PALEOECOLOGICAL RECONSTRUCTION OF A MODERN WHITEBARK PINE (*PINUS ALBICAULIS*) POPULATION IN GRAND TETON NATIONAL PARK, WY

by

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B.S., Pittsburg State University, 2012

A THESIS

submitted in partial fulfillment of the requirements for the degree

MASTER OF ARTS

Department of Geography
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2014

Approved by:

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Abstract

Whitebark pine (*Pinus albicaulis)* is a critically threatened North American conifer. In modern times, it has experienced a significant decline in population due to pine beetle infestations, blister rust infections, fire suppression, and climate change. While climate, fire, and vegetation are strongly linked on regional and global scales, the relative roles of these three factors are not well-documented during the Holocene in high elevation mountain sites of North America. Recent anthropogenic changes in climate and fire management practices are underway, but the potential responses of subalpine vegetation to these environmental changes remain relatively unknown. Here, I documented the paleoecology of a watershed surrounding an unnamed, high-altitude pond containing a large number of whitebark pine trees located at 2805m elevation in Grand Teton National Park, U.S.A. Using a 1.5 meter lacustrine sediment core collected in 2010, I generated a Holocene-scale fire and vegetation record using fossil pollen, charcoal, and macrofossils preserved within the core. I also conducted a dendrochronological study of the current stand of whitebark pine in the watershed to determine both approximate dates of establishment and responses to past climate change of this modern stand.

Sedimentary charcoal data indicate significant variability in both fire frequency and fire intensity during the Holocene. The fire regime observed in the past 1000 years is seemingly unprecedented at this site, with lower fire frequency and higher fire intensity than any other time during the Holocene. Sedimentary pollen data suggest the study site has been primarily dominated by whitebark pine until the last 1000 years, with brief periods of vegetation dominated by non-arboreal taxa that indicate the presence of either successional dynamics or shifts in treeline location. Ages of individual living whitebark pine trees average 365 years, and

dendrochronology data suggest that ring widths of the current stand have been declining since 1991. Statistical analyses of PRISM climate data with ring width data suggest that this decrease in annual growth is likely the result of decreased growing season temperature ranges driven by a warming climate. While this stand of whitebark pine is threatened by both warming climate and fire suppression, there is the potential for low-intensity prescribed burns to play a role in conservation and restoration management plans for this threatened conifer.

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Acknowledgements

This work would not have been possible without the guidance of several people. First, I wish to thank Kendra McLauchlan for her unwavering support, encouragement, and mentorship. Her constant enthusiasm for science has challenged me to become a better researcher. I also wish to thank my committee members, John Harrington and Jack Oviatt, for their helpful input and guidance on this work. This work would not have been possible without the help of Sarah Spaulding, who provided the sediment core used in this study. Additionally, I would like to acknowledge the individuals at LacCore, who prepared and processed pollen samples. This research and associated fieldwork would not have been possible without funding provided by the Department of Geography at Kansas State University in the form of a GGRG and R.B. Marston Scholarship.

I would like to express my sincere gratitude to members of the Paleoenvironmental Lab at Kansas State University, past and present, for their advice, assistance, and emotional support. In particular, I would like to thank our undergraduate lab technician Scott McConaghy for his hard work and, specifically, for spending countless hours at the microscope; without his help, this project would not have been possible. I would also like to thank Scott for allowing me to be a mentor to him, though I suspect he has taught me more than I could have ever taught him. I also would like to thank Laci Gerhart-Barley and Claire Ruffing for their assistance with fieldwork and bear-evasion tactics.

Lastly, I would like to thank my family, friends, and loved ones who have been unconditionally supportive during this process. While my love of trees, mud, and fire has not always made sense to them, they have always been the best support system anyone could ask for.

Dedication

This thesis is dedicated to my undergraduate mentors, Joe Arruda, Peter Chung, and Catherine Hooey, for challenging, guiding, and supporting me from the beginning.

Chapter 1 - Introduction

Subalpine forests of the western United States are experiencing a variety of stresses, including changes in fire regimes, droughts, and beetle outbreaks (Mohat et al. 2008). One of the most vulnerable tree species seems to be whitebark pine (*Pinus albicaulis*; hereafter 'whitebark pine'), a high-elevation keystone species that serves to preserve animal and water resources in the Rocky Mountains (Miller et al. 2012). This severely-threatened high-elevation conifer historically occupied around 10-15% of forests in the western United States (Keane 2001). However, it has been suggested that whitebark pine has experienced as much as a 90% decrease in population throughout its native range (Mohatt et al. 2008). Whitebark pine is "functionally extinct in 1/3 of its range" (Tomback et al. 2001; Schrag et al. 2008) due to a combination of climate change, anthropogenic fire suppression, and epidemics of pine beetle and blister rust infections (Schrag et al. 2008). Disentangling the interactions and effects of these multiple, slow-acting threats represents a unique challenge which requires a more thorough understanding of long-term dynamics of whitebark pine ecosystems.

Whitebark pine is a long-lived, early seral species found only at high elevation sites occurring in subalpine ecosystems of the Northern Rocky and Cascade Mountains in the United States (Keane and Parsons, 2010). Whitebark pine is considered a keystone species of subalpine forest ecosystems for three reasons. First, more than 100 animal species, including the endangered grizzly bear (*Ursus arctos horribilis*), depend on its high-calorie, fatty seeds for survival (Felicetti et al. 2003). If whitebark pine should vanish from its native range, endangered animal species would be forced to lower elevations in search of food, thus increasing the potential for humans and human-caused casualties. Second, the presence of whitebark pine in subalpine ecosystems helps to slow the melting of accumulated wintertime snowpack, in turn reducing the threat of down-slope flooding events. And third, by slowing the melt of snowpack, whitebark pine provides a high quality source of water to plants and animals during the summer melting season (Keane and Parsons 2010). Whitebark pine is not a single-function species. The species functions simultaneously as a food, water, and flood-prevention resource. Successful management of this resource translates directly into the successful management of water resources and endangered animal species. Currently, there is not enough data available on the long-term dynamics of whitebark pine ecosystems to effectively manage the species for all functions simultaneously.

Two drivers of modern whitebark pine decline, climate change and changes in fire regime, are slow-acting processes operating at timescales of centuries to millennia. Despite hints that these two ecological controls are affecting whitebark pine populations, little is known about their long-term effects. Given the long lifespan of individual trees, it is important to know how whitebark pine responded to the variable climates during the Holocene and 20th century. Tree-line whitebark pine populations are adapted to function within narrow environmental constraints and are most limited in their geographic distribution by temperature (Schrag et al. 2008). Climate models suggest a 1.5-4.5° C global temperature increase during the next century; a climatic shift more extreme than that associated with the end of the Pleistocene epoch (Romme and Turner 1991). Schrag et al. (2008) have suggested that such a temperature increase would completely remove whitebark pine from its native range in the Greater Yellowstone Area (hereafter, ‘GYA’) and Grant Teton National Park (hereafter, ‘GTNP’), creating the opportunity for competing species such as subalpine fire (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) to invade this ecological niche.

In addition to climate, whitebark pine communities are also sensitive to fire regimes. Whitebark pine is an early-successional species, and must experience regular, mixed-severity fire events to prevent replacement by later-successional species (Keane and Parsons, 2010). Regular fire events favor the survival and dominance of whitebark pine by removing competing, fire-intolerant species from the landscape. Whitebark pine trees are better adapted to high-frequency fire regimes than their fire-intolerant competitors due to their thick bark, deep roots, and thin crowns (Keane 1991). When exposed to high-severity fires, whitebark pine lacks proper defenses and is removed from the ecosystem along with its competitors.

There is some paleoecological information about the long-term dynamics of whitebark pine communities. During the 11,000 year period of glacial retreat following the late-Pinedale glaciations in the GYA and GTNP, climate conditions interacted with elevation to produce dynamic shifts in treeline locations (Whitlock 1993). The role of long-acting processes on subalpine communities was further investigated by Richardson et al. (2002) who found that the past biogeography and distribution of tree-line conifers, specifically whitebark pine, were likely heavily influenced by insolation amounts, climate change and glaciations. These are processes that, along with fire regimes, are known to act on temporal timescales from several centuries to millennia. One study from the Wind River Range, Wyoming, suggested that whitebark pine treeline is sensitive to moisture and advanced during a period of higher effective moisture from 1800 and 800 cal. yr BP (Morgan et al. 2014). This intriguing suggestion has not been tested in other locations. Long-term changes in temperature, precipitation, and fire regimes will produce profound ecological consequences for modern populations of whitebark pine and other subalpine conifers.

Here, I have reconstructed in great spatial and temporal detail, the paleoecology of a subalpine forest ecosystem including whitebark pine in Grand Teton National Park, Wyoming. The location and size of my study site allowed an investigation of long-term dynamics of a whitebark pine population on a detailed spatial scale that will complement existing regional assessments. Because 10%-15% of the surviving North American population of whitebark pine exist in the GYA and GTNP (Schrag et al. 2008), there remains a need to investigate the species from a paleoecological perspective to aid in the development of sustainable conservation plans. More specifically, I asked: (i) how have fire frequency and severity changed through time, both locally and regionally? (ii) what has been the Holocene vegetation history of the site? (iii) what have been the growth trends of the stand of living *P. albicaulis* during the 20th century, and (iv) how have *P. albicaulis* growth trends been affected by climate?

Chapter 2 - Study Site

Fire, vegetation, and dendrochronological histories were examined at a small, un-named subalpine lake (known informally as Whitebark Moraine Pond; 43.79 N, 110. 110.79 W; elevation 2800 m) and the surrounding watershed in Grand Teton National Park, WY, USA (Jones 2013) (Figure 2-1). The lake and surrounding watershed are located at treeline in the uppermost reaches of Paintbrush Canyon, approximately 5 km NW of Jenny Lake. The lake has a maximum depth of 4 m and a watershed of 0.76 ha. The watershed contains no inlet or outlet systems, and the majority of hydrologic input is provided by summer snowmelt.

Whitebark Moraine Pond, a moraine-dammed lake, was produced by late Pinedale glacial activity (Jones 2013; Pierce 2003). Moraine-dammed lakes generally form when glacial meltwater collects behind terminal moraine debris as a glacier retreats (Richardson & Reynolds 2000). Whitebark Moraine Pond likely resulted from the retreat of a Pinedale glacier which reached its maximum extent in Grand Teton National Park approximately 9000 yr BP (Marston et al. 2005). As the Pinedale glacier retreated, resulting meltwater became trapped by terminal moraine debris and was prevented from flowing downslope, resulting in the formation of a dammed lake. The terminal moraine and rocky debris are still present in the south-east section of the study site.

The modern vegetation community of the study area can be characterized as a subalpine conifer forest. Canopy species dominate the watershed and consist primarily of whitebark pine (*Pinus albicaulis*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). Shade produced by the dense canopy results in a sparse understory including a small number of grasses and forbs. However, likely due to environmental constraints, vegetation approaching watershed boundaries (i.e. higher in elevation) is almost exclusively composed of whitebark pine.

Typical of most high-elevation ecosystems, soils in the watershed generally lack well-developed horizons (Tomback et al. 2001). The lack of soil profile development is primarily caused by a combination of steep slopes and high rates of eolian erosion (Weaver 2001). As a result of poor development, soils in the watershed have a relatively low water-holding capacity; it has been estimated that approximately 35-60% of all annual precipitation becomes surface runoff in high elevation watersheds, though soil drought is uncommon (Tomback et al. 2001). Soils in the watershed contain a large portion of organic matter (>20%; Jones 2013) due to the high annual production of conifers and slow decomposition characteristic of cold climates.

Annual growing season (May-July) precipitation at the site from 1895-2012 averaged 310 mm, and showed no significant trends during the available time period. Annual growing season maximum temperature averaged 15 °C for the same time period, and annual growing season minimum temperature averaged -2 °C. The average annual range in temperature for the time period was 13 °C and has been steadily decreasing since the 1990s. This decrease in annual temperature range is attributed to an increase in average growing season minimum temperatures, specifically, increases in July minimum temperatures. Annual July minimum temperatures have increased 7 °C since 1991 at the study site.

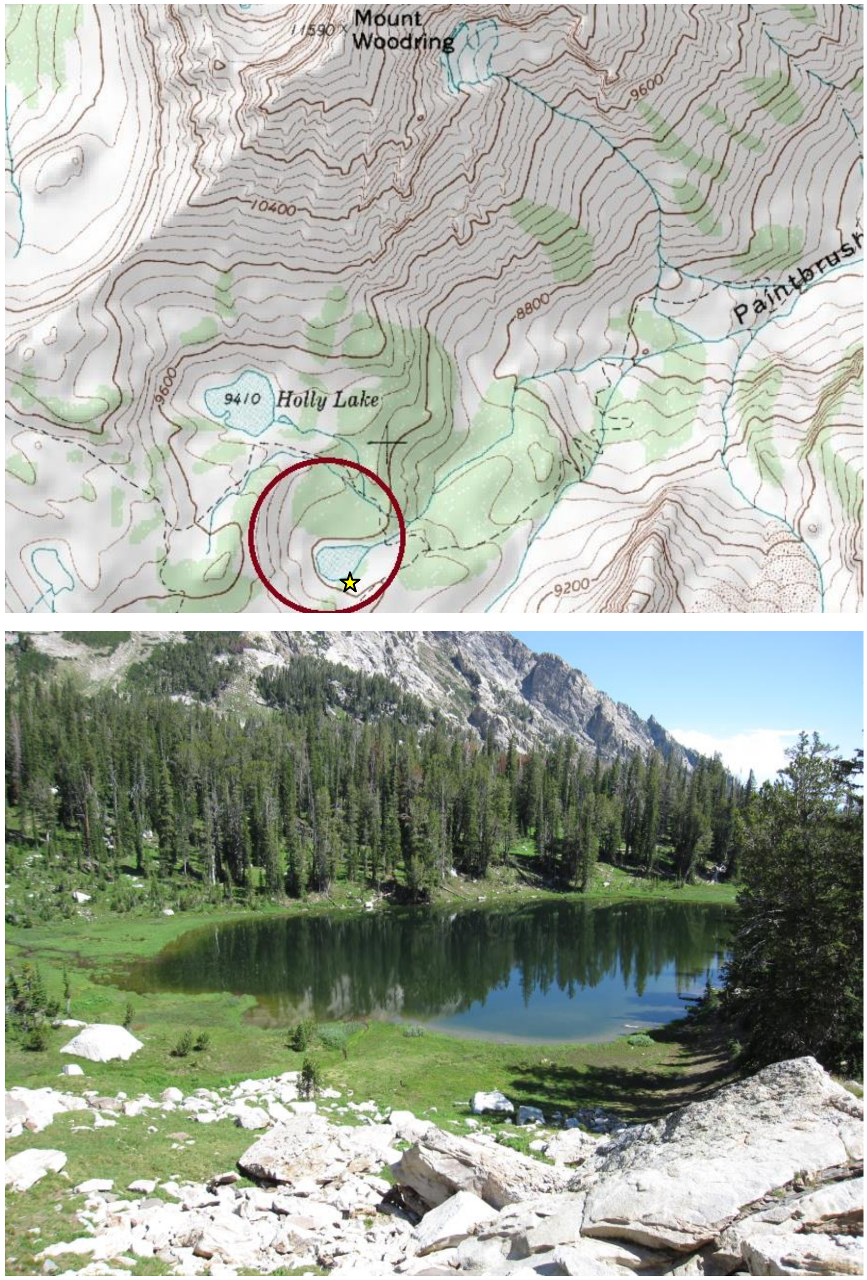

Figure 2-1 Top panel: Topographic map with study site circled in red showing its location relative to other landmarks. The specific geographic location of the stand used for dendrochronological analyses is indicated by the yellow star. Bottom panel: Photo of Whitebark Moraine Pond. Photos from USGS and Dr. Sarah Spaulding.

