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I am submitting herewith a dissertation written by Maegen Lee Rochner entitled "Tree-Ring Evidence of Climate and Environmental Change, Beartooth Mountains, Wyoming, U.S.A.." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Geography.

Sally P. Horn, Matthew Bekker, Major Professor

We have read this dissertation and recommend its acceptance:

Nicholas Nagle, Kelsey N. Ellis, Michael L. McKinney

Accepted for the Council:

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Tree-Ring Evidence of Climate and Environmental Change, Beartooth Mountains, Wyoming, U.S.A.

A Dissertation Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Maegen Lee Rochner
May 2019

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DEDICATION

I would like to dedicate this dissertation to my husband,
who stood by me during the grueling process of completing my PhD.
Without him, I would not have survived.

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I would first like to thank my committee co-chairs, Drs. Sally Horn and Matthew Bekker, who stepped in last minute to help during an incredibly tough time. My dissertation was much improved by their thoughtful guidance. I thank them both for putting in the extra hours to help me write, re-write, edit, and re-edit my dissertation chapters. I also thank Drs. Kelsey Ellis, Nicholas Nagle, and Michael McKinney for agreeing to serve on my committee and for providing valuable expertise in data, climate, and environment. I thank every member of my committee for his or her help in completing my dissertation.

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ABSTRACT

Long-lived, subalpine tree species like whitebark pine and Engelmann spruce may eventually cease to exist due to the combination of climate change and exacerbated native and invasive biological threats. While this loss would have dire consequences for mountain ecosystems, it would also result in the irreversible loss of valuable climatological and ecological data preserved in the growth rings of these trees. The purpose of this dissertation research was to develop extended whitebark pine and Engelmann spruce tree-ring chronologies for use in regional analyses of climate and disturbance, and more importantly to demonstrate the potential of these tree species and the need for increased tree-ring based work. From a high-elevation site in the Beartooth Mountains of Wyoming, I collected hundreds of samples from both living and remnant whitebark pine and Engelmann spruce, and used dendrochronological methods to develop two millennial-length tree-ring chronologies for these species. Using information gained from these chronologies, I examined evidence of climate and environmental change. First, I reconstructed the millennial-length history of a subalpine "ghost" forest. I determined that massive whitebark pine and Engelmann spruce trees had established and lived in the Beartooth Mountains during the warm and dry Medieval Warm Period but perished during the colder Little Ice Age. Next, I evaluated climate drivers of tree growth and implications for ongoing climate change. I discerned the key climatic factors controlling whitebark pine and Engelmann spruce growth, but also discovered that tree responses to climate may be changing. Finally, I investigated the influence of volcanic cooling events in the Beartooth Mountains. I discovered frost and narrow rings associated with climate-changing volcanic eruptions and contributed important information to our understanding of volcanic cooling. I hope that my work may serve as a guide for future efforts to collect and analyze data from whitebark pine and other species that are, and may be, threatened with extinction. I also call for increased contribution of tree-ring data, from whitebark pine especially, but also from other subalpine species, to accessible archives, such as the International Tree-Ring Data Bank (ITRDB), which will make tree-ring data available for current and future scientists.

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CHAPTER ONE

INTRODUCTION

1.1 Motivation and Purpose

1.1.1 Whitebark Pine Ecosystems

Whitebark pine (*Pinus albicaulis* Engelm.) is a hardy, long-lived, generally slow-growing tree species found at elevations near treeline in the western United States (Arno and Hoff 1990; Tomback *et al*. 2001). The species is considered both keystone and foundational in its ecosystem because of its role as a wildlife food source (Tomback 2001; MacFarlane *et al*. 2013; Resler *et al*. 2014) and as a facilitator in the development of tree communities in harsh, high-elevation conditions (Resler *et al*. 2014; Tomback *et al*. 2014). The tree species provides a range of valuable ecosystem services, including delayed summer snowmelt, increased soil stability, and improved water quality downstream (Tomback *et al.* 2016), and has historical or cultural value to the many Native American tribes and First Peoples that have relied on it for food, medicine, heat, and building materials (Keane *et al*. 2012; Pojar and MacKinnon 2013; Tomback *et al*. 2016). The historical and ecological value of whitebark pine is currently threatened by anthropogenic influences, including climate change and altered fire regimes (Tomback *et al*. 2001; Perkins 2015). Warming temperatures have also exacerbated other threats, such as the native mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and the invasive white pine blister rust (*Cronartium ribicola* J.C. Fisch.), which were previously limited by the colder conditions found near treeline (Tomback *et al*. 2001, 2016; Bentz *et al*. 2010, 2015; Logan *et al.* 2010; Jewett *et al.* 2011; MacFarlane *et al*. 2013)**.**

The one-two punch of climate warming (Leung *et al.* 2004; Bentz *et al.* 2010; Iglesias *et al.* 2015) and resulting increases in infestation and disease are exerting major stresses on whitebark pine ecosystems. More than 50% of whitebark pine trees are currently dead or dying (McLane and Aitken 2012), and studies have projected possible extirpation of the species in some areas (Schrag *et al.* 2008; Jewett *et al.* 2011). With continued warming, whitebark pine is projected to lose up to 99 percent of suitable habitat in some areas (Chang *et al*. 2014; Hansen and Phillips 2015). The species was recommended for listing as endangered in the United States in 2011 (Dooley *et al.* 2015; Perkins 2015; Tomback *et al*. 2016) but is currently only listed as endangered by the IUCN Red List (Mahalovich and Stritch 2013). Whitebark pine was listed in Canada in 2012 under the Species at Risk Act of 2002 (Perkins 2015; Tomback *et al*. 2016). The loss of this important keystone species will lead to dramatic ecosystem changes, such as reduced biodiversity and altered treeline structure, throughout its range (Callaway 1998; Tomback *et al*.

2001; Tomback and Kendall 2001; MacFarlane *et al*. 2013; Tomback *et al*. 2016). As part of a complicated network of ecological relationships, natural and invasive threats, and human intervention, whitebark pine represents a management challenge.

Although listed as a species of least concern because of relative abundance and fewer threats (Farjon 2013), Engelmann spruce (*Picea engelmannii* Parry ex Engelm) also faces the combined effects of climate change, bark beetle infestations, and altered fire regimes (DeRose and Long 2007; Bentz *et al*. 2010; Hart *et al*. 2014; Foster *et al*. 2017). Bark beetles are one of the most important disturbance agents shaping western forests (Temperli *et al*. 2015; Bakaj *et al*. 2016), and one in particular, the spruce beetle (*Dendroctonus rufipennis* Kirby), is exceptionally destructive, with recorded mortality rates of greater than 90% in some areas (DeRose and Long 2007; Hart *et al*. 2014; Bakaj *et al* 2016). Despite some variability, bark beetles in general are expected to benefit from projected warming, and outbreaks of both mountain pine and spruce beetles are exacerbated by warmer and drier conditions (Hebertson and Jenkins 2008; Bentz *et al*. 2010; Hart *et al*. 2014). In an uncertain future, Engelmann spruce and other subalpine tree species might also face the threat of extinction.

1.1.2 Species Potential as Natural Archives

Tree-ring chronologies from both whitebark pine and Engelmann spruce have the potential to provide long records of environmental change. While most Engelmann spruce trees tend to live in the range of 250–450 years (USDA 2003), some with ages exceeding 850 years have been identified (Brown *et al*. 1995). Whitebark pine is one of only a few tree species that can live in excess of 1,000 years (Perkins and Swetnam 1996; Youngblut and Luckman 2013). Remnant (dead) wood from both of these species, and especially from whitebark pine, the wood from which is more resinous and therefore more resistant to weathering, can extend these records back even further. In addition, whitebark pine trees grow in harsher, subalpine environments with consistently cold temperatures, high winds, and thin soils that are inhospitable to most tree species (Tomback *et al*. 2001; Youngblut and Luckman 2013). In these conditions, where climate is likely the dominant limiting factor influencing growth (Fritts 2001), long-lived tree species such as whitebark pine and Engelmann spruce are likely to provide climate-sensitive tree-ring chronologies. Millennial-length tree-ring chronologies are also of high importance to dendroclimatological study because of their potential to track low-frequency climate variability

(Briffa *et al*. 2001; Esper *et al*. 2003; Helama *et al*. 2005; Youngblut and Luckman 2013). Given the potential ages of whitebark pine and Engelmann spruce trees, as well as the limiting climates in which they live, both species can provide valuable climate records.

As with other high-elevation conifers (Peterson and Peterson 1994; Ettl and Peterson 1995; Peterson *et al*. 2002), relationships with growing season temperatures have been found to dominate the climate signal in both whitebark pine (Perkins and Swetnam 1996; Biondi *et al*. 1999; Bunn *et al*. 2005; Larocque and Smith 2005; Kipfmueller 2008; Kipfmueller and Salzer 2010; Youngblut and Luckman 2013) and Engelmann spruce (Peterson and Peterson 1994; Luckman *et al*. 1997; Luckman and Wilson 2005). Significant relationships with winter snowpack have also been identified for whitebark pine (Perkins and Swetnam 1996; Carlson *et al*. 2017). However, despite this evidence of dendroclimatological potential, few studies have focused on whitebark pine for climate reconstruction (Biondi *et al*. 1999; Kipfmueller 2008). Regional climate reconstructions focused on Engelmann spruce are more numerous but are concentrated in the Canadian Rockies (Luckman *et al*. 1997; St. George and Luckman 2001; Wilson and Luckman 2002, 2003; Luckman and Wilson 2005). Engelmann spruce and other spruce species have been increasingly included in emerging research using blue intensity, a surrogate for maximum latewood density (MXD), which has been shown to be a strong proxy for summer temperatures (Wilson *et al*. 2014; Österreicher *et al*. 2015; Kaczka *et al*. 2018).

The relatively infrequent use of whitebark pine in climate reconstructions is most likely due to high rates of disturbance in these stands, especially in recent decades, that limit the suitability of the species for dendroclimatological study in some areas (Larocque and Smith 2005; Youngblut and Luckman 2013). Growth decline, due to mountain pine beetle, white pine blister rust, increasing temperatures, or any combination of these three may lead to changes in climate-growth responses or diminish the climate signal (Youngblut and Luckman 2013; van de Gevel *et al*. 2017). In addition, tree-ring patterns in whitebark pine, as in other high-elevation conifers, often exhibit low inter-annual variability and high first-order autocorrelation (St. George and Luckman 2001; Wilson and Luckman 2003; Laroque and Smith 2005; Youngblut and Luckman 2013). Because of this, the most useful whitebark pine chronologies should have a suitable length to capture low-frequency climate variability, and are often used in combination with chronologies from other species (Biondi *et al*. 1999; Kipfmueller 2008; Youngblut and Luckman 2013). Such chronologies however, may soon disappear from the landscape. Rather than serve as a disincentive to perform whitebark pine research, I suggest that the decline of the species should serve to motivate the capture of more tree-ring data, especially from relatively healthy whitebark pine ecosystems, before increasing threats make such research unfeasible.

While increasing threats to both whitebark pine and Engelmann spruce may eventually reduce the value of the species for climatological studies, changes in growth due to such threats, such as bark beetles and altered fire regimes, are valuable data in themselves. Given that both species co-evolved with bark beetles (DeRose and Long 2007; Raffa *et al*. 2013), multi-century tree-ring chronologies might inform spatiotemporal trends, including physical and climatological influences on outbreaks (Berg *et al*. 2006; Hart *et al*. 2014; Bakaj *et al*. 2016; Derderian *et al*. 2016). Tree rings have been used to study mountain pine and spruce beetle disturbances (Eisenhart and Veblen 2000; Alfaro *et al*. 2003; Berg *et al*. 2006; Axelson *et al*. 2009; Jarvis and Kulakowski 2015), including in whitebark pine (van de Gevel *et al*. 2017) and Engelmann spruce (DeRose and Long 2007; Hart *et al*. 2014; Bakaj *et al*. 2016; DeRose *et al*. 2017). In a similar fashion, tree-ring chronologies that include scars and other evidence of fire can inform spatiotemporal patterns of wildfire (Speer 2010), which is increasingly necessary as fire regimes continue to change under climatic and anthropogenic influences (Pechony and Shindell 2010; Peterson *et al*. 2011; Parisien *et al*. 2016; Balch *et al*. 2017). In addition to disturbance, tree-ring data can provide information on stand age and structure, establishment, and mortality (Speer 2010), and certain ring anomalies, such as frost rings, can provide a proxy for dramatic, but short-term climate changes (Scuderi 1990; Bailey and McAneney 2015). In this way, even without climatological information, tree-ring chronologies from whitebark pine and Engelmann spruce hold value as archives of ecological change.

1.1.3 Call to Action

Whitebark pine may eventually cease to exist, and old Engelmann spruce trees may be greatly reduced in number, due to the combination of climate change and exacerbated native and invasive biological threats. While this loss would have dire consequences for mountain ecosystems, it would also result in the irreversible loss of proxy data of climatological and ecological value. The need to capture data from a disappearing foundation species was argued by Hessl and Pederson (2012), who proposed the Hemlock Legacy Project (HeLP) to inspire increased collection from old growth eastern (*Tsuga canadensis* L.) and Carolina hemlock

(*Tsuga caroliniana* Engelm.) trees, which are being devastated by the invasive hemlock wooly adelgid (*Adelges tsugae*). In a similar manner, I call for increased contribution of tree-ring data from whitebark pine especially and from other subalpine species to accessible archives, such as the International Tree-Ring Data Bank (ITRDB), to make important proxy data available for current and future scientists. Despite the potential of whitebark pine in dendroclimatological and dendroecological research, few accessible chronologies for this species exist. In the United States, only fifteen whitebark pine chronologies are published on the ITRDB (2019) (Figure 1.1, see Appendix for all Figures and Tables), and only fourteen are available in Canada (Table 1.1). Only two chronologies are published for the Greater Yellowstone Ecosystem, which is the focus area of this dissertation. Of the 29 whitebark pine chronologies on the ITRDB, nine pre-date, or nearly pre-date the year 1000 CE, demonstrating the potential to develop millennial-length chronologies from the species (Table 1.1). Data are much more common for Engelmann spruce (over 100 chronologies on the ITRDB, 2019), although only four published chronologies extend over 1000 years (Table 1.1). Many whitebark pine and Engelmann spruce chronologies that are published on the ITRDB also need to be updated, as most of them end in the 1980s. The relative scarcity of published whitebark pine chronologies means that those with unpublished data should work to publish, but also that tree-ring scientists should seek to collect more data from the tree species. This includes data from dead, or remnant trees, which have the potential to extend tree-ring chronologies back for millennia.

Under certain conditions, remnant (sometimes “relic” or “subfossil”) wood has been observed to persist on the landscape, sometimes preserved in ice or water, for hundreds to even thousands of years (LaMarche 1973; Scuderi 1987; Carrara *et al.* 1991; Hormes *et al.* 2001; Scapozza *et al.* 2010; Morgan *et al.* 2014; Carrara and McGeehin 2015; Salzer *et al.* 2019). However, as with living whitebark pine, remnant wood is also disappearing from the landscape. At some sites, such as the one chosen for this dissertation research, firewood collection and campfires are permitted for any dead and down wood, and in some areas, changes in moisture due to climate change may increase rates of decay. Remnant wood with the potential to inform paleoclimate is a finite resource that will eventually disappear from the landscape. Because of this, I emphasize not only the necessity of capturing data from living whitebark pine, but the need for more studies that include important data from remnant wood. While this wood may not always be dateable using tree-ring methods, I encourage tree-ring dating where possible because of the climatological and ecological information that chronologies can provide. For whitebark pine and other threatened species, these data could assist in ongoing conservation efforts, but would also serve to capture information on past climate and ecology that might otherwise be lost forever. The overarching purpose of this dissertation research is to develop extended whitebark pine and Engelmann spruce chronologies with the potential for use in regional analyses of climate and disturbance. This study is meant not only to provide data that will be archived in the ITRDB, but to serve as an example of the potential of these tree species and the need for increased tree-ring based work. Along with Hessl and Pederson (2012), I hope that my work may serve as a guide for future efforts to collect and analyze data from whitebark pine and other species that are, and may be, threatened with extinction.

1.2 Dissertation Study Site

The study site, Fantan Lake (FTL, 44.926°N, 109.544°W), is a mixed subalpine forest community located in the Beartooth Mountains, near the Beartooth Highway (U.S. 212), in the Shoshone National Forest (Figure 1.1), within the Greater Yellowstone Ecosystem. FTL is characterized by high-elevation (2800 to 3020 m) meadows and small "islands" of relatively young (< 300 years old) whitebark pine, Engelmann spruce, and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) trees, which tend to concentrate on outcrops of the three to four billion-year-old granite and metamorphic rocks of the mountain range (Lageson and Spearing 1991). The site is also characterized by the remains of extremely large trees (Figure 1.2). The exceptional number of large, intact remnant trees is what originally drew me to the FTL site, as it suggested some extensive mortality event, or series of events. While whitebark pine was the original focus of this study, I eventually identified some of these large remnants as Engelmann spruce, which led me to expand the project to include the species. The discovery of equivalent-age remnant spruce logs made it clear that this species is a crucial part of the story at FTL and a necessary component to any research regarding climate and ecology at the site.

1.3 Dissertation Objectives

For this dissertation research, I use methods in tree-ring science, or dendrochronology, to complete the following objectives:

1. Develop millennial-length whitebark pine and Engelmann spruce tree-ring chronologies for the Greater Yellowstone Ecosystem (Chapter 2);
2. Examine the influence of late Holocene climate change on temporal patterns of establishment and mortality at the FTL site (Chapter 2);
3. Analyze climate drivers of growth in living whitebark pine and Engelmann spruce trees at the FTL site and assess implications of climate relationships for the future of whitebark pine in a changing climate (Chapter 3);
4. Evaluate the potential of paleoclimate reconstruction using the FTL whitebark pine and Engelmann spruce chronologies (Chapter 3);
5. Investigate the potential of the FTL whitebark pine and Engelmann spruce chronologies to record volcanic cooling events (Chapter 4).

1.4 Dissertation Organization

My dissertation consists of five chapters: this introduction, three individual manuscripts prepared for submission to peer-reviewed journals, and a final chapter that summarizes the dissertation research and describes potential future work. In Chapter 2, I address the question that originally drew me to the FTL study site: What killed the massive trees (Figure 1.2) that used to grow there? I hypothesized that the large remnants represent the remains of an open woodland that thrived during the Medieval Warm Period (MWP) (ca. 900–1350 CE) and perished during the Little Ice Age (LIA) (ca. 1350–1850). To test this hypothesis, I used dendrochronology to absolutely date the tree rings from 106 remnant trees. This allowed me to determine approximate mortality dates, and in some cases establishment dates for the remnant trees. In addition, I crossdated and estimated establishment dates for 148 living whitebark pine and 118 living Engelmann spruce trees. With these data, I examined temporal patterns of establishment and mortality at the FTL site and related these changes to the MWP and LIA. As a result of this work, I ultimately developed two millennial-length chronologies for the FTL site, one for whitebark pine and another for Engelmann spruce.

In Chapter 3, I evaluate the potential of paleoclimate reconstruction using the millennial-length tree-ring chronologies from FTL. To test for significant relationships between tree growth and monthly and seasonal aggregates of temperature and moisture variables, I used correlation analyses. I then used forward and backward evolutionary analyses to determine if these relationships remained stable through the instrumental period 1896–2016 CE. With these methods, I also examined how past climate, and potentially modern climate change, have affected and may affect growth in whitebark pine and Engelmann spruce at FTL. Finally, in Chapter 4, I evaluate the potential of the FTL chronologies to record volcanic cooling events. I combined frost ring, tree-ring minima (narrow rings), and evidence of suppressed growth with climate records and ice core and tree-ring proxy data from other sources to examine where multiple lines of evidence support volcanic cooling in my study area. First, I developed a frost-ring chronology using synchronous, frost-damaged rings. I then used relative growth change analyses to identify pointer years (extremely narrow years) and periods of suppressed growth, and compared these with ring-width minima (narrowest 5% of ring-width indices) and multi-year periods of reduced growth (at least three minimum years within a decade) within the FTL chronologies. Then, to examine temporal associations between tree-ring evidence and recorded volcanic events, I compared frost rings and combined single and multi-year periods of decreased growth with other published proxies of volcanic activity. To account for the confounding influence of drought, I also investigated correspondence between tree-ring evidence and years with severe (≥ –3.00) values of reconstructed Palmer Drought Severity Index (PDSI), and performed comparative superposed epoch analysis.

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Appendix

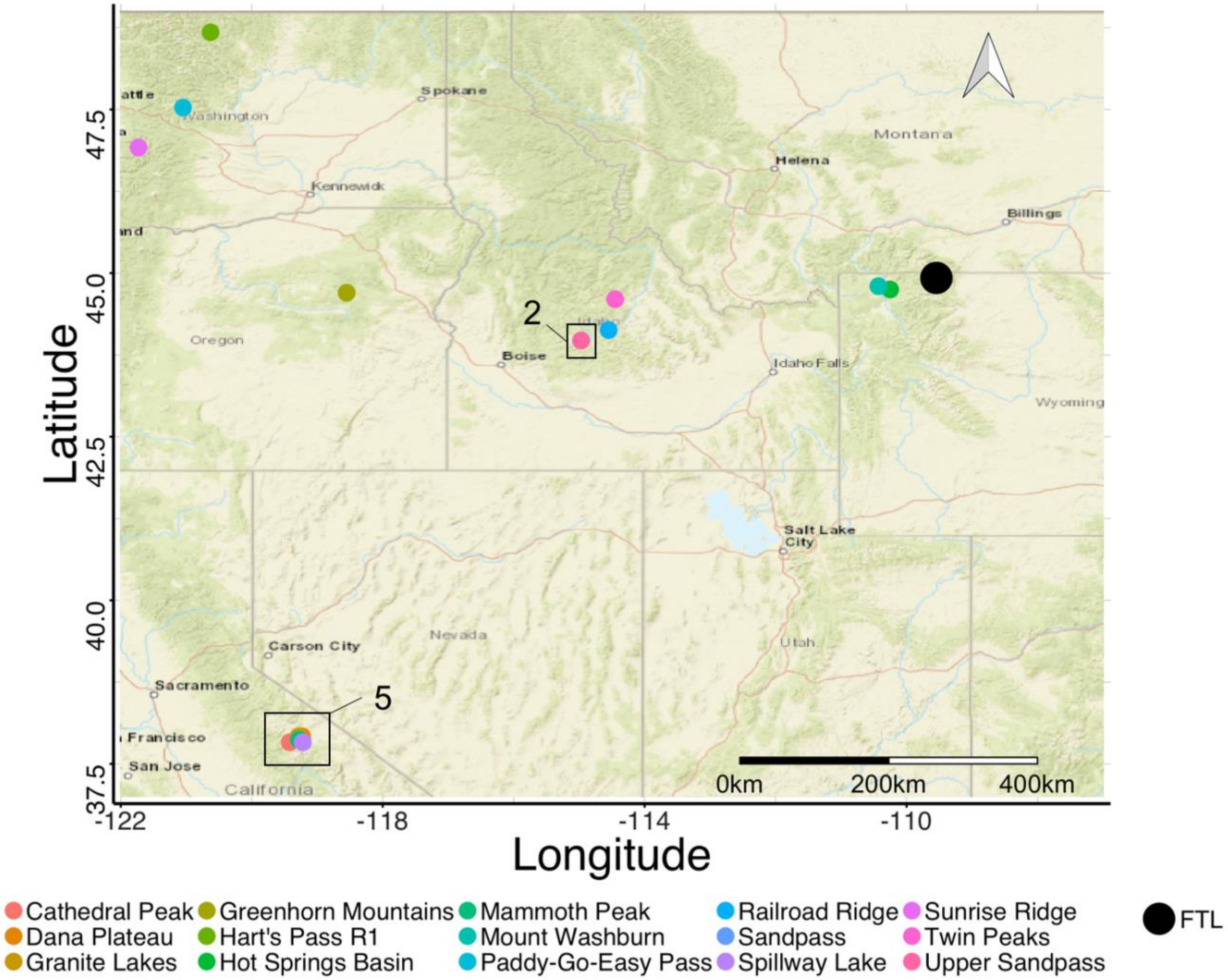

Figure 1.1 FTL and ITRDB Chronology Locations: Locations of the FTL study site and of 15 published whitebark pine chronologies for the U.S. that are available on the ITRDB. Source map data and imagery © OpenStreetMap contributors (www.openstreemap.org/copyright).

Figure 1.2 FTL Remnant: A massive remnant whitebark pine log at the FTL site. (Photo courtesy of Lauren Stachowiak)

Table 1.1 ITRDB Published Chronologies: Top: Whitebark pine chronologies published on the ITRDB for the United States, Middle: Whitebark pine chronologies published on the ITRDB for Canada, and Bottom: Published pre-1000 CE Engelmann spruce chronologies.

Site	Latitude (°)	Longitude (°)	State/ Province	Author	Innermost Year (CE)	Outermost Year (CE)
Sunrise Ridge	46.92	-121.73	WA	Brubaker	1605	1976
Paddy-Go-Easy Pass	47.53	-121.05	WA	Graumlich	1430	1980
Cathedral Peak	37.83	-119.42	CA	King	1532	1991
Dana Plateau	37.92	-119.23	CA	King	1430	1996
Granite Lakes	37.92	-119.28	CA	King	1520	1996
Greenhorn Mountains	44.70	-118.55	OR	King	1740	2002
Hot Springs Basin	44.75	-110.25	WY	King	1390	2005
Mammoth Peak	37.87	-119.28	CA	King	885	1996
Mount Washburn	44.80	-110.43	WY	King	937	1998
Spillway Lake	37.83	-119.22	CA	King	800	1996
Railroad Ridge	44.13	-114.55	ID	Perkins	726	1992
Sandpass	43.97	-114.97	ID	Perkins	955	1992
Twin Peaks	44.60	-114.45	ID	Perkins	965	1992
Upper Sandpass	43.97	-114.97	ID	Perkins	1210	1992
Hart's Pass R1	48.68	-120.63	WA	Peterson, Peterson	1669	1991
Vicary Mine	49.77	-114.53	CANA	Sauchyn	1488	2010
Bennington	52.68	-118.33	CANA	Luckman, Youngblut	1104	1996
Peyto Forfield and Num-ti-jah	51.68	-116.50	CANA	Luckman, Youngblut	1000	1999
Blaeberry	51.65	-116.68	CANA	Luckman, Youngblut	1519	1999
Grassy Mountain	49.57	-116.08	CANA	Luckman, Youngblut	932	1999
Graves Lookout	50.20	-115.22	CANA	Luckman, Youngblut	1720	1999
Jumbo Pass	50.50	-116.33	CANA	Luckman, Youngblut	1390	1997
Lakit	49.72	-115.58	CANA	Luckman, Youngblut	1477	1999
Lavina	50.25	-116.90	CANA	Luckman, Youngblut	1571	1999
McMurdo	51.10	-117.15	CANA	Luckman, Youngblut	1715	1999
Mt. Forster	50.58	-116.28	CANA	Luckman, Youngblut	1489	1999
Obelisk	49.63	-116.45	CANA	Luckman, Youngblut	1303	1999
Saskatchewan	52.15	-117.08	CANA	Luckman, Youngblut	950	1998
Trout Lake	50.63	-117.37	CANA	Luckman, Youngblut	1670	1999
Athabasca Glacier 2	52.22	-117.23	CANA	Luckman, Wilson, St. George	920	1987
Peyto Glacier snags	51.70	-116.52	CANA	Luckman, Reynolds, St. George	760	1326
Robson Glacier snags	53.15	-119.11	CANA	Luckman	867	1345
Athabasca, historisch	51.42	-117.33	CANA	Schweingruber	1072	1991

CHAPTER TWO

TREE-RING DATING AND EVIDENCE OF CLIMATE-INDUCED MORTALITY IN A SUBALPINE "GHOST FOREST"

This chapter is in preparation for submission to a journal. The use of "we" within the text refers to me and my co-authors, Matthew Bekker and Sally Horn. As first author, I led on study design, data collection and analyses, and writing the manuscript.

Abstract

The greatest temperature increases with global warming are projected to occur at high latitudes and altitudes. Consequences of this warming include shifting and altered treelines, which in mountainous regions will lead to changes in the ecosystem services provided by high-elevation forests. Upslope migration by tree-line tree species in response to warming will be limited by varied environmental and ecological factors, with mountain height providing an absolute limit. Eventually, some migrating species could run out of refugia, and face extinction. One avenue for investigating the potential effects of warming temperatures on alpine treelines is to examine how high-elevation ecosystems responded to past climate change. For this study, we used methods in tree-ring science, or dendrochronology, to investigate how past climate changes during the Medieval Warm Period (ca. 900–1350 CE) and Little Ice Age (ca. 1350–1850 CE), affected temporal patterns of mortality and establishment in a subalpine, whitebark pine ecosystem. We collected establishment and mortality data from living and remnant whitebark pine and Engelmann spruce trees from a site in the Beartooth Mountains of Wyoming. At this site, a "ghost forest" of massive dead trees indicated major ecosystem changes. Our results demonstrate that large whitebark pine and Engelmann spruce trees thrived at the study site under more climatically favorable conditions during the Medieval Warm Period, but perished during the subsequent Little Ice Age, a finding that indicates that whitebark pine ecosystems may be more robust to warming temperatures than current thought. Perhaps whitebark pines will persist, given successful management of other threats, despite global warming.

Keywords: dendrochronology, global warming, environmental change, treeline, whitebark pine

2.1 Introduction

Summer temperatures are the primary driver of tree growth at both high latitudes and high altitudes (Kauppi and Posch 1985; Fritts 2001; Rossi *et al*. 2008), and with ongoing climate change, these locations are expected to experience the greatest temperature increases (IPCC 2013; Mountain Research Initiative 2015). Consequences of this warming include northward and upward shifts in the limits of plant species (Grace *et al*. 2002; Körner 2003; Holtmeier and Broll 2005; Schwörer *et al*. 2017), and altered treeline composition and structure because of changes in growth, recruitment, and population density of component tree species (MacDonald *et al*. 1998). These ecological changes can subsequently impact ecosystem services, microclimate factors, biodiversity, and at some scales, surface energy budgets and related climate feedbacks (MacDonald *et al*. 1998; Smith *et al*. 2009; Schwörer *et al*. 2017). For subalpine species that already exist in relatively narrow climate niches, upward migration will be limited by suitable habitat, competition, and other factors, and eventually by limits in the topography itself (La Sorte and Jetz 2010; Dirnböck *et al*. 2011; Elsen and Tingley 2015). High-elevation species will eventually run out of refugia, leading to local extinction (Elsen and Tingley 2015).

In the western United States and Canadian Rocky Mountains, high-elevation whitebark pine ecosystems are currently threatened by the combination of warming temperatures and exacerbated threats from increased and more widespread outbreaks of native bark beetles (Tomback *et al*. 2001; Bentz *et al*. 2010) and more rapid spread of the invasive white pine blister rust (*Cronartium ribicola* J.C. Fisch.) (Resler and Tomback 2008). For whitebark pine, altitudinal migrations with warming temperatures will be limited by soil development and eventually, the tree species will run out of room on mountaintops. In addition, while the general consensus is that whitebark pine will move northward and upward out of its current range, questions surround whether or not the species will be able to migrate without assistance (Romme and Turner 1991; Weaver 2001; McLane and Aitken 2012; Palmer and Larson 2014). Whitebark pine migration is expected to lag behind climate change because the species is slow to mature reproductively, is often outcompeted by other tree species, exists in relatively isolated mountaintop communities, and relies on the Clark's nutcracker for seed dispersal and recruitment (McLane and Aitken 2012). Whether whitebark pine migration is rapid or lagged, changes in treeline structure and biodiversity will occur that are expected to negatively impact important ecosystem services, including delayed summer snowmelt, water storage, and soil stability (Callaway 1998; Tomback *et al.* 2001; Tomback and Kendall 2001; MacFarlane *et al.* 2013; Tomback *et al.* 2016).

