LATE QUATERNARY AND HOLOCENE PALEOECOLOGY OF INTERIOR MESIC FORESTS OF NORTHERN IDAHO

by

ERIN MAURYEEN HERRING

A DISSERTATION

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Student: Erin Mauryeen Herring

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This dissertation has been accepted and approved in partial fulfillment of the requirements for the Doctor of Philosophy degree in the Department of Geography by:

Daniel G. Gavin	Chair
Patrick J. Bartlein	Core Member
W. Andrew Marcus	Core Member
Gregory J. Retallack	Institutional Representative

and

J. Andrew Berglund	Dean of the Graduate School

Original approval signatures are on file with the University of Oregon Graduate School.

Degree awarded September 2014

DISSERTATION ABSTRACT

Erin Mauryeen Herring

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The mesic forests distributed within the Rocky Mountains of northern Idaho are unique because many species contained within the forest are separated from their main distribution along the Pacific Northwest coast. It remains unclear whether most species within the inland disjunction survived the glacial periods of the Pleistocene, or whether they were more recently dispersed from coastal populations. To see if the dominant tree taxa of the mesic forests today could have persisted in a refugium south of the large ice sheets, four sediment cores were used to reconstruct the vegetation and climate history of the region. A nearly continuous record of pollen and sediment composition (biogenic silica and inorganic and organic matter) over the last ca. 120,000 years provides evidence of a dynamic ecosystem. Over a long timescale, the slow shifts in vegetation are attributed to the changes in climate. During the last interglacial period, the region was warmer and drier with a *Pinus* dominated mixed conifer forest. Approximately 71,000 years ago, a *Pseudotsuga/Larix* forest became established in the area as a response to the increased available moisture. As climate cooled and glaciers expanded the *Pinus* and

Picea forest was the dominant vegetation type until ca. 40,000 years ago. The environment during the Last Glacial Maximum (LGM) was so harsh that no vegetation record was recorded. After the LGM, climate warmed, enabling a *Pinus* and *Picea* forest to establish and persist until the Holocene.

The mesic taxa that dominate the modern forests did not arrive in northern Idaho until the mid- to late-Holocene. The recent arrival of the dominant tree species, *Thuja plicata* and *Tsuga mertensiana,* suggests that they likely did not persist in a refugium during the last glaciation. Instead, these species recently dispersed from coastal populations, but expansion into their interior distributions was likely limited by both climate and species competition in already established forests. During the late-Quaternary, the deposition of thick tephra layers (>20 cm) from the eruptions of Glacier Peak (ca. 13,400 years ago) and Mt. Mazama (ca. 7,600 years ago) also facilitated an abrupt and persistent change in vegetation in northern Idaho.

CURRICULUM VITAE

NAME OF AUTHOR: Erin Mauryeen Herring

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon, Eugene
Northern Arizona University, Flagstaff
Humboldt State University, Arcata, California

DEGREES AWARDED:

Doctor of Philosophy, Geography, 2014, University of Oregon
Master of Science, Quaternary Sciences, 2009, Northern Arizona University
Bachelor of Science, Botany, 2007, Humboldt State University
Bachelor of Science, Geology, 2005, Humboldt State University

AREAS OF SPECIAL INTEREST:

Long-term environmental change
Fire-vegetation-climate linkages
Tephra-vegetation linkages

PROFESSIONAL EXPERIENCE:

Graduate Research Assistant, Department of Geography,
University of Oregon, 2008-2014

Course Instructor, Department of Geography, University of Oregon
Biogeography, Fall 2012, Summer 2014
The Natural Environment, Summer 2010, Winter 2012

Graduate Teaching Fellow, Department of Geography, University of Oregon, 2009-2012
Biogeography, Global Environmental Change, Introduction to Physical Geography, and Geomorphology

Graduate Teaching Fellow, Department of Biology, University of Oregon, 2008-2010
Biological Diversity, Introduction to Ecology, Systematic Botany

Graduate Research Assistant, Department of Quaternary Sciences, Northern Arizona University, 2005-2008

Laboratory Instructor, Department of Biology, Northern Arizona University, 2007-2008
Introduction to Biology

Researcher/Field Assistant, Department of Biology, Northern Arizona University, Summer 2007

Laboratory Instructor, Department of Geology, Northern Arizona University, 2005-2007
Introduction to Geology, Invertebrate Paleontology, Natural Disasters

GRANTS, AWARDS, AND HONORS:

Outstanding Graduate Student Poster, Northwest Scientific Association, 2012

Northwest Scientific Association Student Grant Award ($1500), 2012

PUBLICATIONS:

Gavin, D.G., Fitzpatrick, M., Heath, K., Rodriguez-Sanches, F., Dobrowski, S., Hampe, A., Hu, F.S., Ashcroft, M., Bartlein, P., Blois, J., Carstens, B., Davis, E., de Lafontaine, G., Edwards, M., Fernandez, M., Henne, P., Herring, E., Holden, Z., Kong, W.S., Liu, J., Magri, D., Matzke, N., McGlone, M., Saltre, F., Stigall, A., Tsai, Y., Williams, J., 2014. Climate refugia: joint inference from fossil records, species distribution models, and phylogeography. New Phytologist, 204, 37-54.

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I dedicate this to my grandmothers Miriam Herring and JoAnne Walsh, my mother Nancy Herring, my aunt Christine Walsh Ramirez, and my cousin and best friend Rebecca Marker.

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CHAPTER I

INTRODUCTION

The mesic forests within the northern Rocky Mountains of northern Idaho are unique in that many species of this region are separated from their main distribution along the Pacific Northwest coast. Within these mesic forests, there are over 100 vascular plant species, including the dominant trees, *Thuja plicata, Tsuga heterophylla,* and *Tsuga mertensiana* with both coastal and interior distributions (Björk, 2010). Prior to the Miocene, mesic forests were contiguous across the region. During the late Miocene (~10 million years ago), the Cascade Range was uplifted and volcanic mountains formed throughout the northwestern United States (Reiners et al., 2002). This orogeny led to the development of a pronounced rain shadow to the east. The decrease in moisture produced a sharp rainshadow that extends eastward to the northern Rocky and Columbia Mountains.

The repeated glaciations of the Pleistocene and the eruption of Mt. Mazama (ca. 7600 cal yr BP; (Zdanowicz et al., 1999) have had a large effect on species distributions (Whitlock, 1992; Brunelle & Whitlock, 2003; Brunelle et al., 2005; Long et al., 2014). It remains unclear whether most species in the inland disjunction survived the glacial periods within a north-Idaho refugium, (the Clearwater Range of northern Idaho) or whether these species were redistributed into the region during the Holocene. In the past decade, several studies have taken a genetic approach to answer this question (Brunsfeld & Sullivan, 2005; Brunsfeld et al., 2007; Carstens & Richards, 2007). The results of these phylogeographic studies provide broad support for refugial presence of a glacial refugium for some plant and amphibian taxa, and recent dispersal for other taxa. However, there has been no fossil evidence recovered from this area in northern Idaho.

Few paleovegetation or paleoclimate records exist from the interior mesic forests, and none that extend to the Last Glacial Maximum (LGM). In this dissertation I present the first climate and vegetation reconstructions from sediment cores taken within the mesic forests of northern Idaho. To reconstruct the environmental context in northern Idaho, I used a combination of pollen and sediment composition (biogenic silica and measures of inorganic and organic matter) analyses to infer the past climate and vegetation history of the interior mesic forests from four sediment cores. If this region existed as a mesic refugium in the past, then the pollen record should contain mesic taxa prior to the onset of the Holocene. I also examine the response of vegetation assemblages to changing climate conditions and natural disturbances such as tephra from Cascade volcanic eruptions.