Chapter 3 - Methods

Sediment Core

The 155 cm lacustrine sediment core used in this study was collected from the deepest part of the lake in August 2010 using a light percussion corer and was obtained following operational protocols outlined by Nesje (1992) and Wright (1967). Subsamples for pollen, charcoal, and macrofossil analyses were obtained in December 2012 at the University of Colorado, Boulder Institute for Arctic and Alpine Research (INSTAAR) using freeze dried sediment sections and the archived half of the original sediment core, respectively.

Core Chronology

Five accelerated mass spectrometry (AMS) ^{14}C dates were obtained from conifer macrofossils (Table 3-1). Targets for ^{14}C analysis were prepared at the Laboratory for AMS Radiocarbon Preparation and Research at INSTAAR (University of Colorado, Boulder), and final AMS values were obtained at the W.M. Keck Laboratory (University of California, Irvine). Radiocarbon dates were calibrated using OxCal Software (version 4.1) and the IntCal09 calibration curve (Jones 2013).

Table 3-1 Radiocarbon dating results (From Jones 2013).

Absolute Depth (cm)	Composite Depth (cm)	Macrofossil Type	Age (^{14}C yr BP)
17.75	25.75	Conifer twig	555 ± 15
27.75	35.75	Conifer bark	1185 ± 15
100.25	108.25	Twig	4675 ± 20
120.75	128.75	Twig	5685 ± 20
148.25	156.25	Mazama ash	7687 ± 20
152.25	160.25	Conifer cone	6960 ± 20

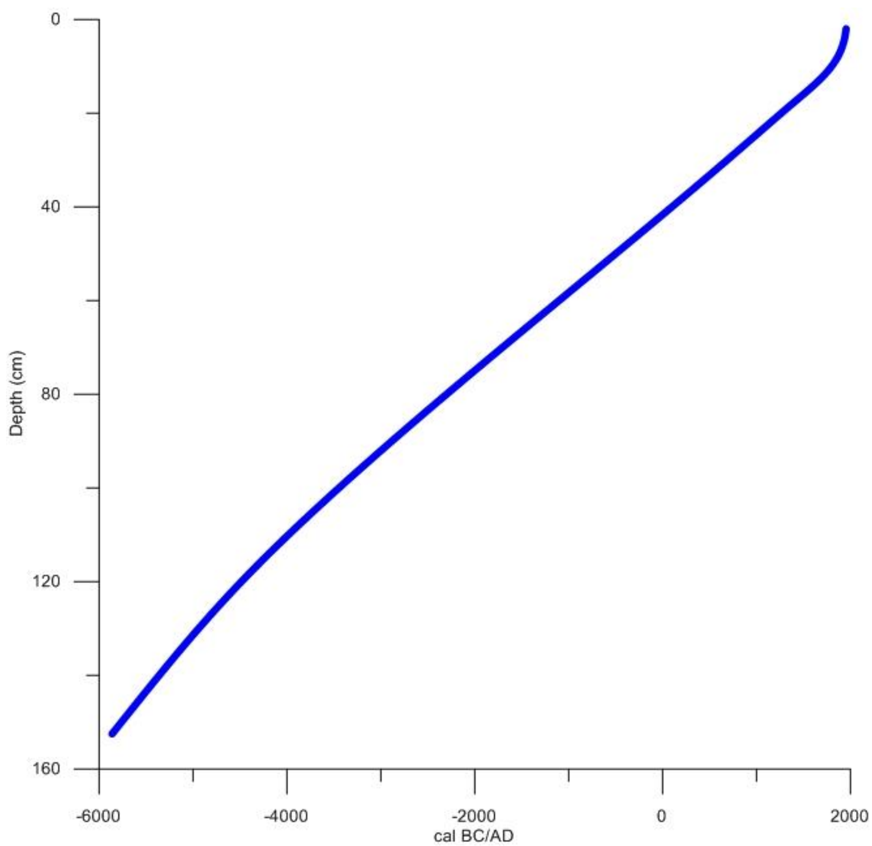

Figure 3-1 Age versus depth model for Whitebark Moraine Pond. Model based on radiocarbon ages from Table 3-1.

A 2 cm layer of Mazama ash was observed 148.5 cm from the top of the sediment core and was used to determine basal chronology. The eruption of Mount Mazama represents one of the most identifiable tephra layers in the United States and southwest Canada, and is documented as one of the most destructive eruptions of the late Quaternary (Zdanowica et al. 1999). The ash layer present in the sediment core was confirmed to be of Mazama origin through geochemical analysis of ash shards using electron microprobe analysis, conducted at the University of Alberta (Jones 2013). The date for the Mazama eruption is 7700 cal y BP.

A classical, non-Bayesian age-depth model was created using CLAM (Blaauw 2010) in the open-source statistical package R (Figure 3-1). ^{14}C and tephra dates were used as individual data points. The resulting age model was smoothed to reduce noise (Hutchinson & de Hoog 1985) using a cubic spline function. The resulting age-depth model indicates an incredibly low sedimentation rate during the entire sedimentary record. Low sedimentation rates are typical of high-elevation ecosystems (Yeend 1969).

Charcoal

Sediment subsamples of 1 cc each were taken at continuous 0.5 cm intervals along the length of the archived core. Subsamples were collected starting 2.0 cm from the top of the core due to a loss of sediment at the soil/water interface that occurred during field sampling. Methods of charcoal extraction generally followed guidelines summarized by Whitlock & Anderson (2003). Due to the high organic matter content of the core, subsamples for charcoal analysis were rinsed through a 1 mm sieve to allow removal and preservation of these organic macrofossils for further analysis. Sieved subsamples were then soaked for 48 hours in a 10% hydrogen peroxide solution to bleach any organic matter remaining in the sample. Bleached subsamples were rinsed through two stacked sieves of 250 µm and 125 µm. Subsamples were examined under a dissecting microscope, and all charcoal particles were counted and categorized according to source type (arboreal and non-arboreal) by identifying morphology types of individual charcoal pieces (Jensen et al. 2007).

Raw charcoal counts were ultimately converted to charcoal accumulation rates (CHAR, particles cm^{-1} per $year^{-1}$) using CharAnalysis; a modeling program designed to reconstruct local fire histories by detecting peaks in fire activity (Higuera 2009). Accumulation rate data were further broken down to separate background charcoal (C_{back}, BCHAR) from charcoal associated with fire episodes (C_{peak}) (Higuera et al. 2009). BCHAR is the low-frequency trend in charcoal production representative of the long-term trends in charcoal production, while C_{peak} represents peaks in fire activity identified by digressions in the BCHAR record, indicating charcoal influx from a local fire event (Long et al. 1998). BCHAR was estimated using a LOWESS (locally weighted scatter plot smoothing) method resistant to outliers with a 500 year window. Peaks in the charcoal record were identified by subtracting BCHAR values from the total CHAR values (Higuera et al. 2009). Resulting peaks were tested for significance using a threshold value of (t) =0.95. Peak components exceeding the threshold value were then considered significant peaks: peaks resulting from fire-related events. Peak components were then screened to eliminate peaks that failed to meet the cut-off probability for minimum count analysis, where (p) =.05 (Higuera 2009). That is, peaks with ≥5% chance of coming from the same distribution as the maximum charcoal count associated with the peak were rejected.

Pollen

Pollen was analyzed from freeze dried sediment to characterize vegetation changes at the Whitebark Moraine Pond site, and, ultimately, to assess altitudinal shifts in tree-line through time. Subsamples of freeze dried sediment of 1 cc volume were collected at 4 cm intervals along the entire length of the core. Freeze dried samples were rehydrated by gradually adding 1 mL portions of dH_2O to samples until the freeze dried sediment was completely saturated. Rehydrated samples were then sent to the University of Minnesota's National Lacustrine Core Facility (LacCore) where they were prepared for pollen analysis in accordance with traditional extraction protocols (Faegri and Iverson 1989). Extracted pollen samples were spiked with a solution with a known concentration of microspheres and suspended in silicon oil.

Samples were mounted on microscope slides and examined at 400X magnification. Individual pollen grains and spores were identified and recorded until a minimum of 300 terrestrial pollen grains had been counted. Totals for each species of pollen were then converted to frequencies to represent the ratio of each individual species to the total pollen influx at each sampled depth (Davis 1963). Species frequencies for each sampled depth were calculated as follows:

$$\text{Frequency of Species A} = \frac{\text{\# grains of Species A}}{\text{\# of total pollen grains}}$$

Final frequency data were used to create a pollen diagram illustrating changes in vegetation through time. The pollen diagram was created by plotting individual frequencies of each species against its associated age (cal yr BP) (Davis 1963). C2, a Microsoft program designed for analyzing paleoecological data, was used to create the final pollen diagram in this study.

Macrofossils

Macrofossil data are often used as a supplementary proxy to pollen analysis. Pollen analysis is inherently limited in treeline situations where local pollen production is usually low. This low local production can lead to misleading vegetation data because non-local pollen rain may easily mask the local pollen signal. Macrofossil analysis can help mediate this limitation by providing more accurate vegetation information because macrofossils are more locally distributed than pollen (Birks & Birks 2000).

Methods of macrofossil preparation and analysis generally followed procedures outlined by Gavin et al. (2013). Samples used for macrofossil analysis were collected during the charcoal preparation process, resulting in continuous 0.5 interval samples representative of 1 cc of raw sediment (described above). Samples were shaken continuously for 3-5 minutes in a 4% sodium hexametaphosphate (NaHMP) solution and then soaked in the solution for approximately 1 hour (Jiménez-Moreno &Anderson 2012). Soaked samples were washed through a 250 µm sieve and examined under a lighted dissecting microscope. The total number and types of macrofossils greater than 250 µm were counted and categorized according to taxonomy (excluding fossil charcoal). Final macrofossil data were superimposed as histograms on the pollen assemblage diagram (Gavin et al. 2013).

Dendrochronology

Demographic Survey

The area located south of the lake contains a continuous stand of conifers encompassing the highest concentration of whitebark pine, as well as the oldest whitebark pine trees in the watershed. A demographic survey was conducted to determine the abundance of whitebark pine in the watershed as compared to other competing species attributed to its modern decline using the stand as a representative sample for the watershed (Sala et al. 2000, Zeglen 2002).

Transect methods roughly followed those outlined by Anderson et al. (1979) and Eberhardt (1978). Four parallel line transects of 12-18 m each were run on the south side of the pond along an east/west gradient. Each transect line was initiated at the tree closest to the pond, and was spaced approximately 10 m from the neighboring transect. Data were collected every 3 m along each transect. At each point, the closet tree on each side of the transect line was identified and its dbh recorded. GPS locations of whitebark pine encountered during the survey were recorded with a handheld GPS unit. Light meter measurements were also recorded at each point using an Extech EasyView Light Meter to determine the effect of out-shading by competing species on the abundance of whitebark pine in the stand.

GPS Data

While the overall geographic range of whitebark pine is well documented, precise locations of individual stands remain largely undocumented. The absence of detailed locational data of whitebark pine stand locations is likely due to the species seldom being used as a timber resource (Environment 1991). Because whitebark pine is considered to be an ecological resource, rather than a commercial resource, studies documenting local stand locations are rare (Zeglen 2002).

The location of each of the 20 sampled trees on the south side of the watershed was recorded using a handheld Garmin GPS unit with 2 m resolution. Whitebark pine trees counted in the demographic study were also included in the total sample size. The latitude and longitude coordinates of each tree were recorded and stored in the Garmin unit. Stored GPS coordinates were used to document the exact physical location of each sampled tree in the watershed as it relates to other physical features such as the pond.

Increment Cores

Increment cores from 20 of the largest living whitebark pine *(Pinus albicaulis*) trees in the watershed were taken in June and July 2013 from the study site to determine age and dates of establishment of the current population of whitebark pine. Increment cores were taken using standard dendrochronological techniques with a 5.15 mm diameter Haglöf increment borer 1.3 m above the soil surface and stored in paper straws in the field (Elliot 2011). The borer was rinsed with a 70% ethanol solution after obtaining each sample to prevent the spread of pathogens, such as blister rust infections, between trees. Geographic coordinates, diameter at breast height (dbh), and height were measured for each sampled tree using a Garmin GPS unit, standard dbh tape, and electronic clinometer, respectively.