One avenue for better understanding the potential magnitude and effects of ongoing warming is to examine how whitebark pine ecosystems have responded to climate change in the past. This includes examinations of potential treeline changes. For this study, we use methods in tree-ring science, or dendrochronology, to examine the influence of late Holocene climate change, specifically the Medieval Warm Period (MWP) and the Little Ice Age (LIA), on temporal patterns of establishment and mortality in a subalpine whitebark pine ecosystem of the Greater Yellowstone region. Scientists concur that the MWP (*ca.* 900–1350 CE) was a period of anomalous warmth in the Northern Hemisphere (Crowley and Lowery 2000; Bradley *et al.* 2003; Mann *et al.* 2009; Reinemann *et al.* 2014), but the magnitude and spatial patterns of warming continue to be a topic of debate (Crowley 2000; Crowley and Lowery 2000; Reinemann *et al.* 2014). In the western United States, a prolonged drought from 900–1300 CE occurred during the MWP, followed by generally wetter conditions during the LIA (*ca.* 1350–1850 CE) (Stine 1994; Cook *et al.* 2004; Herweijer *et al.* 2007; Wanner *et al.* 2008). Site-specific variability within these periods has been identified by dendroclimatological research in the northern U.S. Rocky Mountains and Canadian Rockies (Luckman *et al.* 1997; Biondi *et al.* 1999; Luckman 2000; Luckman and Wilson 2005; Kipfmueller 2008), suggesting that more studies are needed to adequately describe Holocene climate change in the mountainous regions of the western United States.

2.1.1 Regional Records of Climate and Environmental Change

In the Greater Yellowstone region and western United States, several studies have used paleoenvironmental records to examine Holocene climate change and shifts in forest composition. Treeline advance and other post-glacial changes during the early to middle Holocene, including during the warmer Climatic Optimum, have been documented using evidence in lake sediment cores (*e.g.* pollen, charcoal, wood fragments, conifer needles) collected from the Wind River Range of northwestern Wyoming (Fall *et al.* 1995; Lynch *et al.* 1998), the Snowy Range of southeastern Wyoming (Mensing *et al.* 2011), and in Yellowstone and Grand Teton National Parks (Whitlock 1993; Krause and Whitlock 2013; Krause *et al.* 2015). Few of the above studies mention treeline changes during the MWP or LIA and instead conclude that modern treeline established by 5750–3000 cal. yr. BP, largely based on pollen assemblages (Whitlock 1993; Mensing *et al*. 2011). Other paleoenvironmental records have provided evidence of MWP and LIA climate and environmental change, although not treeline change, in Yellowstone National Park. Studies of alluvial stratigraphy indicated increased fire-related sedimentation during warmer and drier periods, including the MWP (Meyer *et al*. 1992; Pierce *et al*. 2004). Parts of the drier northwest U.S. and northern Rocky Mountains experienced increased fire activity during this time (Whitlock *et al*. 2003). Fire-related sedimentation decreased and alluvial material was eroded during the cooler and wetter conditions of the LIA (Meyer *et al*. 1992), and while wetter conditions during this time increased available fuels, cooler temperatures and higher canopy moisture limited stand-replacing fires (Pierce *et al*. 2004). The transition from the MWP to the LIA has even been marked by shifts in fossil diatom assemblages in Yellowstone National Park (Bracht *et al*. 2008).

Another important proxy for environmental change during the MWP and LIA is sub-fossil, remnant wood at treeline. Several studies in the western U.S. have used radiocarbon and tree-ring dates from remnant wood to document higher-than-present treelines during intervals of the Holocene, including for the White Mountains of California (LaMarche and Mooney 1967, 1972; LaMarche 1973), the Snake Range of Nevada (LaMarche and Mooney 1967), the Rocky Mountain Front Range of Colorado (Carrara and McGeehin 2015), the Sierra Nevada of California (Scuderi 1987; Lloyd and Graumlich 1997), and the Wind River Range of Wyoming (Morgan *et al*. 2014). However, these studies indicate wide variability in the timing of treeline advance and decline. A few document higher-than-present treelines that predate the MWP by hundreds to over 1000 years (LaMarche and Mooney 1967, 1972; Carrara and McGeehin 2015), while others suggest that higher-than-present treelines declined into and during the early MWP (LaMarche 1973; Scuderi 1987; Lloyd and Graumlich 1997). Only two document changes specific to the MWP and LIA. In the Sierra Nevada of California, Lloyd and Graumlich (1997) determined that treeline had experienced two declines in the last 1000 years, one during the MWP, attributed to drought stress, and another during the LIA, attributed to cooling. Morgan *et al*. (2014) also documented treeline decline during the MWP, based on radiocarbon dating of remnant trees in the Wind River Range. Overall, and despite abundant paleoenvironmental records, we still know very little about the timing and spatial extent of the MWP and LIA.

2.1.2 Study Site: A Subalpine "Ghost Forest"

We discovered the study site of Fantan Lake (FTL, 44.926°N, 109.544°W, 2800 to 3020 m elevation) while conducting other research in the Beartooth Mountains of northwest Wyoming. The site, which is located near the Beartooth Highway (U.S. Highway 212) in the Shoshone National Forest, is a mixed subalpine ecosystem characterized by alpine meadows and clusters, or "islands," of whitebark pine, Engelmann spruce, and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) trees, which tend to concentrate on outcrops of Precambrian granite and metamorphic rocks (Lageson and Spearing 1991) (Figures 2.1 and 2.2, see Appendix for all Figures and Tables). Our attention was drawn to the site by the remains of massive trees, scattered within the living tree islands, but also isolated in the alpine meadow (Figure 2.3). The abundance of remnant trees at the site evoked images of a "tree graveyard." None of the living trees in the same area could match the size of the remnant trees. Many of the remnant trees still had intact outer rings. Originally, we assumed that all of the remnants would be whitebark pine, due to the resinous nature of the tree species and therefore decreased rates of decay. However, we discovered that some of the large remnants were equivalent-aged Engelmann spruce. We were immediately intrigued by the unique story that these trees, and the site, might have to tell about past climate and environmental change and began to form hypotheses about the history of the "ghost forest" and what that history might suggest about future changes in the ecosystem.

2.1.3 Hypothesis

We hypothesized that the whitebark pine and Engelmann spruce remnant logs represent the remains of an open woodland that established and thrived during the warmer conditions of the MWP and was destroyed by a return to cooler conditions and more persistent snowpack during the LIA. We based this hypothesis first on the fact that many of the remnant trees still had intact bark, which indicates more recent mortality, second on the fact that growing season temperatures are most limiting to growth in high-elevation trees (Fritts 2001; Rossi *et al.* 2008), and third on the importance of growing-season length to ring formation in whitebark pine, which does not occur when growing-season length falls below three months, most often due to cold (Weaver 2001). We considered cold temperatures during the LIA to be the most likely cause of mortality. Given the evidence of recent regeneration at the site, we also hypothesized that the establishment dates for living trees at the FTL site would post-date the end of the LIA.

2.2 Methods

2.2.1 Field and Laboratory Methods

From each of 148 living whitebark pine and 118 living Engelmann spruce (Figure 2.2.), we collected at least two cores at ground level using a Haglof increment borer. From each of 106 remnant trees (Figure 2.2), we collected at least one cross section or wedge using a chainsaw. In the lab, we sanded all cores and cross sections to a fine polish to ensure visibility of tree-ring boundaries and then measured all rings to the nearest 0.001 mm using scanned images and the software WinDENDRO (Regents, Inc. ver. 2012a). Where the resolution of scanned images was inadequate for measuring extremely narrow or resinous rings, we used a Velmex measuring system coupled with Measure J2X (VoorTech, ver. 5.0) software. For some samples, we were unable to measure all rings or crossdate them, and so used ring counts to determine inner and outer ring dates. To quality-check absolute dating and develop tree-ring chronologies from the living whitebark pine and Engelmann spruce trees, we performed statistical crossdating in the software COFECHA (Holmes 1983), which uses segmented, time-series correlation analyses to identify problem rings or misdating. We evaluated 40-year segments, lagged by 20 years, and used an interseries correlation cutoff of ≥ 0.40 to consider a tree-ring series as crossdated with the other series. We used a 32-year smoothing spline in the R dendrochronology program library (dplR) (Bunn 2008) to standardize the raw measurements and develop final chronologies for the living whitebark pine and Engelmann spruce. Once properly dated, we determined or estimated establishment dates, using pith estimators when no pith (tree center) was present (Applequist 1958). We used frequency distribution graphs to examine temporal patterns of establishment in relation to climate shifts.

2.2.2 Absolute Dating of Remnants

We used COFECHA to first relatively date and then absolutely date the tree rings on remnant samples, analyzing 50-year ring segments lagged by 25 years (Holmes 1983). To begin, we entered measurement series into COFECHA as undated. COFECHA then attempts to crossdate each series with all of the others and provides an output containing potential matches (relative dating adjustments and correlations) and associated t-values. We used a standard t-value of ≥ 3.5 to indicate statistical crossdating between different series (Holmes 1983), but t-values were often much higher (e.g., > 6.0 and as high as 12.0) because of series lengths (often over 400 rings). We used the dating adjustments and t-values provided by COFECHA to develop a set of measurement series that were relatively dated (to each other), but not yet anchored in time. We standardized the raw measurements using a two-thirds (0.67) smoothing spline in the R dendrochronology program library (dplR) (Bunn 2008) and developed initial, undated (or "floating") whitebark pine and Engelmann spruce chronologies. We then absolutely dated the floating FTL chronologies against whitebark pine (King, Mount Washburn, WY050, 44.8°N 110.4°W, 937–1998 CE) and Engelmann spruce (Briffa and Schweingruber, Sylvan Pass, WY023, 44.37°N 110.13°W, 1388–1983 CE) reference chronologies downloaded from the International Tree-Ring Data Bank (ITRDB 2019).

Once the initial chronologies were absolutely dated, we used them as reference chronologies for dating the remaining samples, which we tested one at a time against the growing data set. We added a series to the chronology when its interseries correlation coefficient was ≥ 0.40 and when COFECHA suggested a temporal adjustment that was identical for all or most of the segments tested. We used the program EDRM (Holmes 1992) to manually adjust series to exact calendar years. Crossdating of rings on remnant samples provided the innermost and outermost (possibly terminal) ring dates for each remnant tree. To evaluate remnant tree mortality, we recorded if remnant trees still possessed: (1) sapwood, (2) curvature, and/or (3) bark. These classifications indicate death dates (curvature and/or bark) or dates near the time of death (sapwood). Remnant trees with remaining curvature had a smooth outer surface that followed a ring boundary for all or a portion of remnant circumference. We used 50-year bins for mortality estimates, based on estimated rings per cm, calculated from intact sapwood on living and remnant trees.

2.2.3 Final Chronology Development

We developed the living and remnant chronologies separately because of initial lack of overlap between the two. Once the four separate chronologies were complete, we merged the living and remnant whitebark pine and Engelmann spruce chronologies. We used a two-thirds (0.67) smoothing spline in the R dendrochronology program library (dplR) (Bunn 2008) to develop final, standardized chronologies for each species. We evaluated the strength of the common signal in these chronologies using the interseries correlation statistics in COFECHA (Holmes 1983) and the expressed population signal (EPS) (Wigley *et al.* 1987), calculated using functions in the R dendrochronology program library (dplR) (Bunn 2008). The EPS statistic relies on mean interseries correlation and sample size, and is used to explain how well a subsample represents a larger, infinite sample (Wigley *et al.* 1987; Buras 2017). For the purposes of this paper, we used the EPS statistic only to evaluate the representative power of the final chronologies and to identify the points at which low sample size or low interseries correlation potentially reduce predictive power. In addition, we maintained the arbitrary threshold of 0.85 to indicate a strong common signal in the chronologies. We recognize that this common signal may be explained by non-climatic variables (Wigley *et al.* 1987), and that the 0.85 threshold may not be appropriate for evaluation of the chronologies for eventual climate reconstruction (Briffa and Jones 1990; Buras 2017).

2.3 Results

2.3.1. Remnant Tree Establishment and Mortality

We initially crossdated 15 whitebark pine and 15 Engelmann spruce remnants against the Mount Washburn and Sylvan Pass reference chronologies to develop site-specific reference chronologies for each species (Table 2.1). We then dated an additional 76 remnant trees, for a total of 106 dated remnants from the FTL site (Figure 2.4, Table 2.2), and used the measured series from these remnants to create final remnant chronologies for whitebark pine and Engelmann spruce (Table 2.3). Of the 78 whitebark pine remnants sampled, 37 (47%) contained evidence of preserved outer rings (Table 2.2). Excluding those trees without definitive inner- and/or outer-ring dates, 12 of 21 (57%) whitebark pine remnants with pith and sapwood and/or curvature indicated inner-ring dates before or during the MWP and terminal dates in the LIA, and an additional seven of the 21 (33%) had inner-ring dates before 1500 CE (during the LIA) and terminal-ring dates during the LIA. One of two samples with bark (FTL026) had an inner-ring date during the MWP (1089 CE) and an outer-ring date during the LIA (1663 CE). Of 14 whitebark pine remnants without pith but possessing sapwood and/or curvature, 11 had terminal-ring dates during the LIA. In total, 31 of the 37 (84%) whitebark pine remnants with evidence of outer rings indicated terminal dates during the LIA (Table 2.2, Figure 2.4). Two of the remnants with pith and sapwood and/or curvature (FTL070 and 058) had inner dates (811 and 869 CE respectively) that predate the onset of the MWP and outer-ring dates (1294 and 1329 CE respectively) that fell within the MWP. Three of the remnants without pith but with sapwood and/or curvature (FTL012, 069, and 018) had outer dates that fell within the MWP (1144, 1271, and 1319 CE respectively), and one of the remnant samples with bark had an outer-ring date of 1959 CE (Table 2.2).

We found similar results for the Engelmann spruce remnants. Of the 28 Engelmann spruce remnants sampled, 19 (68%) contained evidence of preserved outer rings (Table 2.2). Excluding those trees without definitive inner and/or outer ring dates, four of seven (57%) Engelmann spruce remnants with pith and sapwood and/or curvature indicated inner-ring dates before or during the MWP and terminal dates in the LIA, and an additional two of the seven (29%) had terminal-ring dates during the LIA. All of the Engelmann spruce remnants without pith but possessing sapwood and/or curvature (eight of eight) had terminal-ring dates during the LIA. In total, 14 of the 19 (74%) Engelmann spruce remnants with evidence of outer rings indicated terminal dates during the LIA (Table 2.2, Figure 2.4). One of the remnant samples with pith and curvature had an inner date during the LIA (1672 CE) and an outer-ring date of 1924 CE. Two of the four samples with bark (FTL052 and 003) were similar, with inner- (1576 and 1685 respectively) and outer- (1876 and 1905 respectively) ring dates during the LIA. One sample with bark, FTL053, had inner- and outer-ring dates during the MWP. The remaining Engelmann spruce remnant sample, BP001, contained bark and had an outer-ring date of 2007 CE (Table 2.2). For both species combined, 45 of 56 (80%) total remnant samples with preserved outer rings had terminal-ring dates during the LIA (Figures 2.4 and 2.5).

2.3.2 Living Tree Establishment

The final living whitebark pine chronology covered the period 1332–2016 CE, and the final living Engelmann spruce chronology covered the period 1652–2016 CE (Table 2.3). For both living tree chronologies, the mean series length was less than 150 years. We obtained or were able to estimate establishment dates for 84% of the crossdated, living trees (for 124 of 128 whitebark pines and 99 of 118 Engelmann spruce trees). Frequency distribution graphs for the species show increasing establishment after the end of the LIA (1850 CE) (Figure 2.6). While establishment dates were not exclusively post-LIA, most whitebark pine (>76%) and Engelmann spruce (>65%) established after 1850 CE. The remaining trees established during earlier portions of the LIA (pre-1715 CE), except for one whitebark pine tree that established during the MWP (~1282 CE) and survived until the present. Only one other whitebark pine had an inner measured ring of 1332 CE, showing it established during the MWP, but we could not determine an establishment date due to irregular growth near the innermost rings. These living trees predate the establishment of the next oldest whitebark pine by nearly 200 years (1506 CE). The oldest living Engelmann spruce that we identified established in approximately 1621 CE.

2.3.3 Final Chronologies

The final whitebark pine chronology covered the period 708–2016 CE, and the final Engelmann spruce chronology covered the period 754–2017 CE (Figure 2.7, Table 2.4). Based on statistical crossdating (Table 2.4), we considered these chronologies as accurately dated and sufficient for determining inner and outer ring dates, especially as we report these dates in bins to account for estimate errors. However, for further analyses using ring-width data, such as for dendroclimatological study, we recommend that the chronologies be truncated at 942 CE for whitebark pine and 1167 CE for Engelmann spruce based on the EPS threshold of 0.85 (Figure 2.7). Further analysis is necessary to determine how much of the common signal is related to climate, and therefore, the EPS statistic cannot be used in this case to evaluate the potential of the chronologies for future use in climate reconstructions. While both chronologies are millennial-length, only the whitebark pine chronology maintains an adequate sample depth for climate analyses prior to 1000 CE.

2.4 Discussion

2.4.1 Establishment, Mortality, and Climate at FTL

Analysis of tree rings in remnant and living trees at FTL provided a basis to evaluate the influence of past and present climate on growth and establishment in high-elevation whitebark pine and Engelmann spruce. The dating of 106 remnant samples at FTL supports the hypothesis that the massive dead trees represent the remains of an open woodland that established and grew during the MWP and perished during the LIA. Although fire or insect disturbance could have killed trees at the FTL site, the nonsynchronous patterns of mortality at FTL point to climate change as the most likely driver of tree mortality. We found only limited evidence of fires and insect outbreaks in our samples from FTL. The spatial distribution of the handful of cross-sections on which we identified fire scars indicates that the fires were small and isolated, affecting only one to a few trees. While cooler and wetter conditions during the LIA led to increased fuels and fire in other ecosystems of the Greater Yellowstone region (*e.g.* ponderosa pine), these fires were found to be low severity and not stand replacing (Pierce *et al.* 2004). We found little to no evidence of blue stain fungi (including *Ceratocystis montia* Rumb. and *Europhium clavigerum* Robinson and Davidson) in the sapwood of remnant trees, a marker for bark beetles (Reid *et al.* 1967; Whitney 1971; Solheim 1995). Thus we interpret tree death during the LIA as driven by climate.

Mortality and establishment at FTL indicate that the site was potentially affected by shifting treeline during the late Holocene. Although establishment and inner ring dates were spread throughout the MWP and LIA, few of the remnant trees sampled survived the entire LIA. In addition, many of the living whitebark pine (>76%) and Engelmann spruce (>65%) trees that we sampled established after the end of the LIA (1850 CE), suggesting that, although some trees did establish and survive through the LIA, conditions were primarily unfavorable to seedlings as well as mature trees. The near eradication of trees from the FTL site during the mid-to-late LIA suggests drastically different environmental conditions at this time than during the preceding MWP, when most of the large trees established. The few trees that survived the LIA likely occupied more favorable microclimates within the complex site topography; microclimates together with facilitation would also have influenced establishment (Bekker 2005; Holtmeier and Broll 2005; Elliott 2011). Facilitation and microclimates have been shown to play an important role in conifer establishment and survival at high elevations (Resler *et al.* 2005; Pyatt *et al.* 2016), and topography is known to be an important local driver of treeline migration (Holtmeier and Broll 2005; Elsen and Tingley 2015).

2.4.2 Comparison to Regional Records

Several studies performed in the Rocky Mountains have provided evidence of treeline fluctuations during the middle to late Holocene, although most of these studies suggest a pre-MWP warm period, with estimated, higher-than-average treelines before and sometimes declining into the MWP (LaMarche and Mooney 1967, 1972; LaMarche 1973; Scuderi 1987; Carrara and McGeehin 2015). Other studies have focused on treeline and other post-glacial changes that occurred even earlier, during warmer periods of the early to middle Holocene (Whitlock 1993; Fall *et al.* 1995; Lynch 1998; Mensing *et al.* 2011; Krause and Whitlock 2013; Iglesias *et al.* 2015; Krause *et al.* 2015). Despite these records, however, relatively little is known about how the MWP affected subalpine ecosystems in the Greater Yellowstone region. Variability in regional paleoclimate records make them difficult to compare, and many of the tree-ring based temperature reconstructions from the area do not describe conditions prior to the late MWP (Biondi *et al*. 1999; Kipfmueller 2008). We identified only one treeline study in the region that documented changes specific to the MWP, and this study indicated treeline decline, not advance, during that period (Morgan *et al*. 2014).

At a site approximately 180 km from FTL, Morgan *et al*. (2014) documented treeline decline during the MWP, based on radiocarbon dating of remnant trees in the Wind River Range of Wyoming. They interpreted evidence of tree death and treeline decline to reflect drought stress during the MWP, contrary to our findings at FTL that trees established and thrived during the that time. While this difference may represent real disparities between FTL and the nearby Wind River Range, it may partly reflect differences in scope and methods. Radiocarbon dating can only provide ranges of potential dates, the length of which can depend on calibration datasets and other factors. For example, we re-calibrated the fifteen dates obtained by Morgan *et al*. (2014) using a different program, Calib 7.0.2 (Stuiver and Reimer 1993), and the updated IntCa13 dataset (Reimer *et al*. 2013). This technique yielded calibrated ranges (95% probability) that were somewhat narrower than those reported by Morgan *et al*. (2014) but still spanning from 67 to 194 years (Figure 2.8). Four of the 15 calibrated ranges fall within the five centuries prior to the start of the MWP at 900 CE (as used in our study), three overlap the beginning of the MWP, and eight indicate death between 981 and 1250 CE, during the MWP (Figure 2.8). Alternatively, the annual resolution provided by tree-ring dating can provide exact dates, which is especially important when relating these dates to short-term changes like the MWP and LIA.

Because they found remnant trees up to 100 m above modern treeline, Morgan *et al*. (2014) could definitively conclude that treeline was once higher at their study site. However, based on our experience at FTL, we propose that interpretations of remnant death dates would benefit from combining radiocarbon with tree-ring dating techniques, such as seen in other studies of remnant wood at treeline (LaMarche 1973; Carrara and McGeehin 2015). Tree-ring dating would have allowed Morgan *et al*. (2014) to also examine the establishment dates of remnant trees. Still, we recognize that real differences may exist between the history of treeline forests at our sites. Because of data limitations, we cannot rule out some decline at FTL during the MWP; many of the remnant trees at our site established after the mid- to late-MWP, and many of those that established earlier did not survive the period (Figure 2.4). The potential exists for two declines: one drought-induced change during the early MWP and another, temperature-induced change during the LIA, such as recorded by Lloyd and Graumlich (1997) in the southern Sierra Nevada. Warm and dry conditions are known to have caused downslope movement of whitebark pine elsewhere in the Yellowstone region during the middle Holocene (Fall *et al.* 1995). However, more data are necessary to determine if this is true at FTL.

Results from this study agree with regional paleoclimate records that document a cooler, and potentially wetter, LIA and especially with those that document cold conditions during the first half of the nineteenth century (Schweingruber *et al.* 1991; Luckman *et al.* 1997; Biondi *et al.* 1999; Luckman and Wilson 2005; Kipfmueller 2008). While mortality dates were spread throughout the LIA, few of the remnant trees survived past the end of the LIA at 1850 CE, and more than 60% of living trees established after this date. Growth rates, indicated by tree-ring width, for the whitebark pine and Engelmann spruce trees that survived the LIA were some of the lowest of the millennial record (Figure 2.7). The most extreme growth suppression for whitebark pine occurred during the 1830–1850 CE period (Figure 2.7). These findings of exceptionally low temperatures during the late LIA are also coincident with documented glacial advances in the western U.S. and Canada (Carrara 1989; Osborn and Gerloff 1997; Luckman 2000; Marcott *et al.* 2009), as well as with hemispheric temperature reconstructions (Bradley and Jones 1993, 1995; Crowley 2000; Mann *et al.* 2008, 2012). This correspondence demonstrates the potential of FTL tree rings to record late Holocene climate changes.

2.4.3 Ecosystem Implications in a Changing Climate

Recent temperatures in the Greater Yellowstone region have exceeded those of the last 6000 years (Shuman 2012), and with projected warming, decreased winter snows, and increased moisture deficits in the western U.S., dramatic environmental and ecological changes are likely to occur (Leung *et al.* 2004; Mote 2006; Shuman 2012; Iglesias *et al.* 2015; Sepulveda *et al.* 2015). Results from this study, however, suggest that both whitebark pine and Engelmann spruce may be robust to warmer and drier conditions. At FTL, whitebark pine and Engelmann spruce established during the MWP, lived through the late MWP and early LIA, and perished during the late LIA. If the next decades are characterized by conditions similar to the MWP, successful management of other threats could allow both species to persist despite global warming. At FTL, both species will likely experience initial increases in growth and recruitment under warming temperatures, such as purported during the MWP and documented during even greater post-glacial warming in the Greater Yellowstone region (Whitlock 1993; Fall *et al*. 1995; Lynch *et al*. 1998; Mensing *et al*. 2011; Krause and Whitlock 2013; Krause *et al*. 2015; Iglesias *et al*. 2015). During warmer periods of the past in this region, high-elevation sites typically transitioned from tundra to pine/spruce parkland and eventually to closed, mixed stands of pine, spruce, and fir, with some variation based on local geology, hydroclimate, and topography (Fall *et al*. 1995; Lynch *et al*. 1998; Krause and Whitlock 2013; Krause *et al*. 2015). We documented recent encroachment of both whitebark pine and Engelmann spruce into the alpine meadow at FTL, more than likely because of a shift toward drier conditions and a longer, warmer growing season. The landscape at FTL may eventually transition back into open woodland, such as existed during the MWP.

Despite the potential robustness of whitebark pine and Engelmann spruce to changing climate conditions, we do not discount complex interactions between climate, disturbance, and competition. For the future of the FTL site, much will depend on the interplay of these factors in a warming climate, and eventually on the ability of whitebark pine and Engelmann spruce to migrate upslope. Warmer and drier future conditions are likely to affect important competitive and facilitative relationships, including between whitebark pine and Engelmann spruce (Callaway 1998; Tomback *et al*. 2001; Weaver 2001; MacFarlane *et al*. 2013; Tomback *et al*. 2016; Hill *et al*. 2018), and threats to both species, including bark beetle outbreaks, devastating wildfires, and spreading invasive species, are expected to increase under warming conditions (Westerling *et al*. 2006, 2011; Hebertson and Jenkins 2008; Resler and Tomback 2008; Bentz *et al*. 2010; Hart *et al*. 2014; Buermeyer 2016). The threat of local extinction of high-elevation species in the face of warming temperatures, shifting ranges, and changes in fire regimes, forest pests, and diseases underscores the need for continued study of the ecology and history of vulnerable treeline species, to better anticipate change and to inform conservation and management. Our results provide insight into how past climate change affected important treeline species and environments of the Greater Yellowstone region.

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Appendix

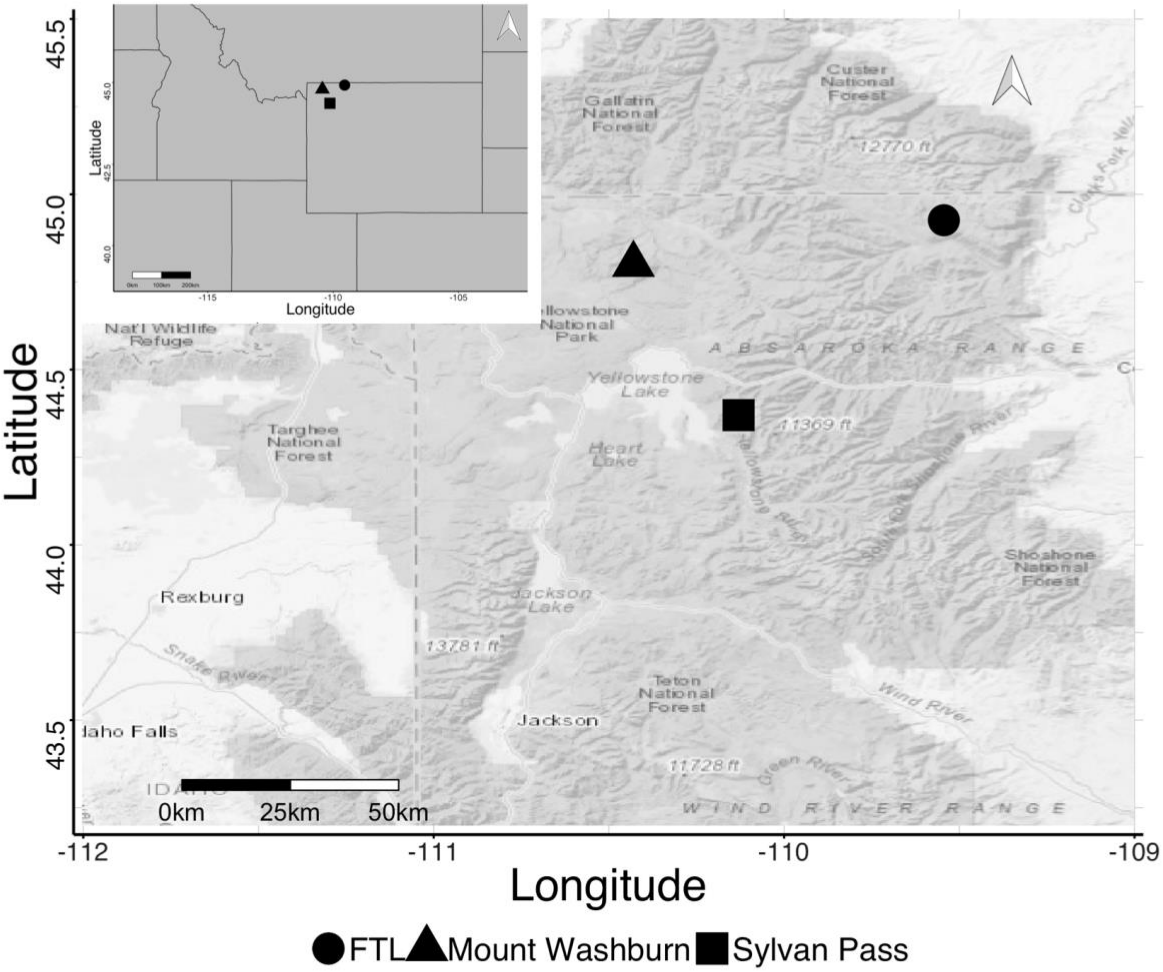


Figure 2.1 FTL and Reference Chronology Locations: Locations of the FTL study site and of the sampling locations for the reference chronologies (Mount Washburn and Sylvan Pass) in Yellowstone National Park used to date the floating chronology developed from remnant cross sections. Source map data and imagery © OpenStreetMap contributors (www.openstreemap.org/copyright).