In Chapter II, I present a late Pleistocene and Holocene vegetation and climate record from a nearly continuous, ca. 120,000-year-long sediment and peat core located near the southern end of the distribution of the mesic *Thuja plicata* forests in northern Idaho. Star Meadows is located 140 km south of the maximum extent of the Cordilleran ice sheet and was not occupied by alpine glaciers. Based on previous phylogenetic research (Carstens et al., 2004; Brunsfeld & Sullivan, 2005; Brunsfeld et al., 2007; Carstens & Richards, 2007) this location may have existed as a refugium during the last glaciation. I describe the long-term response of vegetation to climate change over the last ca. 120,000 years. Additionally, I examined the pollen record for evidence of a mesic refugium that existed throughout the last glacial cycle. This chapter details the first long (>14,000 year) record of climate and vegetation from northern Rockies.

Chapter III describes the regional vegetation of the last 7,600 years from Dismal, Horseshoe, and Rocky Ridge Lakes, mid- to high-elevation sites, in the Northern Rocky Mountains of Idaho. Each of these lakes are surrounded with varying abundances of *Tsuga mertensiana*, one of the dominant trees of the mesic forest, and are located near the southern edge of its modern distribution. The goals of this research were to: 1) create a new range map of *T. mertensiana*, 2) examine the relationship between *T. mertensiana* pollen abundance and distance from a known location, 3) determine the timing of the establishment of *T. mertensiana* in its disjunct interior distribution in northern Idaho, and 4) determine how climate and/or dispersal limitation may have influenced its modern distribution. The timing of *T. mertensiana* arrival at the southern disjunct population was then compared to the time of arrival at the northern disjunct population in British Columbia to examine if there were similar climatic events leading to the expansion of both disjunctions.

In Chapter IV, I extend the sediment record from Dismal Lake back to 13,600 years. I used a multi proxy (pollen, plant macrofossil, loss-on-ignition, and magnetic susceptibility) approach to present a high resolution record of a 10-m sediment core. Tephra from the eruption of Mt. Saint Helens (1980 AD), Mt. Mazama (ca. 7,600 cal yr BP; (Zdanowicz et al., 1999), and Glacier Peak (ca. 13,400 cal yr BP; (Kuehn et al., 2009) are preserved in the record. The effects of the Mt. Mazama eruption and its effects on fire and vegetation have been the focus of some recent studies in the Cascade Range (Long et al., 2011, 2014), but all vegetation changes observed in those studies were attributed to climatic variations, and not driven by tephra deposition. The aim of this chapter was to determine the effect of thick tephra deposition in past environments far from the source of the tephra. This chapter provides the first high resolution vegetation record from the mesic forests of northern Idaho and evidence of tephra-mediated vegetation change from the Glacier Peak eruption. Chapter V summarizes the major findings of this dissertation research.

CHAPTER II

CLIMATE AND VEGETATION SINCE THE LAST INTERGLACIAL (MIS 5E) IN A PUTATIVE GLACIAL REFUGIUM, NORTHERN IDAHO, USA

1. Introduction

Worldwide there are very few terrestrial climate and vegetation records that span the interval from the last major interglacial, marine isotope stage (MIS) 5e (ca. 130 to 123 ka, or thousands of calendar years before present), though the Last Glacial Maximum (LGM; 26-19 ka), to the present. Less than ten such vegetation records exist south of the Cordilleran Ice Sheet in North America (Jiménez-Moreno et al., 2010), therefore little is known about how major vegetation types responded to changing climates during the last interglacial and subsequent stadial and interstadial events of the late Quaternary. Pollen records from northern Utah (Jiménez-Moreno et al., 2007), western Washington (Whitlock & Bartlein, 1997), and central, coastal, and southern California (Adam et al., 1981),indicate that the climate was cooler and drier during MIS 5 (130 to 71 ka) than our current interglacial (the Holocene, 11.7 ka to present). During the Last Glacial Maximum (LGM), there is considerably more evidence of climate and vegetation south of the Cordilleran Ice Sheet. In general, pollen records indicate reduced forest cover and increases in pollen types typical of cold and dry climates (Mehringer et al., 1977; Heusser et al., 1999; Jiménez-Moreno et al., 2007). However, most of these records occur within the Coast and Cascade ranges. Currently no paleovegetation records exist in the northern Rocky Mountains that extend back to the LGM (Thompson, 2007). The closest site to the northern Rocky Mountains in northern Idaho that dates to the LGM or earlier is Carp Lake in Washington (Whitlock et al., 2000). Paleoclimate simulations and existing pollen records suggest that the LGM vegetation across this broad mountainous region was a cold sagebrush steppe or tundra with sparse vegetation (Braconnot et al., 2007).

Within the northern Rocky Mountains of the USA, most terrestrial paleoecology research has focused on the late glacial and Holocene periods (Mehringer et al., 1977; Karsian, 1995; Doerner & Carrara, 1999, 2001; Millspaugh et al., 2004; Brunelle & Whitlock, 2003; Millspaugh et al., 2000; Brunelle et al., 2005; Power et al., 2006). A distinctive feature of the vegetation of this region is a zone of mesic forests extending northward from northern Idaho. These mesic forests are unique because they support at least 22 endemic plant species and more than 100 vascular plant species (including the canopy-dominant tree *Thuja plicata*) that are disjunct from their main population distribution along the Pacific Northwest coast (Björk, 2010). It remains unclear whether most species in the inland disjunction survived the glacial periods within a north-Idaho refugium, or whether these species were recently dispersed from coastal populations (Gavin, 2009). In the past decade, several studies have taken a genetic approach to this question (Brunsfeld & Sullivan, 2005; Brunsfeld et al., 2007; Carstens & Richards, 2007). These phylogeographic studies provide broad support for the presence of a glacial refugium for at least two plant and three amphibian taxa within the Clearwater Range of northern Idaho (Ritland et al., 2000; Nielson et al., 2001; Carstens et al., 2004; Brunsfeld & Sullivan, 2005; Thompson & Russell, 2005; Brunsfeld et al., 2007). However, few paleovegetation or paleoclimate records exist from the interior mesic forests, and none that extend to the LGM or earlier, to support these inferences of refugia.

In this study, I present a late Pleistocene and Holocene vegetation and climate record from a nearly continuous sediment and peat core located near the southern end of the distribution of the mesic *Thuja plicata* forests in northern Idaho (Figure 2.1). The study site, Star Meadows, is adjacent to the Lochsa River, and 140 km south of the maximum extent of the Cordilleran Ice Sheet. Although the mountains in the surrounding area, especially to the north and at high elevations, underwent extensive glaciation during the Pleistocene, Star Meadows is located down-valley of late Pleistocene terminal moraines (Figure 2.1b). The Lochsa River and other river canyons in the surrounding Clearwater National Forest comprise the putative glacial refugia (Daubenmire, 1975; Brunsfeld & Sullivan, 2005; Brunsfeld et al., 2007; Carstens & Richards, 2007). To reconstruct the environmental context of this region, I used a combination of fossil pollen and sediment composition (biogenic silica and measures of inorganic and organic matter) to infer the past climate and vegetation history of the interior mesic forests. If this region existed as a mesic refugium in the past, then the pollen record should reveal indicators of a mesic climate, such as continuous forest cover or the presence of mesic-adapted taxa, through the LGM.