In the laboratory, increment cores were sanded, scanned, and ring widths were counted and measured to establish chronologies. Chronologies and ring widths were obtained using the dendro-chronological software programs Coo Recorder and C Dendro. Final ring widths were detrended in C Dendro to account for variability in ring widths associated with differences in growth rates during early tree development (Szeicz and MacDonald, 1993, Briffa et al. 1998).

Response to Climate

An analysis of tree ring widths aimed to provide information about the generalized climatic trends over time, as well as how these climate trends impacted the growth and stability of each sampled tree on a local scale. Methods generally followed those of a larger study of climate and local-scale factors on upper treeline in the Rocky Mountains (Elliot 2012). Because climate stations are rare at higher elevations in the Rocky Mountains, Precipitation-elevation Regressions on Independent Slopes Model (PRISM) data were used for the study site (Daly et al. 2008). PRISM uses point data, in the form of climate data collected from individual weather stations at lower elevations, to extrapolate high elevation climate histories and produce gridded (0.25 square mile cells) climate maps. PRISM data provided climatic information including maximum temperature, minimum temperature, dew point, and precipitation for each year ranging from 1895-2012 C.E.

PRISM and annual ring width data were analyzed to determine how climatic variables influence the development of annual rings in whitebark pine using a series of linear regression analyses in the statistical software program “R.” Linear regression analyses allowed for statistically significant climate variables, defined by their strong correlation with ring width data, to be identified.

Chapter 4 - Results

Charcoal

Summary of Holocene Fire Regimes

Fire regime reconstructions indicate that both fire frequency and severity were highly variable throughout the Holocene (Figure 4-1). Two distinct fire regimes were observed in the sedimentary record: (1) high frequency, low intensity fire episodes during the early and middle Holocene, and (2) low frequency, high intensity fire episodes during the late Holocene.

Fire Frequency and Severity (Early to Middle Holocene)

Two peaks in fire frequency were observed during the early and middle Holocene. The peak in fire frequency during the early Holocene occurred at 6,500 cal yr BP and was characterized by an increase in fire episodes from 0.5 fire episodes per $1000a^{-1}$ to 4 episodes per $1000a^{-1}$, as well as an increase in BCHAR influx during the time period (Figure 4-1a). Severity of fire episodes corresponding to the peak in fire activity, indicated by peak magnitude of individual events, is lower (0.1-10 pieces cm^{-2}) than during times of intermediate fire frequency following this peak in activity. The mid-Holocene peak in fire frequency occurred at 3,000 cal yr BP. This period of increased fire activity was characterized by an increase in fire episodes from 1 episode per $1000a^{-1}$ at 5,000 cal yr BP to 3.8 episodes per $1000a^{-1}$ at 3,000 cal yr BP. This increase in fire frequency also corresponds to an increase in BCHAR influx. Similar to the peak identified during the early Holocene, the mid-Holocene peak in fire activity corresponds to fire episodes that were lower (0-5 pieces cm^{-2}) than during times of intermediate fire frequency.

Fire Frequency and Severity (Late Holocene to Present)

Fire frequency has decreased from 1,000 cal yr BP towards present. This decrease in fire frequency is marked by a decrease in episodes from 2-3 episodes per $1000a^{-1}$ to 0 episodes per $1000a^{-1}$. This decline in frequency is coupled with an increase in fire intensity. The only two fire episodes occurring since 1,000 cal yr BP have higher peak magnitudes than any other identified peaks throughout the entire record. These increases in peak magnitudes are further supported by the observation of the largest influxes of BCHAR present throughout the entire sedimentary record.

Holocene Fuel Sources

Determination of fuel sources was accomplished by comparing the ratio of non-arboreal charcoal pieces to the total number of charcoal pieces observed, where values near 0.0 represent arboreal fuel sources and values near 1.0 represent non-arboreal fuel sources. Fire episodes fueled by arboreal vegetation produce more intense fire episodes due to the large amount of available biomass, while fires fueled by non-arboreal sources typically produce less severe fires as a result of lower fuel loads. Fuel sources were highly variable throughout the Holocene indicating the presence of a mixed-fuel system (Figure 4-1c). However, the majority of data points fall below 0.5, indicating that fire episodes were fueled by vegetation composed of more arboreal species than non-arboreal species, particularly during the most recent 1000 years.

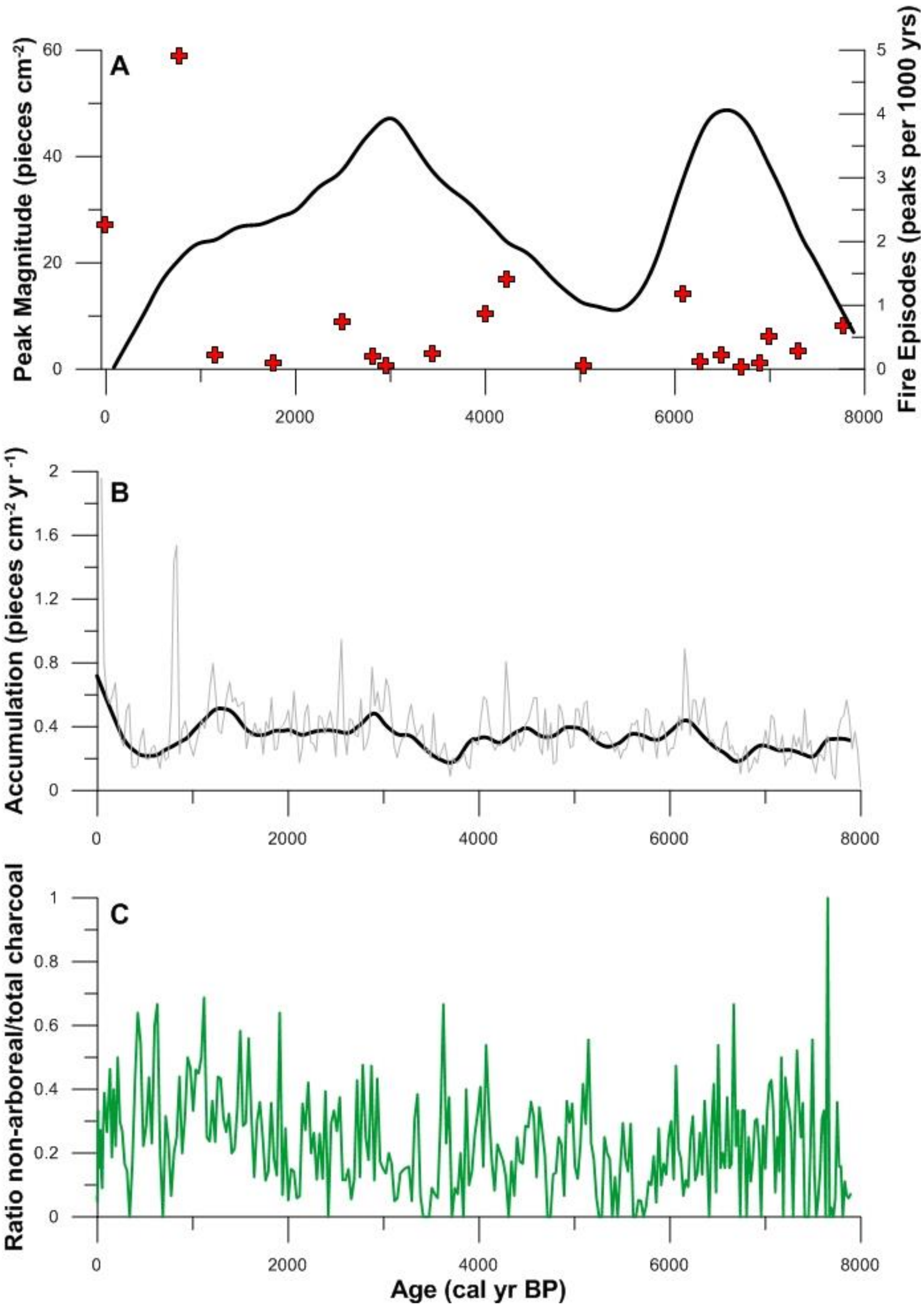

Figure 4-1 Whitebark Moraine Pond sedimentary charcoal record. (A) Fire episode frequency plotted as fire events per 1,000 years. Crosses represent peak magnitudes of fire events plotted as pieces of charcoal per cm^{-2}. (B) Charcoal accumulation rates with BCHAR, black line, superimposed. (C) Ratio of charcoal morphology types for each 0.5 cm sediment interval. Values near 1.0 indicate non-arboreal fuel sources. Values near 0 indicate arboreal fuel sources.

Pollen

Summary of Holocene Vegetation

Whitebark Moraine Pond experienced few major shifts in vegetation type during the Holocene (Figure 4-2). Holocene vegetation at the site included the presence of 15 taxa, with *Pinus* and *Artemisia* being the two most dominant taxa. The morphology of all *Pinus* pollen grains found in these samples is from the Haploxylon subgroup, of which *P. albicaulis* is a member. In the Holocene record, *Pinus*, indicative of subalpine vegetation, has comprised between 30% and 70% of the upland pollen sum, while *Artemisia*, indicative of tundra vegetation, has comprised between 20% and 60% of the upland pollen sum. Specifically, early and middle-Holocene vegetation was characterized by periods of alternating dominance between *Pinus*, *Artemisia*, and competing arboreal taxa (*Abies*, *Larix*, *Picea*), with herbaceous taxa occurring in small percentages. Similar to late-Holocene charcoal data, late-Holocene vegetation (from 1,000 cal yr BP towards present) represents a unique period in the vegetation record. From 1,000 cal yr BP to present, peaks in *Pinus* were lower than any other time during the Holocene, making up only 20% of the total upland pollen sum. Conversely during this time period, *Artemisia* peaks were higher than any other time during the Holocene, making up 55%-60% of the total upland pollen sum. Additionally, pollen from competing arboreal taxa have shown higher abundances and may have occupied a greater portion of the landscape in the most recent 1,000 years than at any other time during the Holocene.

Macrofossil data were used to validate pollen results. Because macrofossils travel less readily than airborne pollen grains, they were used as an indicator of local climate and vegetation. Times of high coniferous pollen influx were supported by times of high coniferous macrofossil influx, thereby supporting the sedimentary pollen results.

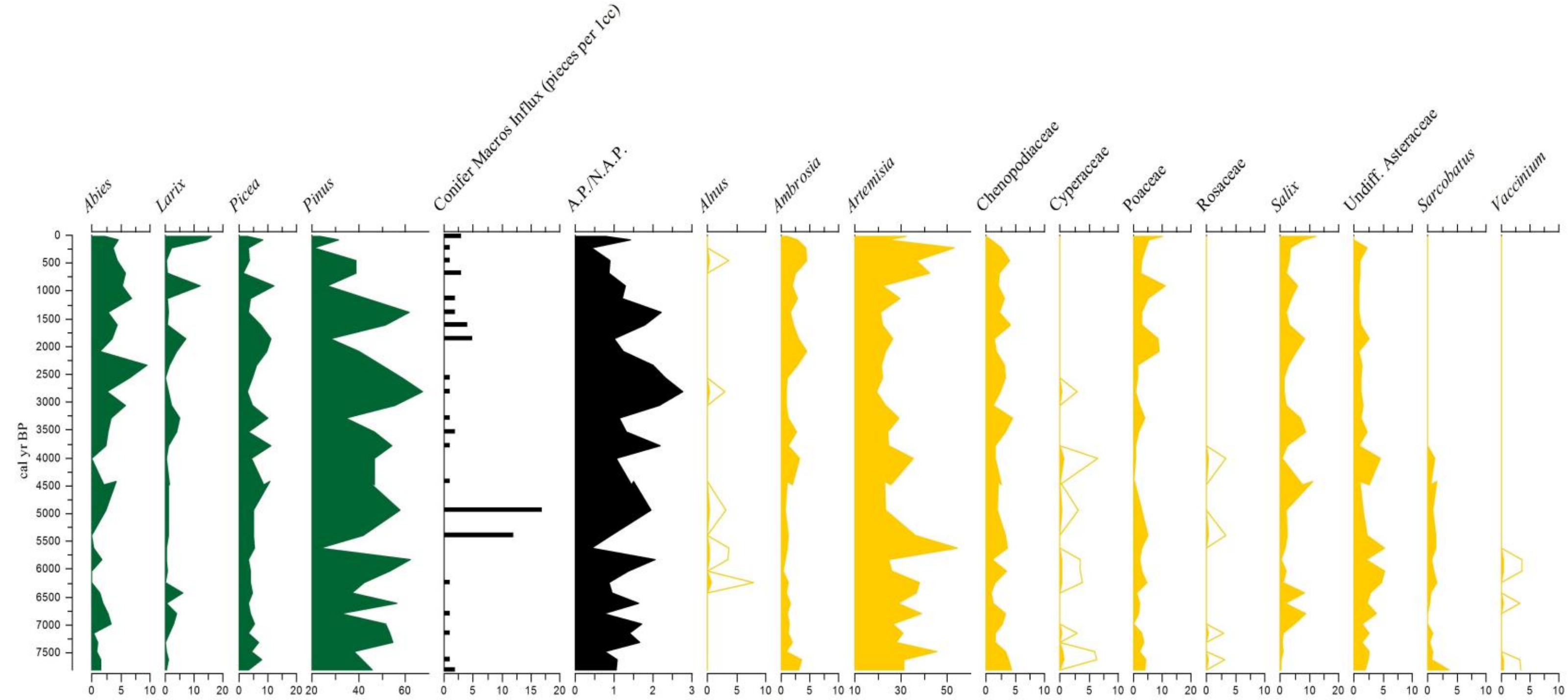

Figure 4-2 Pollen percentages of plant taxa from the Whitebark Moraine Pond sediment core. Percentages of each taxon are plotted against the age of the sediment core. Exaggeration lines are scaled at 10%.