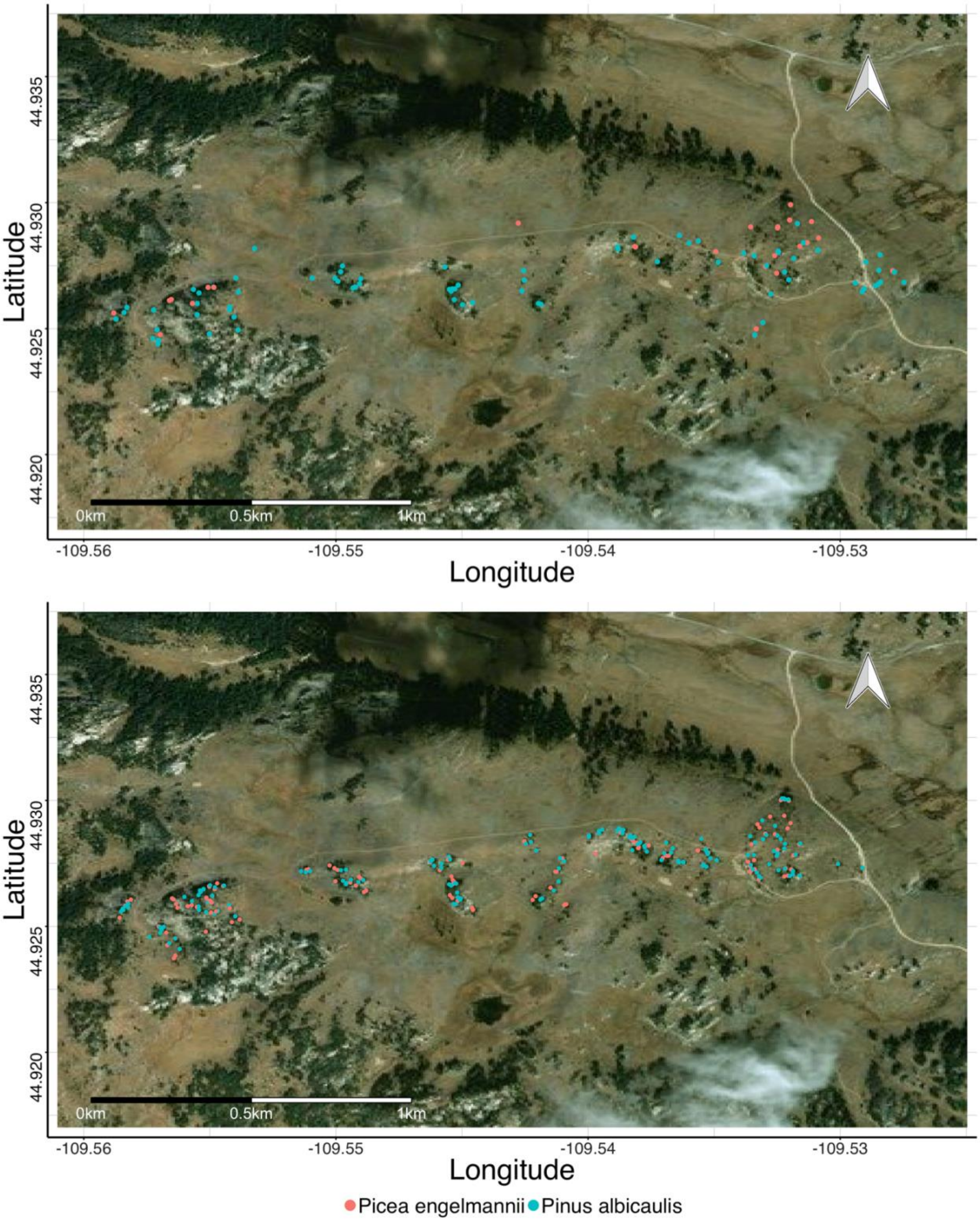


Figure 2.2 Locations of Sampled Trees: Locations of sampled remnants (top) and living trees (bottom) at the FTL study site. Source map data and imagery © OpenStreetMap contributors (www.openstreemap.org/copyright).

Figure 2.3 Examples of FTL Remnants: Photographs of remnant trees at the FTL site. Top left: One remnant with author for scale.

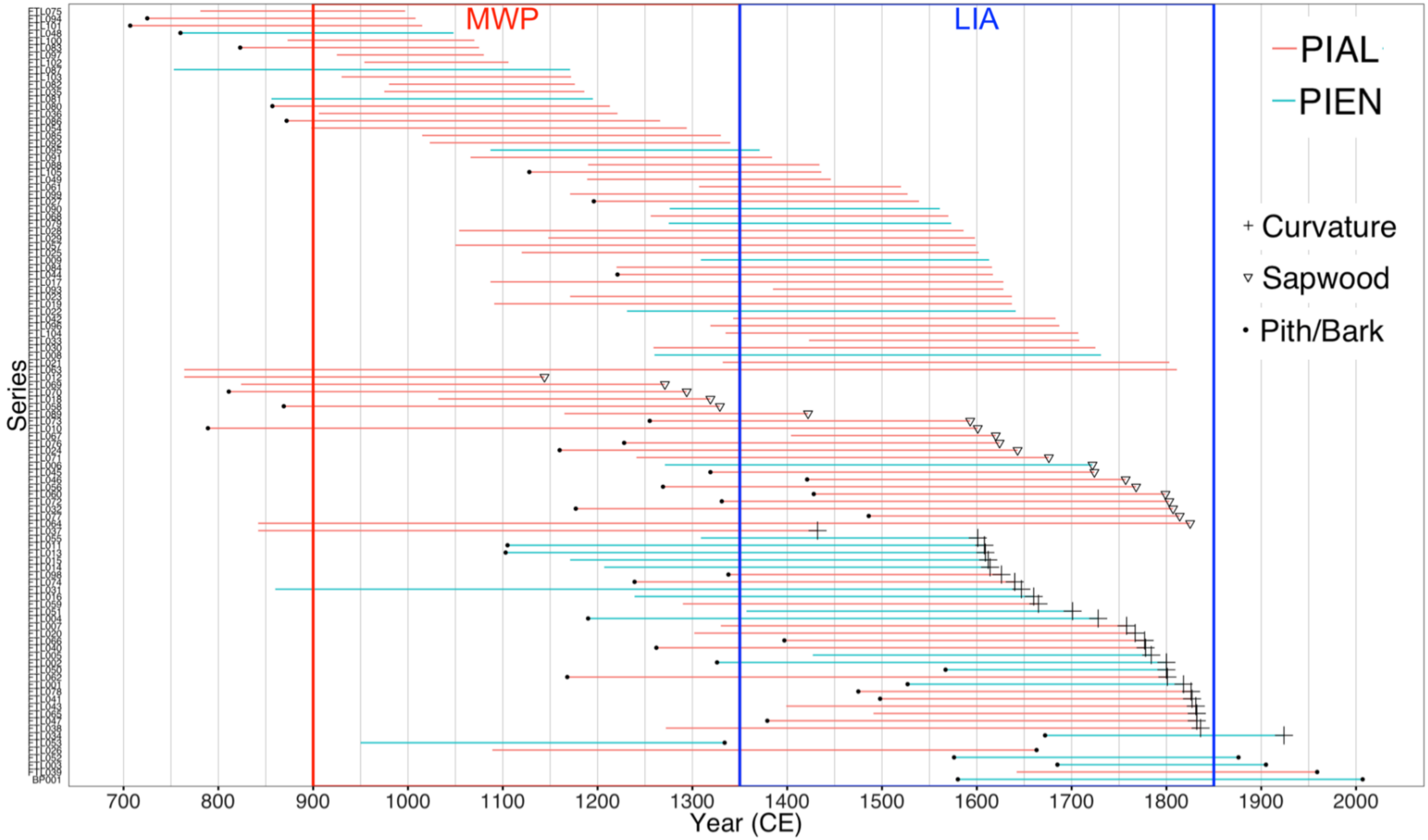


Figure 2.4 Remnant Time Spans: Plot of series time spans, which shows inner and outermost rings (and ring types) in relation to the MWP and LIA. Note that despite establishment, few trees survived the extent of the LIA.

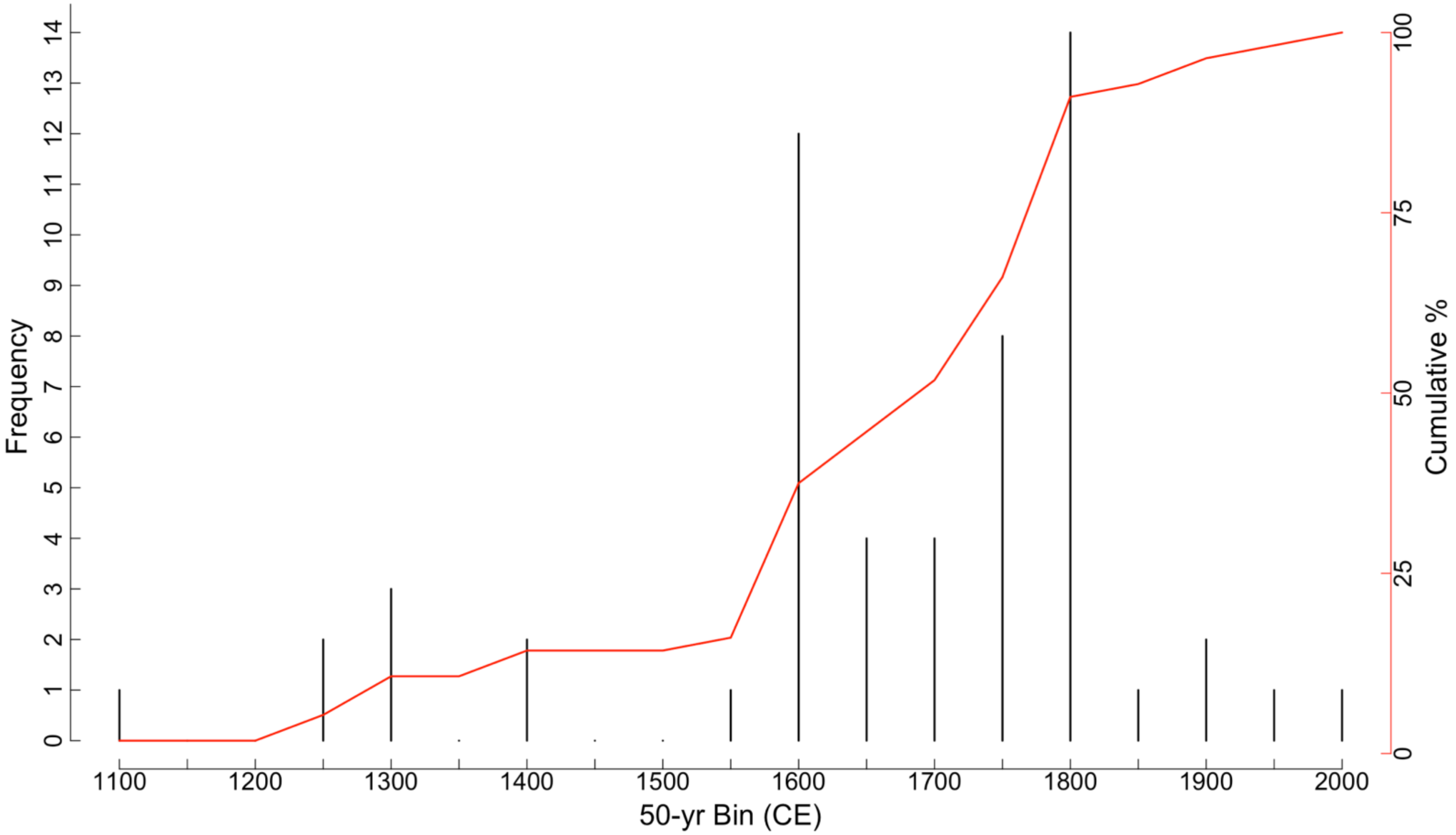
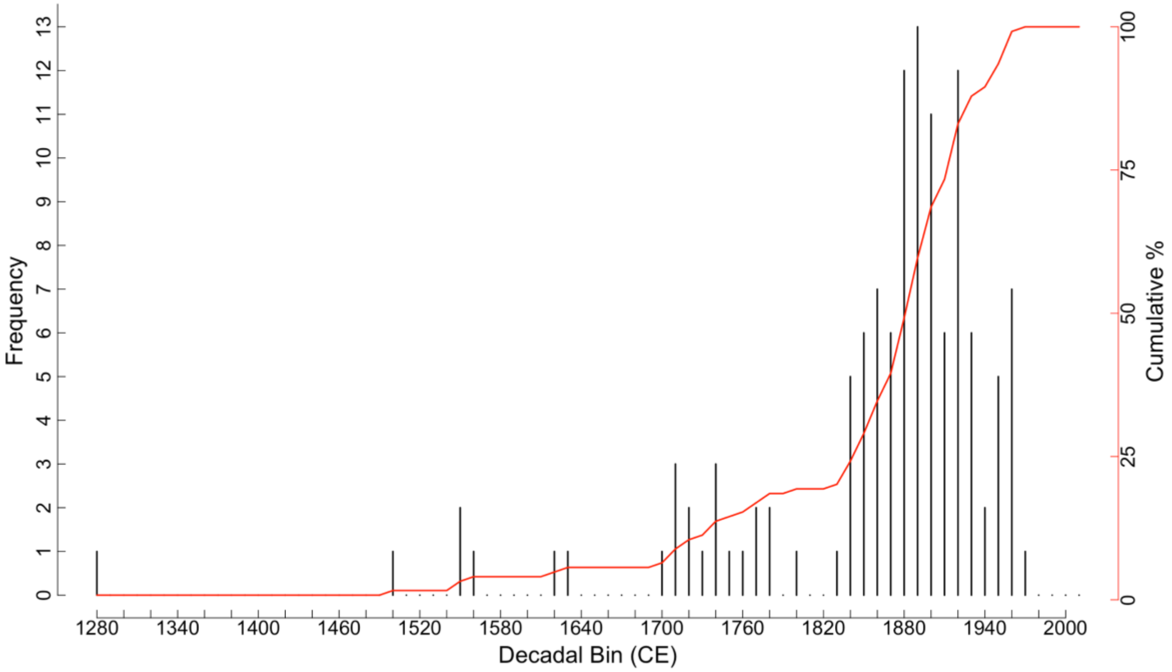


Figure 2.5 Frequency Distribution Plot of Mortality: Frequency distribution plot for mortality of remnant trees with preserved outer rings, placed in 50-year bins. Note that a majority of these remnant trees (45/56, 80%) indicate mortality during the LIA, 1350–1850 CE, and especially after 1600 CE.



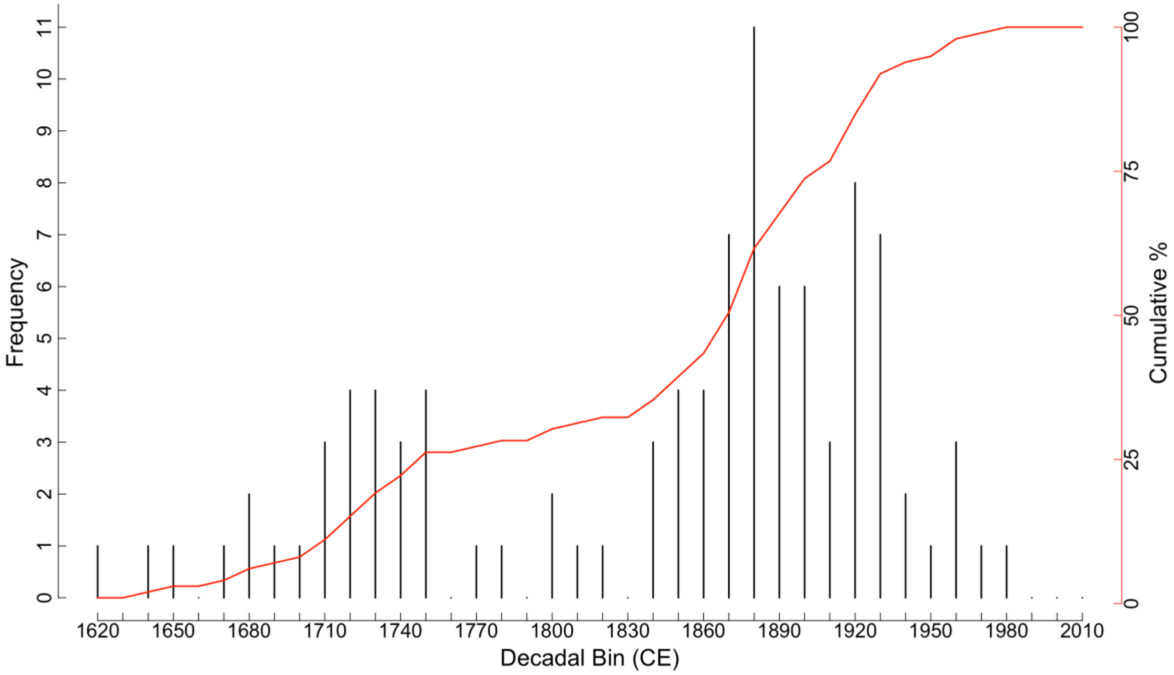


Figure 2.6 Frequency Distribution Plots of Establishment: Frequency distribution plots for whitebark pine (top) and Engelmann spruce (bottom) establishment, using decadal bins. The black bars represent frequency of trees that established in each bin. The red line is the cumulative percentage. Notice the steeper increase in cumulative percentage beginning after 1850, especially for whitebark pine. (Note: The x axis scales are not the same.)

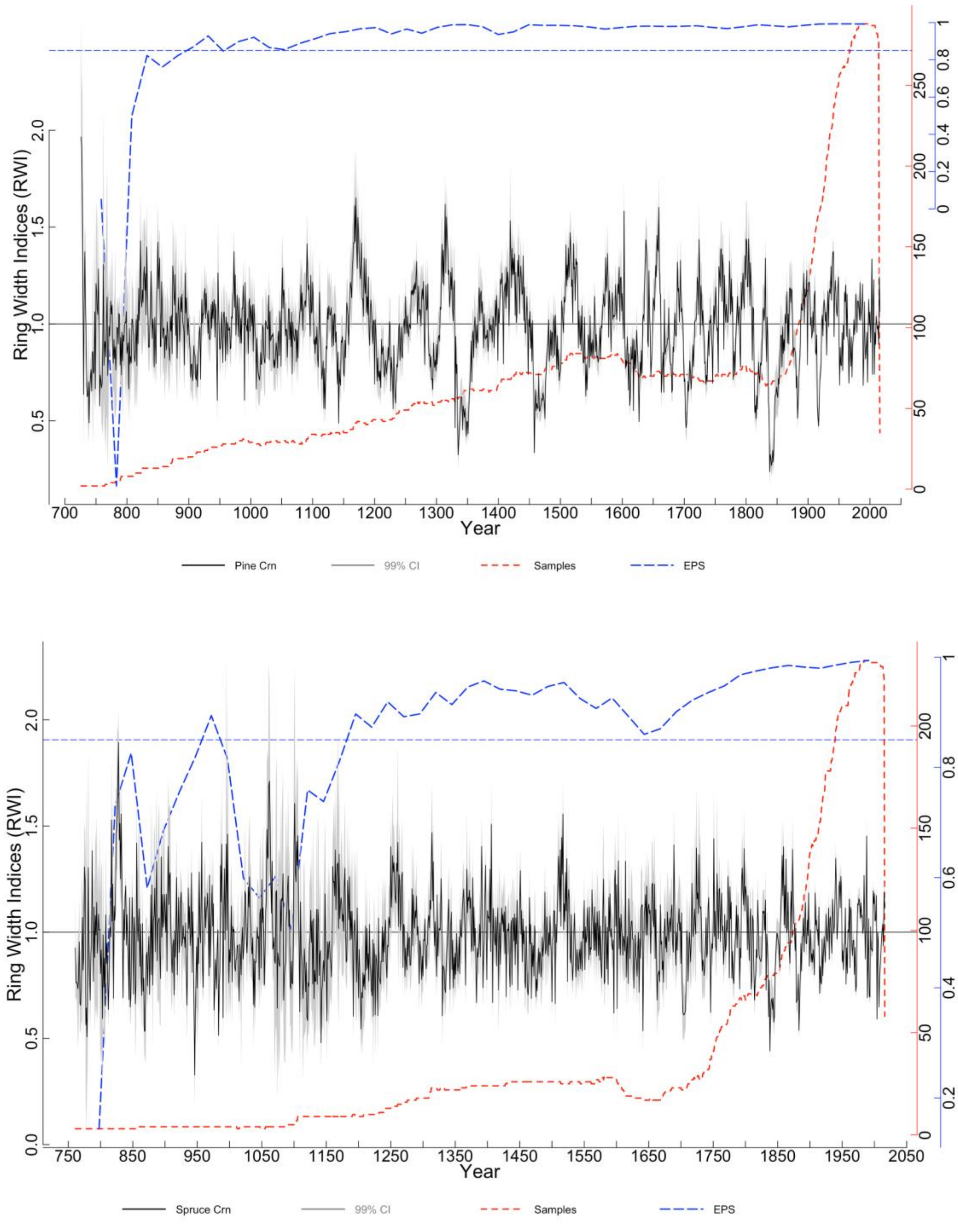


Figure 2.7 Final Chronologies: Final FTL whitebark pine (top) and Engelmann spruce (bottom) chronologies and statistics.

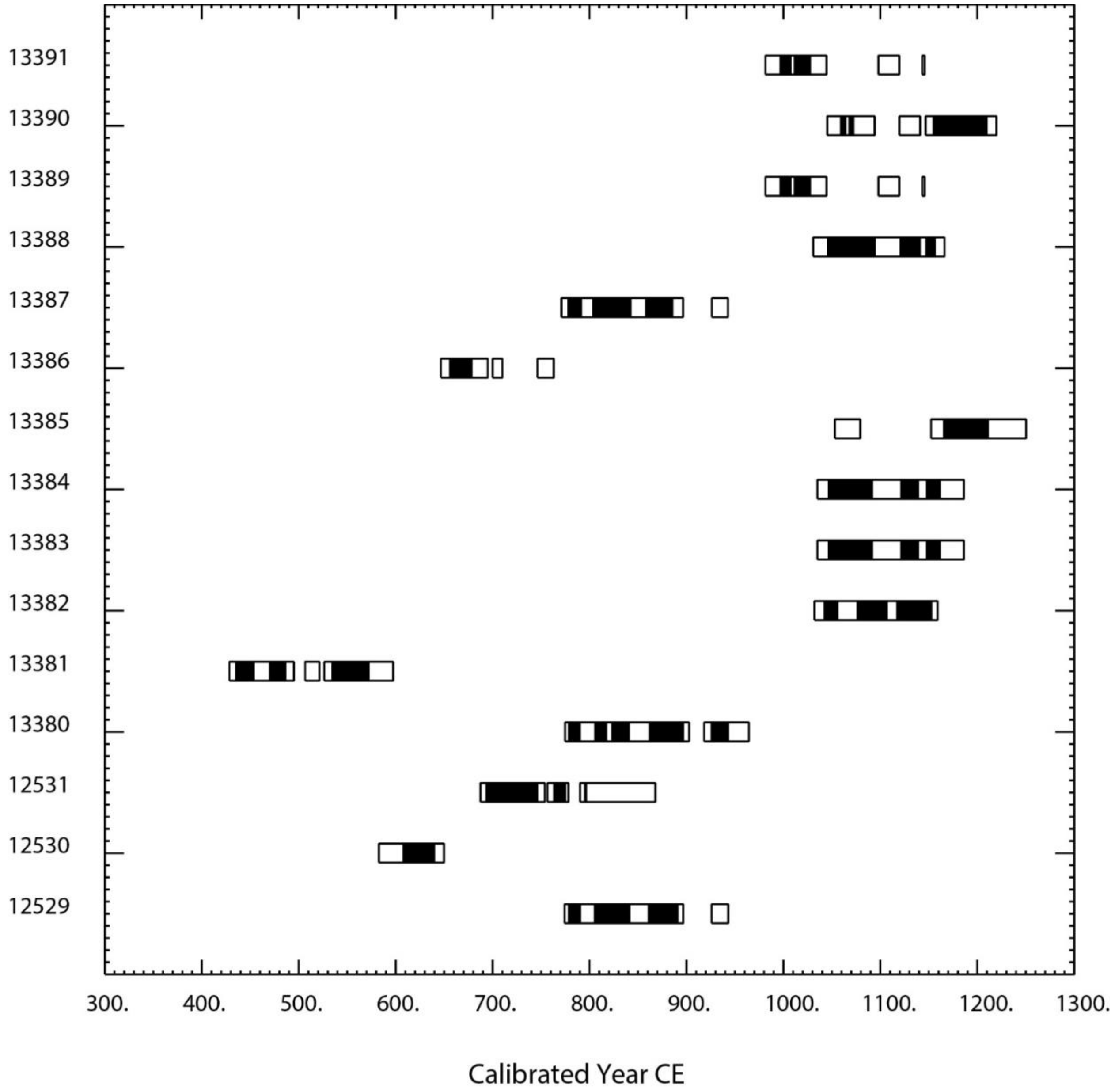


Figure 2.8 Radiocarbon Dating Block Plots: Multi-sample block plots showing the calibrated age ranges for the fifteen radiocarbon dates on remnant wood at a site in the Wind River Range obtained by Morgan *et al*. (2014). The plot was produced using Calib 7.0.2 (Stuiver and Reimer, 1993) using the IntCa13 database (Reimer et al., 2013). The black portions of the bars indicate the 67% probability range and the unshaded portions together with the shared portions indicate the 95% probability range. The numbers on the y axis are the lab numbers (all samples run at the Center for Applied Isotope Analysis at the University of Georgia).

Table 2.1 Initial Chronology Stats: Chronology statistics for the initial whitebark pine and Engelmann spruce remnant chronologies developed for use as local reference chronologies for dating remaining remnant samples.

Species[1]	**Measured Series**	**Total Trees**	**Length (yrs)**	**Average Interseries Correlation**	**Average Mean Sensitivity**	**Segments Tested**	**Segments Flagged[2]**	**Percent Flagged**	**Dating Adjustment[3]**	**Segments**	**Average Interseries Correlation**	**Absolute Dating (CE)[4]**
PIAL	30	15	1021	0.58	0.22	496	29	5.85	789	23 of 40	0.56	790–1810
PIEN	26	15	920	0.67	0.21	388	9	2.32	1087	17 of 36	0.47	1104–2007

[1] ITRDB Species Codes, where PIAL = whitebark pine (*Pinus albicaulis* Engelm.) and PIEN = Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)

[2] Indicates tested segments that fell below the statistical threshold for significance at the 0.01 level. These were re-inspected and found to be correctly placed in time.

[3] Dating adjustment given by COFECHA when testing against the Mount Washburn and Sylvan Pass reference chronologies.

[4] Absolute dating against the reference chronologies: PIAL ($r = 0.45$, $n = 874$ years, $t = 14.88$, $p < 0.0001$), PIEN ($r = 0.43$, $n = 596$ years, $t = 11.61$, $p < 0.0001$).

Table 2.2 Remnant and Living Chronology Stats: Final remnant and living chronologies developed by this study and associated statistics.

Chronology[1]	Measured Series	Total Trees	Length (yrs)	Mean Length Series (yrs)	Average Interseries Correlation	Average Mean Sensitivity	Segments Tested	Segments Flagged[2]	Percent Segments Flagged	Time Span (CE)[3]
Remnant PIAL	134	78	1250	340.7	0.54	0.22	1826	182	9.97	708–1958
Remnant PIEN	44	28	1253	341.4	0.63	0.22	595	22	3.70	754–2007
Living PIAL	299	148	684	136.0	0.60	0.24	1936	191	9.87	1332–2016
Living PIEN	232	118	364	148.0	0.63	0.23	1636	145	8.86	1652–2016

[1] ITRDB Species Codes, where PIAL = whitebark pine (*Pinus albicaulis* Engelm.) and PIEN = Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)

[2] Indicates tested segments that fell below the statistical threshold for significance at the 0.01 level. These were re-inspected and found to be correctly placed in time.

[3] For remnants: Absolute dating against the reference chronologies: PIAL ($r = 0.49$, $n = 1022$ years, $t = 17.95$, $p < 0.0001$), PIEN ($r = 0.43$, $n = 596$ years, $t = 11.61$, $p < 0.0001$).

Table 2.3 Dated Remnant Data: Absolute dating of remnants and indicators of innermost and outermost dates. The presence of pith indicated a near establishment date while the presence of bark, sapwood, and/or curvature indicated a death or near date.