2. Methods

2.1. Site description and field collection

Star Meadows is a 3.2 ha seasonally inundated meadow located on undulating terrain at 1109 m a.s.l. and 53 m above the Lochsa River in northern Idaho (Figure 2.1). Based on the height of the outlet at the northern end of the meadow, only 20 cm of water can fill the modern meadow. The meadow and other wetlands are located on the apparent

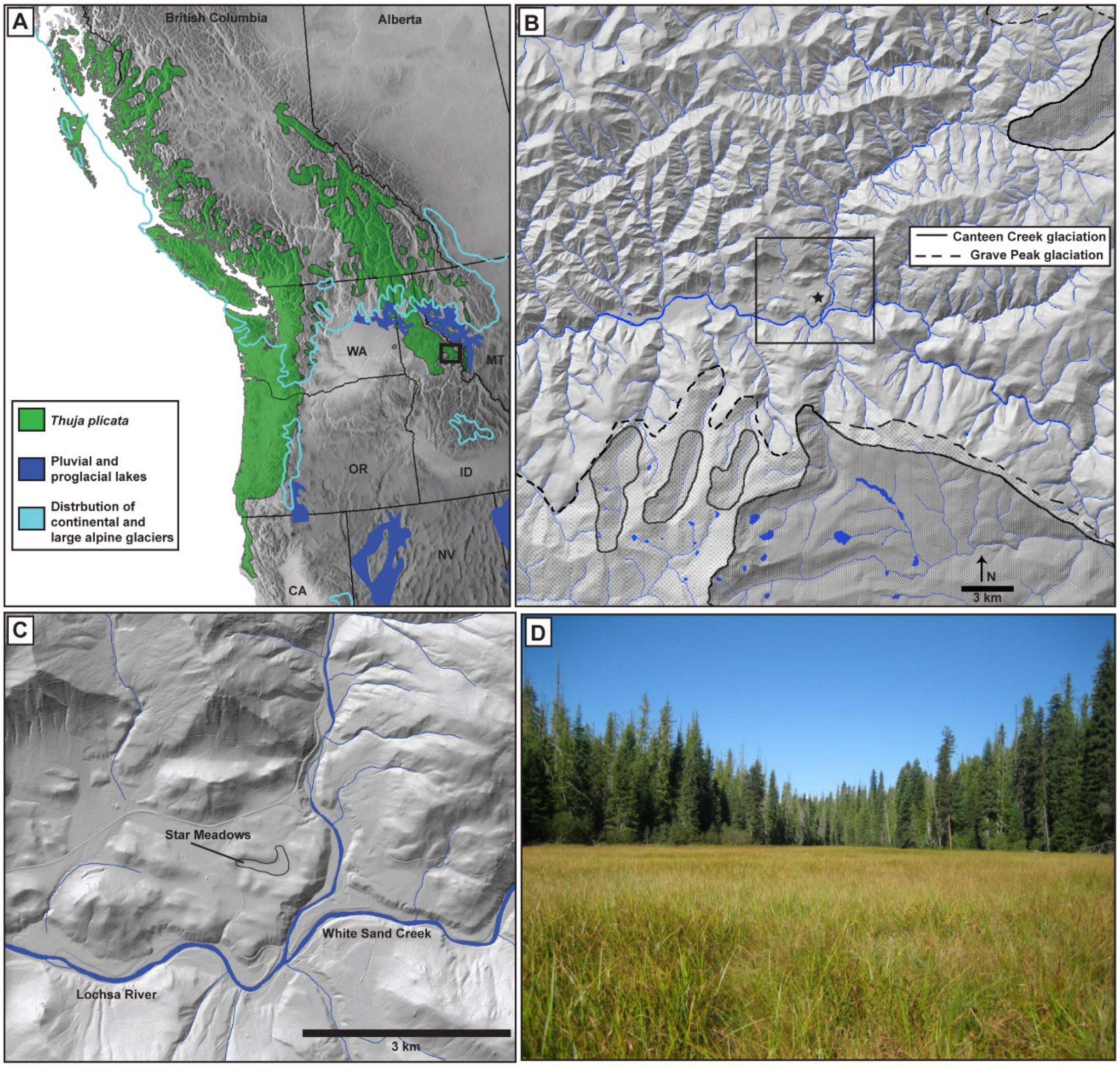


Figure 2.1. (A) The modern distribution of *Thuja plicata* in north-west North America (Little, 1971) plotted on a shaded relief map. Also shown are the locations of major pluvial lakes, proglacial lakes, and ice extent at 17 ka (Dyke et al., 2003). Square indicates enlarged map in (B). (B) Shaded relief map showing the location of Star Meadows (star icon) in the Lochsa River watershed. Late Pleistocene glacier extent correspond to two glaciations mapped by Dingler and Breckenridge (1982). Square indicates enlarged map in (C). (C) Shaded relief map showing the location of Star Meadows located on a landslide runout. (D) Photograph of Star Meadows showing the surrounding forest (dominated by *Thuja plicata*) and meadow vegetation (mainly *Carex* spp.).

run-out (Figure 2.1c). The wetland depressions may have originated from abandoned channels of the Lochsa River created before the river down-cut through the landslide debris. The vegetation of Star Meadows is dominated by *Carex aquatilis, Comarum palustre,* and other *Carex* spp. (Figure 2.1d). *Sphagnum* is limited to the southwestern edge of the meadow. The surrounding forest is dominated by *Thuja plicata,* with *Abies grandis*, *Picea engelmannii,* and minor amount of *Pseudotsuga menziesii* and *Pinus monticola*. A survey of the forest understory revealed 148 vascular plant species (Curtis Björk, personal communication). Common vascular plant and fern species include *Adiantum pedatum, Asarum caudatum, Coptis occidentalis, Disporum hookeri, Fragaria virginiana, Galium triflorum, Goodyera oblongifolia, Gymnocarpium dryopteris, Linnaea borealis, Smilacina stellate, Tiarella trifoliate,* and *Viola orbiculata*. *Thuja plicata* forests can extend up to 1675 m in elevation and are most abundant on riparian or poorly-drained sites (Daubenmire, 1980; Cooper et al., 1991). Above 1400 m, *T. plicata* forests transition into subalpine forests that are dominated by *Abies lasiocarpa, Pinus contorta,* and/or *Tsuga mertensiana*. Tree line within the Bitterroot Mountains does not often extend higher than 2300 m. The species list from the vegetation survey is in Appendix A.

Despite its interior location, the study region experiences a maritime west-coast climate with snowy winters. Mean annual precipitation is 97 cm distributed roughly evenly through the year, with approximately 35% as snow during the winter months. Snow cover persists, on average, from mid-November to early April (WRCC, 2014). In July the daily maximum and minimum temperatures are 27.6°C and 7.2°C, respectively (average=17.3°C). In December the daily maximum and minimum temperatures are -

1.2°C and -9.1°C, respectively (average=-5.2°C).

In August 2010 I obtained an 809 cm long core from the visually wettest location (46°30’56.8’’N, 114°40’55.7’’W) of the meadow using a modified square-rod Livingstone piston corer (Wright et al., 1984). To reduce friction from sediment along the drive rods, between each Livingstone core drive I widened the core hole by using a bucket auger attached to drive rods. However, resistance became too great to continue coring more than 8 meters. Continued use of the bucket auger, which could not retrieve samples, indicated peaty sediment continued to at least 900 cm. During the recovery of two core sections the piston slipped resulting in the loss of two short segments (342-367 cm and 698-706 cm). A second core (91.5 cm) was taken three meters from the first core, in order to ensure that I recovered a continuous sediment sequence above the Mazama ash, 7.63 ka. I extruded and wrapped each core section in the field. I transported the core to the Paleoecology and Biogeography Laboratory at University of Oregon and stored it at 4°C.

