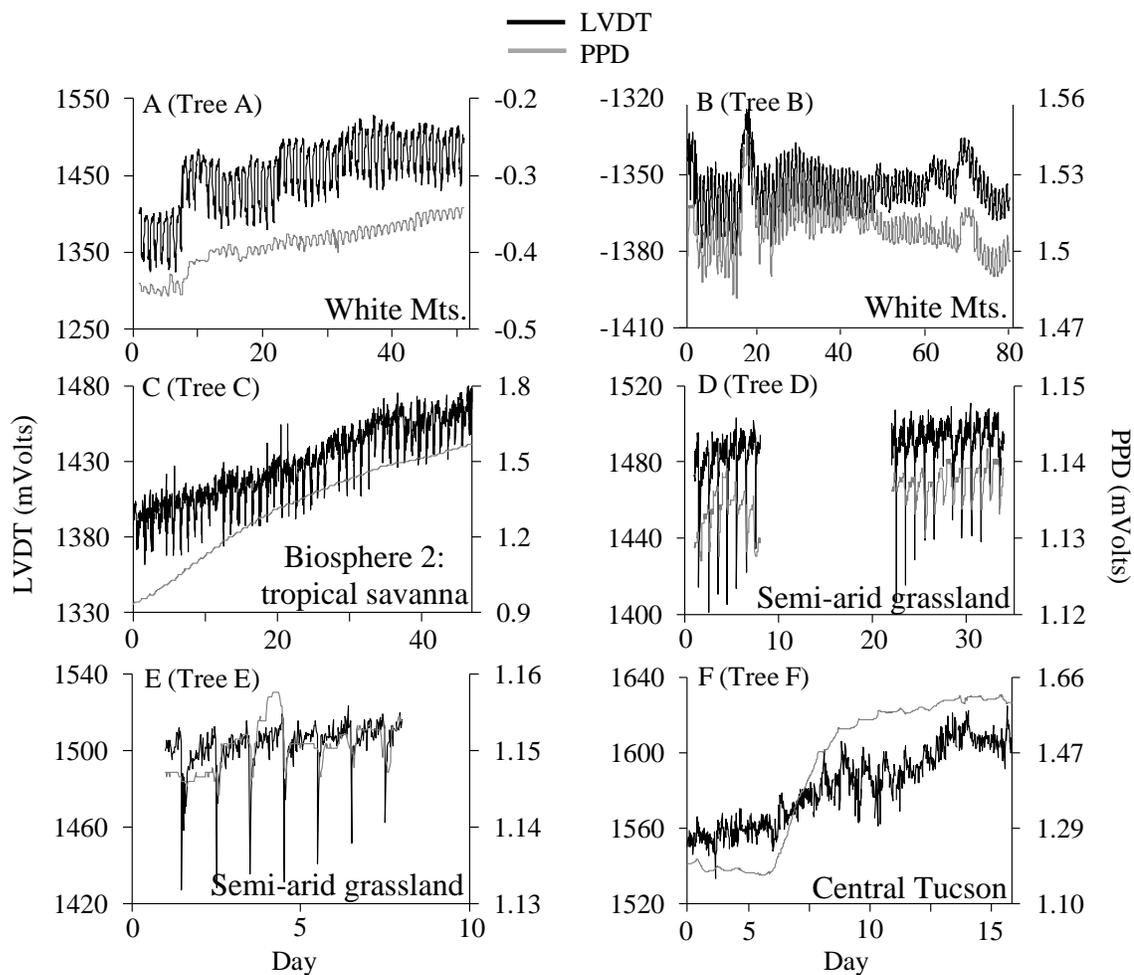


Figure C3. Visual seasonal comparison of both point dendrometer types. Graphs with negative integers have been inverted to resolve wiring issues.

C.10 Supplemental materials

C.10.1 Materials

Point Potentiometer Dendrometer (PPD)

- 4.5-inch long, 1-inch diameter PVC pipe
- two 1-inch PVC flat end caps
- one MMR 10 (shaft spring return) with 8 mm electrical stroke potentiometer, 2 K ohms resistance values (www.p3america.com)
- 3 x 18 gauge insulated wire
- heat shrink tubing
- 18 gauge butt splice connectors
- silicone
- two #2 bolts
- two #2 nuts

Mount Assembly

- 2.5-inch angle bracket
- two 6 x 24 x 6 inch threaded rods
- four 6 x 24 coupling nuts
- one 1-inch electrical conduit clamp

Datalogger

Four-channel indoor and outdoor HOBO® dataloggers (<http://onsetcomp.com/>) and a cable with a stereo jack were also utilized. Indoor HOBO® dataloggers were housed in six-inch-long 3-inch diameter ABS with a 3-inch ABS cap, 3-inch ABS female iron pipe adaptor and 3-inch male iron pipe plug.

C.10.2 Design of Point Potentiometer Dendrometer

A 4.5-inch long section of 1-inch diameter PVC pipe was cut for the body of the Point Potentiometer Dendrometer (Figure C1). In order to slide the front cap onto the PVC body, a file or dermal tool was used to bevel the PVC body where the two potentiometer mounting bolts were inserted. The potentiometer was mounted to the PVC

body using #2 bolts and existing holes in the potentiometer. A hole was drilled in one of the flat PVC caps so that the potentiometer plunger had a place to exit. When the front cap was pushed onto PVC body, the cap must be pushed straight or the potentiometer plunger will be bent. In cases where it was necessary to remove the front cap, it was removed with a file or cut. The potentiometer plunger broke when the front cap was twisted. A hole was drilled in the rear PVC cap to allow the 3 x 18 gauge insulated wire a location to exit. Heat shrink tubing was slid onto the potentiometer wiring. The potentiometer wiring was connected to the 3 x 18 gauge insulated wire using butt splice connectors. Then each splice was taped and the heat shrink tubing was pulled over connectors. Once the tubing was in place, heat was applied in order to seal. Lastly, the rear cap was pushed onto PVC body and the wire was sealed with silicone.

C.10.3 Installation and Issues

Using the bracket as a guide, holes were drilled in a tree with 7/64th-inch aircraft drill bit. Threaded rods were inserted into the tree using an electric drill. One coupling nut was threaded onto each rod until it contacted the bark. Then the bracket was placed on the threaded rods. Two additional coupling nuts were used to hold the bracket in place. The bracket angle relative to tree was adjusted with first set of coupling nuts. Bark was scraped where the potentiometer plunger rested. The PPD was inserted into the 1-inch electrical conduit clamp and tightened to finger tightness (Figure C2). The cable stereo jack was inserted into the HOBO®. While the HOBO® datalogger was connected to the computer, under instrument type “2.5 stereo” was selected and the datalogger was launched.

Indoor HOBO® dataloggers were placed in ABS housing for protection from the weather. A 3-inch ABS cap was glued onto a six-inch-long 3-inch diameter ABS pipe with an attached 3-inch ABS female iron pipe adaptor. A slot was cut into the iron pipe adaptor to allow cable insertion. The indoor datalogger was placed in ABS housing then a 3-inch male iron pipe plug was utilized to close the housing. Finally, silicone was used to waterproof the housing around the cables.

The major problem encountered during the testing of the PPD involved rodents. On three occasions, cables were destroyed. Cables to the HOBO® datalogger were buried when possible. Cables above ground were sprayed with cayenne pepper and inserted through 1/4-inch diameter irrigation tubing.