Tree	Species	Inner Date	Pith? (Y or *)	Inner Measured Date	Outer Measured Date	Outer Ring	Sapwood? (Y or *)	Curvature? (Y or *)	Bark? (Y or *)
BP001	Picea engelmannii	1580	Y	1581	2007	2007	Y	Y	Y
FTL001	Picea engelmannii	1527	Y	1528	1817	1818	Y	Y	*
FTL002	Picea engelmannii	1326	Y	1327	1799	1800	Y	Y	*
FTL003	Picea engelmannii	1685	Y	1686	1904	1905	Y	Y	Y
FTL004	Picea engelmannii	1190	Y	1191	1727	1728	Y	Y	*
FTL005	Picea engelmannii	1427	*	1428	1783	1784	Y	Y	*
FTL006	Picea engelmannii	1271	*	1272	1721	1722	Y	*	*
FTL007	Pinus albicaulis	1330	*	1331	1757	1758	Y	Y	*
FTL008	Picea engelmannii	1260	*	1261	1730	1731	*	*	*
FTL009	Picea engelmannii	1309	*	1310	1612	1613	*	*	*
FTL010	Pinus albicaulis	789	Y	790	1600	1601	Y	*	*
FTL011	Picea engelmannii	1105	Y	1106	1607	1608	Y	Y	*
FTL012	Pinus albicaulis	764	*	765	1143	1144	Y	*	*
FTL013	Picea engelmannii	1103	Y	1104	1608	1609	Y	Y	*
FTL014	Picea engelmannii	1207	*	1208	1613	1614	Y	Y	*
FTL015	Picea engelmannii	1171	*	1172	1611	1612	Y	Y	*
FTL016	Picea engelmannii	1239	*	1240	1628	1660s	Y	Y	*
FTL017	Pinus albicaulis	1087	*	1088	1627	1628	*	*	*
FTL018	Pinus albicaulis	1032	*	1033	1318	1319	Y	*	*
FTL019	Pinus albicaulis	1091	*	1093	1636	1637	*	*	*
FTL020	Pinus albicaulis	1302	*	1303	1766	1767	Y	Y	*
FTL021	Pinus albicaulis	1332	*	1333	1802	1803	*	*	*
FTL022	Picea engelmannii	1231	*	1232	1640	1641	*	*	*
FTL023	Pinus albicaulis	1171	*	1172	1636	1637	*	*	*
FTL024	Pinus albicaulis	1160	Y	1161	1642	1643	Y	*	*
FTL025	Pinus albicaulis	1120s	*	1166	1601	1602	*	*	*
FTL026	Pinus albicaulis	1089	*	1090	1662	1663	Y	Y	Y
FTL027	Pinus albicaulis	1196	Y	1197	1538	1539	*	*	*
FTL028	Pinus albicaulis	1054	*	1055	1585	1586	*	*	*
FTL029	Pinus albicaulis	1148	*	1149	1597	1598	*	*	*
FTL030	Pinus albicaulis	1259	*	1260	1724	1725	*	*	*
FTL031	Picea engelmannii	860s	*	1368	1646	1647	Y	Y	*
FTL032	Pinus albicaulis	1177	Y	1506	1806	1807	Y	*	*
FTL033	Pinus albicaulis	1423	*	1426	1707	1708	*	*	*
FTL034	Picea engelmannii	1672	Y	1673	1923	1924	Y	Y	*
FTL035	Pinus albicaulis	975	*	976	1185	1186	*	*	*
FTL036	Pinus albicaulis	906	*	907	1220	1221	*	*	*
FTL037	Pinus albicaulis	842	*	1096	1431	1432	Y	Y	*
FTL038	Pinus albicaulis	1272	*	1273	1835	1836	Y	Y	*
FTL039	Pinus albicaulis	1642	*	1643	1958	1959	Y	Y	Y
FTL040	Pinus albicaulis	1262	Near	1263	1777	1778	Y	Y	*
FTL041	Pinus albicaulis	1498	Y	1499	1826	1827	Y	Y	*
FTL042	Pinus albicaulis	1343	*	1344	1682	1683	*	*	*

Table 2.3 Continued

Tree	Species	Inner Date	Pith? (Y or *)	Inner Measured Date	Outer Measured Date	Outer Ring	Sapwood? (Y or *)	Curvature? (Y or *)	Bark? (Y or *)
FTL043	Pinus albicaulis	1399	*	1400	1830	1831	Y	Y	*
FTL044	Pinus albicaulis	1221	Y	1222	1616	1617	*	*	*
FTL045	Pinus albicaulis	1319	Y	1320	1723	1724	Y	*	*
FTL046	Pinus albicaulis	1421	Y	1422	1756	1757	Y	*	*
FTL047	Pinus albicaulis	1379	Y	1473	1831	1832	Y	Y	*
FTL048	Picea engelmannii	760	Y	761	1047	1048	*	*	*
FTL049	Pinus albicaulis	1189	*	1190	1445	1446	*	*	*
FTL050	Picea engelmannii	1567	Y	1568	1799	1800	Y	Y	*
FTL051	Picea engelmannii	1357	*	1358	1700	1701	Y	Y	*
FTL052	Picea engelmannii	1576	Y	1577	1875	1876	Y	Y	Y
FTL053	Picea engelmannii	950s	Y	1016	1333	1334	Y	Y	Y
FTL054	Pinus albicaulis	898	*	899	1293	1294	*	*	*
FTL055	Picea engelmannii	1309	*	1310	1600	1601	Y	Y	*
FTL056	Pinus albicaulis	1269	Y	1270	1767	1768	Y	*	*
FTL057	Pinus albicaulis	1050	*	1051	1598	1599	*	*	*
FTL058	Pinus albicaulis	869	Y	870	1328	1329	Y	*	*
FTL059	Pinus albicaulis	1290	*	1291	1664	1665	Y	Y	*
FTL060	Pinus albicaulis	1428	Y	1429	1798	1799	Y	*	*
FTL061	Pinus albicaulis	1307	*	1308	1519	1520	*	*	*
FTL062	Pinus albicaulis	1168	Y	1169	1800	1801	Y	Y	*
FTL063	Pinus albicaulis	1409	*	1410	1810	1811	*	*	*
FTL064	Pinus albicaulis	1580	*	1581	1824	1825	Y	*	*
FTL065	Pinus albicaulis	1491	*	1681	1831	1832	Y	Y	*
FTL066	Pinus albicaulis	1397	Y	1398	1776	1777	Y	Y	*
FTL067	Pinus albicaulis	1404	*	1405	1619	1620	Y	*	*
FTL068	Pinus albicaulis	1256	*	1257	1569	1570	*	*	*
FTL069	Pinus albicaulis	824	*	825	1270	1271	Y	*	*
FTL070	Pinus albicaulis	811	Y	812	1293	1294	Y	*	*
FTL071	Pinus albicaulis	1241	*	1242	1675	1676	Y	*	*
FTL072	Pinus albicaulis	1331	Y	1511	1802	1803	Y	*	*
FTL073	Pinus albicaulis	1255	near	1256	1592	1593	Y	*	*
FTL074	Pinus albicaulis	1239	Y	1240	1637	1640s	Y	Y	*
FTL075	Pinus albicaulis	781	*	782	996	997	*	*	*
FTL076	Pinus albicaulis	1228	Y	1229	1623	1624	Y	*	*
FTL077	Pinus albicaulis	1486	Y	1487	1813	1814	Y	*	*
FTL078	Pinus albicaulis	1475	Y	1476	1825	1826	Y	Y	*
FTL079	Picea engelmannii	1275	*	1276	1572	1573	*	*	*
FTL080	Pinus albicaulis	857	Y	858	1212	1213	*	*	*
FTL081	Picea engelmannii	856	*	857	1194	1195	*	*	*
FTL082	Pinus albicaulis	980	*	981	1175	1176	*	*	*
FTL083	Pinus albicaulis	823	Y	824	1074	1075	*	*	*
FTL084	Pinus albicaulis	1220	*	1221	1615	1616	*	*	*
FTL085	Pinus albicaulis	1015	*	1016	1329	1330s	*	*	*
FTL086	Pinus albicaulis	872	Y	873	1265	1266	*	*	*
FTL087	Picea engelmannii	753	*	754	1170	1171	*	*	*
FTL088	Pinus albicaulis	1190	*	1191	1433	1434	*	*	*

Table 2.3 Continued

Tree	**Species**	**Inner Date**	**Pith? (Y or *)**	**Inner Measured Date**	**Outer Measured Date**	**Outer Ring**	**Sapwood? (Y or *)**	**Curvature? (Y or *)**	**Bark? (Y or *)**
FTL089	Pinus albicaulis	1165	*	1166	1421	1422	Y	*	*
FTL090	Picea engelmannii	1276	*	1313	1560	1561	*	*	*
FTL091	Pinus albicaulis	1066	*	1067	1383	1384	*	*	*
FTL092	Pinus albicaulis	1023	*	1024	1333	1340s	*	*	*
FTL093	Pinus albicaulis	1385	*	1386	1627	1628	*	*	*
FTL094	Pinus albicaulis	725	Y	726	1007	1008	*	*	*
FTL095	Picea engelmannii	1087	*	1088	1370	1371	*	*	*
FTL096	Pinus albicaulis	1319	*	1320	1686	1687	*	*	*
FTL097	Pinus albicaulis	925	*	926	1082	1080s	*	*	*
FTL098	Pinus albicaulis	1338	Y	1339	1625	1626	Y	Y	*
FTL099	Pinus albicaulis	1171	*	1172	1526	1527	*	*	*
FTL100	Pinus albicaulis	873	*	874	1069	1070	*	*	*
FTL101	Pinus albicaulis	707	Y	708	1014	1015	*	*	*
FTL102	Pinus albicaulis	954	*	955	1105	1106	*	*	*
FTL103	Pinus albicaulis	930	*	931	1171	1172	*	*	*
FTL104	Pinus albicaulis	1335	*	1336	1706	1707	*	*	*
FTL105	Pinus albicaulis	1128	Y	1129	1435	1436	*	*	*

The following symbols: * or Y, indicate the presence (Y) or absence (*) of the indicator (pith, sapwood, curvature, bark).
Non-definite years (e.g. 1080s) indicate estimates based on ring counts.
The use of “near” for pith indicates where innermost rings were near pith (within 1–5 yrs) but pith was not present.

Table 2.4 Final Chronology Stats: Chronology statistics for the final whitebark pine and Engelmann spruce chronologies developed for the FTL site.

Chronology[1]	Measured Series	Total Trees	Length (yrs)	Mean Length Series (yrs)	Average Interseries Correlation	Average Mean Sensitivity	Segments Tested	Segments Flagged[2]	Percent Segments Flagged	Time Span (CE)
PIAL	433	226	1308	199.0	0.57	0.23	3395	261	7.69	708–2016
PIEN	276	146	1262	178.0	0.63	0.23	1937	70	3.61	754–2016

[1] ITRDB Species Codes, where PIAL = whitebark pine (*Pinus albicaulis* Engelm.) and PIEN = Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)

[2] Indicates tested segments that fell below the statistical threshold for significance at the 0.01 level. These were re-inspected and found to be correctly placed in time.

CHAPTER THREE

CLIMATE DRIVERS AND IMPLICATIONS OF A CHANGING CLIMATE FOR WHITEBARK PINE AND ENGELMANN SPRUCE ON THE BEARTOOTH PLATEAU, WYOMING, U.S.A.

This chapter is in preparation for submission to a journal. The use of "we" within the text refers to me and my co-authors, Matthew Bekker and Sally Horn. As first author, I led on study design, data collection and analyses, and writing the manuscript.

Abstract

Long-lived, subalpine tree species like whitebark pine and Engelmann spruce may eventually disappear due to the combination of climate change and exacerbated native and invasive threats. While this loss would have dramatic circumstances for mountain ecosystems, it would also result in the irreversible loss of valuable climatological and ecological data. As part of ongoing research in the Beartooth Mountains of northwestern Wyoming, we developed two millennial-length tree ring chronologies, one for whitebark pine and another for Engelmann spruce. With these newly collected chronologies, we endeavor to address gaps in the Greater Yellowstone tree-ring record, and to provide tree-ring data from whitebark pine Engelmann spruce that are suitable for paleoclimate reconstruction. The objective of this paper is to evaluate the potential of paleoclimate reconstruction using these chronologies. We used correlation analyses to test for relationships between tree growth and monthly and seasonal aggregates of temperature and moisture variables and then used evolutionary analyses to determine if these relationships remained stable through the instrumental period 1896–2016 CE. While we identified multiple, significant relationships with temperature and moisture variables, results suggest that high-elevation species, and especially whitebark pine, may not respond positively to future climate, especially if drier conditions accompany warming. Emerging negative growth responses to previous summer temperatures, along with emerging, and in some cases strengthening, positive growth responses to previous summer moisture, suggest that the moisture conditions that accompany warming will greatly influence future growth.

Keywords: dendrochronology, climate-growth relationships, Greater Yellowstone Ecosystem

3.1 Introduction

Whitebark pine (*Pinus albicaulis* Engelm.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) are co-occurring subalpine tree species of the western United States and Canada. While only whitebark pine is currently facing extirpation in some regions (Schrag *et al.* 2008; Jewett *et al*. 2011), both species are threatened by the combined effects of climate change, bark beetle infestations, altered fire regimes, and other pressures (Tomback *et al*. 2001; DeRose and Long 2007; Hart *et al*. 2014; Perkins 2015; Foster *et al*. 2017). Currently, more than 50% of whitebark pine trees are dead or dying (McLane and Aitken 2012), and with continued warming, whitebark pine is projected to lose up to 99 percent of suitable habitat in some regions (Chang *et al*. 2014; Hansen and Phillips 2015). Engelmann spruce, although listed as a species of least concern because of relative abundance and fewer threats (Farjon 2013), may also face an uncertain future, especially as bark beetles, including the exceptionally destructive spruce beetle (*Dendroctonus rufipennis* Kirby), are expected to benefit from projected warming (Hebertson and Jenkins 2008; Bentz *et al*. 2010; Hart *et al*. 2014). The loss of these tree species, and especially of whitebark pine, a keystone species, would lead to dramatic ecosystem changes and altered treeline structures in the western United States and Canada (Callaway 1998; Tomback *et al*. 2001; Tomback and Kendall 2001; MacFarlane *et al*. 2013; Tomback *et al*. 2016). It would also result in the irreversible loss of proxy data of climatological and ecological value.

Both whitebark pine and Engelmann spruce tree-ring chronologies have the potential to provide multi-century records of climate and environmental change that can track low-frequency climate variability (Briffa *et al*. 2001; Esper *et al*. 2003; Helama *et al*. 2005; Youngblut and Luckman 2013). While most Engelmann spruce trees live in the range of 250–450 years (USDA 2003), some with ages exceeding 850 years have been identified (Brown *et al*. 1995), and whitebark pine is one of only a few tree species that can live in excess of 1,000 years (Perkins and Swetnam 1996; Youngblut and Luckman 2013). Remnant (dead) wood from both of these species, and especially from whitebark pine, the wood from which is more resinous and therefore more resistant to weathering, can extend these records back even further. In addition to age, both whitebark pine and Engelmann spruce trees grow as isolated individuals in harsh subalpine environments, where climate rather than completion or stand dynamics is the dominant limiting factor influencing growth (Fritts 2001). As with other high-elevation conifers (Peterson and Peterson 1994; Ettl and Peterson 1995; Peterson *et al*. 2002), relationships with growing season temperatures dominate the climate signal in both whitebark pine (Perkins and Swetnam 1996; Biondi *et al*. 1999; Bunn *et al*. 2005; Larocque and Smith 2005; Kipfmueller 2008; Kipfmueller and Salzer 2010; Youngblut and Luckman 2013) and Engelmann spruce (Peterson and Peterson 1994; Luckman *et al*. 1997; Luckman and Wilson 2005). Given the potential ages of whitebark pine and Engelmann spruce trees, as well as the limiting climates in which they live, both species can provide valuable climate records.

Despite the potential of whitebark pine in paleoclimate and ecological research, few accessible tree-ring chronologies for this species exist. The International Tree-Ring Data Bank (ITRDB) only includes 15 whitebark pine chronologies for the United States, and only two whitebark pine and four Engelmann spruce chronologies for the Greater Yellowstone Ecosystem (ITRDB, February 2019) (Figure 3.1, see Appendix for all Figures and Tables). The avoidance of whitebark pine by tree-ring researchers, especially for climatological study, has been attributed to high rates of disturbance in the species and low inter-annual variability and high first-order autocorrelation (St. George and Luckman 2001; Wilson and Luckman 2003; Larocque and Smith 2005; Youngblut and Luckman 2013). Growth decline due to pine beetle infestation, increasing temperatures, or any combination may lead to changes in climate-growth responses or diminish the climate signal (Youngblut and Luckman 2013; van de Gevel *et al*. 2017). Consequently, few studies have focused on whitebark pine for climate reconstruction (Biondi *et al*. 1999; Kipfmueller 2008). Regional climate reconstructions focused on Engelmann spruce are more common but concentrated in the Canadian Rockies (Luckman *et al*. 1997; St. George and Luckman 2001; Wilson and Luckman 2002, 2003; Luckman and Wilson 2005).

Inconsistencies in expected tree-growth relationships with temperature during recent decades have brought into question important assumptions of paleoclimate research. During recent decades, tree-ring width and maximum latewood density have diverged from temperature trends, especially in high altitude and high latitude forests (Jacoby and D’Arrigo 1995; Briffa *et al*. 1998, 2000; D’Arrigo *et al*. 2004, 2008). Decreased growth after the mid-20th century is the opposite of what would normally be expected due to a warming climate. This “divergence” between tree growth and temperature was first noted in the late 1990s (Jacoby and D’Arrigo 1995; Briffa *et al*. 1998). Multiple causes have been proposed since then, including increased atmospheric carbon dioxide, increased pollutants such as nitrates and phosphates, soil chemistry changes, global “dimming,” increased UV-B radiation, and drought stress (D’Arrigo *et al*. 2008).

Divergence in tree-ring chronologies, while not ubiquitous, is problematic because resulting models have the potential to underestimate temperatures, especially during warm periods (Anchukaitis *et al.* 2013). Changes in climate response over time also violate the uniformitarianism principle that modern processes have operated in the same way through time, an important assumption of paleoclimate reconstruction (Fritts 2001). Because of this, relationships between tree growth and climate must now be tested for temporal stability prior to climate reconstruction (Briffa *et al.* 1998; D'Arrigo *et al.* 2008). Testing for temporal stability is also important when working with tree species that experience high rates of disturbance. Disturbances leading to changes in growth might overshadow tree responses to climate and alter climate-growth relationships over time.

Documenting the climate response of long-lived whitebark pine and Engelmann spruce trees can reveal how they may be affected by ongoing climate change. It can also aid in reconstructing past climate variability beyond the instrumental record, which can provide important context for modern change. We developed two, millennial-length tree ring chronologies, one for whitebark pine and another for Engelmann spruce. With these newly collected chronologies, we endeavor to address gaps in the Greater Yellowstone tree-ring record, and to provide tree-ring data from whitebark pine Engelmann spruce that are suitable for paleoclimate reconstruction. The objective of this paper is to evaluate the potential for paleoclimate reconstruction using these chronologies, and to assess the implications of the climate relationships we document for the future of whitebark pine in a changing climate. We do this by first identifying the dominant climate drivers of tree growth and second by determining if these relationships are stable through time. Divergence, or other changes in tree-growth response to climate will not only affect the potential for paleoclimate reconstruction, but may indicate emerging new and potentially negative shifts in whitebark pine and other high-elevation ecosystems.

3.2 Methods

3.2.1 Study Area

We developed tree-ring chronologies from living and sub-fossil whitebark pine and Engelmann spruce collected from a mixed subalpine forest community on the Beartooth Plateau of northwest Wyoming (Figure 3.1). The study site, Fantan Lake (FTL; 44.926°N, 109.544°W), covers 125 hectares with an elevation range of 2800 to 3020 m. The area is characterized by alpine meadows and small clusters of whitebark pine, Engelmann spruce, and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) trees, which tend to concentrate on outcrops of Precambrian granite and metamorphic rocks of the mountain range (Lageson and Spearing 1991). Climate in the region (NCEI Yellowstone Drainage, 4801) is consistently cool and relatively wet all year long (Figure 3.2) (NCEI 2018). However, over 70% of annual precipitation falls as snow during the period November to June, and most winter snow in the region falls during the month of March (Sepulveda *et al*. 2015). Snow telemetry data from nearby Beartooth Lake (2853 m elevation) indicate winter snowpack depths of one to nearly three meters from 2003 to 2019 CE (SNOTEL 2019). These conditions are consistent with the average climate of whitebark pine ecosystems reported by Weaver (2001). Based on the persistence of snowpack at the FTL site into June and sampling of living trees in July, growing season at the site is likely only three to four months long, ending in September. Based on a June to September growing season at FTL, the average growing season temperature would be ca. 12°C with average total growing season precipitation ca. 186 mm.

3.2.2 Tree-Ring Data

We sanded increment cores from living trees and cross-sections from sub-fossil trees to a fine polish using progressively finer sand paper (Stokes and Smiley 1996; Speer 2010), and then measured ring-widths to the nearest 0.001 mm using scanned images and the software WinDENDRO (Regents, Inc. ver. 2012a). To quality check absolute dating and develop raw (tree-ring measurement) chronologies from the living whitebark pine and Engelmann spruce trees, we performed statistical crossdating in the software COFECHA (Holmes 1983), which uses segmented, time-series correlation analyses to identify problem rings and/or misdating. The final whitebark pine and Engelmann spruce chronologies extended back to 708 and 754 CE respectively (Table 3.1), but for the purposes of this paper, we only considered the period that overlaps with the instrumental climate record of 1896–2016 CE (Figure 3.3). To remove age- and disturbance related trends, and therefore maximize the climate signal, we standardized the raw tree-ring measurements using a 32-year spline and combined detrended series using bi-weight robust mean estimation in the R dendrochronology program library (dplR) (Mosteller and Tukey 1977; Cook 1985; Bunn 2008).

3.2.3 Climate Data

We tested our FTL chronologies against instrumental climate data for monthly average temperature (TEMP), monthly maximum temperature (TMAX), monthly minimum temperature (TMIN), total monthly precipitation (PRECIP), monthly standardized precipitation index (SP01), and monthly Palmer Drought Severity Index (PDSI) extracted from the National Center for Environmental Information climate divisional data (nClimDiv) for the Yellowstone Drainage division (4801) of northwest Wyoming (NCEI 2018). In 2014, the NCEI Monitoring Branch transitioned from the original Drd964x divisional dataset to the more robust nClimDiv dataset, which includes additional station records, accounts for observation biases, and uses climatologically-aided interpolation to better account for topographic and network variability (Willmott and Robeson 1995; Vose *et al*. 2014). For the nClimDiv dataset, divisional values are calculated using area-weighted averages of interpolated gridpoint (5 km) values (Vose *et al*. 2014). Divisional errors are highest for earlier portions of the record, although estimated by Vose *et al*. (2014) as less than 0.5°C for temperature and 20 mm for precipitation.

3.2.4 Climate Response and Temporal Stability

We assessed climate-growth relationships in whitebark pine and Engelmann spruce using a combination of analyses in the R package treeclim (Zang and Biondi 2015). We performed all analyses over the common period 1896–2016 CE, extending from previous May to current October, to include the lagged effect of influences from the previous year on current year growth. First, we used bootstrapped correlation analysis to test for static relationships between individual climate variables and tree-ring data. We also investigated tree-growth relationships with aggregate seasons of each climate variable, spanning three, six, and 12 months, using the seascorr function in the R package treeclim (Zang and Biondi 2015). The function seascorr allows for the input of primary and secondary climate variables. Relationships with the primary variable are expressed as correlations (Pearson's r), while relationships with the secondary variable are expressed as partial correlations with the influence of the primary variable removed (Meko *et al*. 2011; Zang and Biondi 2015). Significance is calculated using simulation (Gaussian circulant embedding) (Percival and Constantine 2006; Meko *et al*. 2011; Zang and Biondi 2015). We initially entered temperature variables as primary and precipitation variables as secondary, and then reversed these positions to more thoroughly evaluate primary climate drivers. We then used forward and backward evolutionary analysis to detect changes in climate-growth relationships over time (*i.e.* temporal stability) (Biondi 1997). We designated the significant relationships found using correlation analysis as temporally stable if they were maintained throughout the twentieth century under both forward and backward evolutionary analysis. Relationships considered "maintained" remained consistent (*i.e.*, did not switch from positive to negative or weaken substantially) and significant through all or most of the instrumental period. For evolutionary analyses, we determined significance based on standard bootstrapped confidence bounds calculated by treeclim.

3.3 Results and Discussion

3.3.1 Climate Drivers of Growth

We found multiple significant relationships (all at $p \leq 0.05$) between tree growth and temperature and moisture variables at the FTL site (Figure 3.4, Table 3.2). Overall for whitebark pine, significant relationships occurred across monthly and seasonal aggregates for previous fall and current growing season temperatures and winter precipitation (Figures 3.4 and 3.5). All significant relationships with temperature were positive, indicating that warmer conditions in certain months are more favorable to growth in whitebark pine at the FTL site. More specifically, monthly relationships with spring (previous and current May and June) and fall (previous September) temperatures (Figure 3.4) indicate that whitebark pine growth has been tightly linked with growing season length and temperature. On average, the growing season for whitebark pine begins in May and June and ends in September (Weaver 2001). However, based on data from our sampling, which indicate that some whitebark pine trees had not yet initiated cambial growth in July, we estimate that growing season, or at least wood production at FTL can sometimes be limited to July, August, and September. Warmer May and June temperatures during the current year would therefore be beneficial to growth by lengthening the growing season by one to two months.

Growth relationships with monthly temperature variables during previous September (Figure 3.4), and with seasonal temperatures ending in previous October/November (Figure 3.5), indicate that an extension of the previous year growing season is also beneficial to growth in whitebark pine for the current year. A warmer September is most likely beneficial to growth because it would allow trees more time to complete cambial growth and harden for the winter.

Colder September temperatures would leave whitebark pine less physiologically prepared for the following year, and could lead to frost damage that would negatively influence growth in the following year (Weaver 2001). A similar relationship was identified by Carlson *et al.* (2017) in the Southern Coast Mountains of British Columbia, except there, autumn snowfall resulted in an early truncation of the previous year growing season and negatively impacted whitebark pine growth in the current year. In extreme cases, when the growing season is reduced to less than three months, whitebark pine may not grow at all (Weaver 2001).

The importance of growing-season length to whitebark pine growth may also be reflected in negative relationships with winter snow. Whitebark pine growth at FTL was negatively correlated with previous December and current January precipitation (Figure 3.4), as well as with precipitation during the three- and six-month periods ending in February and March (Figure 3.5). This indicates that winter precipitation, in this case in the form of snowpack, is not favorable to growth in whitebark pine. This is contrary to many high-elevation tree species that prefer increased snowpack and therefore increased soil moisture availability in the spring and summer (Perkins and Swetnam 1996; Carlson *et al.* 2017). However, heavy snows can delay melt-out dates, especially for younger trees, and can cause damage to the crown, which can both delay the start of growing season and reduce growth in subsequent years (Peterson *et al.* 1990). At the FTL site, winter snow depth can reach up to three meters (SNOTEL 2019), which is more than high enough to nearly or completely bury many of the whitebark pine trees at the site. In addition, much of this snow appears to fall after December (SNOTEL 2019). In this case, a snowy December may be indicative of increased winter snowfall and therefore greater snow depth. Deeper snows at FTL would delay the onset of the growing season, especially for buried juvenile trees.

Growing-season length and temperature may also be linked with complex physiological processes in whitebark pine. While cambial growth begins in late May, given optimal conditions, a majority of wood production occurs between bud break and shoot growth in June and winter bud formation in August (Weaver 2001). This pattern is reflected by our observations of cambial growth at the FTL site. Cone formation in whitebark pine is a fourteen-month process, also beginning in June, and ending in August of the following year (Weaver 2001). Warmer temperatures, especially during May and June, can increase the overall amount of energy available, allowing for increased cambial growth earlier in the growing season. Colder temperatures during the early part of the growing season would alternatively increase the risk of frost damage to buds and shoots, which could negatively influence growth in the current year, and likely in the following year. These and other biological relationships, such as needle retention and nutrient storage, may influence tree response to climate. However, we cannot fully assess their contributions to ring width in our study, as the detrending methods we used maximize climate signatures over the signals left by biological processes (Fritts 2001).

The climate response of FTL Engelmann spruce was more complex, although also driven by growing season length and temperature. Overall, significant relationships occurred across monthly and seasonal aggregates for previous and current growing season temperatures, previous growing season precipitation, and winter precipitation (Figures 3.4 and 3.6). Growth relationships with temperature variables were consistently negative with previous summer (July and August), positive with previous fall (September, October), and positive with current summer (July, August). As with FTL whitebark pine, a warmer previous September, or warmer previous fall, lengthens the previous growing season, allowing for increased physiological preparedness. However, other relationships with temperature were less direct. While growth was positively correlated with temperatures during the current year, and especially with current July temperatures, it was negatively correlated with previous year summer temperatures (Figures 3.4 and 3.6). Warmer temperatures during the current year led to increased growth, but warmer temperatures during the previous year led to decreased growth. A similar relationship was identified by Peterson and Peterson (1994) in the North Cascade Mountains and attributed to two possible conditions. One possible cause of the inverse relationship is drought stress and increased respiration, which can diminish carbohydrate reserves for the next year. Warmer temperatures can also boost cambial growth to the point that fewer resources are devoted to roots or food reserves (Peterson and Peterson 1994). Both can limit growth in the following year.

The potential influence of previous year drought stress is corroborated by significant tree-growth relationships with previous-year precipitation and PDSI. Combined, negative responses to temperature and positive responses to moisture during the previous year (Figures 3.4 and 3.6) indicate that previous-year drought stress negatively impacts current year growth in Engelmann spruce at FTL. Inversely, cooler and wetter conditions benefit growth in the following year. We identified a similar, but inverse relationship during current year July (Figure 3.4), such that warmer and drier conditions during current year July would be beneficial to growth. However, seasonal analyses did not indicate a significant response to current summer precipitation. As with FTL whitebark pine, Engelmann spruce was also responsive to winter precipitation (Figures 3.4 and 3.6), indicating that increased winter snowfall leads to decreased growth in the following year.

3.3.2 Temporal Stability of Response

Results from this study suggest that growing season temperatures have been the most important climate drivers of whitebark pine and Engelmann spruce growth at the FTL site, consistent with previous research on both species (Peterson and Peterson 1994; Perkins and Swetnam 1996; Luckman *et al*. 1997; Biondi *et al*. 1999; Bunn *et al*. 2005; Larocque and Smith 2005; Luckman and Wilson 2005; Kipfmueller 2008; Kipfmueller and Salzer 2010; Youngblut and Luckman 2013). However, results also indicate potential changing relationships at our study site. Using forward evolutionary analysis (FEA) alone, climate-growth relationships appeared stable throughout the instrumental period, but many of these relationships did not persist through backward evolutionary analysis (BEA). In whitebark pine, only the relationships with previous September and current June average and minimum temperature, and with previous December and current January precipitation and SP01, remained temporally stable through both FEA and BEA. But despite these stable signals, BEA revealed an emerging negative growth response to previous summer temperatures in recent decades and an emerging positive growth response to previous summer precipitation in recent decades (Figure 3.7). This emerging response is also evident in BEA of whitebark pine growth relationships with PDSI (Figure 3.8), and indicates an overall negative response to warm and dry previous summers (alternatively, a positive response to cool and wet previous summers). In a warming world, growing season length, influenced by spring and fall temperatures and winter snowpack, may no longer limit growth of whitebark pine. Instead, growth may be largely affected by previous year drought stress.

Climate-growth relationships in Engelmann spruce at FTL were more stable, but results again suggest that the influence of previous year moisture may be increasing. Relationships with previous July, August, and September average and maximum temperature, previous September minimum temperature, previous October minimum temperature, current July average, maximum, and minimum temperature, and current June minimum temperature proved temporally stable though both FEA and BEA. Relationships with previous June, July and December total monthly precipitation and SP01, current July total monthly precipitation and SP01, and previous July and August PDSI were also temporally stable. No major shift in climatic response occurred during recent decades, although growth responses to previous summer precipitation (positive) were stronger and more significant in recent decades. A new, positive relationship with previous August precipitation emerged as a part of this change (Figure 3.9). While neither of these changes represent a shifting or emerging response in Engelmann spruce, they may represent the increasing influence of moisture stress under warming conditions, as also indicated by changing relationships in whitebark pine. Of the two species, whitebark pine is more resistant to drought, but modern conditions may be exceeding that tolerance. Despite the apparent stability of climate response in Engelmann spruce, the future does not bode well for either species. The increased importance of previous summer precipitation suggests that the moisture conditions that accompany warming will greatly influence future growth at the FTL site.

3.3.3 Potential for Paleoclimate Reconstruction

Our analyses show that complex and unstable responses affect the potential use of the FTL whitebark pine and Engelmann spruce tree-ring chronologies in paleoclimate reconstructions. The spruce chronology is most likely to provide reliable predictors of summer temperatures for climate reconstruction. Relationships with current July mean, minimum, and maximum temperatures, as well as with seasonal temperatures (three-month period ending in current August, Figure 3.6), were the strongest that we identified in this study and were also temporally stable through the instrumental period. Despite temporal stability in whitebark pine relationships with previous fall (September) and current Spring temperatures (June), the potential emergence of new responses indicates that the overall climate signal in FTL whitebark pine may not be stable. Because of this instability, the whitebark pine chronology is unlikely to represent a reliable climate predictor. However, it still provides useful insight into how climate change may be affecting growth. Ultimately, climate change, rather than disturbance, seems to be disrupting the climate response of whitebark pine at the FTL site. Continued study and sampling at FTL and similar sites will allow us to test whether the apparent shift to previous year water stress is sustained.