2.2. Laboratory analysis

2.2.1. Core description, magnetic susceptibility, CT-scan, and biogenic silica

I split the cores longitudinally and described the sediment stratigraphy by visual and microscopic inspection. Lithology was described by using guidelines outlined by (Schnurrenberger et al., 2003). The upper 91.5 cm of the cores were correlated by visual inspection. I measured magnetic susceptibility using a Bartington MS2 meter at one-cm intervals and photographed each core section using a line-scan camera on a GEOTEK “bench-top” split core MSCL-XY track (Marine Geology Repository at Oregon State

University). High resolution photos from the GEOTEK is in Appendix A.

Bulk density was measured on 44 samples (1 cm^3), followed by measurement of organic content using loss-on-ignition (at 550°C). To estimate bulk density at a resolution of ca. 0.5 mm, I scanned the core using a Toshiba CT-scan at Oregon State University College of Veterinary Medicine. I selected a longitudinal image of each core image using RadiAnt (free software; http://www.radiantviewer.com/) to locate the section with the fewest cracks, void spaces, and sediment disturbance due to root growth. Radio-opacity values were averaged at each depth along a 5-mm wide transect using ImageJ (free software; http://rsbweb.nih.gov/ij/). To express the opacity values as bulk density, I developed a linear relationship between measured bulk density (n=44) and the corresponding opacity values (r^2=0.897).

I analyzed percent organic carbon and nitrogen on 155 subsamples every ca. 5 cm using a Costech ECS 4010 CHN analyzer at the University of Illinois at Urbana-Champaign. Samples were oven dried and ground with a mortar and pestle until the samples had the consistency of a fine powder prior to analysis.

A total of 205 samples were analyzed for biogenic silica (BSi) using a wet digestion extraction procedure outlined by Mortlock and Froelich (1989). After six hours of digestion in a hot sodium carbonate solution, I assayed for Si concentration using the molybdate-blue method (Mortlock & Froelich, 1989).

2.2.2. Chronology

Six accelerator mass spectrometry (AMS) radiocarbon dates were obtained from the sediment core. I attempted to find charcoal or wood for each radiocarbon date, but at four depths I resorted to dating a 1 cm^3 sample of bulk sediment (pre-treated with 10% KOH and 10% HCl). The sediment of these samples was highly decomposed peat and the resultant dates are concordant with tephra and dates of macrofossils and thus consistent with an absence of a hard-water effect. Radiocarbon dates were calibrated to calendar years BP and rounded to the nearest decade using CALIB 5.0 (Stuiver & Reimer, 1993; Reimer et al., 2004). I created an age model using CLAM (Blaauw, 2010) with a monotonic spline between the six AMS dates and the Mazama tephra layer (Zdanowicz et al., 1999) for the portion of the core that was dateable by radiocarbon (<251 cm).

Absolute dating of the lower 558 cm of the core (older than 50,000 years) was not possible due to the absence of mineral matter suitable for optical-spin luminescence dating. To estimate the ages of this portion of the core, I noticed astrong visual correlation of percent organic carbon and the SPECMAP (Imbrie et al., 1984) $\delta^{18}O$ record, which would be expected if warm periods resulted in greater organic matter production. I attempted to use the NGRIP $\delta^{18}O$ record (North Greenland Ice Core Project Members, 2004), but the resolution of the Star Meadows core was not as high as the NGRIP record so correlation between the two records was problematic. I created two age models with alternative tie points between SPECMAP (1000 year resolution) and Star Meadows record to determine which match had the strongest correlation. I employed several rules in order to be consistent with each model: 1) all tie points between the percent organic carbon curve and $\delta^{18}O$ curve were limited to depths below the oldest radiocarbon age (251 cm), and 2) only two tie points, one at a peak and another at a trough in the organic carbon curve, were assigned to each pollen zone (see below for pollen zonation). In other words, for each peak (or trough) in percent organic matter, I selected a specific peak (or trough) in $\delta^{18}O$ from SPECMAP. I selected the age model that had a high percent organic content vs. SPECMAP correlation and that also produced an overall climate reconstruction that was consistent with glacial and interglacial periods.

2.2.3. Pollen analysis

I processed 179 (0.5 cm^3) samples for pollen analysis following standard methods (Krzywinski et al., 2000) with the addition of a second KOH extraction. Processed samples were stained and pollen was examined at 400X magnification. I identified pollen to the lowest taxonomic level possible based on published keys (Krzywinski et al., 2000; Kapp, 2000) and the modern pollen reference collection at the Paleoecology and Biogeography Laboratory at the University of Oregon. Asteraceae pollen types were differentiated into four categories: Tubuliflorae-type (sunflower); *Ambrosia*-type (bursage); Liguliflorae-type (lettuce subfamily), and *Artemisia* (sagebrush). *Pinus* (pine) grains were differentiated into *Pinus* and *Strobus* subgenera-types based upon the presence or absence of verrucae on the leptoma. All aquatic pollen types, algae, and Cyperaceae were excluded from the pollen sum. Cyperaceae was excluded from the total pollen sum because the meadow is currently dominated by *Carex* sp. If *Carex* were included in the pollen sum, it would strongly influence trends in the upland pollen types. I identified a minimum of 350 terrestrial pollen grains in the pollen sum, resulting in 367 to 953 total identified pollen grains per sample.

After all samples were counted, 10 *Betula* grains were measured at 20 levels in order to differentiate *Betula* grains to species level (*B. glandulosa* or *B. papyrifera*). *Betula* grain pore size and diameter were measured following the procedures outlined by

(Ives, 1977) and (Clegg et al., 2005). Pollen zones are based on a constrained cluster analysis (Grimm, 1987) using the total sum of squares method. Placement of zone boundaries was guided by other sediment properties (i.e., percent organic carbon and biogenic silica).

Table 2.1. AMS ^{14}C results for the Star Meadows core. All samples were analyzed at Lawrence Livermore National Laboratory.

Depth (cm)	14C age (yr BP)	Calibrated age (median cal yr BP and 2 σ range)	Item dated
58-59	4300 ± 220	4880 (4300-5500)	~60 pieces of charcoal
96-97	9845 ± 40	11240 (1200-11300)	1 cm^3 bulk sediment
177-178	27300 ± 130	31450 (31200-31700)	1 cm^3 bulk sediment
213-214	32120 ± 380	36500 (35300-37700)	1 cm^3 bulk sediment
230-231	38630 ± 430	42950 (42200-43700)	1 cm^3 bulk sediment
250-251	46370 ± 560	49450 (48470-50000)	Single piece of wood

3. Results

3.1. Core description, magnetic susceptibility, CT-scan and biogenic silica

The lithology of the Star Meadows core alternates between highly fragmental granular peat, sapropel, and sapropelic clays (inorganic silt and clay; Schnurrenberger et al., 2003; Figure 2.2). The base of the core (751-809 cm) consists of very dense fragmented granular peat. There is a diffuse contact with the dark-brown sapropelic silt and clay (706-751 cm) above the base peat layer. Above a gap in the core (697-706 cm), the sediment is a medium-brown sapropelic silt and clay from 564 to 697 cm above the gap in the core. Within this section, there are several thin (<1-cm) bedded very dark brown color bands. There is a diffuse contact to a fragmental granular peat layer that extends between 510 and 564 cm. The fragmental granular peat has very thin (< 1 cm) beds that consist of slight color changes (black and dark brown). The peat gradually grades into a very dark brown sapropelic silt and clay section extending from 367 to 510 cm. Above a 25-cm core gap (342-367 cm) is a dark brown sapropelic silt and clay extending from 313 to 342 cm. The core then transitions diffusely into a light brown silt and clay with little organics from 298 to 313 cm. At 298 cm there is a sharp contact to medium brown sapropelic silt and clay, which grades diffusely at 144 cm into a very light brown silt and clay layer with little organics. This layer has slight orange and green mottling from 90 to 124 cm. At 90 cm there is a sharp contact with the Mazama ash (73-90 cm). The ash layer has a diffuse contact with a light gray massive diatomaceous silt and clay, which extends from 40 to 73 cm. The diatomaceous layer has a diffuse contact with the fragmental granular peat, which extends from 43 to 0 cm. Photos of the core are in Appendix A.