Dendrochronological Analyses

Demography of Current Stand

The average date of establishment for the current stand of whitebark pine is 1751 C.E., however, individual dates of establishment range from 1324 C.E. to 1919 C.E. Of the 16 trees that were cored to the center, 75% were established between 1600 C.E. and 1800 C.E. (Figure 4-3a). With the exclusion of the oldest individual, dbh is inversely related to date of establishment (R^2 = 0.62); that is, older individuals are typically larger than younger individuals (Figure 4-3b). Transect data indicate that only 14% of the current stand is composed of whitebark pine, with subalpine fir and Engelmann spruce occupying 81% and 5%, respectively. All new growth within the survey area consisted of subalpine fir.

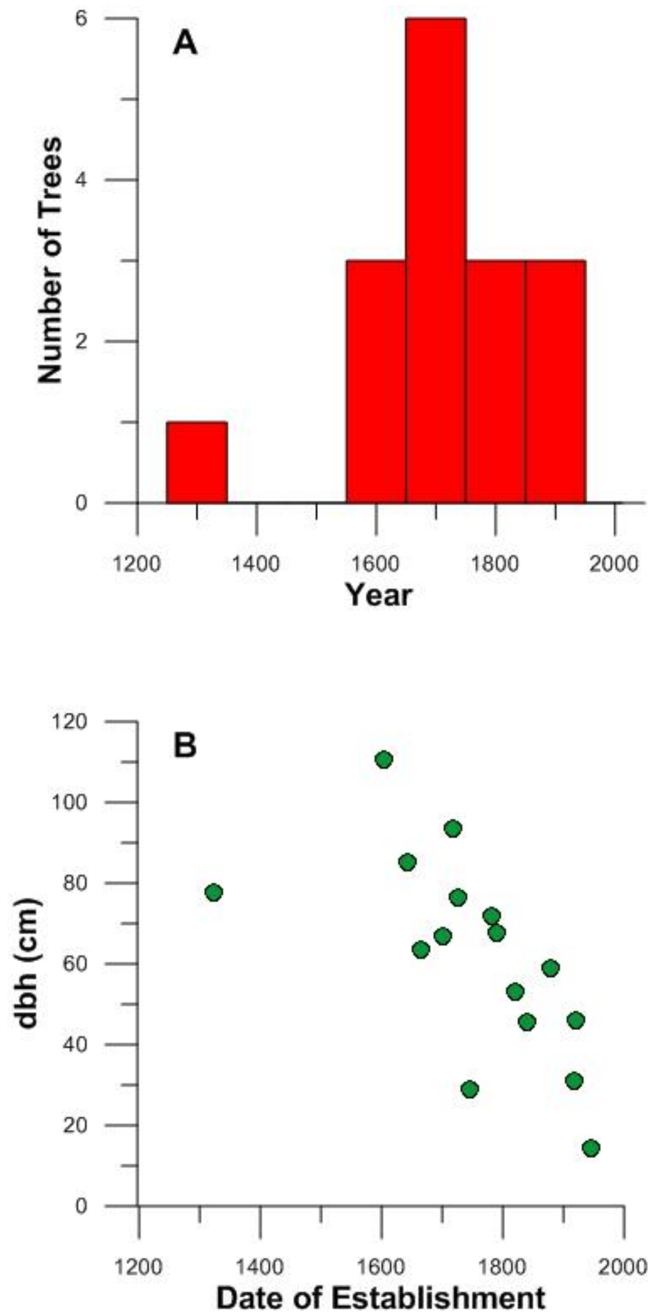

Figure 4-3 Demography of the current stand of whitebark pine. (A) Dates of establishment for all trees cored to the pith. (B) Dates of establishment plotted against dbh values; $R^2 = 0.62$.

Annual Growth and Climate

Average yearly ring widths ranged from 1.23 mm in 1950 to 0.60 mm in 2011 for the period of available climate data (1895-2012) (Figure 4-4a). A breakpoint analysis confirmed the presence of a change point at 1949 (±4.5 years) and further indicated that average ring widths increased until 1949, and then began to decline to their current widths.

Average July minimum temperature (Tmin) was identified as the most statistically significant variable affecting annual ring widths ($p < 0.001$) (Figure 4-4b). Other temperature and precipitation variables had no significant effect on the growth of whitebark pine at this site. Until 1991 (±2 years), average July Tmin values experienced no significant variation and remained relatively constant through time. A maximum value of 37.38 F was reached in 1945, with a spread in data of 8.07 ˚F. After 1991, however, average July Tmin values exhibited more variability and increased to temperatures higher than any other time during the record. Values reached a maximum in 2011 with an average July Tmin of 45.7 ˚F with a spread of 13.34 F from 1991-2011.

Average July Tmin values were plotted against average annual ring widths to determine the effect of climate on tree growth (Figure 4-4c). Analyses indicated that average July Tmin values were a significant ($p < 0.001$) predictor of whitebark pine growth. The resulting relationship between the two variables reveals that the modern decline in whitebark pine growth at the study site can be attributed to increasing July minimum temperatures.

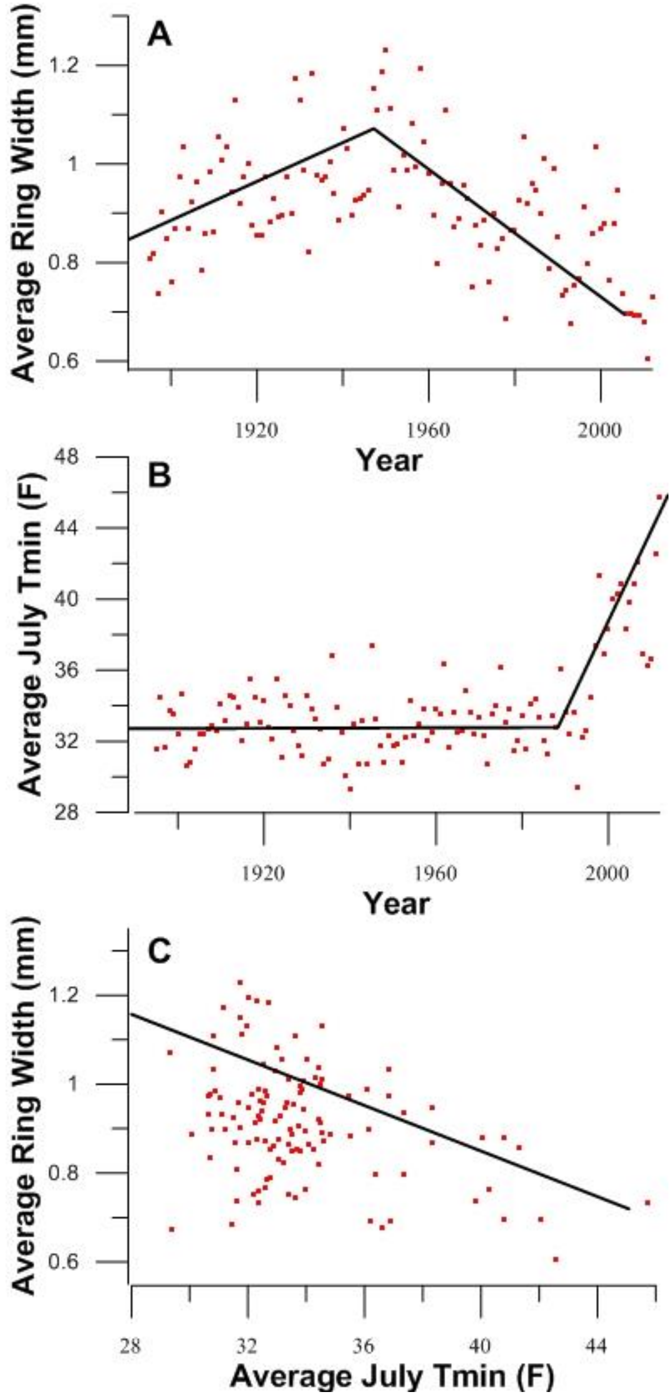

Figure 4-4 Modern tree growth and climate trends. (A) Average ring width values through time. Breakpoint analysis indicates a sharp decline at 1991 C.E. (B) Average July minimum temperature values through time. Breakpoint analysis indicates a sharp increase at 1949 C.E. (C) Average annual ring widths plotted against average July Tmin values indicating an inverse relationship; $p<.001$.

Chapter 5 - Discussion

Until the most recent 1,000 years, the study site has been dominated by whitebark pine when treeline was at or above its current location, and experienced regular, low to moderate intensity fire events. Past climate and fire regimes aided in reinforcing whitebark pine as the dominant vegetation type at the site. From 1,000 cal yr BP to present, whitebark pine has experienced an unprecedented decline in population due to a combination of anthropogenic fire suppression and climate change. At present, the current stand of whitebark pine is being displaced by competing coniferous species, namely subalpine fir, due to fire suppression and, indirectly, to increasing summer temperatures. It is suspected that the current stand of whitebark pine is a relic population.

A shift in fire regime observed during the most recent 1,000 years from frequent, low and moderate intensity fires to infrequent, severe fires is likely due to climate and anthropogenic fire suppression. Fire is perhaps the most important abiotic factor in determining the distribution and survival of whitebark pine because of its status as an early seral species. For whitebark pine to survive and maintain dominance over other subalpine conifer species, the surrounding ecosystem must be kept in a constant state of early succession (Keane 2001). Frequent, low-severity fire regimes allow for whitebark pine to maintain dominance by killing its less fire-tolerant competitors (Figure 5-1). Because whitebark pine is better adapted to fire events than its competitors, the regime characterized by frequent, low intensity events during the early and middle Holocene allowed for the perpetuation of whitebark pine as the dominant ecosystem component. Conversely, high intensity fire events, such as those observed during the most recent 1000 years, are fatal to both competing species and whitebark pine and are contributing to the modern decline of the species.

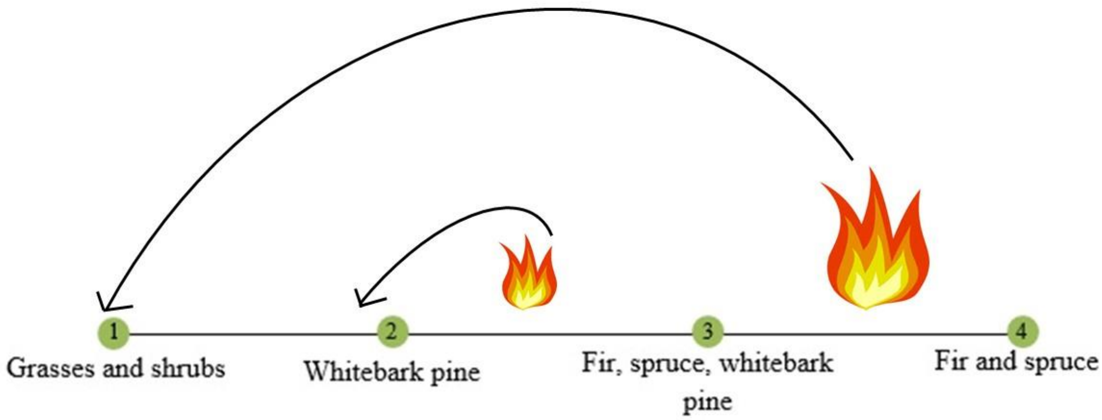

Figure 5-1 Conceptual diagram of succession in relation to disturbance events in subalpine conifer ecosystems. During times of whitebark pine dominance, small, frequent fire episodes move the successional trajectory back in time to sustain whitebark pine as the dominant vegetation type by killing off only competing coniferous species. During times characterized by multiple coniferous vegetation types, and, consequently, severe fire events, the successional trajectory is reset to the beginning, killing off all coniferous species, including whitebark pine.

The largest charcoal peak magnitude in the sedimentary record coincides directly with the Medieval Warm Period (MWP). During the MWP, the western United States experienced rapidly warming temperatures and a series of megadroughts (Cook et al. 2004). The warmer temperatures and droughts associated with the MWP have long been associated with increased incidences of fire as the result of increased ignitions in the western United States (Clifford & Booth 2013). It is possible that the observed peak in fire activity is a result of dry climatic conditions associated with the MWP. The most recent peak in fire activity is assumed to be the result of anthropogenic fire suppression. While long-term fire history records are non-existent in

GTNP, data acquired since the onset of anthropogenic fire suppression in the park indicate that most fires events are ignited by lightning or accidentally by humans (Teton Interagency Fire 2014). Fire suppression practices of the last 100 years have allowed considerable amounts of ignitable fuel to accumulate on the forest floor, resulting in high-intensity fires that occur infrequently. Similar to this study, displacement of whitebark pine by subalpine fir driven by fire suppression has been observed in the Bitterroot Mountain Range of northwestern Montana (Keane & Arno 1993).

Long-term trends in fire regime are reflected in the vegetation record. The two periods of fire activity characterized by frequent, low-intensity burns, regimes crucial for perpetuating whitebark pine as the dominant ecosystem component, correspond with periods of high pine dominance in the pollen record. For example, during the peak in frequent, low-intensity fire activity observed around 6500 cal yr BP, the pollen record shows high abundances of *Pinus* pollen (~60%) and low abundances of competing taxa (*Abies*, *Picea)*, as well as low abundances of the tundra-indicating species, *Artemisia*. I interpreted the time periods with high *Pinus* abundance and corresponding periods of low-intensity fires to indicate the importance of these fire regimes to the survival of whitebark pine. The modern period of fire activity characterized by infrequent, high-intensity burns is also reflected in the pollen record. The fire regime observed from 1000 cal yr BP towards present is abnormal in comparison to the rest of the sedimentary record and is not conducive to the survival of whitebark pine. During these times of high-severity fires, the pollen record indicates low abundances of *Pinus*, *Abies*, and *Picea*, but high abundances of *Artemisia*. I interpreted these results to indicate that high severity fires kill off a large portion of living conifers, and reset the successional trajectory to the first stage.