While disturbance, and in our study climate change, have minimized the usefulness of whitebark pine chronologies for paleoclimate study by affecting climate response (Larocque and

Smith 2005; Youngblut and Luckman 2013), changes in growth due to disturbances, such as bark beetles and altered fire regimes, are valuable data in themselves. Whitebark pine and Engelmann spruce co-evolved with bark beetles (DeRose and Long 2007; Raffa *et al.* 2013), and centuries-long tree-ring chronologies can potentially inform spatiotemporal trends in insect outbreaks, including physical and climatological influences (Berg *et al.* 2006; Hart *et al.* 2014; Bakaj *et al.* 2016; Derderian *et al.* 2016). Tree rings have been used to study mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and spruce beetle disturbances in whitebark pine (van de Gevel *et al.* 2017), Engelmann spruce (DeRose and Long 2007; Hart *et al.* 2014; Bakaj *et al.* 2016), and other species (Eisenhart and Veblen 2000; Alfaro *et al.* 2003; Berg *et al.* 2006; Axelson *et al.* 2009; Jarvis and Kulakowski 2015). Whitebark pine tree-ring chronologies that include fire scar data can similarly inform spatiotemporal patterns of wildfire (Harley *et al.* 2018), which is increasingly necessary as fire regimes change under climatic and anthropogenic influences (Pechony and Shindell 2010; Peterson *et al.* 2011; Parisien *et al.* 2016; Balch *et al.* 2017). Finally, tree-ring data can also provide information on stand age and structure, establishment, and mortality (Speer 2010). Even if the whitebark pine chronology from FTL does not have high climatological value, it holds value as an archive of ecological change.

3.3.4 Implications for Whitebark Pine Ecosystems and Management

Many studies have attempted to model the impact of climate change on whitebark pine (Romme and Turner 1991; Bartlein *et al.* 1997; Weaver 2001; Schrag *et al.* 2008; Chang *et al.* 2014), but with mixed results based on whether increased or decreased precipitation will accompany warming (Buermeyer 2016). Results from this study suggest that future warming in the Greater Yellowstone region, especially if accompanied by drier conditions, will negatively affect both whitebark pine and Engelmann spruce. Even though growing season temperatures have historically been the dominant climate driver at the FTL site, increasing water stress, most likely due to increasing summer temperatures, may be leading to emerging and/or shifting climate responses in high-elevation whitebark pine. In a study of recent climate change in the GYE, Sepulveda *et al.* (2015) documented increases in both winter and summer temperatures. While increasing winter temperatures may initially benefit young whitebark pine by decreasing snow depth, eventually, warming temperatures will lead to water stress and soil drought in previously unaffected regions (Weaver 2001). Emerging negative responses to previous summer temperature and positive responses to previous summer moisture are occurring during previous July and August, which are already the warmest and driest months of the year for the Yellowstone region (Figure 3.2). The potential shift of whitebark pine response toward that already shown by Engelmann spruce may indicate that the more drought-tolerant whitebark pine may be reaching its own limit, which does not bode well for the less drought-tolerant Engelmann spruce.

In addition to affecting the growth of whitebark pine and Engelmann spruce trees, warming, drying, and lengthening growing seasons will also affect species distributions, leading to altered treelines in the western U.S. and Canada. Whitebark pine is considered a "stress tolerator" (Tomback *et al.* 2016) that thrives in conditions unsuitable for other tree species (i.e. high-elevation, dry and cold slopes with poor soil). Because of this, whitebark pine trees are often the first to colonize harsh, high-elevation landscapes, improving site conditions and facilitating continued conifer establishment (Callaway 1998; MacFarlane *et al.* 2013; Tomback *et al.* 2016). This facilitation is reflected in relationships between whitebark pine and Engelmann spruce establishment. For Engelmann spruce, successful seedling establishment is dependent on moisture (Gill *et al.* 2015; Andrus *et al.* 2018; Hill *et al.* 2018), and seedlings are more likely to establish in protected microsites with higher moisture retention (Hill *et al.* 2018). These microsites can be provided by whitebark pine trees, which provide shelter, shade, and wind protection (Tomback *et al.* 2001). These complex interactions between species, which are in some cases essential for species survival, may be dramatically altered by warmer and drier conditions at treeline.

Other threats to whitebark pine ecosystems will be limited or exacerbated by the moisture conditions that accompany warming temperatures. Warmer and drier conditions are expected to benefit bark beetles, including the spruce and mountain pine beetles (Hebertson and Jenkins 2008; Bentz *et al.* 2010; Hart *et al.* 2014; Buermeyer 2016), and extreme fire seasons are expected to become more frequent in the Greater Yellowstone Ecosystem (Westerling *et al.* 2011). On the other hand, the invasive white pine blister rust (*Cronartium ribicola* J.C. Fisch.) is limited by cold, dry conditions and requires humid, mild conditions to complete its life cycle (Resler and Tomback 2008). Wetter conditions will promote the spread of white pine blister rust, and will also increase competition from more water-dependent species, including subalpine fir (Weaver 2001; Buermeyer *et al.* 2016). In either case, altitudinal migrations as a result of warming temperatures will be limited by available refugia, as whitebark pine ecosystems are already isolated in high-elevation habitats.

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Appendix

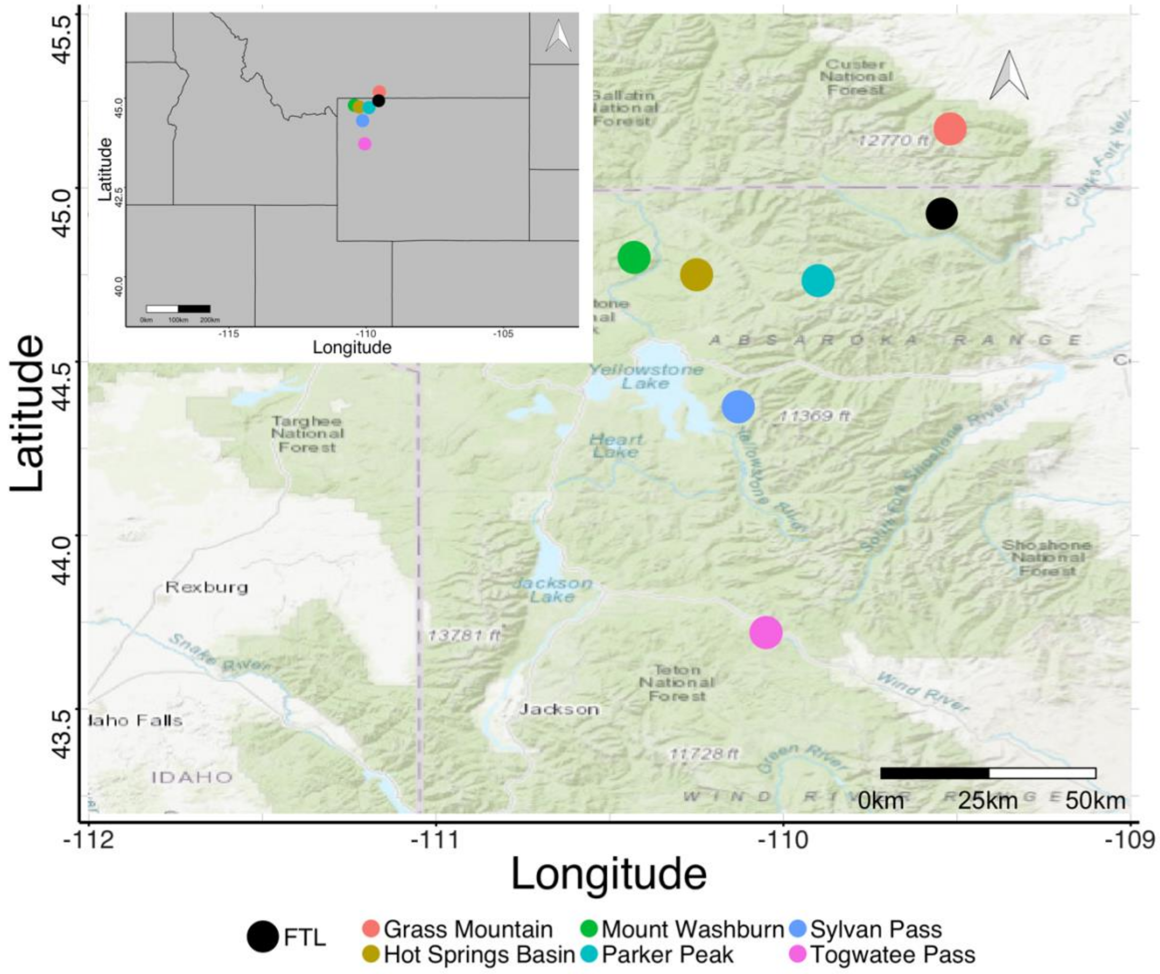

Figure 3.1 FTL and GYE Chronology Locations: Locations of the FTL study site and of the six other whitebark pine and Engelmann spruce tree-ring chronologies included on the ITRDB for the Greater Yellowstone region. The Mount Washburn and Hot Springs Basin chronologies are pine, and the other four are spruce. Source map data and imagery © OpenStreetMap contributors (www.openstreemap.org/copyright).

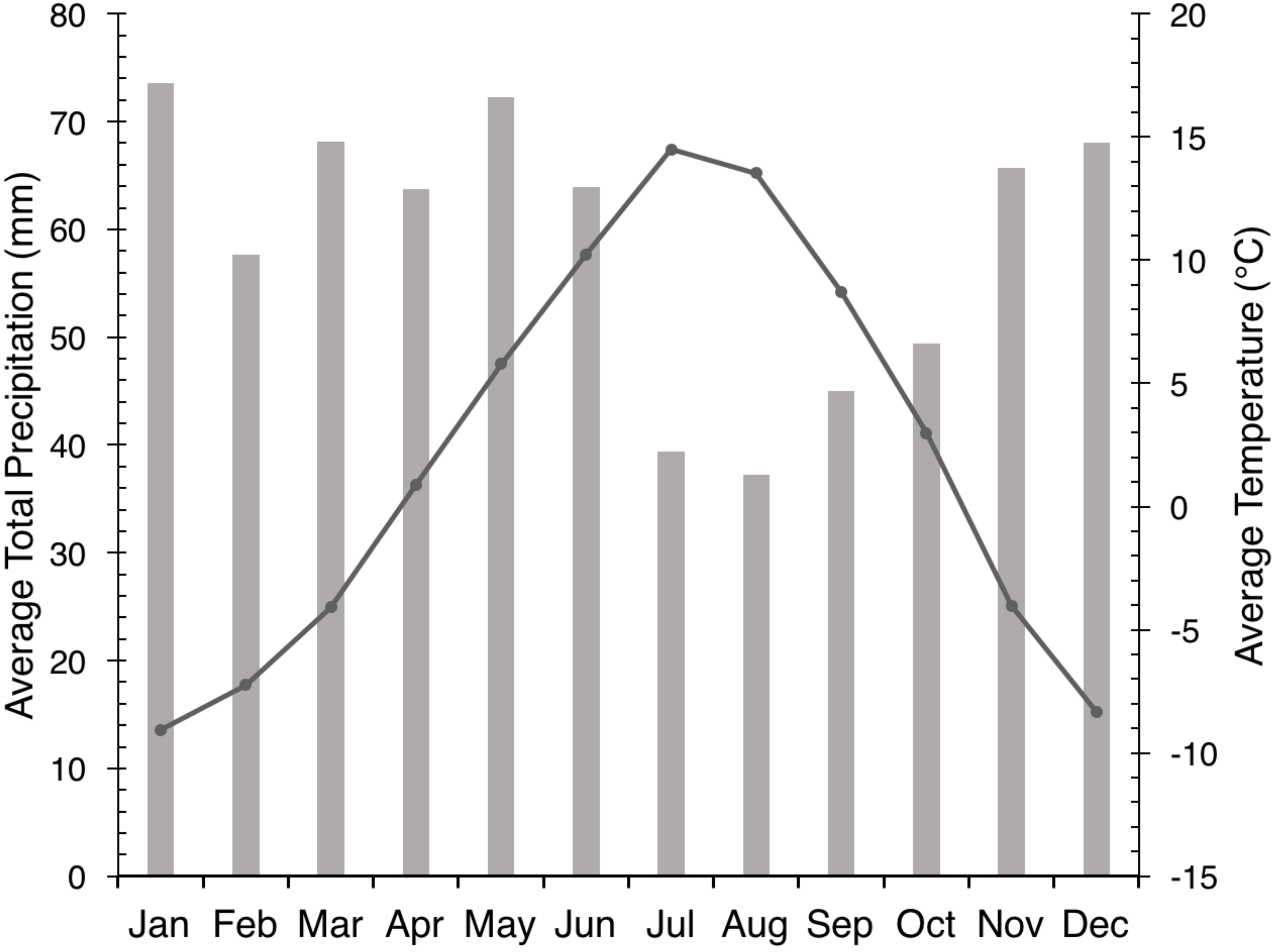

Figure 3.2 GYE Climograph: Climograph for the NCEI Yellowstone Drainage region, based on monthly averages over the instrumental period, 1895–2017 CE (NCEI 2018).

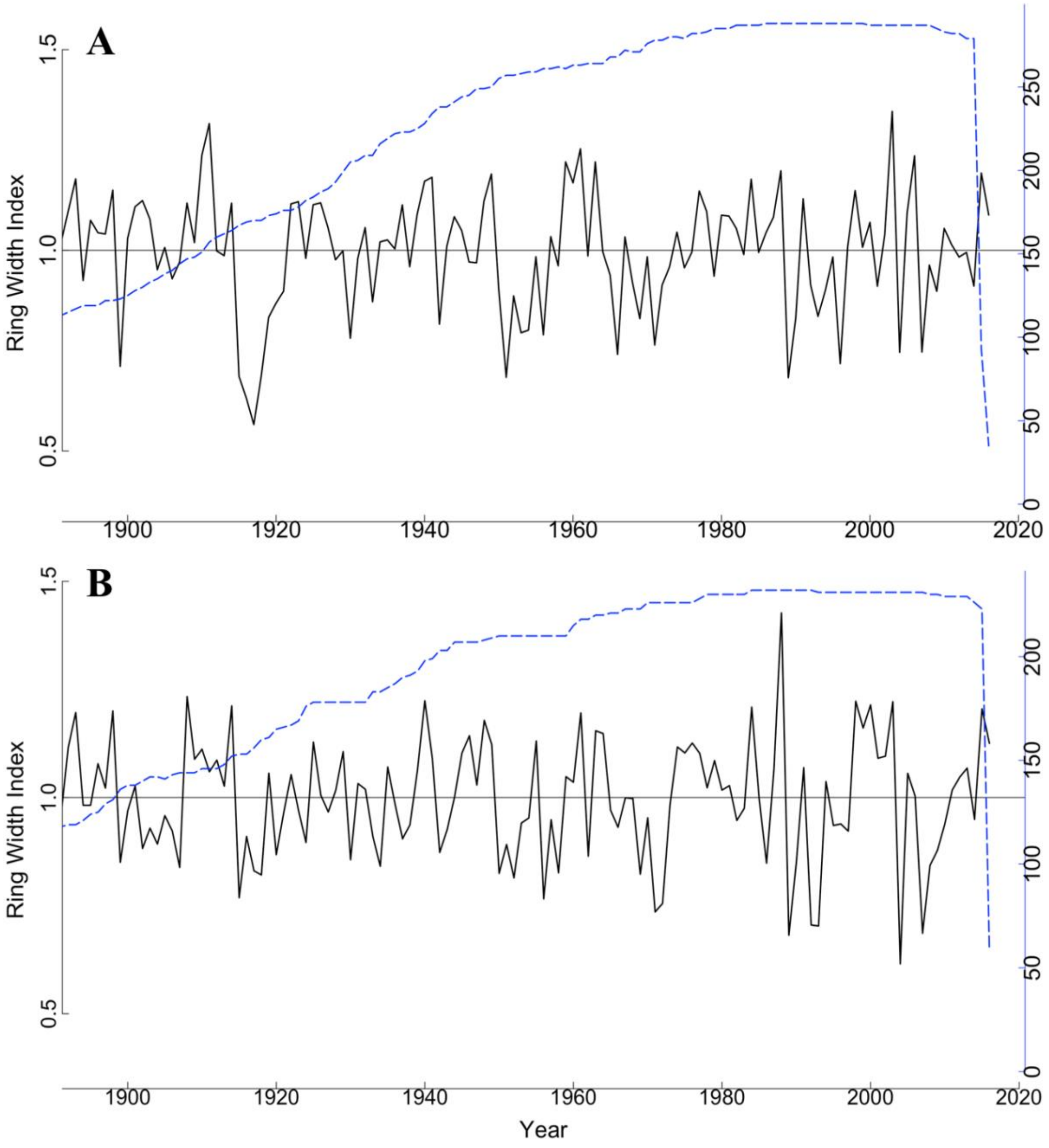

Figure 3.3 Overlap Chronologies for Instrumental Period: Time series plots (1896–2016 CE) of the detrended whitebark pine and Engelmann spruce chronologies used for correlation and evolutionary analyses.

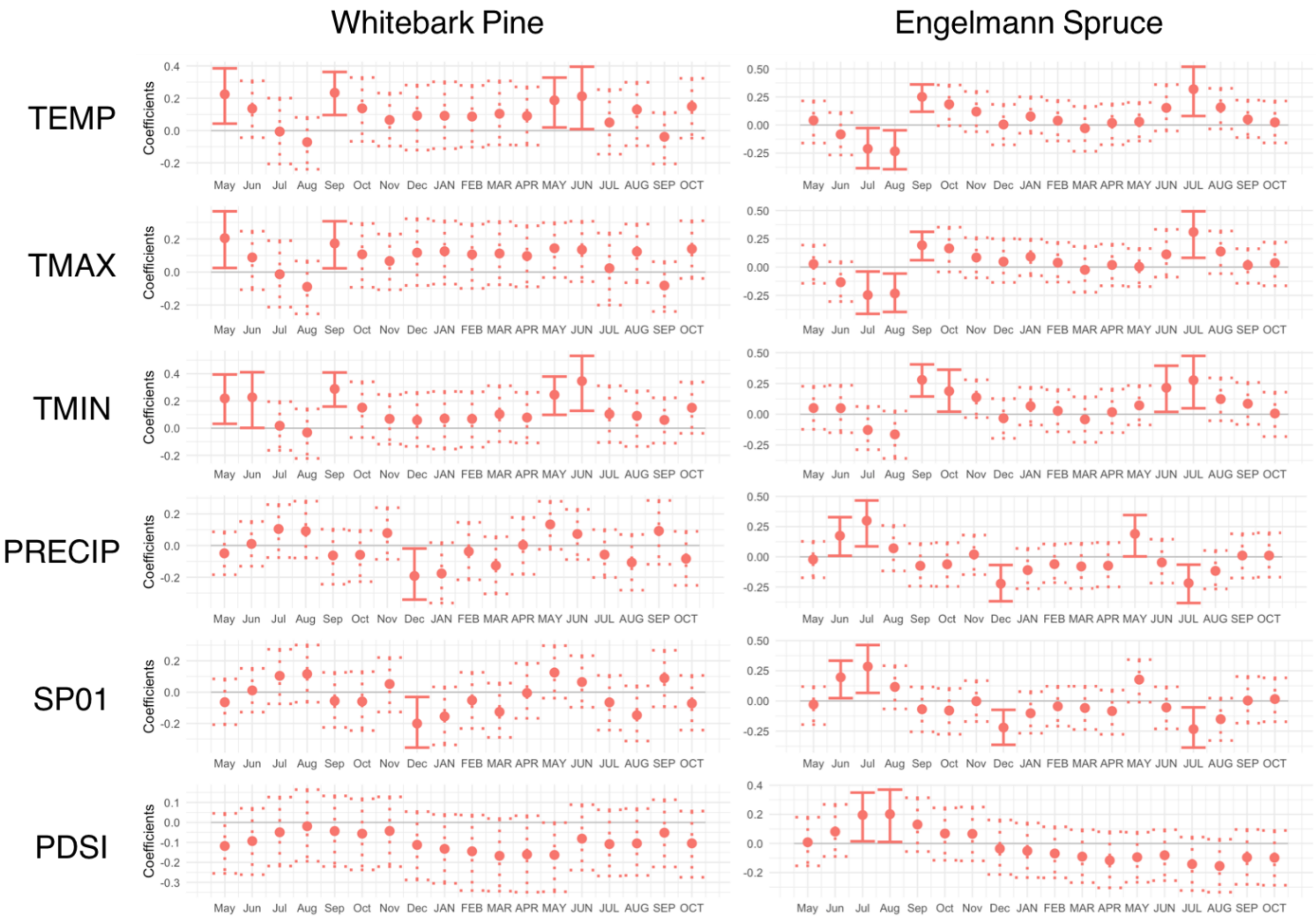

Figure 3.4 Climate-Growth Relationships: Climate-growth relationships in whitebark pine and Engelmann spruce. Statistically-significant ($p < 0.05$) relationships are indicated by solid red bars. Lower-case months are previous year while upper-case months are current year.

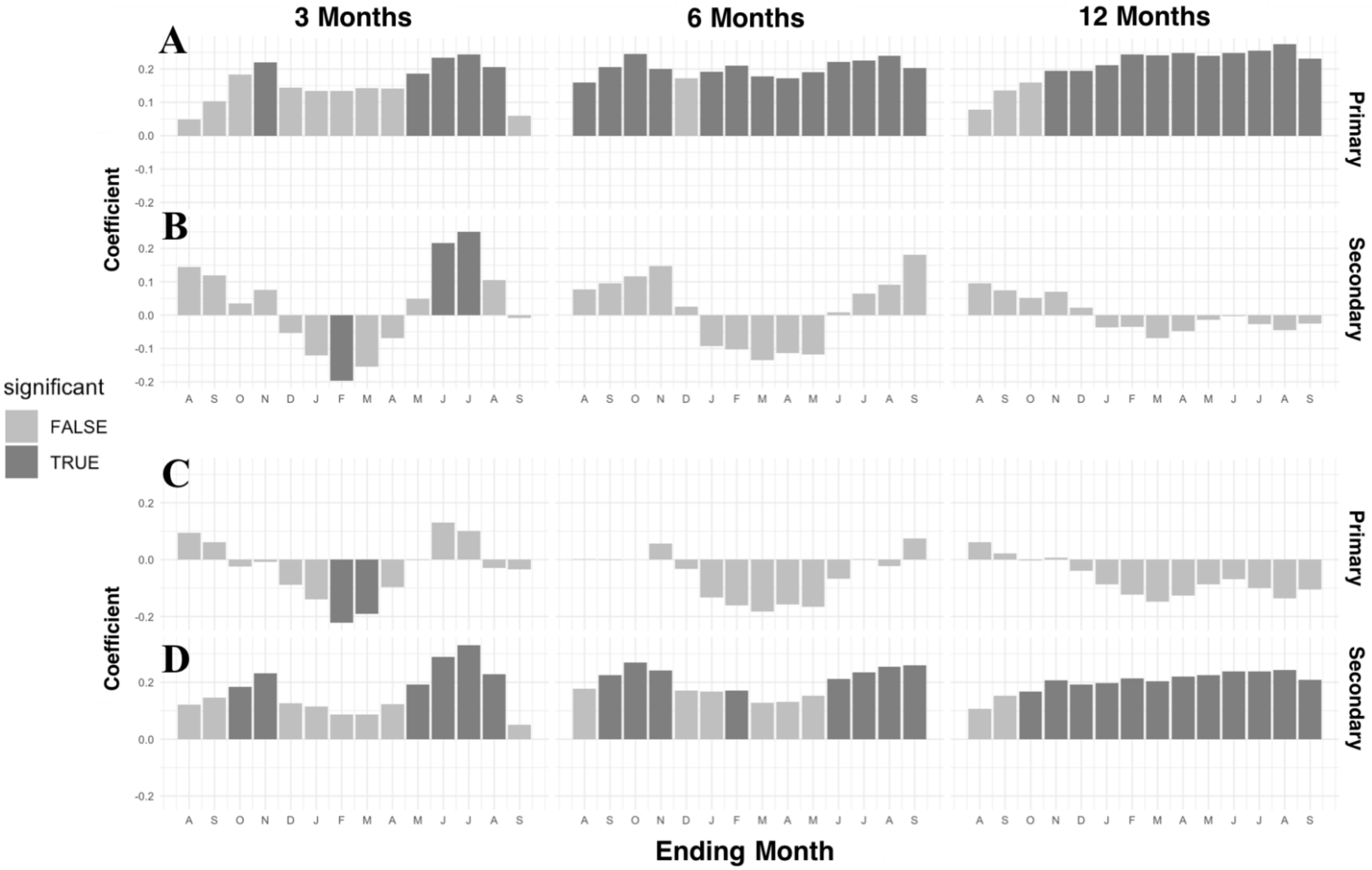

Figure 3.5 Seascorr Plot for Whitebark Pine: Top: Correlations between the FTL whitebark pine chronology and seasonal temperature (A) and remaining partial correlations with seasonal precipitation (B). Bottom: Correlations between the FTL whitebark pine chronology and seasonal precipitation (C) and remaining partial correlations with seasonal temperature (D). Months are from left to right: previous August to current September.

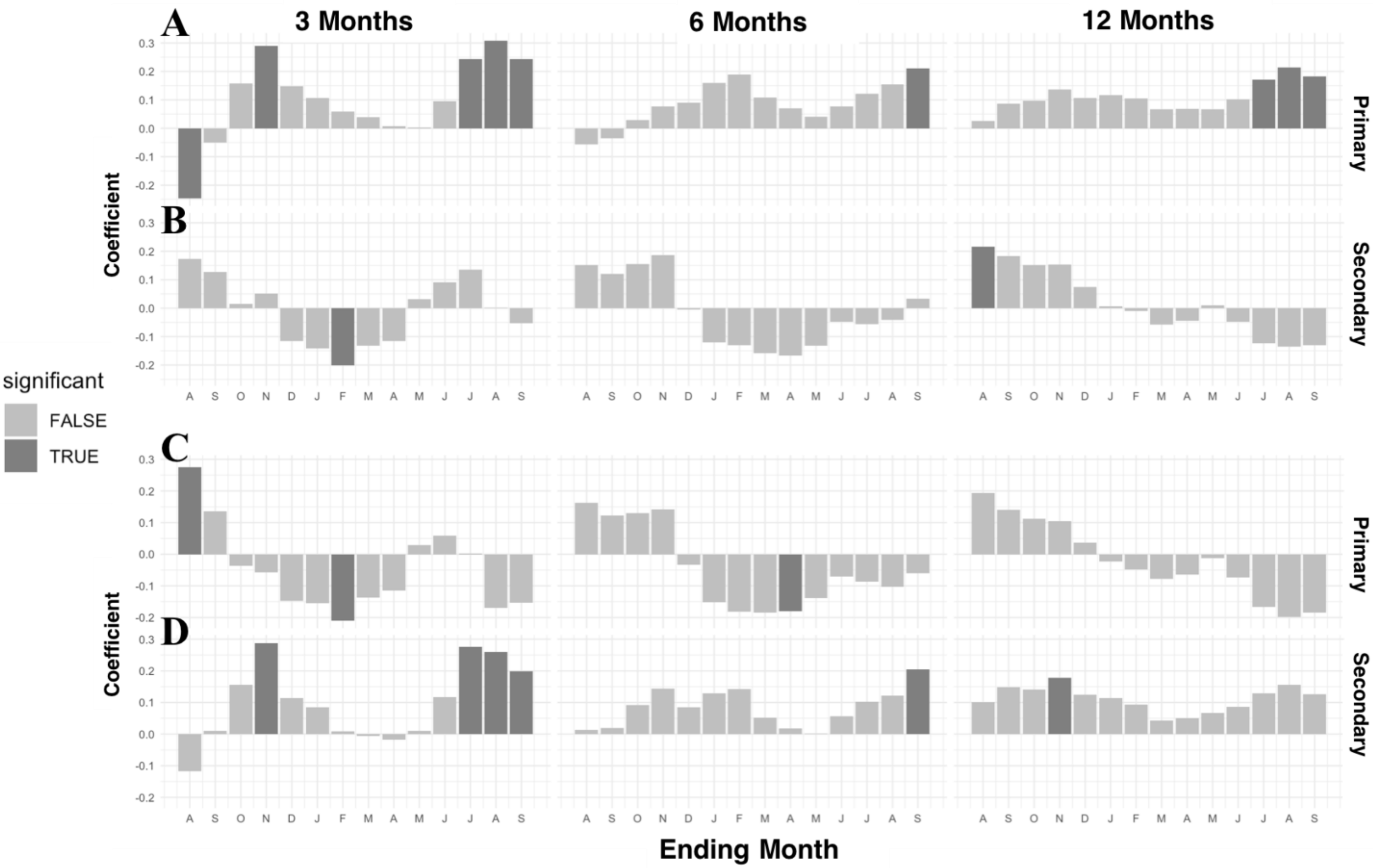

Figure 3.6 Seascorr Plot for Engelmann Spruce: Top: Correlations between the FTL Engelmann spruce chronology and seasonal temperature (A) and remaining partial correlations with seasonal precipitation (B). Bottom: Correlations between the FTL Engelmann spruce chronology and seasonal precipitation (C) and remaining partial correlations with seasonal temperature (D). Months are from left to right: previous August to current September.

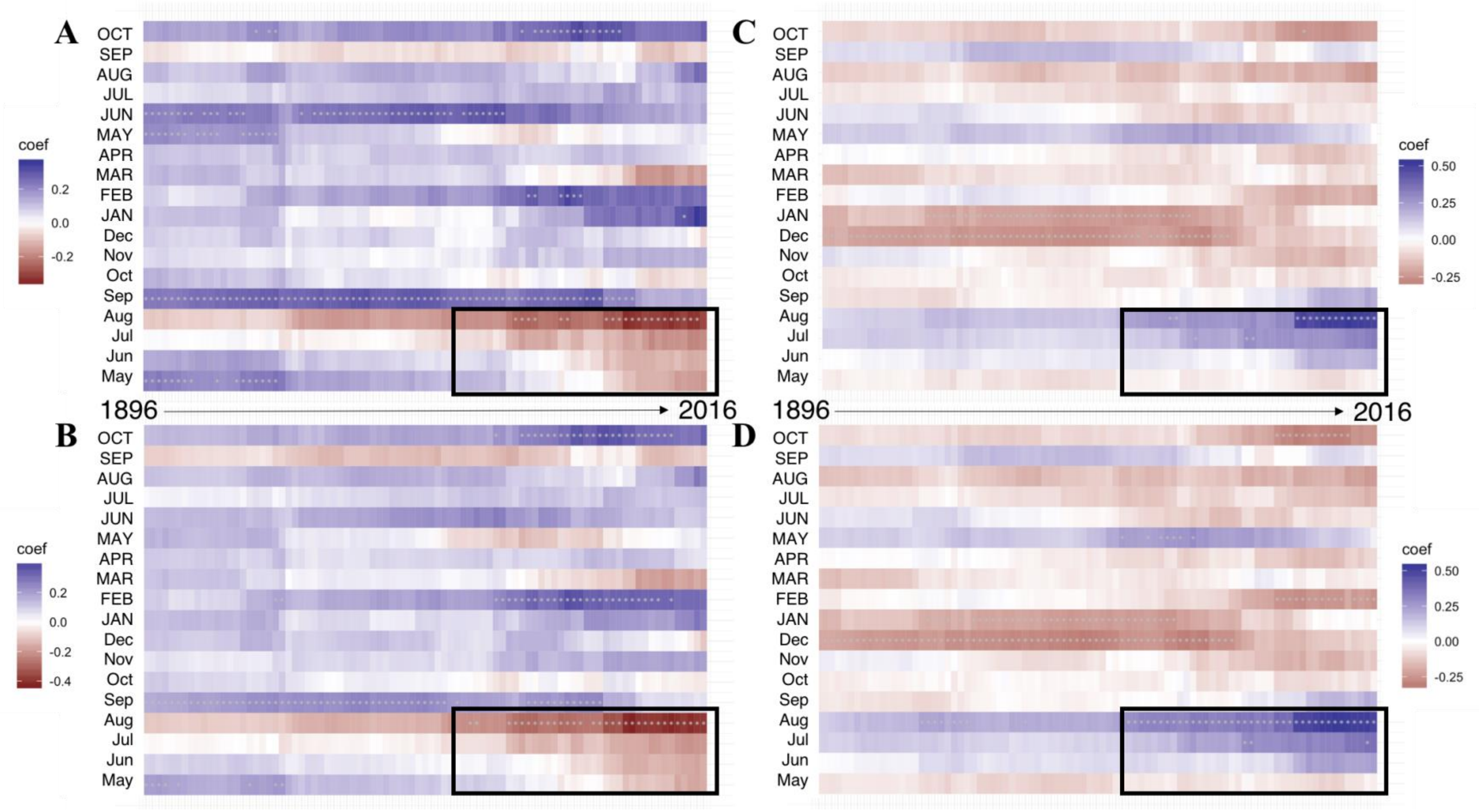

Figure 3.7 Temporal Stability Plots for Whitebark Pine: Temporal stability (Backwards Evolutionary Analysis) of climate-growth relationships in whitebark pine: (A) TEMP, (B) TMAX, (C) PRECIP, and (D) SP01, over the common period 1896–2016. Note the emerging negative relationships with previous summer temperature (A and B) and positive relationships with previous summer moisture (C and D). Stars indicate significance ($p \leq 0.05$).