Percent organic carbon varies from 0.3 to 59.7%. The highest percent organic carbon occurs within the peat-rich sediments (0-20, 514-549, and 734-809 cm). The lowest percent organic carbon occurs in clay and tephra-rich sections (64-175 cm) (Figure 2.2). Percent organic nitrogen varies from 0.03 to 3%. Variations in percent organic nitrogen mirror fluctuations in percent organic carbon, with the highest percentages occurring in the fragmental granular peat sections (0-20, 504-554, and 734-809 cm). C:N ratios, with the exception of five samples, are all greater than 10 indicating the source of sediment was mainly terrestrial (Meyers, 1994). The C:N ratio is higher in the lower two peat segments (21-34 and 18-45 respectively), suggesting the organic matter in these sections of the core were deposited from a terrestrial source and not an aquatic source. The percent of biogenic silica (BSi) varies from 0.6% (784 cm) to 54.9% (40 cm). The highest percentages (>40%) of BSi occur near the top (30 to 67 cm). There are three sections (103-137, 514-559, and 757-802 cm) containing < 6% BSi.

Bulk density estimated from radio-opacity (CT-scan) varied between 0.1 and 1.2 g/cm^3. A total of four peaks in bulk density were observed occurring at 79, 106, 212, and 297 cm. Magnetic susceptibility (MS) varies from $-1.3x10^{-5}$ to $2.5x10^{-5}$ SI with major peaks at approximately the same depths as high bulk density values. The lowest MS values occur in areas with high organic content.

3.2. Chronology

For the top 251 cm of the sediment core, a constrained spline age-depth model was used to create a chronology (Table 2.1; Figure 2.3). For the remainder of the core, I examined correlations between alternative age assignments for the percent organic carbon and the $\delta^{18}O$ record from SPECMAP. The first age-assignment model placed the base of the core at ca. 227 ka (r=-0.66) (Figure 2.3). The second model estimated the base at ca. 125 ka (r=-0.61). Additional attempts could not yield a higher correlation. I used the climatic interpretation of the pollen and sediment proxies to choose among the two models. I found no clear evidence of the penultimate (Illinoian) glaciation (MIS 6) in the sediment or pollen records that is similar in organic content and pollen assemblages to the LGM. There was also no evidence of any tephra deposits (i.e. Medicine Lake andesite tuff, various tephras from Mt. St. Helens, and Summer Lake JJ) below 251 cm that could provide another age constraints (Kuehn, personal communication; (Herrero-Bervera et al., 1994; Whitlock et al., 2000; Lanphere et al., 2002; Colman et al., 2006). Therefore, I

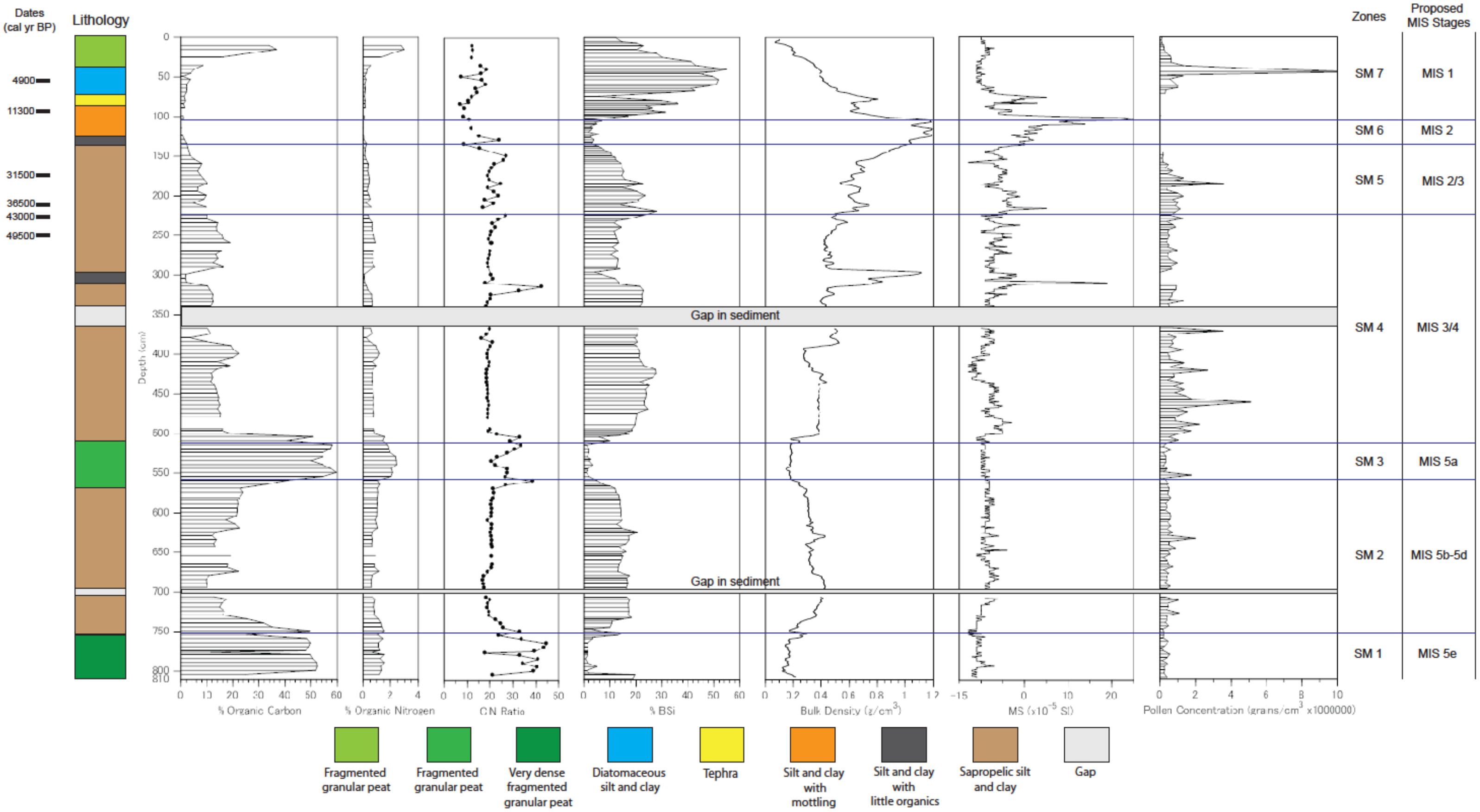


Figure 2.2. Sediment composition (% organic carbon, % organic nitrogen, C:N ratio, % BSi, bulk density, magnetic susceptibility (MS), and pollen concentration) of the Star Meadows core.