Pollen records from subalpine ecosystems can be used as a proxy for treeline location. Tinner et al. (1996) suggested that long-term records of fossil pollen are useful in tracking treeline advances and retreats during the Holocene, which was also supported in a regional synthesis of pollen data in the European Arctic region (Fang et al. 2013). While Holocene-scale shifts in treeline have been well-documented throughout Yellowstone National Park (Whitlock 1993), factors driving treeline fluctuations in Grand Teton National Park have not been as thoroughly investigated. Using sedimentary pollen data and a model of typical subalpine vegetation as it relates to elevation (Whitlock 1993), I was able to characterize changes in boundaries between different vegetation zones (Figure 5-2). The three major vegetation zones found around the study site include tundra (*Artemisia*), *Pinus albicaulis*, and mixed *Picea, Abies, Pinus*. Vegetation zones are dynamic features that respond to a variety of climate variables. Because the lake is a stationary point on the landscape, changes in boundaries between these vegetation zones were reflected as different zones moved up and down in elevation relative to the lake used here, thus changing the pollen rain that was ultimately accumulated in the lake sediments. For example, the pollen record indicates a period around 700 cal yr BP where the abundance of both *Pinus* and *Artemisia* were low, but the abundance of whitebark pine competitors, *Abies*, *Picea,* and *Larix,* were high. This period does not correspond with sedimentary charcoal data, indicating that the vegetation observed at this time period was not the result of successional dynamics associated with fire activity. I interpreted this unique period of vegetation to indicate that the boundary between the *Picea-Abies* and *Pinus albicaulis* zones had shifted upward in elevation to some point above the location of the lake. The upward movement of this boundary would have resulted in increased accumulation of *Picea* and *Abies* pollen in lake sediments. Alternatively, the pollen record indicates a period around 7000 cal yr BP that was characterized by high abundance of *Artemisia*, but low abundance of all conifer species; this period is also not the result of fire activity. I interpreted this as a time when the boundary between the tundra and *Pinus albicaulis* zones had shifted downwards in elevation to a point below the location of the lake, which resulted in high rates of accumulation of *Artemisia*.

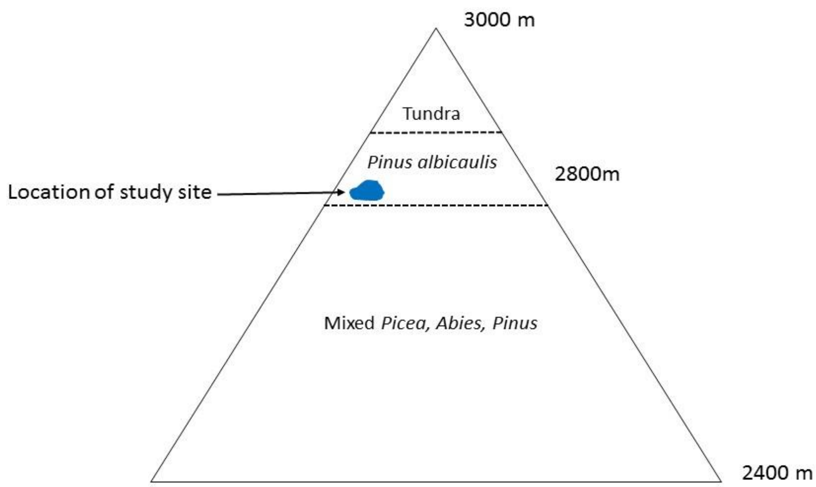

Figure 5-2 Vegetation zones of subalpine ecosystems by elevation in relation to the location of the study site. Boundaries between vegetation zones are dynamic features that may shift through time. Changes in the upward or downward movement of these vegetation boundary zones in relation to the location of the lake are reflected in the pollen record. Modified from Whitlock 1993.

Increasing July minimum temperatures have aided in the displacement of whitebark pine by subalpine fir. The initial onset of declining ring widths around 1949 may have been triggered by an unknown ecological event which subsequently increased the stand’s sensitivity to later temperature changes beginning in 1991, thereby amplifying its effect on the population. *Abies* and *Picea*, competitors of whitebark pine, are better adapted to survive in warmer climates than whitebark pine. While July minimum temperatures were the most significant climate variable of ring width at this site, Perkins and Swetnam (1996) observed a significant inverse relationship between ring widths and May temperatures in *Pinus* in the Sawtooth-Salman River region of Idaho. Further, Morgan et al. (2014) found a role of moisture variables on placement of whitebark pine treeline during the past 1800 years in the Wind River Range, Wyoming. I did not find any evidence of moisture influences (as seen as variables reflecting precipitation in data from PRISM) on tree growth in the past ~200 years in Grand Teton National Park; however, it is possible that whitebark pine is significantly influenced by changes in moisture due to its classification as a xeric species (Larson 2009). While I found the most significant climate variable to be temperature, it is possible that increases in temperature may be indirectly altering moisture availability through soil moisture processes or evaporation. This discrepancy in tree growth response to climate variables may be caused by the geographic difference in site locations and should be investigated further. In both cases, increased growing season temperatures have resulted in altered subalpine conifer communities by allowing warm temperature-adapted species to invade the niche normally occupied by whitebark pine. Because subalpine fir tends to grow much faster than whitebark pine, it acts as a competitor for resources and ultimately restricts the growth of whitebark pine by out-shading. The role of different climate variables on whitebark pine survival is currently not well-understood and should be investigated further. Climate, combined with anthropogenic fire suppression, has set the stage for the modern successional displacement of whitebark pine.

Chapter 6 - Conclusion

Fire, vegetation, and climate are long-term, dynamic drivers of ecosystem composition. The relative role of each driver on the composition and stability of whitebark pine populations has remained relatively undocumented until now. The past stability and subsequent decline of whitebark pine illustrate the direct impact of anthropogenic fire suppression and climate change on biodiversity in subalpine ecosystems. With the extinction of whitebark pine on the horizon, an understanding of the past ecology of the species, through the synthesis of proxy data, will be invaluable when designing conservation and management plans for this keystone species.

The management of this threatened species will require action from park officials. Because climate change is a long-term, global phenomenon, managing whitebark pine for its response to a changing climate on a local scale is not feasible. However, anthropogenic fire suppression can be managed by national park fire ecologists. It is well documented that whitebark pine benefits from frequent, low-intensity fire events. With the introduction of regular prescribed fires that induce low-intensity ground burns, the current decline of whitebark pine may be significantly mitigated. The findings of this study highlight the importance of immediate action; without significant restoration and regeneration efforts, whitebark pine will likely face extinction.

References

Anderson, D. R., J. L. Laake, B. R. Crain & K. P. Burnham (1979) Guidelines for line transect sampling of biological populations. *Journal of Wildlife Management,* 43, 70-78.

Arno, S. F. & R. J. Hoff (1989) Silvics of whitebark pine (Pinus albicaulis). *USDA Forest Service Intermountain Research Station General Technical Report INT-253,* 1-11.

Birks, H. H. & H. J. B. Birks (2000) Future uses of pollen analysis must include plant macrofossils. *Journal of Biogeography,* 27, 31-35.

Blaauw, M. (2010) Methods and code for 'classical' age-modelling of radiocarbon sequences. *Quaternary Geochronology,* 5, 512-518.

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

Clifford, M.J and R.K. Booth (2013) Increased probability of fire during late Holocene droughts in northern New England. *Climatic Change*, 119, 693-704.

Cook, E.R., C.A. Woodhouse, C.M. Eakin, D.M. Meko, D.W. Stahle (2004) Long-term aridity changes in the western United States. *Science*, 305, 1015-1018.

Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. T. Curtis & P. A. Pasteris (2008) Physiographically-sensitive mapping of temperature and precipitation across the conterminous United States. *International Journal of Climatology,* 28, 2031-2064.

Davis, M. B. (1963) On the theory of pollen analysis. *American Journal of Science,* 261, 897-912.

Eberhardt, L. L. (1978) Transect methods for population studies. *Journal of Wildlife Management,* 42, 1-31.

Elliot, G. P. (2011) Influences of 20th- century warming at the upper tree line contingent on local-scale interactions: evidence from a latitudinal gradient in the Rocky Mountains, USA. *Global Ecology and Biogeography,* 20, 46-57.

Elliot, G. P. (2012) Extrinsic regime shifts drive abrupt changes in regeneration dynamics at upper treeline in the Rocky Mountains, USA. *Ecology*, 93, 1614-1625.

Faegri, K. & J. Iverson (1989) (Fourth Edition by K. Faegri, P.E. Kaland, and K. Krzyinski) Textbook of Pollen Analysis. John Wiley and Sons New York 328 p.

Fang, K., J.L. Morris, J. S. Salonen, P.A. Miller, H. Renssen, M.T. Sykes, H. Seppa (2013) How robust are Holocene treeline simulations? A model-data comparison in the European Arctic treeline region. *Journal of Quaternary Science*, 28, 595-604.

Felicetti, L.A., C.G. Schwartz, R.O. Rye, M.A. Haroldson, K.A. Gunther, D.L. Phillips, C.T. Robbins (2003) Use of sulfur and nitrogen stable isotopes to determine the importance of whitebark pine nuts to Yellowstone grizzly bears. *Canadian Journal of Zoology*, 81, 763-770.

Gavin, D. G., L. B. Brubaker, & D. N. Greenwald (2013) Postglacial climate and fire-mediated vegetation change on the western Olympic Peninsula, Washington. *Ecological Monographs,* (In Press).

Higuera, P. E. (2009) CharAnalysis 0.9: Diagnostic and analytical tools for sediment-charcoal analysis. *User's Guide Update,* 1-26.

Higuera, P. E., L. B. Brubaker, P. M. Anderson, F. Sheng Hu & T. A. Brown (2009) Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs,* 79, 201-219.

Hutchinson, M. F. & F. R. de Hoog (1985) Smoothing noisy data with spline functions. *Numerische Mathematik,* 47, 99-106.

Jensen, K., E. A. Lynch, R. Calcote & S. C. Hotchkiss (2007) Interpretation of charcoal morphotypes in sediments from Ferry Lake, Wisconsin, USA: do different plant fuel sources produce distinctive charcoal morphotypes? *The Holocene,* 17, 907-915.

Jimenez-Moreno, G. & R. S. Anderson (2012) Pollen and macrofossil evidence of Late Pleistocene and Holocene treeline fluctuations from an alpine lake in Colorado, USA. *The Holocene,* 23, 68-77.

Jones, E. V. (2013) A spectroscopic approach to inferring charcoal concentrations and fire history from lacustrine sediments. M.Sc. Thesis, University of Alberta: Canada.

Keane, R.E. (2001) Can the fire-depended whitebark pine be saved? *Fire Management Today*, 61, 17-20.

Keane, R.E. and S.F. Arno (1993) Rapid decline of whitebark pine in western Montana: evidence from 20-year remeasurements. *Western Journal of Applied Forestry*, 8, 44-47.

Keane, R.L. and R.A. Parsons (2010) Restoring whitebark pine forests of the northern Rocky Mountains, USA. *Ecological Restoration*, 28, 56-70.

Larson, E. R. (2009) Stand dynamics of whitebark pine (Pinus albicaulis Elgelm.) forests in southwest Montana, central Idaho, and Oregon, U.S.A. Ph.D. Dissertation, University of Minnesota: USA.

Long, C. J., C. Whitlock, P. J. Bartlein & S. H. Millspaugh (1998) A 9000-year fire history from the Oregon Coast Range, based on a high-resolution charcoal study. *Canadian Journal of Forest Research*, 28, 774-787.

Marston, R. A., J. D. Mills, D. R. Wrazien, B. Bassett, & D. K. Splinter (2005) Effects of Jackson Lake Dam on the Snake River and its floodplain, Grand Teton National Part, Wyoming, USA. *Geomorphology*, 71, 79-98.

Millar, C.I., R.D. Westfall, D.L. Delany, M.J. Bokach, A.L. Flint, L.E. Flint (2012) Forest mortality in high-elevation whitebark pine (Pinus albicaulis) forests of eastern California, USA; influence of environmental context, bark beetles, climatic water deficit, and warming. *Canadian Journal of Forest Research*, 42, 749-765.

Mohatt, K.R., C.L. Cripps, M. Lavin (2008) Ectomycorrhizal fungi of whitebark pine (a tree in peril) revealed by sporocarps and molecular analysis of mycorrhizae from treeline forests in the Greater Yellowstone Ecosystem. *Botany*, 86, 14-25.

Morgan, C., A. Losey, L. Trout (2014) Lakte-Holocene paleoclimate and treeline fluctuation in Wyoming's Wind River Range, USA. *The Holocene*, 24, 209-219.

Nesje, A. (1992) A piston corer for lacustrine and marine sediments. *Arctic and Alpine Research,* 24, 257-259.

Perkins, D.L. and T.W Swetnam (1996) A dendroecological assessment of whitebark pine in the Sawtooth-Salman river region, Idado. *Canadian Journal of Forestry Research*, 26, 2123-2133.

Pierce, K. L. (2003) Pleistocene glaciations of the Rocky Mountains. *Development in Quaternary Science*, 1, 63-76.

Richardson, S. D. & J. M. Reynolds (2000) An overview of glacial hazards in the Himalayas. *Quaternary International,* 65/66, 31-47.

Sala, A., E. V. Carey, R. E. Keane & R.M. Callaway (2001) Water use by whitebark pine and subalpine fir: potential consequences of fire exclusion in the northern Rocky Mountains. *Tree Physiology*, 21, 717-725.

Schrag, A.M., A. G. Bunn, L.J. Graumlich (2008) Influence of bioclimatic variables on tree-line conifer distribution in the Greater Yellowstone Ecosystem: implications for species of conservation concern. *Journal of Biogeography*, 35, 698-710.

Tinner, W., B. Ammann, G. Germann (1996) Treeline fluctuations recorded for 12,500 years by soil profiles, pollen, and plant macrofossils in the central Swiss Alps. *Arctic and Alpine Research*, 28, 131-147.

Tomback, D.F., A. J. Anderies, K.S. Carsey, M.L. Powell, S. Mellmann-Brown (2001) Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. *Ecology*, 82, 2587-2600.