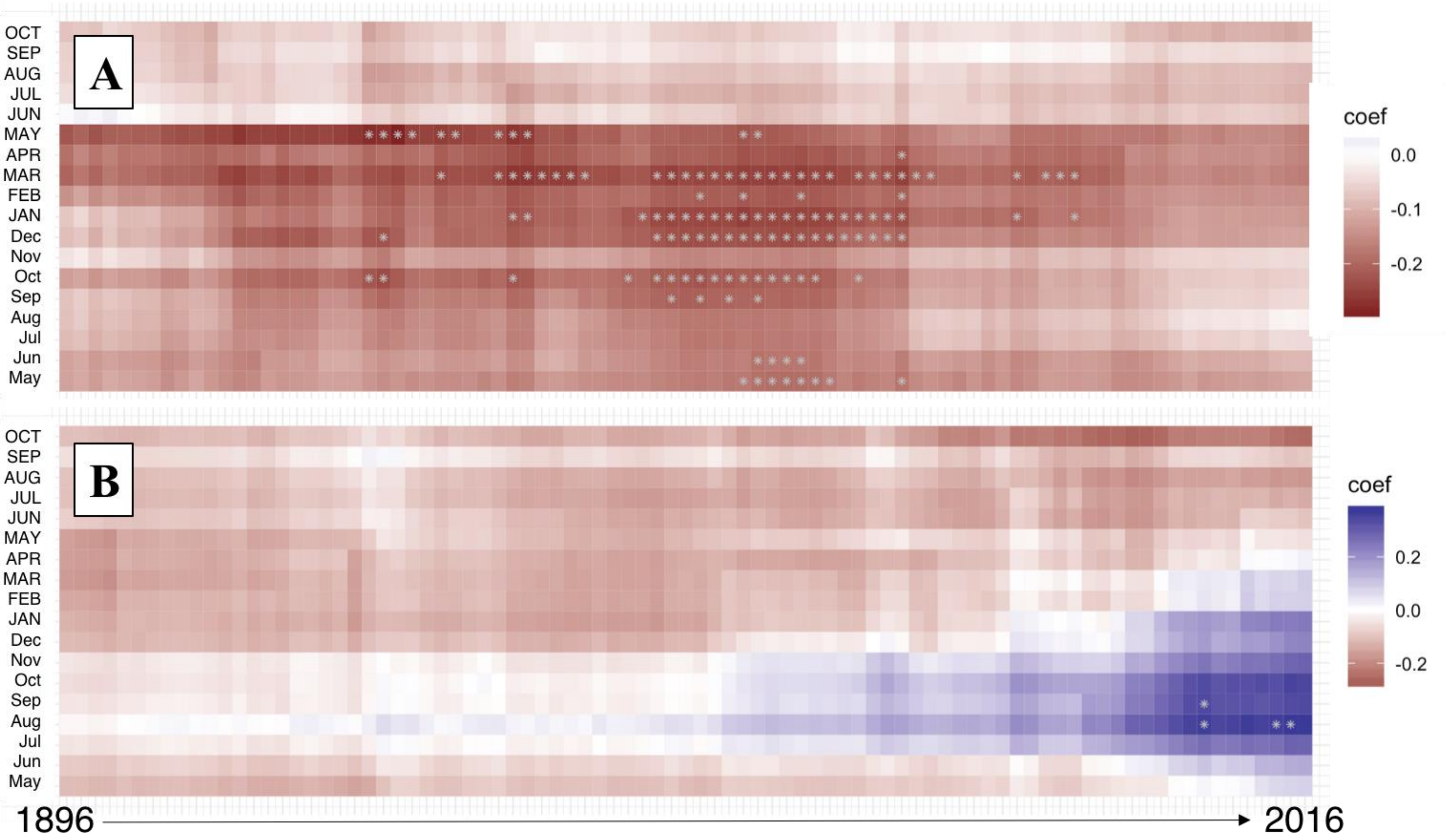

Figure 3.8 Temporal Stability Plot for Whitebark Pine and PDSI: Forward (A) and backward (B) evolutionary analyses of climate-growth relationships in whitebark pine with PDSI, which indicate an emerging positive response to previous year PDSI. Stars indicate significance (p ≤ 0.05).

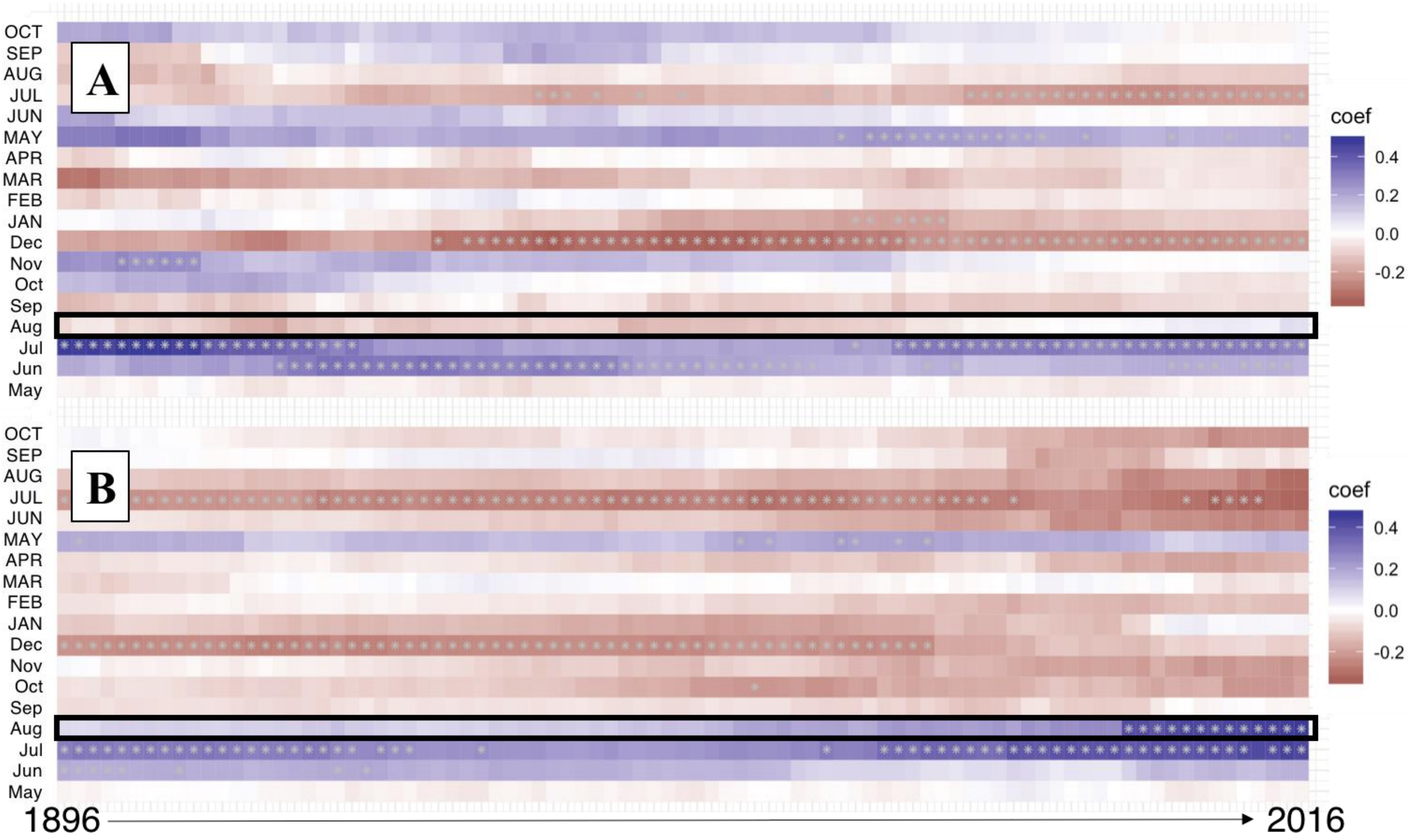

Figure 3.9 Temporal Stability Plot for Engelmann Spruce and Precipitation: Forward (A) and backward (B) evolutionary analyses of climate-growth relationships in Engelmann spruce with total monthly precipitation, which indicate an emerging positive response to previous year August precipitation (black boxes). Stars indicate significance ($p \leq 0.05$).

Table 3.1 FTL Site Chronology Stats: Chronology statistics for the whitebark pine and Engelmann spruce chronologies developed for the FTL site.

Chronology[1]	**Measured Series**	**Total Trees**	**Length (yrs)**	**Mean Length Series (yrs)**	**Average Interseries Correlation**	**Average Mean Sensitivity**	**Segments Tested**	**Segments Flagged**[2]	**Percent Segments Flagged**	**Time Span (CE)**
PIAL	433	226	1308	199.0	0.57	0.23	3395	261	7.69	708–2016
PIEN	276	146	1262	178.0	0.63	0.23	1937	70	3.61	754–2016

[1] ITRDB Species Codes, where PIAL = whitebark pine (*Pinus albicaulis* Engelm.) and PIEN = Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)

[2] Indicates tested segments that fell below the statistical threshold for significance at the 0.01 level. These were re-inspected and found to be correctly placed in time.

Table 3.2 Significant Climate-Growth Relationships

Species[1]	Month	Variable[2]	Correlation[3]
PIAL	Prev May	TEMP	0.23
PIAL	Prev Sept	TEMP	0.23
PIAL	Curr May	TEMP	0.19
PIAL	Curr June	TEMP	0.21
PIAL	Prev May	TMAX	0.21
PIAL	Prev Sept	TMAX	0.17
PIAL	Prev May	TMIN	0.22
PIAL	Prev June	TMIN	0.23
PIAL	Prev Sept	TMIN	0.29
PIAL	Curr May	TMIN	0.25
PIAL	Curr June	TMIN	0.35
PIAL	Prev Dec	PRECIP	-0.19
PIAL	*Curr Jan	PRECIP	-0.18
PIAL	Prev Dec	SP01	-0.20
PIAL	*Curr Jan	SP01	-0.16
PIEN	Prev July	TEMP	-0.21
PIEN	Prev Aug	TEMP	-0.23
PIEN	Prev Sept	TEMP	0.25
PIEN	Curr July	TEMP	0.32
PIEN	Prev July	TMAX	-0.25
PIEN	Prev Aug	TMAX	-0.23
PIEN	Prev Sept	TMAX	0.19
PIEN	Curr July	TMAX	0.31
PIEN	Prev Sept	TMIN	0.28
PIEN	Prev Oct	TMIN	0.19
PIEN	Curr June	TMIN	0.22
PIEN	Curr July	TMIN	0.28
PIEN	Prev June	PRECIP	0.17
PIEN	Prev July	PRECIP	0.30
PIEN	Prev Dec	PRECIP	-0.22
PIEN	Curr May	PRECIP	0.19
PIEN	Curr July	PRECIP	-0.22
PIEN	Prev June	SP01	0.20
PIEN	Prev July	SP01	0.29
PIEN	Prev Dec	SP01	-0.22
PIEN	Curr July	SP01	-0.23
PIEN	Prev July	PDSI	0.20
PIEN	Prev Aug	PDSI	0.20

[1] ITRDB Species Codes, where PIAL = whitebark pine (*Pinus albicaulis* Engelm.) and PIEN = Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)

[2] Monthly average temperature (MNTM), monthly maximum temperature (TMAX), monthly minimum temperature (TMIN), total monthly precipitation (TPCP), monthly standardized precipitation index (SP01), and monthly Palmer Drought Severity Index (PDSI).

[3] Significant at $p < 0.05$.

*Not significant but temporally stable relationship

CHAPTER FOUR

TREE-RING EVIDENCE OF VOLCANIC COOLING EVENTS DURING THE LAST MILLENIUM FROM THE BEARTOOTH MOUNTAINS, WYOMING, U.S.A.

This chapter is in preparation for submission to a journal. The use of "we" within the text refers to me and my co-authors, Matthew Bekker and Sally Horn. As first author, I led on study design, data collection and analyses, and writing the manuscript.

Abstract

Explosive volcanic eruptions are a well-known cause of natural climate variability, but local and regional proxy records from tree rings and other natural archives are needed to identify the spatial extent of past volcanic influences on surface temperatures. Tree-ring characteristics including frost rings, narrow rings (tree ring minima), and maximum latewood density have been used to examine temporal associations between volcanic eruptions and tree-ring records and to thereby infer the influences of volcanic forcing at a variety of scales. For this study, we investigated the potential of two millennial-length tree-ring chronologies to record volcanic cooling events in the Beartooth Mountains of northwest Wyoming. We combined frost-ring years, tree-ring minima, and periods of suppressed growth in our chronologies with climate records and ice core and tree-ring proxy data to identify times when multiple lines of evidence support volcanic cooling in our study region. We identified tree-ring evidence indicating cooling in response to five volcanic events and longer periods of activity. We identified whitebark pine frost rings associated with the eruptions of Huaynaputina, Peru in 1600 CE, Parker, Philippines and others in 1640/1641 CE, and Agung, Bali in 1963–1964 CE, tree-ring minima and periods of growth suppression associated with the eruptions of Tambora, Indonesia in 1815 CE and Cosigüina, Nicaragua in 1835 CE, and other potential volcanic events during the early nineteenth century that contributed, along with solar forcing, to cooler than average conditions across the western U.S. The combination of tree-ring evidence with ice core signals and other tree-ring studies highlights the ability of tree rings in the high plateaus of the Beartooth Mountains to record volcanic events and to thereby provide more information about the spatial extent of past volcanic influences.

Keywords: dendrochronology, frost rings, volcanic history, whitebark pine

4.1 Introduction

Explosive volcanic eruptions are a major driver of natural climate variability (Robock 2000; Salzer and Hughes 2007). Volcanic aerosols, formed when ash, sulfur dioxide, and other gases are erupted into the atmosphere, affect Earth's radiative balance by reflecting or absorbing incoming radiation, reducing ozone concentrations, and absorbing outgoing longwave radiation, depending on particle sizes and the altitude of aerosol layers in the atmosphere. Volcanic aerosols most often lead to cooler surface temperatures, but sometimes to warmer winter temperatures (Rampino and Self 1982; Sear *et al.* 1987; Robock and Mao 1992; Crowley 2000; Robock 2000). Efforts to quantify the effects of volcanic eruptions on climate were limited until recent decades by sparse temperature and proxy data (Robock 2000). Knowledge of the areal extent of volcanic influence largely depends on local or regional proxies, such as coral isotope or tree-ring based evidence of cooling (Crowley *et al.* 1997; D'Arrigo and Jacoby 1999; Baille and McAneney 2015). Some proxies, such as ice core records from Antarctica and Greenland, document past volcanic histories but do not provide information on climatic response (D'Arrigo and Jacoby 1999; Salzer and Hughes 2007). Annually-resolved tree-ring chronologies have the potential to clarify volcanic signals in ice core records, and by providing localized evidence of cooling, can also provide data on the spatial extent and magnitude of volcanically-influenced changes in climate (D'Arrigo and Jacoby 1999; Baille and McAneney 2015). Such data are necessary for more accurate modeling and prediction of climate changes following modern volcanic eruptions.

In North America, tree-ring evidence attributed to volcanism has included frost-damaged rings (LaMarche and Hirschboeck 1984; Brunstein 1996; Salzer and Hughes 2007), narrow rings (tree-ring minima) (Scuderi 1990; Salzer and Hughes 2007), and low maximum latewood density (MXD) values (Jones *et al.* 1995; Briffa *et al.* 1998; D'Arrigo and Jacoby 1999). Frost rings (Figure 4.1, see Appendix for all Figures and Tables) occur when temperatures well below freezing occur during the growing season, which can lead to intracellular freezing and the deformation of cell structure. This deformation leaves a distinct ring of anatomical damage, a frost ring, within an annual ring (Glerum and Farrar 1966; LaMarche and Hirschboeck 1984; Brunstein 1996). While other anomalies in tree rings can be caused by multiple factors, frost rings are only formed by freezing temperatures, making them the most reliable proxy for examining sudden and severe cooling events in tree-ring series (Scuderi 1990; Bailey and

McAneney 2015). LaMarche and Hirschboeck (1984) identified notable frost rings coincident with the then unknown 1600 CE eruption of Huaynaputina, Peru, as well as with known eruptions of Tambora (Indonesia) in 1815 CE, Cosigüina (Nicaragua) in 1835 CE, Krakatoa (Indonesia) in 1883 CE, Katmai (Alaska, U.S.) in 1912 CE, and Agung (Bali) in 1963–1964 CE. Other studies with bristlecone pine also linked frost-damaged rings to volcanic events. Brunstein (1996) identified multiple frost-ring years associated with climatic cooling during the early nineteenth century, attributed in part to a cluster of volcanic eruptions during that period, including the eruptions of Tambora in 1815 CE and Cosigüina in 1835 CE. Salzer and Hughes (2007) identified frost rings associated with the 1600 CE eruption of Huaynaputina, and with the eruptions of Kuwae (Vanuatu) in 1452 CE and Krakatoa in 1883 CE.

While of great use as indicators of freezing events, frost rings are relatively uncommon and more likely to occur in younger trees, seedlings, or branches (LaMarche and Hirschboeck 1984; Brunstein 1996). Younger trees are more vulnerable during their first few centimeters of growth, before thicker bark can better protect the cambium (Schweingruber 2007; Payette *et al.* 2010). Frost rings that occur in mature, well-established trees are more likely to reflect notable frost events, but are relatively rare. This has led researchers to examine other tree-ring indicators for links to volcanic cooling. Salzer and Hughes (2007) and Scuderi (1990) examined relationships between tree-ring minima and volcanic events in the western United States. Salzer and Hughes (2007) identified periods of decreased growth (narrowest 5% of years) in bristlecone pine associated with the following eruptions and clusters of eruptions: (1) Kuwae, Pelée, (Martinique), and Kelut (Indonesia) from 1452–1463 CE; (2) Huaynaputina in 1600 CE; (3) Colima (Mexico) and Raoul (New Zealand) in 1622 CE; (4) Parker (Philippines) and Komagatake (Japan) in 1641 CE; (5) Gamkonora (Indonesia) in 1674 CE; (6) Tongkoko (Indonesia) in 1680 CE; and (7) Cosigüina in 1835 CE. However, they did not find evidence of cooling during the eruptions of Laki (Iceland) in 1783 CE, Tambora in 1815 CE, or Katmai in 1912 CE. Scuderi (1990) identified tree-ring minima associated with these three eruptions, in addition to the eruptions of Huaynaputina in 1600 CE and Komagatake and Awu (Indonesia) in 1640/1641 CE. The eruption of Awu is believed to have been misattributed, with the source actually Parker, in the Philippines, according to Briffa *et al.* 1998 (because of this misattribution, we henceforth use Parker in place of Awu).

Other studies (Jones *et al*. 1995; Briffa *et al*. 1998; D'Arrigo and Jacoby 1999) have taken a different, and larger-scale approach, by examining low MXD values as a proxy for volcanic cooling at hemispheric and continental scales. For high-elevation or high-latitude tree species, MXD has been considered more reliable than tree-ring width for indicating volcanic cooling, because of both (1) a stronger summer temperature response and (2) a stronger high-frequency response (D'Arrigo *et al*. 1992; D'Arrigo and Jacoby 1999). Jones *et al*. (1995) were among the first to quantify relationships between MXD and volcanic events. They averaged MXD records from 97 sites in North America and 37 sites in Europe, using z-scores to evaluate the most extreme values. In North America, they found years of extreme low latewood density to be associated with eruptions of Huaynaputina in 1600 CE, Komagatake and Parker in 1640/1641 CE, Long Island (New Guinea) in 1660 CE, and Tarumae (Japan) in 1667 CE. D'Arrigo and Jacoby (1999) focused their MXD analyses on the northern treeline of North America, but rather than averaging series, they reported the 20 most extreme MXD values for each of their thirteen sites. They identified MXD extremes associated with the eruptions of Huaynaputina in 1600 CE, Komagatake and Parker in 1640/1641 CE, Laki in 1783 CE, Tambora in 1815 CE, and Cosigüina in 1835 CE. They found spatial variation in tree response to some of these eruptions: for example, a higher response in eastern North America to the 1815 CE eruption of Tambora and a higher response in Alaska for the 1783 CE eruption of Laki. Briffa *et al*. (1998) expanded MXD analyses to the Northern Hemisphere (383 site averages) and found strong support, once again, for the 1600 CE eruption of Huaynaputina, and associations of low density values with the eruptions of Komagatake and Parker in 1640/1641 CE, Kuwae in 1452 CE, Tambora in 1815 CE, and Katmai in 1912 CE.

From all of the summarized works above, a few notable dates stand out. Across western North America, tree-ring anomalies, including frost rings, minima, and low MXD values, have been found to be associated with the volcanic eruptions of Kuwae in 1452 CE, Huaynaputina in 1600 CE, Komagatake/Parker in 1640/1641 CE, Tambora in 1815 CE, Cosigüina in 1835 CE, and Krakatoa in 1883 CE. Other notable events include the eruptions of Laki in 1783 CE, Katmai in 1912 CE, and Agung in 1963 CE. Combined, the studies support the continental to hemispheric influence of explosive volcanic eruptions, and demonstrate the potential of tree-ring anomalies to document the influences of these eruptions on climate. In this study, we investigated the potential of two millennial-length tree-ring chronologies to record volcanic cooling events at high elevations in the Beartooth Mountains of northwest Wyoming. We combined frost-ring years, tree-ring minima, and suppressed growth evidence with climate records and ice core and tree-ring proxy data from other sources to examine where multiple lines of evidence support volcanic cooling as a driver at our study site.

4.2 Data and Methods

We developed tree-ring chronologies from living and remnant whitebark pine (*Pinus albicaulis* Engelm.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm) collected from Fantan Lake (FTL), at 44.926°N, 109.544°W, a high-elevation site (2800 to 3020 m) in the Beartooth Mountains of northwest Wyoming (Figure 4.2, Table 4.1). We crossdated these chronologies and confirmed our dating using the statistical software COFECHA (Holmes 1983). The absolute dating of individual tree rings allowed for the assignment of frost rings to exact calendar years. For complementary analyses of marker years and growth changes, described below, we used raw tree-ring widths, as well as standardized tree-ring indices, which were generated using a 32-year spline in the dendrochronology program library in R (dplR) (Cook 1985; Bunn 2008). We chose to use a flexible spline for this study to emphasize both the most negative growth years and periods of decreased growth within a decade. In addition, we truncated both chronologies based on an expressed population signal (EPS) threshold of 0.85 (Wigley *et al*. 1987) (Table 4.1). For the purposes of this paper, we used the EPS statistic, which explains how well a subsample represents a larger, infinite sample, to identify where low sample size or low interseries correlation potentially limits the identification of a specific event (Wigley *et al*. 1987; Buras 2017).

We first developed a frost-ring chronology from the combined whitebark pine and Engelmann spruce tree-ring chronologies from FTL. For each sample, and along two radii where possible, we recorded (1) incidence of frost-damaged cells and (2) position within the ring as either earlywood (EW) or latewood (LW). We also recorded other injuries and/or ring anomalies, such as abrupt but un-sustained changes in growth (*e.g.* wide to extremely narrow ring, followed by a return to regular growth rates), traumatic resin ducts (evident only in Engelmann spruce), growth suppression visible to the naked eye, and thin latewood. To reduce bias in the detection of other injuries, we required that they be identified and recorded before absolute dating of the sub-fossil samples. Therefore, we did not go back through dated samples to seek out further evidence, especially evidence recorded as “other injury.” We used the combination of FHAES (Brewer *et al*. 2016) and the R package burnr (Malevich *et al*. 2018) to visualize synchrony among frost events and other injuries. We calculated the annual relative frequency, or number of frost rings divided by the number of trees alive in that year (%) (Payette *et al*. 2010), including and excluding synchronous other injuries, and recognize that many of the trees that may have been alive during the earliest frost years are now potentially missing from the landscape.

In addition to frost ring identification, we used relative growth change analyses (15-year moving window) in the R package PointRes (van der Maaten-Theunissen *et al*. 2015) to identify pointer years (Schweingruber *et al*. 1990) and periods of suppression or release in growth, which may correspond with frost events or recorded volcanic eruptions. For this analysis, we used the raw ring-width chronologies for whitebark pine and Engelmann spruce and set the following thresholds in R: (1) Growth Release: 60% relative growth change; (2) Growth Suppression: 40% relative growth change; and (3) Minimum Percent Recording Trees: 75%, according to Schweingruber *et al*. (1990) and the defaults used in pointRes (van der Maaten-Theunissen *et al*. 2015). We compared pointer years and growth changes detected by relative growth change analyses with ring-width minima (narrowest 5% of ring-width indices) and multi-year periods of reduced growth (at least three minimum years within a decade) within the standardized FTL chronologies. Then, to examine temporal associations between tree-ring evidence and recorded volcanic events, we compared frost rings and combined single and multi-year periods of decreased growth with other published proxies of volcanic activity (Table 4.2). We considered associations as ± five years of ice core records and ± one year of tree-ring proxies (Salzer and Hughes 2007). To examine the potential confounding influence of drought, we also examined temporal association between reduced growth and severe (≥ -3.00) values of reconstructed Palmer Drought Severity Index (PDSI) for a regional grid point in northwest Wyoming (nearest to 44.93°N, 109.54°W), downloaded from the North American Drought Atlas (Cook *et al*. 2010). To examine differences between the influence of frost ring years (extreme and sudden cooling) and extreme drought on growth in whitebark pine and Engelmann spruce, we also performed superposed epoch analysis (SEA) (Lough and Fritts 1987) using functions in dplR (Bunn 2008).

4.3 Results and Discussion

4.3.1 Tree-Ring Evidence of Volcanic Cooling at FTL

From our combined analyses and multiple lines of evidence, we identified five volcanic events that affected climate and tree growth at FTL: Huaynaputina in 1600 CE; Parker in 1641 CE; Tambora in 1815 CE; Cosigüina in 1835 CE; and Agung in 1963–1964 CE. The eruption of Huaynaputina in 1600 CE is well-documented by tree-ring studies in western North America. The event is indicated by the most extreme MXD year (1601 CE) recorded by both Jones *et al.* (1995) and Briffa *et al.* (1998), as well as by extreme density years recorded by D'Arrigo and Jacoby (1999). The year 1601 CE is also marked by narrow ring widths in foxtail pines of the Sierra Nevada (Scuderi 1990) and frost rings in southwestern bristlecone pine (LaMarche and Hirschboeck 1984; Salzer and Hughes 2007). Summer temperature reconstructions for the western U.S. show marked decreases following the eruption of Huaynaputina (Briffa *et al.* 1992; Biondi *et al.* 1999), and summer temperatures in the year 1601 CE were the lowest reconstructed by Briffa *et al.* (1992). At the FTL site, the Huaynaputina eruption is marked by a latewood 1601 frost ring in mature whitebark pine trees (Table 4.3) and by the third most severe narrow ring (1601 CE) in Engelmann spruce (Table 4.4). The 1601 frost ring was identified in other studies of whitebark pine (Kipfmueller 2003; Larson *et al.* 2009). While a severe drought year did occur during the year of the Huaynaputina eruption (-3.674 PDSI), the combined occurrence of a frost ring and a narrow ring, in addition to tree-ring and ice core evidence of a global volcanic event in 1600 (Table 4.3) support findings that 1601 CE was anomalously cold at the FTL site.

Another event that has been well-documented by tree-ring studies in western North America occurred in 1640/1641, but the potential cause is less clear. A 1640/1641 CE event is reflected by the third most negative density year (1641 CE) recorded by both Jones *et al.* (1995) and Briffa *et al.* (1998), and by negative density values in records from five of the 13 northern treeline sites studied by D'Arrigo and Jacoby (1999). As with the 1600 CE eruption of Huaynaputina, a 1640 CE event is marked by narrow ring widths in Sierra Nevada foxtail pines (Scuderi 1990), and by frost rings in bristlecone pine (LaMarche and Hirschboeck 1984; Salzer and Hughes 2007). Reconstructed summer temperatures for 1641 CE are some of the coldest in California (Briffa *et al.* 1992) and east-central Idaho (Biondi *et al.* 1999). Extreme growth in 1641 CE has been attributed to a cluster of eruptions from 1640–1641 CE: Komagatake, Parker, and Llaima (Chile) (Jones *et al.* 1995; D'Arrigo and Jacoby 1999). Other reports have included an additional eruption at Adiska (Indonesia) in 1641 CE (Scuderi 1990). It appears that a cluster of volcanic eruptions is most likely responsible for tree-ring anomalies in 1641 CE. At the FTL site, this cluster of eruptions is represented by a latewood 1641 frost ring in mature whitebark pine (Table 4.3), although with a relatively low annual relative frequency, as well as by the most extreme narrow ring in Engelmann spruce (Table 4.4). Of the frost ring years at FTL, 1641 CE is associated with the second most commonly identified ice core signal in both hemispheres, behind 1601 CE (Tables 4.2 and 4.3).

In contrast to the explosive eruptions of Huaynaputina in 1600 CE and Parker and others in 1640/1641 CE, the eruption of Agung, Bali in 1963–1964 CE has been less commonly reported by tree-ring studies, although a 1965 frost ring in bristlecone pine was reported in several studies (LaMarche and Hirschboeck 1984; Brunstein 1996; Salzer and Hughes 2007). The year does not seem to be associated with negative ring-width or MXD values in these studies, despite recorded northern hemisphere cooling following the eruption (Hansen *et al.* 1978; Rampino and Self 1982; Mann *et al.* 2012). At FTL, the eruption of Agung is indicated by a notable latewood frost ring in 1965 CE (Figure 4.1, Table 4.3) and a narrow ring in 1966 CE (Table 4.4). The 1965 frost ring was the most commonly noted volcanic indicator for the FTL site (Table 4.3). Unlike with the 1601 and 1641 CE frost rings at the FTL site, instrumental data available for 1965 CE allowed us to compare the 1965 frost ring with monthly average temperature data downloaded for the National Center for Environmental Information (NCEI) climate divisional data for the Yellowstone Drainage region of northwest Wyoming (NCEI 2018). Based on instrumental data from 1895–2017, the Yellowstone Drainage region experiences only five months with average temperatures above 4°C (May–September). Based on our observations of late-lying snowpack in June, and of the beginning of growth ring formation in July, growing season at FTL is likely only three to four months long, culminating in September. The average September temperature for the instrumental period 1895–2017 CE was 8.69°C, and September 1965 CE was the coldest September during the instrumental period, with an average temperature of 3.72°C, nearly 5°C below average. Unusually cool temperatures at the end of the 1965 CE growing season would have created the conditions necessary to form a latewood frost ring.