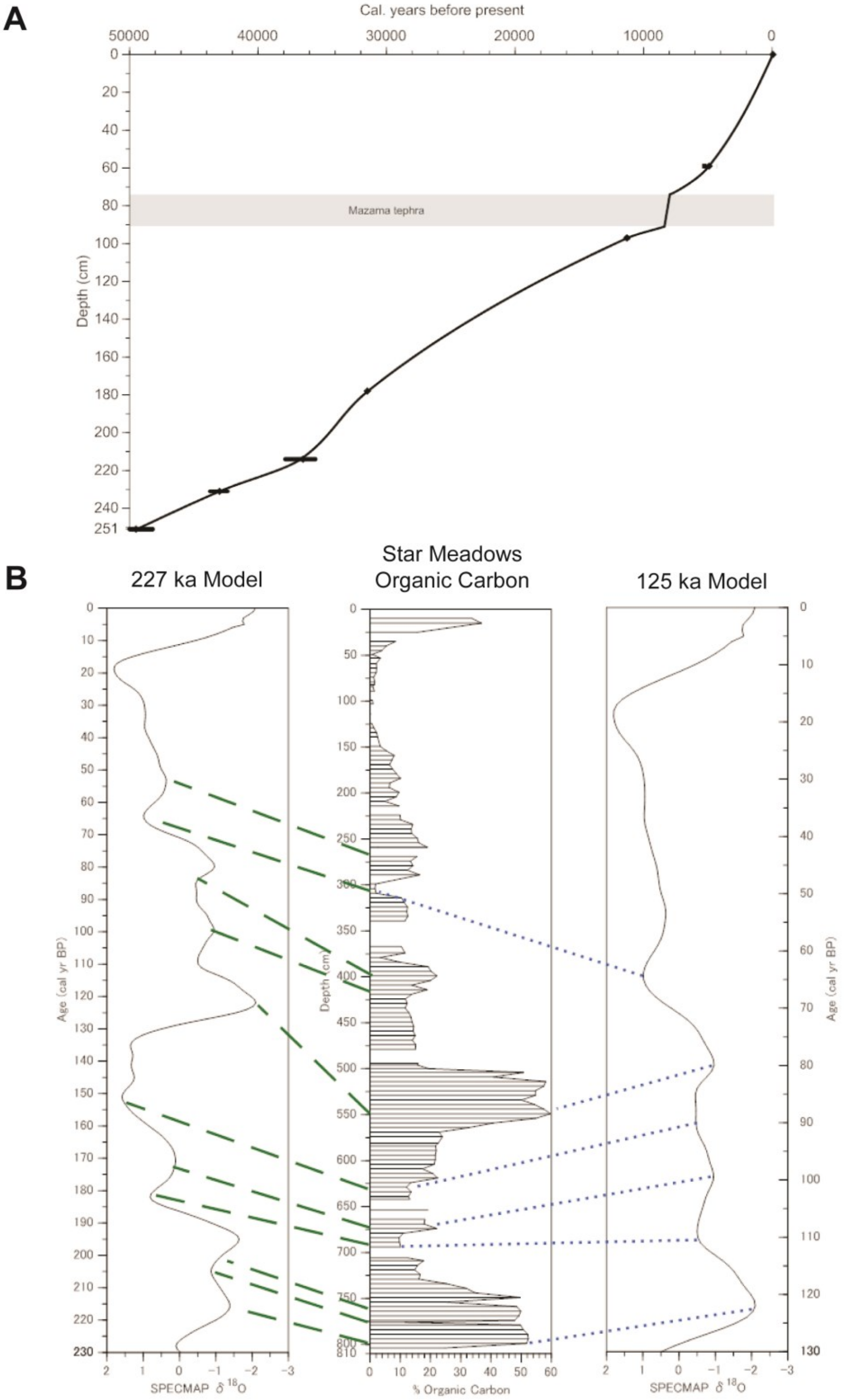


Figure 2.3. (A) Age-depth relationship of the top 251 cm of the Star Meadows core based on six AMS ^{14}C dates and the Mazama tephra (ca. 7.63 ka). (B) Comparison of the 227 ka and 125 ka age models using δ^{18}O SPECMAP (Imbrie et al., 1984) curve and percent organic carbon curve from Star Meadows.

chose the younger age model (125 ka), which places the core base of the core within MIS 5e. MIS stages were then assigned to each pollen zone based on sediment composition and vegetation assemblage interpretations (Figures 2.3 and 2.4).

3.3. Pollen

Pollen was generally well preserved, but concentrations were highly variable ($9x10^3 – 1.1x10^7$ grains/cm^3; Figure 2.2). Pollen could not be recovered from sediments that contained tephra or silt and clay with less than 2% organic carbon, restricted to depths of 72-144 cm and 299-209 cm (Figure 2.4). The 200 *Betula* grains that were measured for species identification, had an average diameter and standard deviation of 20.43 ± 1.41 µm and pore size of 2.55 ± 0.12 µm. *Betula papyrifera* diameters measured by Ives (1977) and Clegg et al. (2005) were 28.78 ± 1.26 µm and 23.03± 3.11 µm, respectively, while *B. glandulosa* diameters measured by the same studies were 23.99 ± 1.82 µm and 20.71± 2.35 µm, respectively. Based upon these results, I conclude that the *Betula* pollen identified at Star Meadows is most likely *B. glandulosa.*

3.3.1. Zone SM-1 (751-809 cm; MIS 5e; ca. 116-125 ka)

This zone consists of 15 pollen samples. This zone is distinguished by having the highest percentages of *Pinus* (60-90%) in the core. The remainder of the arboreal taxa consists of minor amounts of *Picea* (2-6%), *Abies* (2-6%), *Pseudotsuga/Larix*-type (1-5%), *Alnus* (2-10%), and *Betula* (0-2%). Other minor components in the ecosystem include *Salix* (present in the uppermost sample), *Sarcobatus* (0-1%), Ericaceae (0-1%), Rosaceae (0-1%), *Arceuthobium* (0-1%), and *Artemisia* (1-6%). The herbaceous taxa in