Tomback D. F., S. F. Arno, & R. E. Keane (2001) The compelling case for management intervention. In D. F. Tomback, S. F. Arno, & R. E. Keane (Eds.) *Whitebark Pine Communities*: *Ecology and Restoration,* Washington, DC: Island Press, 3-29.

Weaver, T. (2001) Whitebark pine and its environment. In D. F.Tomback, S. F. Arno, & R. E. Keane (Eds.) *Whitebark Pine Communities: Ecology and Restoration*, Washington, DC: Island Press, 41-74.

Whitlock, C. 1993. Postglacial vegetation and climate of Grant Teton and southern Yellowstone national parks. *Ecological Monographs*, 63, 173-198.

Whitlock, C. & R. S. Anderson (2003) Fire history reconstructions based on sediment records from lakes and wetlands. *Ecological Studies,* 160, 3-31.

Wright, H. E. (1967) A square-rod piston sampler for lake sediments. *Journal of Sedimentary Research*, 37, 975-976.

Yeend, W.E. (1969) Quaternary geology of the Grand and Battlement Mesas Area, Colorado. *DOI Geological Survey Professional Paper 617*, 1-49.

Zdanowicz, C. M., Z. A. Zielinski & M. S. Germani (1999) Mount Mazama eruption: calendrical age verified and atmospheric impact assessed. *Geology*, 27, 621-624.

Appendix A - Pollen Data

Raw Counts

Depth (cm)	*Abies*	*Alnus*	*Ambrosia*	*Artemisia*	*Betula*	Chenopod	Cyperaceae	*Larix*
1.0-1.5	5	0	0	11	0	3	0	16
4.0-4.5	6	0	3	84	0	0	0	42
8.0-8.5	11	0	7	59	0	2	0	35
12.0-12.5	11	0	13	158	0	8	0	6
16.0-16.5	12	1	12	99	0	11	0	1
20.0-20.5	16	0	7	116	0	6	0	2
24.0-24.5	13	0	5	54	0	5	0	30
28.0-28.5	22	0	9	94	0	10	0	2
32.0-32.5	9	0	5	66	0	7	0	3
36.0-36.5	14	0	7	69	0	13	0	2
40.0-40.5	8	0	7	59	0	3	0	16
44.0-44.5	3	0	10	52	0	4	0	9
48.0-48.5	27	0	8	61	0	9	0	4
52.0-52.5	20	0	3	67	0	10	0	0
56.0-56.6	9	1	3	65	0	8	1	3
60.0-60.5	18	0	3	73	0	4	0	7
64.0-64.5	8	0	3	70	0	11	0	12
68.0-68.5	5	0	5	44	0	6	0	7
72.0-72.5	8	0	4	81	0	5	0	3

76.0-76.5	0	0	10	108	0	5	2	1
84.0-84.5	4	0	4	50	0	5	0	3
88.0-88.5	8	0	2	43	0	4	0	2
92.0-92.5	8	1	2	74	0	6	1	3
100.0-100.5	0	0	4	108	0	10	0	3
104.0-104.5	1	1	3	146	0	10	0	1
108.0-108.5	5	1	2	70	0	3	1	1
112.0-112.5	0	0	1	74	0	10	1	2
116.0-116.5	0	2	3	97	0	4	1	0
120.0-120.5	3	0	2	79	0	2	0	13
124.0-124.5	6	0	5	88	0	4	0	1
128.0-128.5	5	0	2	71	0	6	0	7
132.0-132.5	7	0	3	56	0	6	0	6
136.0-136.5	1	0	4	102	0	5	1	5
140.0-140.5	3	0	6	84	0	5	0	0
144.0-144.5	3	0	3	152	0	11	2	1
148.0-148.5	5	0	11	99	0	12	2	3
152.5-153.0	5	0	9	95	0	13	0	1

Depth (cm)	*Picea*	*Pinus*	Poaceae	Rosaceae	*Salix*	Undiff. Aster	*Sarcobatus*	*Vaccinium*
1.0-1.5	6	39	4	0	6	0	0	0
4.0-4.5	7	61	26	0	32	0	0	0
8.0-8.5	20	77	13	0	20	0	0	0

12.0-12.5	10	63	13	0	10	7	0	0
16.0-16.5	10	105	8	0	9	3	0	0
20.0-20.5	4	106	7	0	6	3	0	0
24.0-24.5	30	66	27	0	15	2	0	0
28.0-28.5	13	137	16	0	12	3	0	0
32.0-32.5	10	193	9	0	7	3	0	0
36.0-36.5	24	162	9	0	10	4	0	0
40.0-40.5	25	63	19	0	19	6	0	0
44.0-44.5	22	90	20	0	13	2	0	0
48.0-48.5	17	141	4	0	8	4	0	0
52.0-52.5	14	179	4	0	4	4	0	0
56.0-56.6	9	225	2	0	5	4	0	0
60.0-60.5	15	174	7	0	7	5	0	0
64.0-64.5	24	83	9	0	17	3	0	0
68.0-68.5	6	85	3	0	16	4	0	0
72.0-72.5	37	178	2	0	8	3	0	0
76.0-76.5	13	143	2	1	2	14	4	0
84.0-84.5	17	92	0	0	15	5	1	0
88.0-88.5	20	83	1	0	21	2	3	0
92.0-92.5	16	183	9	0	7	5	3	0
100.0-100.5	15	125	15	1	7	7	4	0
104.0-104.5	14	63	8	0	5	14	4	0
108.0-108.5	9	176	6	0	1	6	2	1

112.0-112.5	11	152	8	0	6	15	3	1
116.0-116.5	10	108	12	0	3	12	4	0
120.0-120.5	10	80	2	0	18	6	1	0
124.0-124.5	10	174	7	0	5	7	1	1
128.0-128.5	7	59	3	0	16	7	0	0
132.0-132.5	11	109	0	0	10	3	0	0
136.0-136.5	11	176	9	1	4	9	3	0
140.0-140.5	20	165	11	0	2	4	1	0
144.0-144.5	15	127	7	0	3	9	3	0
148.0-148.5	25	131	14	1	1	8	2	1
152.5-153.0	10	138	12	0	1	6	11	1

Frequencies (Percentages)

cal yr BP	*Abies* (Fir)	*Larix* (Larch)	*Picea* (Spruce)	*Pinus* (Pine)	A.P.	N.A.P.	*Alnus* (Alder)
-10.00	5.56	17.78	6.67	43.33	73.33	26.67	0.00
11.51	2.30	16.09	2.68	23.37	44.44	55.56	0.00
85.05	4.51	14.34	8.20	31.56	58.61	41.39	0.00
235.23	3.68	2.01	3.34	21.07	30.10	69.90	0.00
451.57	4.43	0.37	3.69	38.75	47.23	52.77	0.37
685.83	5.86	0.73	1.47	38.83	46.89	53.11	0.00
916.28	5.26	12.15	12.15	26.72	56.28	43.72	0.00
1146.23	6.92	0.63	4.09	43.08	54.72	45.28	0.00

1378.54	2.88	0.96	3.21	61.86	68.91	31.09	0.00
1613.30	4.46	0.64	7.64	51.59	64.33	35.67	0.00
1850.15	3.56	7.11	11.11	28.00	49.78	50.22	0.00
2088.69	1.33	4.00	9.78	40.00	55.11	44.89	0.00
2328.57	9.54	1.41	6.01	49.82	66.78	33.22	0.00
2569.39	6.56	0.00	4.59	58.69	69.84	30.16	0.00
2810.78	2.69	0.90	2.69	67.16	73.43	26.57	0.30
3052.56	5.75	2.24	4.79	55.59	68.37	31.63	0.00
3293.76	3.33	5.00	10.00	34.58	52.92	47.08	0.00
3534.60	2.76	3.87	3.31	46.96	56.91	43.09	0.00
3774.50	2.43	0.91	11.25	54.10	68.69	31.31	0.00
4013.09	0.00	0.33	4.26	46.89	51.48	48.52	0.00
4484.81	2.04	1.53	8.67	46.94	59.18	40.82	0.00
4417.18	4.23	1.06	10.58	43.92	59.79	40.21	0.00
4946.73	2.52	0.94	5.03	57.55	66.04	33.96	0.31
5395.86	0.00	1.00	5.02	41.81	47.83	52.17	0.00
5614.61	0.37	0.37	5.19	23.33	29.26	70.74	0.37
5828.61	1.76	0.35	3.17	61.97	67.25	32.75	0.35
6037.07	0.00	0.70	3.87	53.52	58.10	41.90	0.00
6239.20	0.00	0.00	3.91	42.19	46.09	53.91	0.78
6434.21	1.39	6.02	4.63	37.04	49.07	50.93	0.00
6621.51	1.94	0.32	3.24	56.31	61.81	38.19	0.00
6801.70	2.73	3.83	3.83	32.24	42.62	57.38	0.00

6978.50	3.32	2.84	5.21	51.66	63.03	36.97	0.00
7144.86	0.30	1.51	3.32	53.17	58.31	41.69	0.00
7309.89	1.00	0.00	6.64	54.82	62.46	37.54	0.00
7471.93	0.89	0.30	4.46	37.80	43.45	56.55	0.00
7632.01	1.59	0.95	7.94	41.59	52.06	47.94	0.00
7811.00	1.66	0.33	3.31	45.70	50.99	49.01	0.00

cal yr BP	*Ambrosia* (Ragweed)	*Artemisia* (Sage)	Chenopodiaceae (Goosefoots)	Cyperaceae (Sedges)
-10.00	0.00	12.22	3.33	0.00
11.51	1.15	32.18	0.00	0.00
85.05	2.87	24.18	0.82	0.00
235.23	4.35	52.84	2.68	0.00
451.57	4.43	36.53	4.06	0.00
685.83	2.56	42.49	2.20	0.00
916.28	2.02	21.86	2.02	0.00
1146.23	2.83	29.56	3.14	0.00
1378.54	1.60	21.15	2.24	0.00
1613.30	2.23	21.97	4.14	0.00
1850.15	3.11	26.22	1.33	0.00
2088.69	4.44	23.11	1.78	0.00
2328.57	2.83	21.55	3.18	0.00
2569.39	0.98	21.97	3.28	0.00
2810.78	0.90	19.40	2.39	0.30
3052.56	0.96	23.32	1.28	0.00
3293.76	1.25	29.17	4.58	0.00
3534.60	2.76	24.31	3.31	0.00
3774.50	1.22	24.62	1.52	0.00
4013.09	3.28	35.41	1.64	0.66
4484.81	2.04	25.51	2.55	0.00

4417.18	1.06	22.75	2.12	0.00
4946.73	0.63	23.27	1.89	0.31
5395.86	1.34	36.12	3.34	0.00
5614.61	1.11	54.07	3.70	0.00
5828.61	0.70	24.65	1.06	0.35
6037.07	0.35	26.06	3.52	0.35
6239.20	1.17	37.89	1.56	0.39
6434.21	0.93	36.57	0.93	0.00
6621.51	1.62	28.48	1.29	0.00
6801.70	1.09	38.80	3.28	0.00
6978.50	1.42	26.54	2.84	0.00
7144.86	1.21	30.82	1.51	0.30
7309.89	1.99	27.91	1.66	0.00
7471.93	0.89	45.24	3.27	0.60
7632.01	3.49	31.43	3.81	0.63
7811.00	2.98	31.46	4.30	0.00

cal yr BP	Poaceae (Grasses)	Rosaceae (Roses)	*Salix* (Willows)	Undiff. Asteraceae	*Sarcobatus* (Greasewood)	*Vaccinium* (Blueberry)
-10.00	4.44	0.00	6.67	0.00	0.00	0.00
11.51	9.96	0.00	12.26	0.00	0.00	0.00
85.05	5.33	0.00	8.20	0.00	0.00	0.00
235.23	4.35	0.00	3.34	2.34	0.00	0.00
451.57	2.95	0.00	3.32	1.11	0.00	0.00
685.83	2.56	0.00	2.20	1.10	0.00	0.00
916.28	10.93	0.00	6.07	0.81	0.00	0.00
1146.23	5.03	0.00	3.77	0.94	0.00	0.00
1378.54	2.88	0.00	2.24	0.96	0.00	0.00
1613.30	2.87	0.00	3.18	1.27	0.00	0.00
1850.15	8.44	0.00	8.44	2.67	0.00	0.00
2088.69	8.89	0.00	5.78	0.89	0.00	0.00

2328.57	1.41	0.00	2.83	1.41	0.00	0.00
2569.39	1.31	0.00	1.31	1.31	0.00	0.00
2810.78	0.60	0.00	1.49	1.19	0.00	0.00
3052.56	2.24	0.00	2.24	1.60	0.00	0.00
3293.76	3.75	0.00	7.08	1.25	0.00	0.00
3534.60	1.66	0.00	8.84	2.21	0.00	0.00
3774.50	0.61	0.00	2.43	0.91	0.00	0.00
4013.09	0.66	0.33	0.66	4.59	1.31	0.00
4484.81	0.00	0.00	7.65	2.55	0.51	0.00
4417.18	0.53	0.00	11.11	1.06	1.59	0.00
4946.73	2.83	0.00	2.20	1.57	0.94	0.00
5395.86	5.02	0.33	2.34	2.34	1.34	0.00
5614.61	2.96	0.00	1.85	5.19	1.48	0.00
5828.61	2.11	0.00	0.35	2.11	0.70	0.35
6037.07	2.82	0.00	2.11	5.28	1.06	0.35
6239.20	4.69	0.00	1.17	4.69	1.56	0.00
6434.21	0.93	0.00	8.33	2.78	0.46	0.00
6621.51	2.27	0.00	1.62	2.27	0.32	0.32
6801.70	1.64	0.00	8.74	3.83	0.00	0.00
6978.50	0.00	0.00	4.74	1.42	0.00	0.00
7144.86	2.72	0.30	1.21	2.72	0.91	0.00
7309.89	3.65	0.00	0.66	1.33	0.33	0.00
7471.93	2.08	0.00	0.89	2.68	0.89	0.00
7632.01	4.44	0.32	0.32	2.54	0.63	0.32
7811.00	3.97	0.00	0.33	1.99	3.64	0.33