The first half of the nineteenth century was dominated by cooler-than-average temperatures in the northern hemisphere, due in large part to combined solar and volcanic forcings (Bradley and Jones 1993, 1995; Crowley 2000; Mann *et al*. 2008, 2012). Regional temperature reconstructions (Schweingruber *et al*. 1991; Biondi *et al*. 1999) and documented glacial advances (Carrara 1989; Osborn and Gerloff 1997; Marcott *et al*. 2009) in the western U.S. reveal a similar pattern. The major eruptions of Tambora in 1815 CE and Cosigüina, in 1835 CE are credited with causing some of this cooling. Signatures of both of these eruptions have been identified in Greenland and Antarctic Ice Cores (GISP2, BIP, Ant1,2, LD, Table 4.2). The 1815 CE eruption of Tambora is marked by narrow foxtail pine tree rings in the Sierra Nevada (Scuderi 1990), two of the five most extreme density years for Northern Hemisphere tree rings (Briffa *et al*. 1998), and an 1817 frost ring in bristlecone pine (LaMarche and Hirschboeck 1984; Brunstein 1996). The 1835 CE eruption of Cosigüina has been identified by narrow rings and decreased growth in bristlecone pine trees (Salzer and Hughes 2007), extreme density years (Briffa *et al*. 1998; D'Arrigo and Jacoby 1999), and an 1837 frost ring in bristlecone pine trees (LaMarche and Hirschboeck 1984; Brunstein 1996). Despite being at one time discounted as a climate-altering eruption (Self *et al*. 1989), the eruption of Cosigüina is now considered one of the most significant in centuries (Longpré *et al*. 2014).

At the FTL site, early nineteenth century cooling, including the eruptions of Tambora and Cosigüina, is reflected in frost rings, narrow ring years, and growth suppression, especially in whitebark pine (Table 4.4). The growth suppressions during the 1810s and 1830/40s are the most extreme in the FTL whitebark pine chronology despite the application of a high-frequency spline (Figure 4.3). Five of the 59 narrowest whitebark pine tree rings cover the period 1814–1818 CE and eight of the 59 narrowest whitebark pine tree rings cover the period 1838–1845 CE (Table 4.4). In addition, half (6/12) of the narrowest 1% of tree-ring minima for whitebark pine occur in the period 1838–1842 and 1844 CE. Relative growth change analyses of raw ring widths in whitebark pine trees also revealed pointer years and suppression in the years 1814 and 1816 CE and from 1838–1844 CE (Figure 4.4). In FTL Engelmann spruce, both 1814 and 1838 CE are ring-width minima, as are 1844 and 1845 CE (Table 4.4). The year 1838 CE was the only pointer year identified by relative growth change analysis in PointRes for Engelmann spruce tree rings at FTL. The 1838 CE growth ring was the most extreme tree-ring minimum in the whitebark pine chronology and the second most extreme in the Engelmann spruce chronology. In addition to decreased growth, we identified a cluster of frost rings in the 1830s; the most frequently recorded occurred in 1832 CE (Table 4.3). We identified other frost rings in 1836 CE (one tree), 1837 CE (three trees), and 1838 CE (one tree). Other than these frost rings, we did not find other tree-ring anomalies associated with either the Tambora or Cosigüina eruptions, and the 1832 frost ring, while notable, pre-dates the 1835 CE eruption of Cosigüina.

In addition to overall cooler temperatures, other unknown volcanic events may have contributed to decreased growth and frost rings at FTL. The 1810s suppression at FTL began in 1814 CE, prior to the eruption of Tambora in 1815 CE. A cluster of volcanic eruptions may have driven cooling, including the 1812 and 1814 CE eruptions of Soufrière (West Indies) and the 1814 CE eruption of Mayon (Philippines) (Jones *et al*. 1995). In addition, an unknown eruption occurring around 1809 CE is proposed based on ice core evidence (Dai *et al*. 1991, Zielinski 1995; Langway *et al*. 1995), reconstructed summer temperatures in 1810 (Briffa *et al*. 1992), decreased foxtail pine growth in the Sierra Nevada (Scuderi 1990), and negative MXD values (Jones *et al*. 1995; Briffa *et al*. 1998). Regarding frost rings, the 1832 CE frost ring at FTL pre-dates the eruption of Cosigüina in 1835 CE. However, a pre-Cosigüina signal (1830–1832 CE) was identified in ice cores from both poles (Langway *et al*. 1995; Zielinski 1995; Cole-Dai *et al*. 1997). This signal was attributed to either the eruption of Klyuchevskaya Sopka (Russia) in 1829 CE or the eruption of Babuyan Claro (Philippines) in 1831 CE by Zielinski (1995). An 1831 frost ring identified in bristlecone pine trees (LaMarche and Hirschboeck 1984; Brunstein 1996) might also reflect a volcanic event, but associations will likely remain unclear. Regardless, volcanic events, with their contribution to nineteenth century cooling, likely played a role in the extreme tree-ring values and growth suppressions at FTL.

4.3.2 Other FTL Ring Anomalies and Potential Events

We identified other ring anomalies within whitebark pine and Engelmann spruce tree rings at the FTL site. However, associations between these anomalies and their causes, including volcanic forcings, are less certain than those previously described. At the FTL site, a seemingly substantial period of cooling is indicated by a 1329 frost ring and decreased growth in following years (Tables 4.3 and 4.4). The years 1330 and 1335 CE are two of the five most extreme tree-ring minima in whitebark pine, and 1330 CE is the tenth most extreme tree-ring minimum in Engelmann spruce. Relative growth change analyses also revealed narrow years and suppression in whitebark pine during the 1330s CE (Figure 4.4). Decreased growth during the 1330s was the most notable growth suppression detected by our analyses, aside from the narrow rings and growth suppressions of the nineteenth century (Figure 4.3). Reconstructed summer temperatures in Idaho (Biondi *et al*. 1999) and the Canadian Rocky Mountains (Luckman *et al*. 1997; Luckman and Wilson 2005) indicate some regional cooling, although a study in the Sierra Nevada (Graumlich 1993) detected warmer temperatures during the mid to latter half of the fourteenth century. Reconstructed PDSI values for the western U.S. (Cook *et al*. 2010) indicate wet conditions for the region during the 1330s (Figure 4.3), making it unlikely that drought is a cause of the suppression. Beyond signals in the GISP2 and BIP ice cores (Table 4.2), we found little other evidence of a 1330s CE volcanic event, although a possible attribution could be to the fourteenth century eruption of Cerro Bravo, Colombia, as reported by Zielinski (1995) for a 1329 GISP2 ice core signal. While the combination of a frost ring with suppressed growth indicates cooler temperatures at the FTL site, the cause remains uncertain.

The 1452 CE eruption of Kuwae, considered the most explosive of the fifteenth century (Robin *et al*. 1994; Briffa *et al*. 1998), may be represented at FTL by a ring width minimum (4th extreme) and pointer year in the year 1458 CE (Figures 4.3 and 4.4), which corresponds with ice core signals from both poles (Table 4.4). However, a majority of the tree-ring evidence for the 1452 CE eruption is found in a notable 1453 frost ring in bristlecone pine (LaMarche and Hirschboeck 1984; Brunstein 1996; Salzer and Hughes 2007) and low average MXD values for the northern hemisphere in 1453 CE (Briffa *et al*. 1998). A 1458 CE recording of the 1452 CE eruption of Kuwae would indicate a substantial six-year lag at the FTL site, which we did not find for eruptions and growth effects in 1601, 1641, 1815, 1835, and 1963 CE. However, more recent ice core and related research (Gao *et al*. 2006; Sigl *et al*. 2014; Esper *et al*. 2017) has suggested re-dating of the Kuwae eruption to 1458 CE. This later date would better correspond with tree-ring evidence at the FTL site, but not with previous work at other sites (LaMarche and Hirschboeck 1984; Brunstein 1996; Briffa *et al*. 1998; Salzer and Hughes 2007); tree-ring associations with the Kuwae eruption await confirmation of the eruption date.

Along with the growth suppressions of the 1810s and 1830s/40s at FTL, two additional periods, 1883–1884 and 1915–1918 CE, form the four major suppressions of the last two centuries (Figure 4.3). These periods are associated with ice core signals for the 1883 CE eruption of Krakatoa and the 1912 CE eruption of Katmai, Alaska (Table 4.4). We observed narrow growth years for 1883 and 1884 CE in both whitebark pine and Engelmann spruce (Table 4.4). The year 1883 CE was the 11th narrowest ring in whitebark pine and the sixth narrowest ring in Engelmann spruce. We only observed growth suppression for the 1915–1918 CE period in whitebark pine, and recorded 1917 CE as the narrowest of this period (Table 4.4).

4.3.3 Additional Information from the Frost Ring Record

Overall, and despite the correspondence of many FTL frost rings with ice core evidence, we cannot determine the causes for many of the remaining FTL frost rings. Only one frost ring (1274 CE) corresponds with ice core signals from both poles (Table 4.3). While the 1880 frost ring appears to correspond with multiple ice core records based on our criterion of ± 5 years, many of those signals most likely represent the 1883 CE eruption of Krakatoa. Only one of the ice core signals associated with an event in 1880 (Table 4.3) was assigned a pre-Krakatoa date of 1881 CE. If this is a true event, it is likely obscured by the signals left by Krakatoa in other ice cores. Only two frost ring years (1472 and 1725 CE) are potentially associated with known volcanic eruptions of Sakurajima, Japan in 1471 and Krafla, Iceland during the period 1724–30 CE, but these associations are tentative (Scuderi 1990; Briffa *et al.* 1998). Of the two, the year 1725 CE was marked by a narrow ring in Sierra Nevada foxtail pines (Scuderi 1990), a frost ring in bristlecone pines (Brunstein 1996; Salzer and Hughes 2007), and by the 15th most extreme MXD year reported by Jones *et al.* (1995). The year was one of the five coldest based on summer temperature reconstructions for the western U.S. (Briffa *et al.* 1992).

Further study of the latewood frost rings at FTL might provide more climate information. First, all of the frost rings included in the frost-ring chronology are latewood frost rings (Table 4.3). Latewood frost rings indicate sudden and severe cooling at the end of the growing season, and in the case of FTL whitebark pine, they likely signal a relatively sudden end to the growing season. Growing-season length is one of the dominant factors influencing whitebark pine growth (Weaver 2001). Volcanic cooling leading to unusually cold fall temperatures, as seen with the 1965 CE frost ring at FTL, can cause latewood frost damage. Second, many of the frost rings at FTL occurred in mature trees (Table 4.3). Because frost rings in mature trees would only form from more extreme events (Schweingruber 2007; Payette *et al.* 2010), we suggest that many of the frost rings at FTL represent particularly strong cooling events caused by volcanic eruptions (LaMarche and Hirschboeck 1984; Payette *et al.* 2010).

Species-specific differences in bark thickness may also play a role in the likelihood of frost-ring formation regardless of age. At FTL, frost rings were more common in whitebark pine trees than in Engelmann spruce trees. We observed only a few frost rings in Engelmann spruce, and these were concentrated in the first few years of growth. SEA of whitebark pine growth during and following a frost ring year indicated average growth during the frost ring year, followed by a negative year and then a recovery year (Figure 4.5). On the other hand, SEA of Engelmann spruce growth around frost-ring years indicates decreased growth during the frost-ring year (Figure 4.5). In other words, frost events in whitebark pine correspond with average growth in the species but narrow rings in Engelmann spruce. Aside from the influence of drought, discussed below, this relationship indicates that whitebark pine is more resistant to cold temperatures but less resistant to frost damage, most likely because of thinner bark. Frost rings are also more likely in wider rings (Schweingruber 2007; Payette *et al*. 2010). The tendency of frost rings to form in average to above average growth years may explain the absence of frost rings during the 1814–1818 CE period of growth suppression in FTL whitebark pine, and especially during the severe 1838–1845 CE period. Frost rings may not have formed because conditions were already limiting, or they may have been obscured by extreme and resinous suppression. The formation of a latewood frost ring suggests that cooling occurred towards the end of the growing season, which may indicate that Engelmann spruce trees, like whitebark pine, simply experienced a relatively abrupt end to growth, signaled by a narrow ring in spruce and a latewood frost ring in pine. For both species, frost events do not appear to lead to sustained growth suppression (Figure 4.5). While whitebark pine trees tended to experience negative growth in the year following a frost ring, this was followed by a positive growth year. For example, the 1603 CE ring in whitebark pine, formed two years after the 1601 frost ring and three years after the volcanic event at Huaynaputina, was the widest in the 1175-year record. While Engelmann spruce trees did not experience above average growth per se following frost years, growth was not significantly reduced.

4.3.4 The Influence of Drought at FTL

While frost rings are indicative of cooler temperatures (Scuderi 1990; Bailey and McAneney 2015), growth suppression can also result from drier conditions. Overall, drought years (≥ –3.00 PDSI) corresponded with few of the tree-ring minima at FTL (Table 4.4). However, a few drought years and/or periods may have served to exaggerate the responses of FTL trees to volcanic cooling. Drier years or periods correspond with or follow many of the suppression periods noted by this study, especially during the last 200 years, but do not exceed the PDSI threshold used in our analysis (Figure 4.3). Despite drier conditions after 1845 CE, whitebark pine growth returned to average after 1846 CE, and suppression during the early 1900s corresponded with a wetter than average period (Figure 4.3). The 1330s CE suppression, as already noted, also corresponded with wetter-than-average conditions (Figure 4.3). Overall, drought years appear to have had little influence on the growth of whitebark pine. SEA of whitebark pine growth during and following drought years revealed no significant response (Figure 4.5). However, for Engelmann spruce, which is less drought tolerant than whitebark pine, we identified a significant negative growth response in the year following a drought year (Figure 4.5). As an example, a signficiant drought year at FTL was 1600 CE (-3.674 PDSI), the same year as the eruption of Huaynaputina, which occurred earlier in the year from February to March. While cold conditions are evident from the 1601 frost ring in FTL whitebark pine, cold and dry conditions combined are likely responsible for the 1601 CE narrow ring in FTL Engelmann spruce. One period of reduced growth, and the only shared by both FTL tree species, 1702–1707 CE, is most likely explained by dry, and potentially cool conditions in the region (Graumlich *et al.* 2003; Luckman and Wilson 2005; Gray *et al.* 2007; Kipfmueller 2008). Overall, historic drought does not appear to have been a major climatic driver of growth in either species, although this may be a consequence of our high-frequency analyses. Further attempts to investigate multi-decadal drivers of growth at FTL will require different detrending methods and analyses.

4.3.5 On Events Absent from the FTL Record

Tree response to volcanic events is not always one-to-one; some major volcanic events may not lead to growth changes, and some growth changes, including frost rings, may not be caused by volcanic cooling (Bailey and McAneney 2015). Certain notable volcanic events appear to be absent from the tree-ring record at FTL: the recorded eruption of Laki, Iceland in 1783 CE and an unknown but well-documented volcanic event around 1259 CE. The 1783 CE eruption of Laki was largely recorded by ice cores and tree rings of the northern hemisphere, leaving records in the GISP2, Crete, GRIP, and DYE ice cores (Crowley *et al.* 1993; Zielinski 1995; Clausen *et al.* 1997), as well as narrow rings and low MXD values within tree-ring records (Scuderi 1990; Briffa *et al.* 1998; D’Arrigo and Jacoby 1999). The unknown 1250s CE eruption, however, left records across the globe, most notably one of the largest sulfate signals found in both Greenland and Antarctic ice cores (Langway *et al.* 1995; Clausen *et al.* 1997). Tree-ring signals from 1257–1260 CE were identified by Scuderi (1990), Brunstein (1996), and Salzer and Hughes (2007). Some have suggested that a large eruption in Mexico led to the large sulfate signal (Palais *et al.* 1992; Zielinski 1995). Others have suggested multiple events, which led to sudden cooling, and perhaps rapid onset of the Little Ice Age (Miller *et al.* 2012). Volcanic influences on climate are complex and influenced by factors such as the sulfur content of eruptions and seasonal timing, as well as by the climate system in place during an eruption (D'Arrigo and Jacoby 1999; Salzer and Hughes 2007; D'Arrigo *et al.* 2013). This leads to complexity in spatial influence, as well as to inconsistent relationships between volcanic eruptions and tree responses, especially within the dynamic context of local and regional climate and other internal and external factors. However, widespread correspondence of findings among both tree-ring and ice core data does point towards a large-scale influence such as a volcanic eruption.

4.4 Summary and Future Work

Our results demonstrate a temporal association between tree-ring characteristics in whitebark pine and Engelmann spruce and explosive volcanic eruptions. We identified tree-ring evidence associated with five volcanic events and periods. At the FTL site, whitebark pine frost rings correspond with the eruptions of Huaynaputina in 1600 CE, Parker and others in 1640/1641 CE, and Agung during 1963–1964 CE. The association of these frost rings with volcanic events is supported by abundant ice core and tree-ring evidence. We also identified tree-ring minima and periods of growth suppression associated with the eruptions of Tambora in 1815 CE, Cosigüina in 1835 CE, and other potential volcanic events that contributed to cooler than average conditions across the western U.S. during the early nineteenth century (Bradley and Jones 1993, 1995; Mann *et al.* 1998; Crowley 2000; Mann *et al.* 2012). At the FTL site, extreme growth suppression occurred during the periods 1814–1818 and 1838–1845 CE, most likely due to additional volcanic forcing on vulnerable trees. Even though we did not identify frost rings associated with these eruptions, we argue that frost rings are less likely in already stressed trees or can be obscured in periods of extreme and resinous suppression. The combination of tree-ring evidence with ice core signals and other tree-ring studies highlights the ability of tree rings in the high plateaus of the Beartooth Mountains to record volcanic events and to thereby provide more information about the spatial extent of past volcanic influences.

We have chosen to highlight only associations between our tree rings series and volcanic events that are supported by multiple lines of evidence. Additional research is necessary to further corroborate temporal associations between tree-ring evidence and volcanic eruptions, and to understand the influence of volcanic cooling events on trees at the FTL site. Additional information may lie in the "other evidence" recorded during our initial analyses. This other evidence mainly comprised (1) abrupt changes in growth from average or wide to narrow rings (as seen in the SEA) and (2) thin latewood (only noted in initial collection of other evidence, compiled in Table 4.3 but not reported in this study). In many cases, these two lines of evidence occurred together. For both whitebark pine and Engelmann spruce, thin latewood may represent years with low MXD values, which would only occasionally be noted with the naked eye. Future study of FTL tree rings should include measurement and analysis of MXD, which has been identified as more reliable than tree-ring width for indicating volcanic cooling because of both stronger summer temperature response and stronger high-frequency response (D'Arrigo *et al.* 1992; D'Arrigo and Jacoby 1999). In addition, future research could examine the timing of frost-ring formation at the seasonal scale. Such research could use instrumental data to investigate how surface temperatures have been and are affected by volcanic forcings, down to the weekly and/or daily level. An example would be a closer examination of how cold September temperatures in particular lead to frost ring formation, as seen with the 1965 CE frost ring at FTL. This would allow for a more detailed understanding of the optimal conditions for frost-ring formation, which would inform past research linking frost rings to volcanic eruptions.

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Appendix

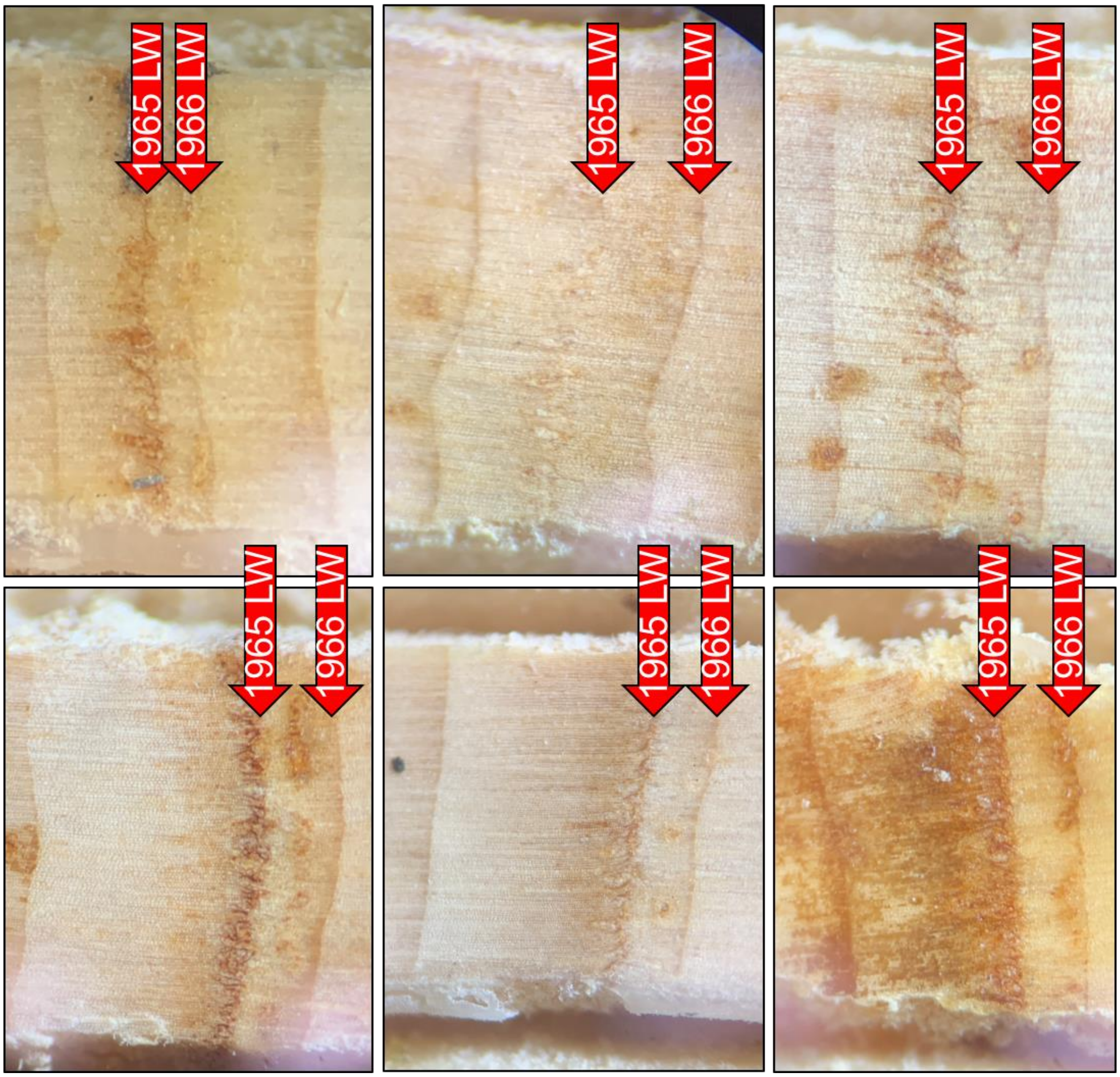

Figure 4.1 Frost Ring Example: Frost ring identified in whitebark pine trees at the FTL site, in this case, multiple variations of a latewood frost ring formed in 1965 CE, which was followed by a narrow ring (confirmed by other samples and crossdating) in 1966 CE. Arrows indicate latewood (LW) boundaries.

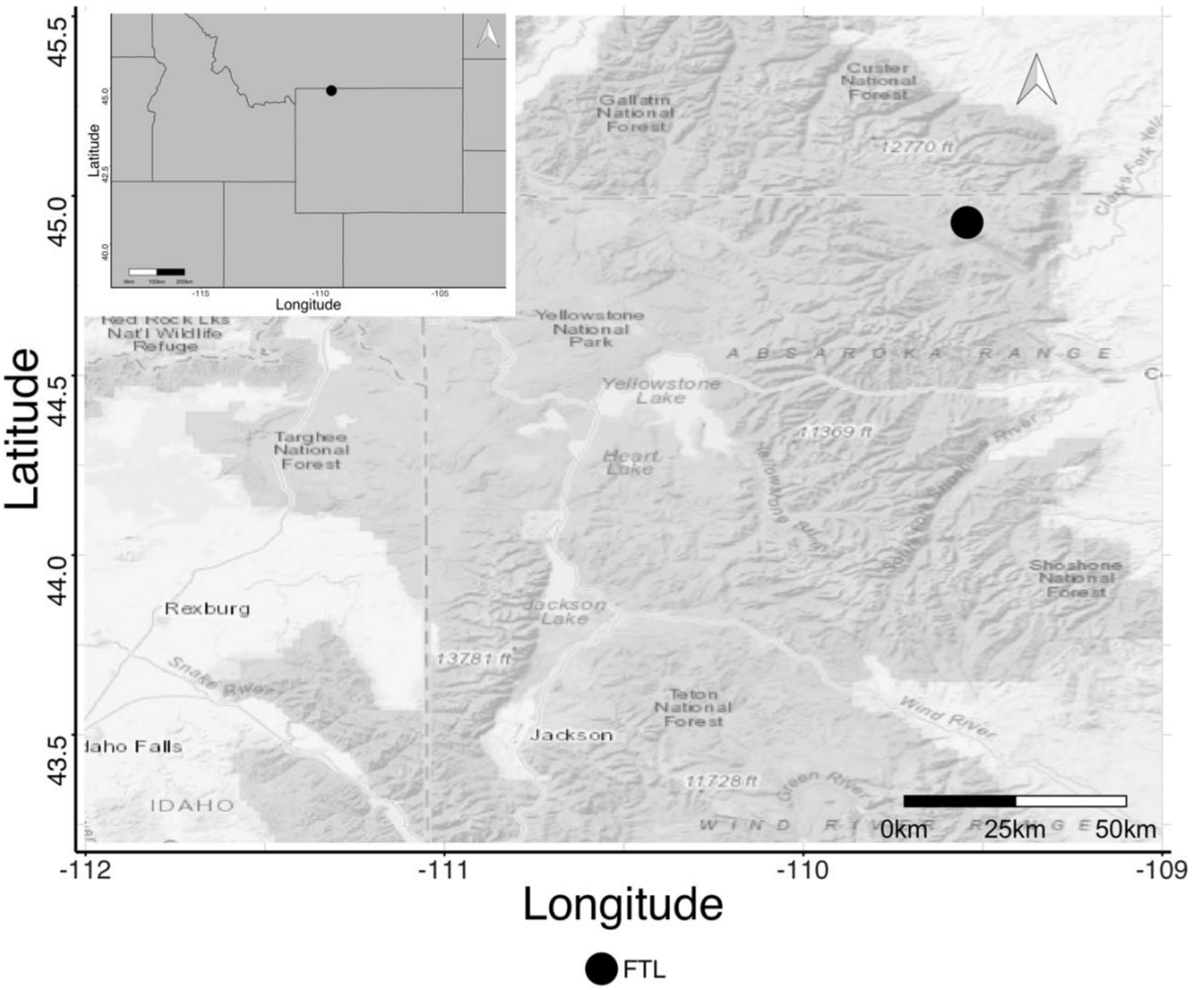

Figure 4.2 FTL Study Site Location: Location of the FTL study site. Source map data and imagery © OpenStreetMap contributors (www.openstreemap.org/copyright).

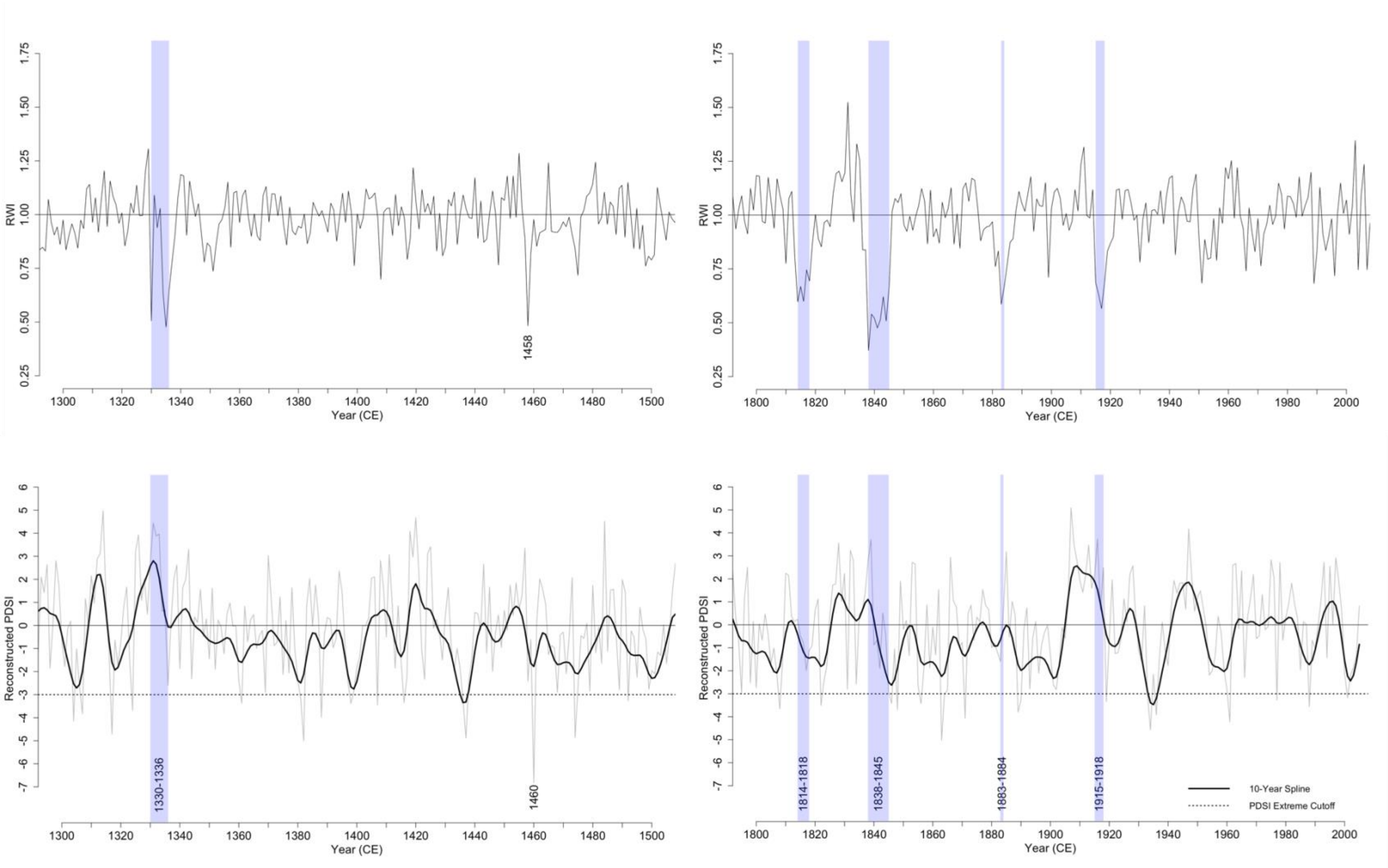

Figure 4.3 Growth Suppression and Drought at FTL: FTL whitebark pine chronology for the periods 1300–1500 CE (top left) and 1800–2000 CE (top right), as compared with reconstructed PDSI for the same periods (bottom), with periods of suppression highlighted.