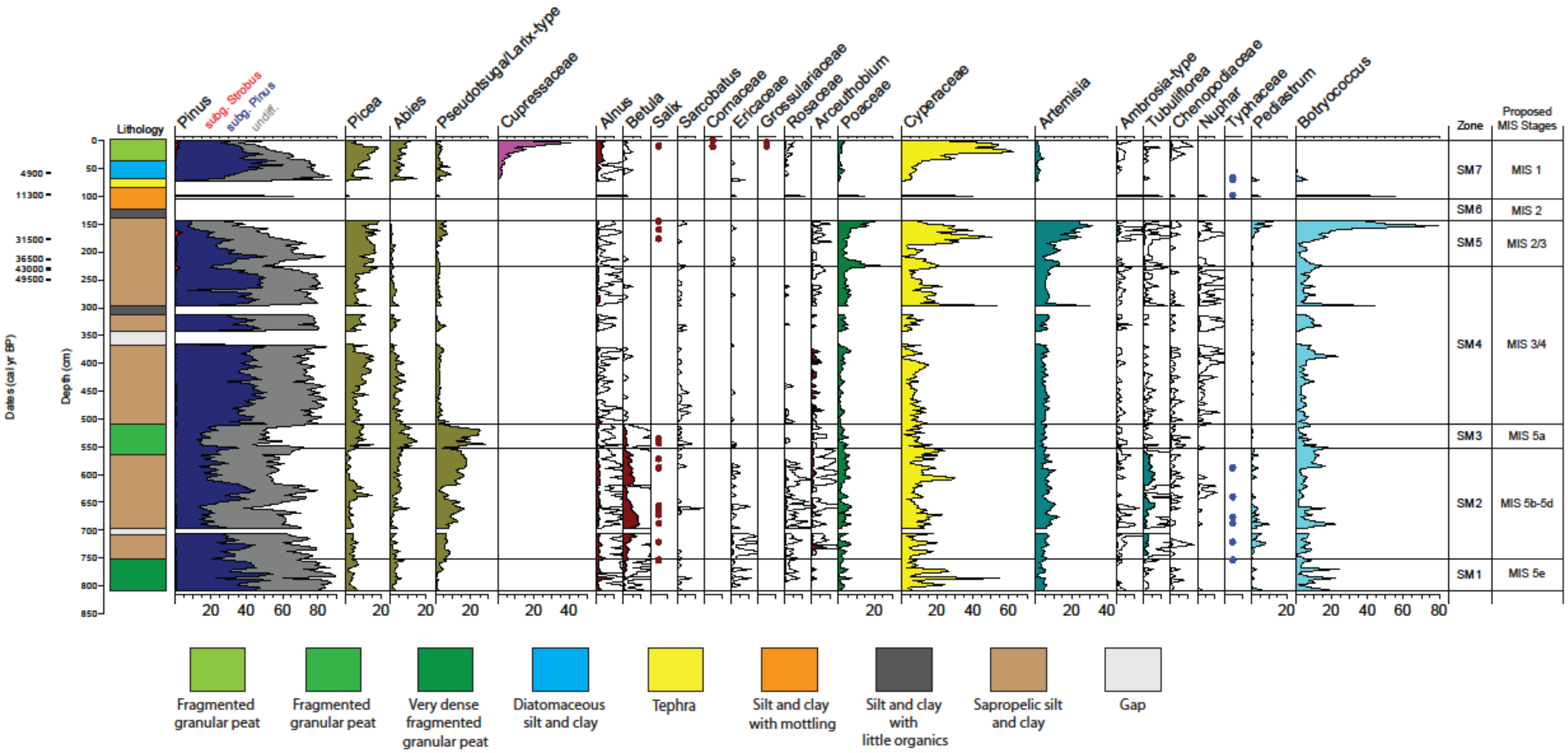


Figure 2.4. The pollen record from Star Meadows. Presence of *Salix*, Cornaceae, Grossulariaceae, and Typhaceae are show by circle symbols. Black lines for *Alnus, Betula, Sarcobatus*, Ericaceae, Rosaceae, *Arceuthobium, Ambrosia*-type, Tubuliflorae, Chenopodiaceae, and *Nuphar* indicate 10x exaggeration.

the understory consists of Poaceae (0-9%) and very minor amounts of members of the Asteraceae family (*Ambrosia*-type 0-1% and Tubuliflorae 0-1%), and Chenopodiaceae (0-1%). The aquatic pollen types represented include highly variable amounts of Cyperaceae (4-55%), *Nuphar* (only present in the bottom-most sample), and Typhaceae (only in the top sample of this zone). *Pediastrum* (0-6%) abundance decreases towards the top of the zone, while *Botryococcus* varies greatly (1-24%).

3.3.2. Zone SM-2 (553-751 cm; MIS 5b-d; ca. 84-116 ka)

A total of 48 pollen samples comprise this zone. This zone stands out from the other pollen zones because both *Pseudotsuga/Larix*-type (2-18%) and *Betula* (0-9%) increase dramatically. The remainder of the arboreal component consists of *Pinus* (37-87%), *Picea* (0.5-15.5%), *Abies* (2-7%), and *Alnus* (1-5%). *Salix* (present), *Sarcobatus* (0-2%), Ericaceae (0-2%), Rosaceae (0-2%), *Arceuthobium* (0-1%), and *Artemisia* (1-6%) make up the remainder of the pollen taxa of woody plants. Poaceae (0-9%) and Tubuliflorae (0-6%) dominate the herbaceous taxa, while *Ambrosia*-type (0-1%) and Chenopodiaceae (0-1%) are minor components. Cyperaceae (4-30%) and Typhaceae (present) can be found throughout the zone, while *Nuphar* (0-1%), is present mainly in the middle of this zone. *Pediastrum* (0-10%) and *Botryococcus* varies greatly within this pollen zone.

3.3.3. Zone SM-3 (510-553 cm; MIS 5a; ca. 71-84 ka)

This zone consists of five samples and has the highest percentage of *Pseudotsuga/Larix*-type (4-28%) observed in the core. The remainder of the arboreal and shrub taxa includes *Pinus* (43-73%), *Picea* (6-10%), *Abies* (5-12%), *Alnus* (1-5%), and

Betula (0-3%). *Salix* (present), *Sarcobatus* (0-1%), Ericaceae (0-1%), Rosaceae (0-1%), *Arceuthobium* (0-1%), and *Artemisia* (0-1%) comprise other woody taxa. The herbaceous component of the zone consists of Poaceae (0-5%), *Ambrosia*-type (0-1%), Tubuliflorae (0-1%), and Chenopodiaceae (0-1%). Cyperaceae (2-17%) dominates the aquatic taxa, while Typhaceae and *Nuphar* are absent from this section. *Pediastrum* (0-1%) and *Botryococcus* (1-8%) are minor components in this zone.

3.3.4. Zone SM-4 (225-510 cm; MIS 3 & MIS 4; ca. 40-71 ka)

This is the largest zone and is comprised of 64 pollen samples. *Pinus* (40-84%) and *Picea* (4-18%) are dominant. *Abies* (0-8%), *Pseudotsuga/Larix*-type (1-7%), *Alnus* (0-3%), and *Betula* (0-1%) comprise the remainder of the arboreal and shrub pollen within this zone. *Salix* is absent from this zone, while *Sarcobatus* (0-1%), Ericaceae (0-1%), Rosaceae (0-1%), and *Arceuthobium* (0-1%) are all present as minor components. *Artemisia* varies little throughout this zone (3-11%) with the exception of a single sample of 30% at 297 cm. Poaceae (0-25%) dominates the non-arboreal taxa and increases towards the top of this zone. *Ambrosia*-type (0-1%), Tubuliflorae (0-2%), and Chenopodiaceae (0-1%) comprise the remainder of herbaceous component. Cyperaceae (2-23%) is highly variable throughout this zone with a large peak (55%) occurring at 297 cm. *Nuphar* (0-3%) is consistently present through most of this zone. There is very little *Pediastrum* (0-2%) and variable amounts of *Botryococcus* (3-24%), with a peak (43%) occurring at 287 cm within the zone.

3.3.5. Zone SM-5 (144-225 cm; ca. 22.8-40 ka)

This zone consists of 20 samples. The highest percentages of *Picea* (8-19%) occur within this zone. *Pinus* (40-82%) declines in abundance towards the top of this zone, while *Abies* (0-3%), *Pseudotsuga/Larix*-type (0-7%), and *Alnus* (0-1%) are not major components of the arboreal taxa. *Betula* is only present as one grain near the base of this section. Other woody taxa within this zone are *Salix* (present only in the upper half of the zone), *Sarcobatus* (0-1%), Ericaceae (0-1%), and *Arceuthobium* (0-1%). *Artemisia* (4-30%) increases dramatically towards the top of this zone. Poaceae (2-24%) decreases at the base of this zone and then increases towards the top. The remainder of the non-arboreal taxa consists of *Ambrosia*-type (0-3%), Tubuliflorae (0-2%), and Chenopodiaceae (0-1%). Cyperaceae (3-50%) pollen is highly variable throughout this zone and increases towards the top. *Nuphar* (0-3%) is present at the base and top of the zone, while Typhaceae is absent. *Pediastrum* (0-12%) and *Botryococcus* (1-80%), have their highest percentages of the entire core occurring at the top of this section.