Appendix B - CHAR Output Data

cm Top_i (cm)	age Top_i (yr BP)	char Count_i (#)	char Vol_i (cm^3)	char Con_i (# cm^{-3})	char Acc_i (# cm^{-2} yr^{-1})	charBkg (# cm^{-2} yr^{-1})	char Peak (# cm^{-2} yr^{-1})	peak Mag (# cm^{-2} $peak^{-1}$)	smPeak Frequ (peaks $1ka^{-1}$)
7.88	82	15	1.00	15.32	0.5210	0.5891	-0.0681	0.0000	0.03
8.87	111	20	1.00	19.78	0.5796	0.5466	0.0330	0.0000	0.10
9.72	140	25	1.00	24.84	0.6546	0.5046	0.1500	0.0000	0.18
10.48	169	17	1.00	17.00	0.4062	0.4632	-0.0570	0.0000	0.26
11.18	198	14	1.00	13.59	0.3029	0.4223	-0.1194	0.0000	0.33
11.82	227	12	1.00	12.27	0.2572	0.3820	-0.1248	0.0000	0.41
12.43	256	24	1.00	24.16	0.4812	0.3430	0.1382	0.0000	0.49
13.01	285	27	1.00	27.47	0.5231	0.3143	0.2088	0.0000	0.56
13.56	314	7	1.00	7.00	0.1291	0.2900	-0.1608	0.0000	0.64
14.09	343	7	1.00	6.77	0.1218	0.2708	-0.1490	0.0000	0.71
14.62	372	8	1.00	8.01	0.1410	0.2562	-0.1152	0.0000	0.79
15.13	401	17	1.00	16.86	0.2923	0.2427	0.0496	0.0000	0.87
15.63	430	21	1.00	21.41	0.3672	0.2299	0.1373	0.0000	0.95
16.13	459	11	1.00	10.51	0.1790	0.2215	-0.0425	0.0000	1.03
16.62	488	10	1.00	10.14	0.1722	0.2184	-0.0463	0.0000	1.12
17.11	517	14	1.00	14.43	0.2449	0.2163	0.0287	0.0000	1.20
17.61	546	15	1.00	15.40	0.2623	0.2171	0.0452	0.0000	1.28
18.10	575	11	1.00	11.48	0.1961	0.2177	-0.0216	0.0000	1.35
18.59	604	7	1.00	6.83	0.1170	0.2192	-0.1021	0.0000	1.42
19.09	633	14	1.00	14.10	0.2424	0.2248	0.0176	0.0000	1.48
19.59	662	10	1.00	9.82	0.1692	0.2354	-0.0661	0.0000	1.53
20.09	691	11	1.00	10.79	0.1864	0.2476	-0.0612	0.0000	1.58
20.59	720	29	1.00	29.42	0.5091	0.2581	0.2510	0.0000	1.63
21.09	749	82	1.00	81.64	1.4152	0.2666	1.1486	0.0000	1.68
21.59	778	87	1.00	87.33	1.5160	0.2748	1.2412	58.7687	1.73
22.10	807	12	1.00	12.02	0.2090	0.2843	-0.0753	0.0000	1.77
22.60	836	21	1.00	21.06	0.3664	0.2946	0.0718	0.0000	1.82
23.11	865	24	1.00	23.89	0.4161	0.3045	0.1116	0.0000	1.86
23.61	894	19	1.00	19.07	0.3323	0.3134	0.0189	0.0000	1.89
24.12	923	15	1.00	14.55	0.2535	0.3227	-0.0692	0.0000	1.93
24.62	952	11	1.00	11.26	0.1963	0.3369	-0.1407	0.0000	1.95
25.13	981	16	1.00	15.79	0.2751	0.3569	-0.0818	0.0000	1.97
25.63	1010	20	1.00	20.18	0.3514	0.3773	-0.0259	0.0000	1.99
26.14	1039	24	1.00	24.31	0.4228	0.3952	0.0276	0.0000	1.99
26.64	1068	21	1.00	21.16	0.3677	0.4147	-0.0471	0.0000	2.00
27.15	1097	26	1.00	26.38	0.4577	0.4309	0.0268	0.0000	2.01
27.65	1126	37	1.00	36.84	0.6382	0.4473	0.1909	0.0000	2.01
28.15	1155	45	1.00	44.94	0.7773	0.4655	0.3118	2.7215	2.03
28.65	1184	33	1.00	33.07	0.5711	0.4837	0.0874	0.0000	2.05
29.15	1213	20	1.00	20.45	0.3528	0.4993	-0.1465	0.0000	2.07
29.65	1242	19	1.00	19.47	0.3353	0.5098	-0.1745	0.0000	2.10
30.15	1271	27	1.00	26.53	0.4563	0.5142	-0.0580	0.0000	2.13

30.65	1300	34	1.00	33.63	0.5775	0.5140	0.0636	0.0000	2.15
31.15	1329	38	1.00	38.42	0.6590	0.5121	0.1470	0.0000	2.18
31.65	1358	31	1.00	31.17	0.5338	0.5087	0.0252	0.0000	2.20
32.14	1387	33	1.00	32.86	0.5622	0.5014	0.0608	0.0000	2.22
32.64	1416	29	1.00	29.45	0.5032	0.4891	0.0141	0.0000	2.23
33.14	1445	31	1.00	30.65	0.5229	0.4712	0.0517	0.0000	2.24
33.63	1474	31	1.00	31.40	0.5352	0.4493	0.0859	0.0000	2.25
34.13	1503	14	1.00	14.17	0.2413	0.4249	-0.1836	0.0000	2.25
34.62	1532	20	1.00	20.09	0.3416	0.4016	-0.0600	0.0000	2.25
35.11	1561	19	1.00	18.70	0.3175	0.3820	-0.0645	0.0000	2.26
35.60	1590	24	1.00	23.82	0.4042	0.3674	0.0368	0.0000	2.26
36.10	1619	20	1.00	19.90	0.3372	0.3575	-0.0204	0.0000	2.27
36.59	1648	22	1.00	21.75	0.3681	0.3511	0.0170	0.0000	2.28
37.08	1677	12	1.00	12.12	0.2049	0.3478	-0.1428	0.0000	2.29
37.57	1706	24	1.00	24.39	0.4122	0.3469	0.0652	0.0000	2.31
38.06	1735	21	1.00	21.49	0.3628	0.3483	0.0145	0.0000	2.32
38.55	1764	33	1.00	33.38	0.5628	0.3524	0.2104	1.2531	2.34
39.04	1793	14	1.00	14.00	0.2358	0.3586	-0.1227	0.0000	2.36
39.53	1822	14	1.00	14.23	0.2396	0.3664	-0.1269	0.0000	2.38
40.01	1851	22	1.00	22.00	0.3701	0.3734	-0.0034	0.0000	2.40
40.50	1880	23	1.00	23.00	0.3864	0.3764	0.0100	0.0000	2.41
40.99	1909	25	1.00	24.96	0.4190	0.3748	0.0442	0.0000	2.42
41.48	1938	29	1.00	28.80	0.4832	0.3738	0.1093	0.0000	2.44
41.96	1967	19	1.00	18.85	0.3159	0.3763	-0.0604	0.0000	2.46
42.45	1996	36	1.00	35.89	0.6010	0.3791	0.2219	0.9882	2.48
42.93	2025	22	1.00	22.43	0.3754	0.3773	-0.0019	0.0000	2.52
43.42	2054	9	1.00	9.15	0.1531	0.3697	-0.2166	0.0000	2.56
43.90	2083	15	1.00	15.04	0.2514	0.3603	-0.1090	0.0000	2.60
44.39	2112	28	1.00	27.81	0.4645	0.3527	0.1117	0.0000	2.65
44.87	2141	31	1.00	31.00	0.5174	0.3491	0.1684	0.0000	2.70
45.36	2170	17	1.00	16.87	0.2814	0.3503	-0.0689	0.0000	2.74
45.84	2199	16	1.00	16.38	0.2732	0.3555	-0.0824	0.0000	2.79
46.33	2228	13	1.00	13.25	0.2209	0.3625	-0.1417	0.0000	2.83
46.81	2257	27	1.00	26.91	0.4481	0.3665	0.0816	0.0000	2.87
47.29	2286	26	1.00	26.07	0.4338	0.3710	0.0628	0.0000	2.90
47.77	2315	20	1.00	20.19	0.3360	0.3742	-0.0383	0.0000	2.92
48.26	2344	24	1.00	23.99	0.3990	0.3758	0.0232	0.0000	2.95
48.74	2373	29	1.00	28.67	0.4765	0.3768	0.0998	0.0000	2.97
49.22	2402	22	1.00	22.47	0.3733	0.3780	-0.0047	0.0000	3.00
49.70	2431	11	1.00	11.45	0.1902	0.3779	-0.1877	0.0000	3.03
50.18	2460	35	1.00	34.95	0.5803	0.3757	0.2046	0.0000	3.07
50.67	2489	56	1.00	55.82	0.9265	0.3733	0.5532	8.9920	3.12
51.15	2518	21	1.00	21.18	0.3515	0.3708	-0.0194	0.0000	3.17
51.63	2547	12	1.00	12.10	0.2007	0.3672	-0.1665	0.0000	3.22
52.11	2576	26	1.00	26.00	0.4312	0.3626	0.0685	0.0000	3.29
52.59	2605	25	1.00	25.11	0.4163	0.3598	0.0565	0.0000	3.35
53.07	2634	20	1.00	19.78	0.3279	0.3614	-0.0336	0.0000	3.41
53.55	2663	19	1.00	19.09	0.3163	0.3690	-0.0526	0.0000	3.48
54.03	2692	33	1.00	33.46	0.5543	0.3819	0.1724	0.0000	3.54
54.51	2721	14	1.00	14.00	0.2319	0.3979	-0.1661	0.0000	3.59

54.99	2750	16	1.00	15.97	0.2646	0.4102	-0.1456	0.0000	3.64
55.47	2779	21	1.00	20.73	0.3432	0.4264	-0.0832	0.0000	3.69
55.95	2808	45	1.00	45.41	0.7521	0.4448	0.3072	2.4006	3.74
56.43	2837	31	1.00	30.74	0.5089	0.4634	0.0455	0.0000	3.78
56.91	2866	36	1.00	36.22	0.5996	0.4775	0.1221	0.0000	3.83
57.39	2895	29	1.00	28.64	0.4741	0.4838	-0.0097	0.0000	3.86
57.87	2924	29	1.00	28.96	0.4794	0.4792	0.0002	0.0000	3.89
58.35	2953	41	1.00	41.16	0.6815	0.4625	0.2190	0.6021	3.92
58.83	2982	37	1.00	37.47	0.6204	0.4388	0.1815	0.0000	3.93
59.32	3011	26	1.00	26.24	0.4345	0.4159	0.0186	0.0000	3.93
59.80	3040	15	1.00	15.11	0.2503	0.3983	-0.1479	0.0000	3.91
60.28	3069	11	1.00	11.07	0.1833	0.3836	-0.2004	0.0000	3.88
60.76	3098	16	1.00	15.93	0.2639	0.3699	-0.1060	0.0000	3.84
61.24	3127	19	1.00	18.65	0.3089	0.3576	-0.0487	0.0000	3.78
61.72	3156	19	1.00	19.05	0.3156	0.3501	-0.0344	0.0000	3.72
62.20	3185	26	1.00	26.44	0.4381	0.3481	0.0900	0.0000	3.66
62.68	3214	31	1.00	31.37	0.5199	0.3492	0.1707	0.4991	3.59
63.16	3243	24	1.00	23.97	0.3975	0.3489	0.0485	0.0000	3.52
63.64	3272	19	1.00	19.25	0.3193	0.3447	-0.0254	0.0000	3.46
64.12	3301	21	1.00	21.26	0.3527	0.3355	0.0173	0.0000	3.39
64.60	3330	24	1.00	23.78	0.3945	0.3213	0.0732	0.0000	3.33
65.08	3359	13	1.00	13.26	0.2202	0.3039	-0.0837	0.0000	3.26
65.56	3388	15	1.00	14.53	0.2413	0.2861	-0.0448	0.0000	3.20
66.05	3417	11	1.00	11.01	0.1828	0.2696	-0.0868	0.0000	3.15
66.53	3446	28	1.00	27.72	0.4608	0.2538	0.2069	2.9851	3.09
67.01	3475	13	1.00	13.00	0.2161	0.2388	-0.0227	0.0000	3.04
67.49	3504	11	1.00	11.04	0.1836	0.2249	-0.0413	0.0000	3.00
67.97	3533	14	1.00	13.83	0.2302	0.2130	0.0172	0.0000	2.95
68.46	3562	17	1.00	16.73	0.2785	0.2034	0.0751	0.0000	2.91
68.94	3591	11	1.00	10.89	0.1814	0.1947	-0.0133	0.0000	2.87
69.42	3620	4	1.00	4.13	0.0689	0.1864	-0.1175	0.0000	2.84
69.91	3649	11	1.00	11.04	0.1841	0.1789	0.0051	0.0000	2.80
70.39	3678	9	1.00	9.15	0.1526	0.1752	-0.0226	0.0000	2.77
70.87	3707	9	1.00	9.47	0.1582	0.1757	-0.0176	0.0000	2.74
71.36	3736	11	1.00	10.70	0.1788	0.1812	-0.0024	0.0000	2.71
71.84	3765	13	1.00	13.02	0.2176	0.1939	0.0237	0.0000	2.68
72.33	3794	8	1.00	8.23	0.1377	0.2143	-0.0766	0.0000	2.64
72.81	3823	7	1.00	6.83	0.1144	0.2408	-0.1264	0.0000	2.61
73.30	3852	18	1.00	17.88	0.2995	0.2694	0.0302	0.0000	2.57
73.78	3881	17	1.00	16.71	0.2802	0.2943	-0.0141	0.0000	2.53
74.27	3910	16	1.00	15.77	0.2645	0.3120	-0.0475	0.0000	2.48
74.76	3939	26	1.00	25.97	0.4361	0.3232	0.1128	0.0000	2.44
75.24	3968	34	1.00	33.82	0.5685	0.3195	0.2490	0.0000	2.39
75.73	3997	33	1.00	32.55	0.5475	0.3271	0.2204	10.3765	2.35
76.22	4026	24	1.00	23.63	0.3979	0.3330	0.0649	0.0000	2.30
76.71	4055	17	1.00	16.62	0.2800	0.3348	-0.0548	0.0000	2.26
77.19	4084	14	1.00	13.75	0.2319	0.3314	-0.0996	0.0000	2.21
77.68	4113	16	1.00	15.71	0.2651	0.3244	-0.0593	0.0000	2.17
78.17	4142	15	1.00	15.34	0.2592	0.3148	-0.0556	0.0000	2.12
78.66	4171	15	1.00	15.12	0.3358	0.3053	0.0305	0.0000	2.07