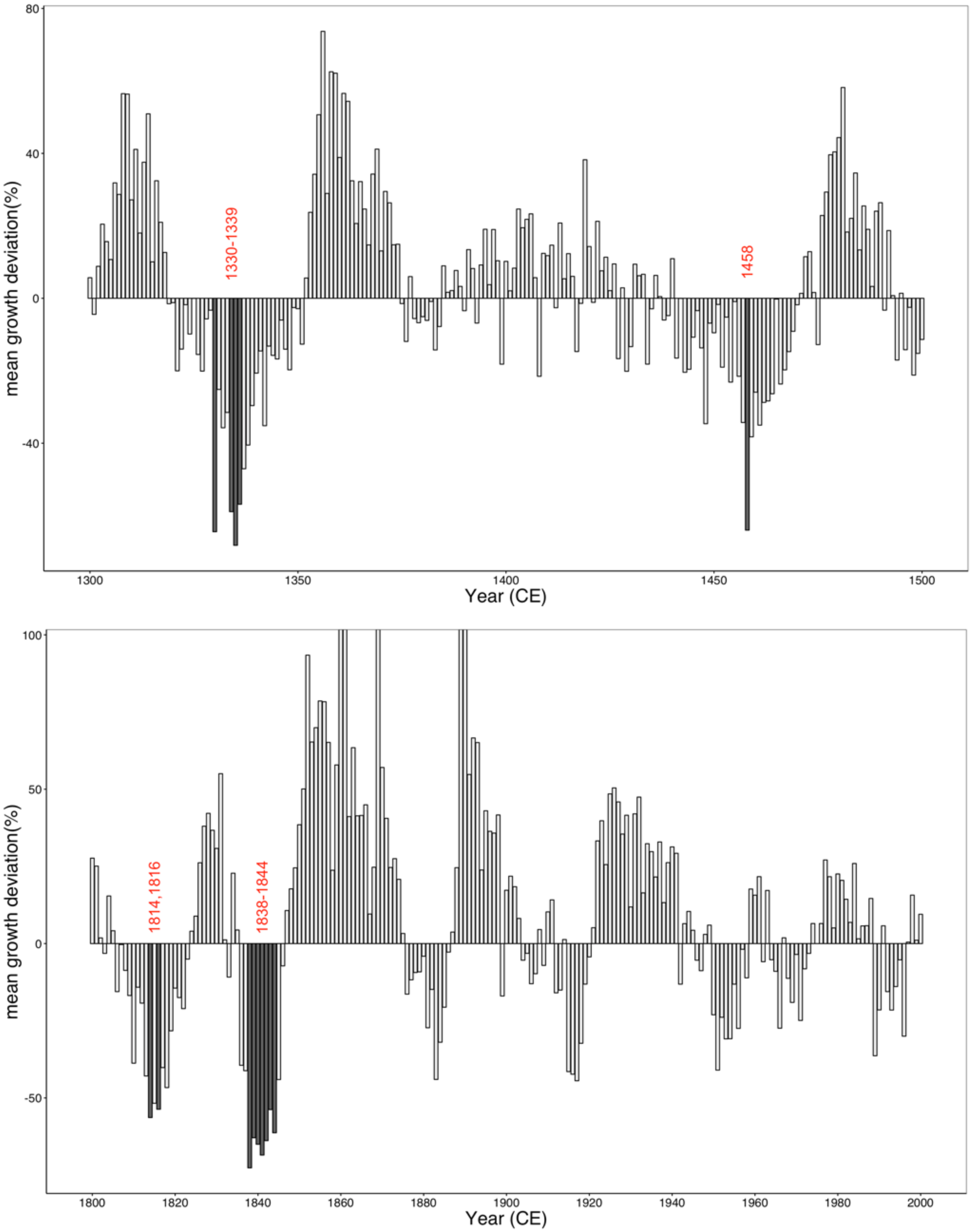

Figure 4.4 Relative Growth Change Analysis: Results from relative growth change analyses of FTL whitebark pine tree rings for the periods 1300–1500 CE and 1800–2000 CE. Darker bars indicate where pointer years met all set criteria.

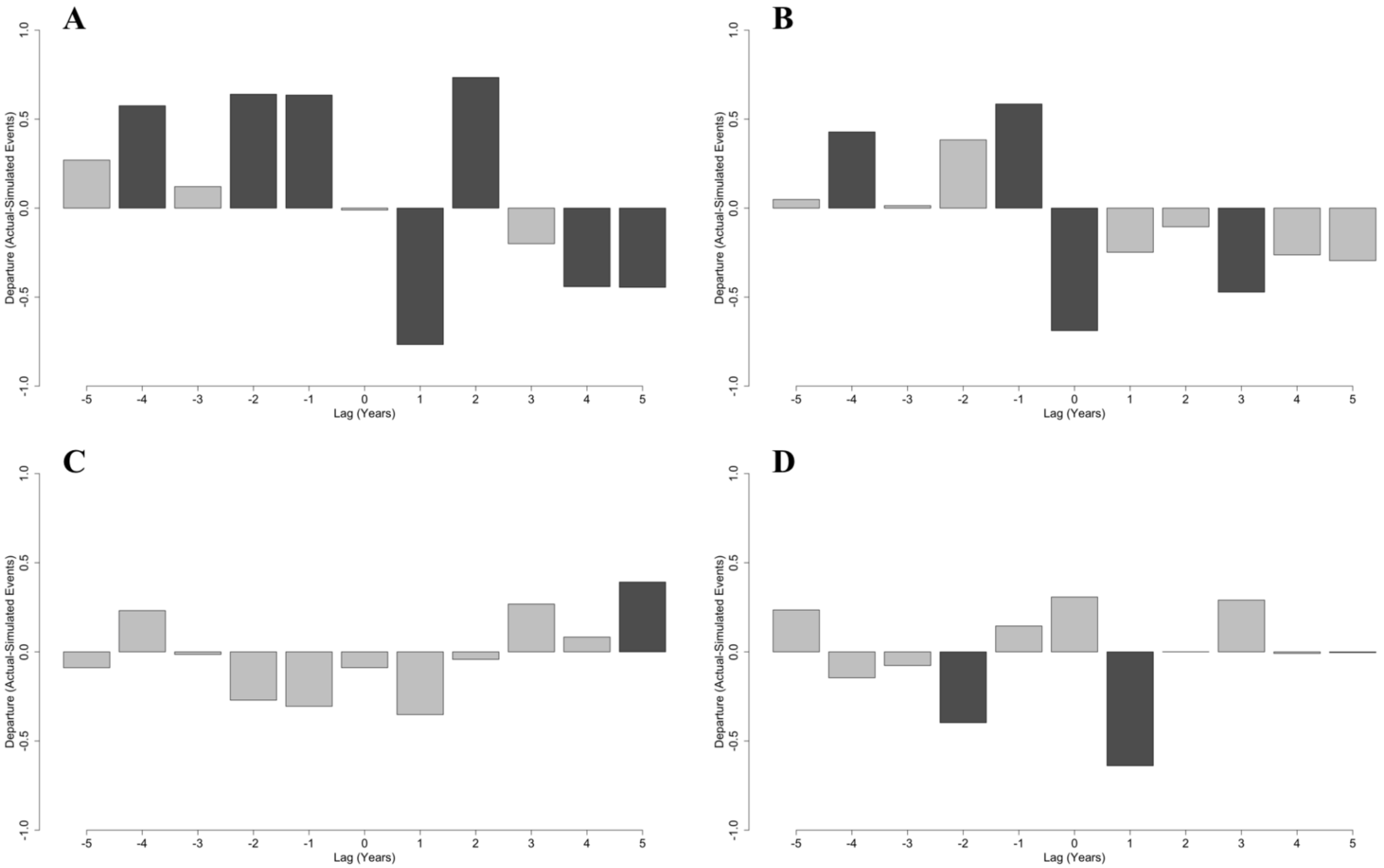

Figure 4.5 Superposed Epoch Analysis (SEA): SEA of tree growth with zero year as frost ring year: (A) whitebark pine and (B) Engelmann spruce, compared with SEA of tree growth with zero year as drought year: (C) whitebark pine and (D) Engelmann spruce.

Table 4.1 FTL Tree-Ring Chronologies: Chronology statistics for the whitebark pine and Engelmann spruce chronologies developed for the FTL site.

Chronology[1]	**Measured Series**	**Total Trees**	**Length (yrs)**	**Mean Length Series (yrs)**	**Average Interseries Correlation**	**Average Mean Sensitivity**	**Segments Tested**	**Segments Flagged**[2]	**Percent Segments Flagged**	**Time Span (CE)**	**Truncated Time Span (CE)**[3]
PIAL	433	226	1308	199.0	0.57	0.23	3395	261	7.69	708–2016	842–2016
PIEN	276	146	1262	178.0	0.63	0.23	1937	70	3.61	754–2016	1167–2016

[1] ITRDB Species Codes, where PIAL = whitebark pine (*Pinus albicaulis* Engelm.) and PIEN = Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)

[2] Indicates tested segments that fell below the statistical threshold for significance at the 0.01 level. These were re-inspected and found to be correctly placed in time.

[3] Truncated based on EPS threshold of 0.85.

Table 4.2 Volcanic Eruption Proxy Records: Other volcanic proxy records (ice core and tree-ring) used for this study.

Ice Core Proxies[1]	**Source**
GISP2 - Greenland	Zielinski 1995
GRIP - Greenland	Clausen *et al*. 1997
DYE - Greenland	Clausen *et al*. 1997
CRETE - Greenland	Crowley *et al*. 1993
BIPOLAR (BIP) - Both Poles	Langway *et al*. 1995
Antarctic1 (AN1)	Budner and Cole-Dai 2003
Antarctic2 (AN2)	Cole-Dai *et al*. 1997
Law Dome (LD) - Antarctica	Plummer *et al*. 2012
Dome C (DC) - Antarctica	Castellano *et al*. 2005
Tree-Ring Proxies[1]	**Source**
West Bristlecone Pine (BC1) Frost Ring	LaMarche and Hirschboeck 1984
Colorado Bristlecone Pine (BC2) Frost Rings	Brunstein 1996
West Bristlecone Pine (BC3) Frost Ring & Minima	Salzer and Hughes 2007
Sierra Nevada Foxtail Pine (FP) Minima	Scuderi 1990
North American Max Latewood Density (NA1)	Jones *et al*. 1995
North American Max Latewood Density (NA2)	D'Arrigo and Jacoby 1999
Northern Hemisphere Mean Density Anomaly (NH)	Briffa *et al*. 1998

[1] With abbreviations used for this study.

Table 4.3 FTL Frost Ring Chronology: Frost ring chronology developed for the FTL site.

Frost Ring Year (CE)	Recorded FR (n)	Recorded OI (n)	Annual Relative Frequency (FR)	Annual Relative Frequency (with OI)	Ring Position	Average No. of Rings to FR	Ice Core Signals[1]	Tree-Ring Proxies[2]
898	2	0	15.38	15.38	LW	13	GISP2, GRIP, DYE	BC3
945	8	6	50.00	87.50	LW	129	GRIP	**BC2**
981	2	5	10.53	36.84	LW	117	Ant1	none
993	1	5	5.26	31.58	LW	136	none	**BC2**
996	2	1	10.53	15.79	LW	83	none	none
1008	2	3	11.11	27.78	LW	220	none	**BC2, BC3**
1049	6	6	30.00	60.00	LW	119	none	none
1066	3	5	15.00	40.00	LW	66	none	**BC2, BC3**
1274	3	0	8.57	8.57	LW	54	BIP, Ant1, LD, DC	BC2, BC3
1329	3	2	8.57	14.29	LW	101	GISP2	**BC2, BC3**
1472	3	1	6.82	9.09	LW	71	GRIP	BC3
1537	10	1	20.40	22.45	LW	150	none	none
1557	6	3	11.76	17.65	LW	131	GRIP, DYE	BC2, **BC3**
1601	17	5	34.00	44.00	LW	180	GISP2, GRIP, CRETE, Ant1,2, LD, DC	**BC1**, **BC3**, FP, NH, NA1, NA2
1641	2	2	5.00	10.00	LW	252	GISP2, GRIP, DYE, CRETE, Ant2, LD	BC1, BC3, FP, NH, NA1, NA2
1725	5	9	13.51	37.84	LW	104	GISP2, CRETE	**BC2**, **BC3**, FP, NA1
1832	16	1	42.11	44.74	LW	99	GISP2, BIP, Ant1,2, LD	**BC1**, **BC2**, BC3
1880	6	0	10.71	10.71	LW	42	BIP, CRETE, Ant2, LD, DC	BC2, BC3, NA1
1965	52	9	37.96	44.53	LW	81	GISP2, CRETE, Ant2, LD, DC	**BC1, BC2, BC3**

[1] ±5 years of ice core signal. See Table 2 for key to abbreviations.

[2] Bold equals exact match to frost ring year, all others ± 1 year. See Table 2 for key to abbreviations.

FR = “Frost Ring” and OI = “Other Injury”

Table 4.4 Tree-Ring Minima: Tree-ring minima (narrowest 5%) from the FTL whitebark pine and Engelmann spruce chronologies.

FTL Whitebark Pine

CE Century	**Year(s)**
9th	847, (*898*)
10th	946*[b], 990, (*945, 981, 993, 996*)
11th	1009*, (*1008, 1049, 1066*)
12th	1118[f], 1120, 1142
13th	1200, 1230[abcdhi], (*1274*)
14th	1330*[a], 1334–1336[ad], 1351[f], (*1329*)
15th	1408[c], 1458[acdfghi], 1475[abci], (*1472*)
16th	1541, (*1537, 1557*)
17th	1612[e], 1618[efg], 1627[egi], 1646[abceg], 1647[abceg], 1663[abcef], 1664[abcef], 1667[abcef], 1680[e], 1681[e] (*1601*, *1641*)
18th	1702–1704, 1755[efi], 1779, 1782[abce], 1791[e], (*1725*)
19th	1814–1818[abcdefghi], 1838–1845[adefgh], 1883[adeghi], 1884[adeghi], 1899
20th	1915–1918[abe], 1951[ae], 1966*[aeghi], 1989, 1996, (*1965*)
21st	none

FTL Engelmann Spruce

CE Century	**Year(s)**
12th	1192[afi]
13th	1204[a], 1223[ad], 1226[abcdhi], 1244, (*1274*)
14th	1321, 1330*[a], 1366, 1383[f], 1393[f], 1399[f], (*1329*)
15th	1408[c], 1417, 1429, 1447[g], (*1472*)
16th	1500, 1505[bcf], 1524, 1596[afgh], (*1537, 1557*)
17th	1601*[abefghi], 1641*[abcegh], 1663[abcef], (*1601*, *1641*)
18th	1704–1707, 1746, 1791[e], (*1725*)
19th	1809[abdfghi], 1814[abcdefghi], 1838[adefgh], 1844[ef], 1845[ef], 1879, 1883[adeghi], 1884[adeghi]
20th	1971[a], 1972[a], 1989, 1992[i], 1993[i]
21st	2004, 2007

*Tree-ring minima ±1 year of frost ring year.
Red years indicate a drought year (≥-–3.00 PDSI)
Frost ring years are in parentheses.
Letters indicate ± 5 year of ice core signal:

[a] GISP2
[b] GRIP
[c] DYE
[d] BIP
[e] CRETE
[f] Ant1
[g] Ant2
[h] LD
[i] DC

CHAPTER FIVE

SUMMARY AND FUTURE WORK

5.1 Summary of Dissertation Research

Long-lived, subalpine tree species like whitebark pine and Engelmann spruce may eventually disappear because of the combination of climate change and exacerbated native and invasive threats. While this loss would entail dire circumstances for mountain ecosystems, it would also result in the irreversible loss of valuable climatological and ecological data. For whitebark pine and other threatened species, these data could assist in ongoing conservation efforts and provide information on potential future effects of ongoing climate change. The overarching purpose of my dissertation research was to develop extended whitebark pine and Engelmann spruce tree-ring chronologies with the potential for use in regional analyses of climate and disturbance. With these newly collected chronologies, I endeavor to address significant gaps in the tree-ring record, especially for whitebark pine in the U.S., for which only 15 chronologies are available in the International Tree-Ring Data Bank (ITRDB). My work is meant to serve as an example of the potential of high-elevation tree species, and especially whitebark pine, to record climate and environmental change, as well as fill a gap in tree-ring data for a keystone subalpine species.

From a high-elevation site in the Beartooth Mountains of Wyoming, I collected hundreds of samples from both living and remnant whitebark pine and Engelmann spruce and developed two millennial-length, tree-ring chronologies for the species using dendrochronological methods. Using information gained from these tree-ring chronologies, I (1) examined environmental change during the late Holocene; (2) evaluated climate drivers of growth and implications for ongoing climate change; and (3) investigated the influence of volcanic cooling events. I hope that my work will serve as a guide for future efforts to collect and analyze data from whitebark pine and other threatened high elevation tree species. I also call for increased contribution of tree-ring data, from whitebark pine especially, but also from other subalpine species, to accessible archives, such as the ITRDB, which will make tree-ring data available for current and future scientists.

5.1.1 Late Holocene Environmental Change

The second chapter of my dissertation represents the origins of my research in the Beartooth Mountains of Wyoming. While conducting other research in the region, I discovered the study site, FTL, and the “ghost forest” that presided there. The abundance of remnant trees at

FTL suggested major ecosystem changes had occurred at the site, and I hypothesized that climate was the likely cause of extensive mortality. Specifically, I hypothesized that the whitebark pine and Engelmann spruce remnant logs at FTL represent the remains of an open woodland that established and thrived during the warmer conditions of the MWP and was killed by a return to cooler conditions and more persistent snowpack during the LIA. Establishment and mortality data from 148 living whitebark pine, 118 living Engelmann spruce, and 106 remnant trees at FTL support the hypothesis. A majority of the remnant trees that I sampled at FTL died during the LIA (45 of 56, 80%), and a majority of the living trees that I sampled at FTL (76% of whitebark pine and 65% of Engelmann spruce) established after the end of the LIA in 1850 CE. These results indicate a climate-caused mortality event at FTL. On the other hand, the establishment and survival of both whitebark pine and Engelmann spruce trees during the MWP suggests that whitebark pine ecosystems may be more robust to warming temperatures than current thought. Perhaps whitebark pines will persist, given successful management of other threats, despite global warming.

5.1.2 Climate Drivers of Growth

As part of my analyses of establishment and mortality at FTL, I developed millennial-length tree-ring chronologies of whitebark pine and Engelmann spruce. The objective of my third chapter was to evaluate the potential of paleoclimate reconstruction using these chronologies. I used correlation analyses to test for relationships between tree growth and monthly and seasonal aggregates of temperature and moisture variables, and then used evolutionary analyses to determine if these relationships remained stable through the instrumental period 1896–2016 CE. Significant, and in some cases temporally stable, climate-growth relationships indicated that growing season length and temperature have been the most important climate drivers of whitebark pine and Engelmann spruce growth at FTL site. However, I also identified emerging (in whitebark pine) and strengthening (in Engelmann spruce) responses to previous year drought stress, which suggest that the moisture conditions that accompany warming will greatly influence future growth. Overall, strong and temporally stable climate-growth relationships in Engelmann spruce indicated that the associated tree-ring chronology may provide reliable predictors for climate reconstruction. Based on emerging responses in whitebark pine, the associated tree-ring chronology is unlikely to provide reliable climate prediction, but has value in understanding stand and disturbance history.

5.1.3 Tree-Ring Evidence of Volcanic Cooling

During inspection and dating of remnant wood, I discovered synchronous frost damage among samples in the year 1601 CE. This frost ring is well-documented by tree-ring studies in Western North America and is known to document extreme cooling following the 1600 CE eruption of the volcano Huaynaputina in Peru. At first, the 1601 CE frost ring simply served as an important marker for the crossdating of FTL remnant samples. However, I soon started to identify other synchronous frost rings. The objective of my fourth chapter was to investigate the potential of the FTL whitebark pine and Engelmann spruce tree-ring chronologies to record volcanic cooling events. I combined frost ring, tree-ring minima (narrow rings), and evidence of suppressed growth in the FTL chronologies with climate records and ice core and tree-ring proxy data to identify times when multiple lines of evidence supported volcanic cooling. I identified whitebark pine frost rings associated with the eruptions of Huaynaputina, Peru in 1600 CE, Parker, Philippines and others in 1640/1641 CE, and Agung, Bali in 1963–1964 CE; tree-ring minima and periods of growth suppression associated with the eruptions of Tambora, Indonesia in 1815 CE and Cosigüina, Nicaragua in 1835 CE; and other potential volcanic events during the early nineteenth century that contributed, along with solar forcing, to cooler than average conditions across the western U.S. The combination of tree-ring evidence with ice core signals and other tree-ring studies highlights the potential of tree rings in the Beartooth Mountains to record volcanic events and to thereby better document the spatial extent of past volcanic influences.

5.1.4 Millennial-Length Tree-Ring Chronologies

The chronologies that I produced for my dissertation research extend the published (available on the ITRDB) whitebark pine record by nearly 200 years and the published Engelmann spruce record by over 600 years for the Greater Yellowstone Ecosystem (GYE). While the final whitebark pine chronology will not be the oldest published on the ITRDB, it will be the oldest published for the GYE. On the other hand, the final Engelmann spruce chronology will be the only published chronology for the species that predates 1000 CE in the United States.

Poor sample depth prior to 1000 CE currently may limit the use of this chronology for climatological study past that point, but through future research with additional remnant samples, I hope to increase sample depth and extend the chronologies for both species back even further. The tree-ring chronologies that I produced for this dissertation represent the majority of the remnant samples collected from FTL, but additional samples have been archived for further study. In addition to simply extending tree-ring records, findings from this study also demonstrate the value of remnant wood for developing long chronologies. Data for most years in the final chronologies came from remnant wood, not living trees; the remnant wood more than doubled the length of the final chronology, which would have originally been limited by dramatic decreases in sample depth past 1800 CE. At the FTL site, living, old whitebark pine and Engelmann spruce were relatively rare on the landscape, a consequence of high mortality during the LIA. Tree-ring dating of remnant wood made it possible to extend the chronologies to millennial lengths.

5.2 Lessons Learned and Other Observations

5.2.1 On Field Identification of the Oldest Samples

The field work to collect samples for this study took place over four summers, and each trip, combined with results from processing and laboratory analysis, improved my ability to identify the oldest samples in the field. Initially, I worked under the assumption that the smallest pieces of wood, which I noted as "true" remnants (no longer bearing any resemblance to a complete tree, *i.e.* highly decayed, no trunk) would be the oldest samples collected. Following this assumption improved my chances of identifying older samples, as 45% of the samples labeled as "true" remnants predated 1000 CE compared to only 13% of others. But the classification was not always a reliable indicator of age, leading me to increasingly rely on other external indicators of age, such as sculpting (from wind/ice abrasion) and burial (sometimes embedded in other living trees). Ultimately, internal evidence of age proved most useful. Once cut, resin saturation became a reliable indicator of advanced age for whitebark pine. A high resin concentration provides resistance to decay, meaning that remnants that are saturated with resin are more likely to persist on the landscape. Nearly all remnant samples contained resin, which in combination with climate likely fostered persistence of remnants at the FTL site, but some were completely saturated. Of the 17 pre-1000 CE whitebark pine samples processed, nine were completely saturated with resin (53%), four contained higher than average amounts of resin (24%), and four were not particularly resinous (24%). The characteristic of resin saturation was not an infallible indicator, but using it increased my chances of identifying older samples.

Eventually, and for the purposes of chronology building only, the combination of external and internal features became the focus of my efforts to find samples predating 1000 CE. While I cannot report these findings with quantitative support, I believe that the indicators described will assist future efforts to identify and collect whitebark pine remnant samples with the ability to considerably extend tree-ring chronologies. As with all studies, however, researchers should be careful not to bias their data through preferential sampling of older samples. All attempts to locate and sample the oldest remnants were guided by a secondary objective to extend my tree-ring chronologies, and with the understanding that the data collected would not inform my original hypotheses. However, the discovery of synchronous disturbances (frost rings, fire scars) in even my oldest samples demonstrated the overall value of long chronologies to studies of both climate and ecology.

5.2.2 On the Collection of Remnant Wood

While I emphasize the inclusion of remnant wood for chronology extension, especially for whitebark pine, I also recognize the limitations of sampling and dating dead wood. First, remnant wood collection requires additional, heavy field gear (*e.g.* chainsaw, PPE, fuel, bar oil) that necessitates a certain skillset (chainsaw use and safety training). In wilderness areas, remnant wood must be collected with handsaws, which requires lighter (though bulkier) equipment, but more time and manpower. Remnant wood sampling also results in much larger samples (cross sections instead of cores), which must be carried out of the field and often, shipped to a lab. I collected hundreds of samples from the FTL site, and shipping costs were in the thousands of dollars. Once returned to the lab, these samples must be stored, and then sanded, which will likely require additional time and lab space. Once measured, the tree-rings in remnant samples may not date against local living trees or even against reference chronologies. Remnant wood represents a gamble in that it may be too old to date with tree-ring methods or available reference chronologies.

5.2.3 On the Dating of Remnant Whitebark Pine

For the samples from the FTL site, initial dating proved difficult, mainly because of low inter-annual variability in tree rings (relative complacency outside of significant marker years) and disturbance (periods of intense suppression, often obscured by resin), both of which were listed as complications in work with whitebark pine (St. George and Luckman 2001; Wilson and Luckman 2003; Larocque and Smith 2005; Youngblut and Luckman 2013). Important marker years included significantly narrow rings (> 2.0 standard deviations), but also included event years, such as the aforementioned 1601 frost ring. However, significantly narrow marker rings were sometimes over 100 years apart. This made it unlikely that samples could be initially dated from a subset of total rings (*e.g.* inner or outer 100–150 rings), a common method for initial dating, and required that I measure all of the tree rings on a sample. Again, this required additional time during the early stages of this study. However, once an initial dataset was complete, sample dating progressed much more quickly. At least for the purposes of crossdating, the problem of complacency in whitebark pine tree rings was overcome by the dating of all rings on samples with at least 300 to 400 rings. It was also aided by the fact that one of the initially dated samples, FTL010, contained over 800 rings. However, this sample was unusual and the average series length for the remnant samples was 340 years. Such potential issues with crossdating, along with the described limitations to sampling, processing, and storage, should be considered before initiating work with remnant samples.

5.3 Call to Action

Despite reluctance to take on the challenge of sampling and dating remnant wood, I recommend that labs with the capability to do so encourage students and researchers to initiate work with whitebark pine and other subalpine species. Some of the described limitations can be overcome by proximity, so labs located near whitebark pine ecosystems should consider working with the species if they are not already. While the ghost forest at FTL is in many ways unique, similar sites of preserved remnant trees likely persist, given that the cold and dry sites occupied by whitebark pine are ideal for preservation of remnants. I also recommend that those with unpublished chronologies work to publish them on the ITRDB, so that more reference chronologies will be available across the ranges of whitebark pine and Engelmann spruce. Following publication, I intend to submit the FTL chronologies to the ITRDB. Despite discussions of being, or not being the oldest published chronologies on the data base, I do not seek to hold “records” but rather to encourage other tree-ring scientists to break them, to publish chronologies that they have already, or to actively seek out whitebark pine sites that may continue to extend chronologies further back in time. Most of all, I submit my work as a call to action. We need to collect and analyze data from whitebark pine and other threatened species before important climatological and ecological records are lost forever.

5.4 Future Work

5.4.1 New and Updated Whitebark Pine Chronologies

The need to capture data from a disappearing foundation species has been expressed by Hessl and Pederson (2012) who proposed the Hemlock Legacy Project (HeLP) to inspire increased collection from old growth eastern (*Tsuga Canadensis* L.) and Carolina hemlock (*Tsuga caroliniana* Engelm.) trees, which are being devastated by the invasive hemlock wooly adelgid (*Adelges tsugae*). In a similar manner, I call for increased contribution of tree-ring data from whitebark pine and other subalpine species to accessible archives such as the ITRDB, which will make tree-ring data available for current and future scientists. With this dissertation work, I extended tree-ring chronologies for the GYE by 200–600 years. With the inclusion of more remnants and the identification of other similar sites, we can extend these and other chronologies back even further. As part of my future research efforts, I will work to develop a project similar to that of Hessl and Pederson (2012), to emphasize the collection of tree-ring data from living and remnant whitebark pine.

As a part of continued work with remnant wood, I also hope to quantify some of the observations described earlier, which were made in an attempt to identify the oldest remnant samples. For the most part in the tree-ring community, techniques for estimating the ages of remnant samples in the field have been qualitatively documented for specific study sites and anecdotally shared. Work to quantify and use discrete decay classes has been performed largely to investigate the influence of woody debris decay on nutrient cycling in forest ecosystems (Harmon *et al*. 1986; Pyle and Brown 1998; Brais and Drouin 2012; Strukelj *et al*. 2013; Alexander *et al*. 2018). Overall, studies relating year of death to decay have found variability and inconsistency (Daniels *et al*. 1997; Alexander *et al*. 2018). More research, especially in the tree-ring community, is necessary to better relate rates of decay to time since death, but the determination of decay classes for sampling and crossdating prioritization may remain study and site specific, developed by researchers who conduct research at the same site for multiple years.

5.4.2 Evidence of Other Disturbances at FTL

Aside from the discovery of frost rings and growth suppression in the FTL tree-ring chronologies, I also found evidence of other climatological and ecological influences on growth. Within living and remnant trees at FTL, I identified (1) traumatic resin ducts (TRDs) in Engelmann spruce, which indicate defoliation or injury to the tree (McKay *et al*. 2003; Stoffel 2008; Arbellay *et al*. 2014; DeRose *et al*. 2017); (2) resin pockets/scars (in remnants) and blue stain fungi (mostly in living trees) in whitebark pine, which indicate mountain pine beetle (Reid *et al*. 1967; Whitney 1971; Solheim 1995; Arbellay *et al*. 2017); and (3) fire scars in both tree species. In some cases, this evidence supplied important marker rings for dating of additional samples that supported the statistical dating of remnant samples. Further study is necessary to analyze the synchrony of these disturbances and likely causes.

5.4.3 Microclimates, Topography, and Facilitation

Facilitation and microclimates have been shown to play an important role in conifer establishment and survival at high elevations (Resler *et al*. 2005; Elliott 2011; Pyatt *et al*. 2016), and topography is known to be an important local driver of treeline migration (Holtmeier and Broll 2005; Elsen and Tingley 2015). Whitebark pine is considered a keystone species because of its role as a facilitator in the development of tree communities in harsh, high-elevation conditions (Resler *et al*. 2014; Tomback *et al*. 2014). As the first tree to establish in harsh, high-elevation conditions, whitebark pine improves site conditions for later arrivals by providing shade, shelter, and wind protection (Callaway 1998; MacFarlane *et al*. 2013; Tomback *et al*. 2016). As a part of future work, I am interested in investigating the influence of these complex interactions on the formation of "tree islands" at FTL, on tree-by-tree climate response, and on tree survival during changing climate conditions. At the FTL site, some of the living whitebark pine and Engelmann spruce trees survived the LIA, most likely due to topographic (aspect, slope, micro-topography) and/or microclimate (facilitation) factors that deserve attention.

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