79.31	4200	27	1.00	27.29	0.7883	0.3003	0.4880	0.0000	2.03
80.14	4229	33	1.00	33.36	0.5656	0.3017	0.2639	16.9887	1.99
80.64	4258	14	1.00	14.44	0.2450	0.3094	-0.0644	0.0000	1.96
81.13	4287	13	1.00	13.18	0.2240	0.3218	-0.0979	0.0000	1.94
81.62	4316	21	1.00	21.15	0.3598	0.3361	0.0237	0.0000	1.91
82.11	4345	15	1.00	15.22	0.2591	0.3497	-0.0906	0.0000	1.90
82.61	4374	17	1.00	17.45	0.2975	0.3613	-0.0638	0.0000	1.88
83.10	4403	23	1.00	23.20	0.3959	0.3706	0.0253	0.0000	1.85
83.60	4432	25	1.00	24.75	0.4229	0.3767	0.0461	0.0000	1.83
84.09	4461	29	1.00	28.72	0.4914	0.3896	0.1018	0.0000	1.79
84.59	4490	33	1.00	32.69	0.5603	0.3912	0.1690	0.0000	1.76
85.09	4519	33	1.00	32.65	0.5601	0.3882	0.1720	0.0000	1.72
85.58	4548	15	1.00	14.69	0.2524	0.3794	-0.1270	0.0000	1.67
86.08	4577	12	1.00	11.87	0.2043	0.3668	-0.1625	0.0000	1.63
86.58	4606	29	1.00	28.63	0.4933	0.3543	0.1390	0.0000	1.58
87.08	4635	13	1.00	13.41	0.2314	0.3447	-0.1134	0.0000	1.53
87.58	4664	23	1.00	23.23	0.4015	0.3385	0.0630	0.0000	1.48
88.08	4693	8	1.00	8.34	0.1442	0.3353	-0.1911	0.0000	1.44
88.58	4722	9	1.00	9.28	0.1608	0.3347	-0.1739	0.0000	1.40
89.09	4751	30	1.00	29.82	0.5177	0.3372	0.1805	0.0000	1.36
89.59	4780	27	1.00	27.33	0.4752	0.3429	0.1322	0.0000	1.32
90.09	4809	20	1.00	20.39	0.3552	0.3522	0.0030	0.0000	1.28
90.60	4838	21	1.00	20.55	0.3585	0.3662	-0.0078	0.0000	1.24
91.10	4867	14	1.00	14.12	0.2468	0.3814	-0.1346	0.0000	1.20
91.61	4896	15	1.00	14.75	0.2581	0.3927	-0.1346	0.0000	1.17
92.12	4925	28	1.00	28.00	0.4911	0.3971	0.0940	0.0000	1.14
92.63	4954	28	1.00	27.78	0.4879	0.3965	0.0913	0.0000	1.10
93.14	4983	21	1.00	20.73	0.3648	0.3952	-0.0304	0.0000	1.07
93.65	5012	30	1.00	29.65	0.5228	0.3940	0.1288	0.0000	1.05
94.16	5041	31	1.00	30.66	0.5417	0.3916	0.1501	0.6257	1.03
94.67	5070	16	1.00	16.30	0.2885	0.3859	-0.0973	0.0000	1.01
95.18	5099	22	1.00	21.69	0.3846	0.3754	0.0092	0.0000	1.00
95.70	5128	16	1.00	15.93	0.2830	0.3611	-0.0781	0.0000	1.00
96.21	5157	17	1.00	17.01	0.3028	0.3453	-0.0425	0.0000	0.99
96.73	5186	20	1.00	19.61	0.3499	0.3289	0.0210	0.0000	0.98
97.25	5215	19	1.00	18.54	0.3315	0.3130	0.0186	0.0000	0.97
97.77	5244	19	1.00	19.45	0.3485	0.2996	0.0489	0.0000	0.95
98.29	5273	17	1.00	17.24	0.3095	0.2889	0.0206	0.0000	0.94
98.81	5302	15	1.00	15.37	0.2766	0.2804	-0.0038	0.0000	0.93
99.33	5331	12	1.00	12.31	0.2221	0.2755	-0.0534	0.0000	0.92
99.85	5360	15	1.00	14.58	0.2636	0.2748	-0.0111	0.0000	0.92
100.38	5389	10	1.00	9.89	0.1793	0.2782	-0.0989	0.0000	0.92
100.90	5418	13	1.00	12.88	0.2339	0.2840	-0.0502	0.0000	0.93
101.43	5447	13	1.00	13.14	0.2393	0.2911	-0.0518	0.0000	0.95
101.96	5476	17	1.00	16.67	0.3043	0.3012	0.0031	0.0000	0.97
102.49	5505	22	1.00	21.83	0.3997	0.3153	0.0844	0.0000	1.00
103.02	5534	21	1.00	21.28	0.3906	0.3314	0.0593	0.0000	1.04
103.55	5563	23	1.00	22.92	0.4218	0.3453	0.0765	0.0000	1.08
104.08	5592	15	1.00	15.24	0.2813	0.3537	-0.0724	0.0000	1.13
104.62	5621	12	1.00	11.89	0.2201	0.3558	-0.1357	0.0000	1.19

105.16	5650	27	1.00	26.55	0.4930	0.3541	0.1389	0.0000	1.25
105.69	5679	26	1.00	25.72	0.4791	0.3507	0.1284	0.0000	1.33
106.23	5708	18	1.00	18.19	0.3399	0.3460	-0.0061	0.0000	1.41
106.78	5737	17	1.00	17.25	0.3235	0.3399	-0.0165	0.0000	1.49
107.32	5766	10	1.00	9.67	0.1819	0.3320	-0.1501	0.0000	1.59
107.87	5795	18	1.00	18.29	0.3453	0.3228	0.0225	0.0000	1.70
108.41	5824	22	1.00	21.84	0.4139	0.3200	0.0939	0.0000	1.81
108.96	5853	18	1.00	18.07	0.3437	0.3174	0.0262	0.0000	1.93
109.51	5882	10	1.00	10.24	0.1956	0.3189	-0.1234	0.0000	2.06
110.07	5911	13	1.00	12.66	0.2427	0.3260	-0.0833	0.0000	2.20
110.62	5940	13	1.00	12.73	0.2450	0.3381	-0.0931	0.0000	2.33
111.18	5969	17	1.00	17.48	0.3376	0.3532	-0.0156	0.0000	2.47
111.74	5998	23	1.00	22.98	0.4458	0.3685	0.0772	0.0000	2.60
112.30	6027	18	1.00	18.31	0.3566	0.3837	-0.0271	0.0000	2.73
112.87	6056	44	1.00	44.38	0.8686	0.4005	0.4681	0.0000	2.85
113.44	6085	35	1.00	34.89	0.6858	0.4174	0.2684	14.2160	2.98
114.01	6114	17	1.00	16.53	0.3266	0.4311	-0.1045	0.0000	3.10
114.58	6143	28	1.00	27.62	0.5481	0.4387	0.1095	0.0000	3.22
115.16	6172	27	1.00	27.16	0.5418	0.4398	0.1019	0.0000	3.33
115.73	6201	19	1.00	19.46	0.3900	0.4337	-0.0437	0.0000	3.44
116.32	6230	24	1.00	23.78	0.4791	0.4201	0.0590	0.0000	3.55
116.90	6259	28	1.00	27.66	0.5601	0.4010	0.1591	1.2886	3.65
117.49	6288	19	1.00	18.68	0.3806	0.3812	-0.0006	0.0000	3.74
118.08	6317	14	1.00	13.85	0.2837	0.3599	-0.0762	0.0000	3.82
118.67	6346	15	1.00	14.60	0.3007	0.3411	-0.0404	0.0000	3.88
119.27	6375	13	1.00	12.85	0.2663	0.3237	-0.0574	0.0000	3.94
119.87	6404	11	1.00	10.57	0.2203	0.3069	-0.0866	0.0000	3.98
120.47	6433	12	1.00	12.09	0.2539	0.2902	-0.0364	0.0000	4.01
121.08	6462	17	1.00	17.15	0.3622	0.2751	0.0871	0.0000	4.03
121.70	6491	19	1.00	19.43	0.4129	0.2631	0.1498	2.6618	4.05
122.31	6520	11	1.00	10.91	0.2333	0.2535	-0.0202	0.0000	4.06
122.93	6549	12	1.00	12.22	0.2631	0.2434	0.0196	0.0000	4.06
123.56	6578	9	1.00	9.47	0.2051	0.2313	-0.0262	0.0000	4.05
124.18	6607	10	1.00	9.50	0.2070	0.2167	-0.0097	0.0000	4.04
124.82	6636	4	1.00	3.87	0.0848	0.2012	-0.1164	0.0000	4.02
125.45	6665	9	1.00	9.41	0.2074	0.1885	0.0190	0.0000	3.99
126.09	6694	12	1.00	11.72	0.2601	0.1824	0.0777	0.4101	3.96
126.74	6723	4	1.00	4.23	0.0944	0.1838	-0.0894	0.0000	3.91
127.38	6752	6	1.00	5.66	0.1270	0.1907	-0.0637	0.0000	3.86
128.03	6781	8	1.00	8.28	0.1870	0.2029	-0.0159	0.0000	3.80
128.69	6810	7	1.00	6.63	0.1504	0.2199	-0.0695	0.0000	3.73
129.35	6839	11	1.00	10.52	0.2401	0.2380	0.0021	0.0000	3.66
130.01	6868	11	1.00	10.78	0.2475	0.2540	-0.0066	0.0000	3.57
130.67	6897	16	1.00	15.56	0.3590	0.2682	0.0908	1.2114	3.48
131.34	6926	10	1.00	10.48	0.2429	0.2787	-0.0358	0.0000	3.39
132.02	6955	19	1.00	19.37	0.4518	0.2831	0.1687	0.0000	3.30
132.69	6984	18	1.00	18.28	0.4282	0.2822	0.1460	6.2344	3.22
133.37	7013	10	1.00	10.47	0.2464	0.2785	-0.0320	0.0000	3.13
134.05	7042	10	1.00	9.79	0.2315	0.2728	-0.0413	0.0000	3.04
134.74	7071	14	1.00	13.76	0.3268	0.2660	0.0608	0.0000	2.95

135.43	7100	5	1.00	5.45	0.1302	0.2588	-0.1286	0.0000	2.86
136.12	7129	7	1.00	7.45	0.1786	0.2532	-0.0746	0.0000	2.77
136.82	7158	7	1.00	7.44	0.1789	0.2508	-0.0719	0.0000	2.68
137.51	7187	14	1.00	13.56	0.3277	0.2523	0.0754	0.0000	2.58
138.21	7216	10	1.00	10.37	0.2515	0.2545	-0.0030	0.0000	2.47
138.92	7245	13	1.00	12.91	0.3142	0.2543	0.0598	0.0000	2.37
139.62	7274	9	1.00	8.74	0.2134	0.2519	-0.0385	0.0000	2.27
140.33	7303	20	1.00	19.92	0.4880	0.2477	0.2403	3.4531	2.17
141.04	7332	10	1.00	9.93	0.2441	0.2414	0.0027	0.0000	2.08
141.76	7361	12	1.00	11.94	0.2944	0.2347	0.0596	0.0000	1.99
142.47	7390	6	1.00	6.25	0.1546	0.2287	-0.0741	0.0000	1.91
143.19	7419	4	1.00	3.56	0.0883	0.2221	-0.1338	0.0000	1.85
143.91	7448	8	1.00	8.34	0.2073	0.2145	-0.0072	0.0000	1.78
144.63	7477	8	1.00	8.04	0.2001	0.2103	-0.0102	0.0000	1.70
145.35	7506	7	1.00	6.61	0.1648	0.2147	-0.0498	0.0000	1.62
146.07	7535	13	1.00	12.91	0.3227	0.2295	0.0933	0.0000	1.54
146.80	7564	11	1.00	11.01	0.2756	0.2532	0.0224	0.0000	1.46
147.52	7593	3	1.00	3.34	0.0838	0.2808	-0.1970	0.0000	1.38
148.25	7622	2	1.00	2.04	0.0511	0.3038	-0.2527	0.0000	1.30
148.98	7651	14	1.00	14.00	0.3516	0.3194	0.0323	0.0000	1.22
149.71	7680	17	1.00	17.14	0.4309	0.3217	0.1092	0.0000	1.13
150.43	7709	18	1.00	17.70	0.4452	0.3227	0.1225	0.0000	1.05
151.16	7738	22	1.00	21.77	0.5477	0.3240	0.2237	0.0000	0.97
151.89	7767	17	1.00	17.49	0.4401	0.3250	0.1151	8.1877	0.89
152.62	7796	10	1.00	9.52	0.2387	0.3250	-0.0863	0.0000	0.82
153.35	7825	14	1.00	13.97	0.3491	0.3235	0.0257	0.0000	0.74
154.08	7854	16	1.00	15.76	0.2309	0.3199	-0.0890	0.0000	0.66
	7883	4	0.28	3.86	0.0000	0.3143	-0.3143	0.0000	0.57