3.3.6. Zone SM-6 (105-144 cm; ca. 14 – 22.8 ka)

The pollen concentration within this zone was too low and degraded (less than 7,000 grains/cm^3) to complete pollen counts. For example, at a depth of 106 cm (ca. 13.5 ka), a total of 89 pollen grains could be identified with significant effort. Of these 89 grains, 53 were *Artemisia* while most of the rest were fragments of *Pinus*.

3.3.7. Zone SM-7 (0-105 cm; MIS 1; ca. 14 ka to present)

A total of 23 samples were counted within this section. At the base of this section, the pollen concentration was too low to complete any pollen counts through much of the Pleistocene to Holocene transition. One sample of early-Holocene age contained sufficient identifiable pollen, marked by high percentages of *Pinus* (58%), Poaceae (15%), and *Ambrosia*-type (7%). The uppermost samples represent the mid to late Holocene vegetation, distinguished by the first appearance of Cupressaceae (most likely *Thuja plicata*) pollen (0-41%). Cupressaceae pollen first appears at 67 cm and increases in an exponential fashion towards the top. The uppermost samples also contain the first appearance of Cornaceae and Grossulariaceae. The rest of the tree taxa consist of *Pinus* (49-87%), *Picea* (2-20%), *Abies* (1-15%), *Pseudotsuga/Larix*-type (1-9%), *Alnus* (0-5%), and *Betula* (0-1%). *Salix* is present in one sample near the top of the core. Ericaceae (0-1%) is present only at two depths, while Rosaceae (0-1%) increases slightly towards the top of the section. *Arceuthobium* is not present while *Artemisia* varies little throughout this zone (0-5%) with the exception of a single sample of 15% at 99 cm. Non-arboreal taxa consist of *Ambrosia*-type (0-1%), Tubuliflorae (0-1%), and Chenopodiaceae (0-1%). Cyperaceae pollen varies greatly in this zone from 4 to 65% with the highest abundance occurring at the top of the core. *Nuphar* (0-1%) is only present at 99 cm, while Typhaceae is present in the lower half of this zone. Percentages are relatively low for both of the algae taxa *Pediastrum* (0-5%) and *Botryococcus* (0-55%) and are only present in the lower half of the zone.

4. Discussion

All interpretations are presented by pollen zone, depth, and assigned age. There is a good correspondence of the CONISS pollen zones with the lithological profile, providing evidence that there were parallel changes in upland vegetation and the wetland environment as controlled by water levels. Zones SM-5 to SM-7 were within the range of radiocarbon dating and zone-boundary ages were estimated to within 100 years. Zones SM-1 to SM-4 were outside the ^{14}C-dated period and correlation-assigned ages were estimated to within 100 years. To aid the interpretation of the paleovegetation, I qualitatively interpreted the pollen data to provide potential modern analogs for each pollen zone. However, these potential analogs require verification using an extensive surface-sample data set (Figure 2.5).

4.1. Zone SM-1 (751-809 cm; MIS 5e; ca. 116-125 ka)

This sediment in this zone is comprised of dense fragmental granular peat with low bulk density and high organic carbon percentages. Vegetation within the meadow was dominated by *Carex.* The meadow was wet periodically as algae were rare (*Pediastrum*) or intermittent (*Botryococcus*), *Nuphar* was mostly absent, and biogenic silica was low (<3%). The meadow was lined with wetland taxa including *Betula glandulosa, Salix,* and *Alnus* (Figure 2.5). I interpret the pollen assemblage as representing a forest dominated by *Pinus contorta,* with minor components of *Picea engelmannii, Abies lasiocarpa*, *Pseudotsuga/Larix*-type*,* and *Vaccinium* shrubs (Ericaceae). A similar vegetation assemblage can be found today to the south in central

Idaho (e.g., montane forests of the Challis National Forest) where climate is warmer and drier than at the Star Meadows region today.

4.2. Zone SM-2 (553-751 cm; MIS 5b-d; ca. 84-116 ka)

The lithology in this zone is a stiff sapropelic silt and clay sediment consistent with a lacustrine origin. Water levels rose within the meadow forming a lake that was able to support *Nuphar.* The persistence of high biogenic silica indicates that the site never dried and maintained a lake level of at least a meter. Bog taxa, such as Typhaceae, *Salix, Betula glandulosa,* Cyperaceae, and possibly *Comarum palustre* (Rosaceae) persisted around the lake margin. *Pinus contorta, Picea,* and *Larix occidentalis* and/or *Pseudotsuga menziesii* form most of the forest composition with minor amounts of *Arceuthobium* and herbaceous taxa (Poaceae, *Ambrosia*-type, and Tubuliflorae) constituting the understory. The forests of this zone may represent a mixed conifer Douglas-fir forest such as is common in the Purcell Mountains of northwestern Montana and southeastern British Columbia (Chadde et al., 1998). The Purcell Mountains are cooler and receive more snow than at Star Meadows.

4.3. Zone SM-3 (510-553 cm; MIS 5a; ca. 71-84 ka)

Several factors including lithology (fragmental granular peat), high C:N, low biogenic silica, absence of *Nuphar* (only one grain present at the base of this zone), and low abundance of algae indicate that the bog dried out and supported a sedge meadow. The forest surrounding the meadow remained similar to forest described in zone SM-2. *Pseudotsuga/Larix*-type is the dominant forest taxon with minor amounts of *Picea, Abies,* and *Pinus* (likely *P. contorta* and/or *P. monticola*). The forest taxa, decreasing amount of *Betula,* and lack of aquatic taxa indicate that climate continued to be warm and but was drier than the previous zone (SM-2; MIS 5b-MIS 5d).

4.4. Zone SM-4 (225-510 cm; MIS 3 & MIS 4; ca. 40-71 ka)

The lithology of this zone is mainly comprised of a sapropelic layer with a short segment of silt and clay containing little organic content from 300 to 314 cm. Relatively high abundances of biogenic silica along with the presence of *Nuphar* throughout most of this zone indicate the presence and persistence of 2-5 m of standing water. Most of the bog taxa such as *Betula,* Typhaceae, and *Salix*, which were present in SM-2 and slightly in SM-3 are no longer present in this zone. *Pinus* (likely *P. contorta*) and *Picea engelmannii* are the dominant trees of the forest while *Pseudotsuga/Larix*-type and *Abies* (likely *A. lasiocarpa*) were only minor components. The pollen assemblage, especially the high *Picea* percentages, suggest the forest was a montane spruce forest such as occur at mid-to-high elevations in the Selkirk Mountains in northern Idaho today. The Selkirk Mountains have a cool continental climate characterized by cold winters and moderately short mild summers. Even though the pollen assemblage suggests a cooler climate than what occurs at Star Meadows today, it was still warm enough for *Nuphar* to be present throughout this zone.

The peaks that occurred in bulk density and magnetic susceptibility with corresponding troughs in percent organic carbon and biogenic silica at 300 cm most likely represent a glacial advance. The inorganic nature of the sediment and lack of pollen preservation in this section (300-314 cm) indicates the effects of this glacial advance was strong and had a profound effect on the region. Perhaps this silt layer represents an extreme stadial event, such as the Heinrich event at 66 ka (H6) event, during MIS 4 (Bond et al., 1992; Rashid et al., 2003; Hemming, 2004; McDonald et al., 2012). The cool temperatures during this advance caused the tree line in the surrounding mountains to lower, increasing *Picea* and *Pinus* abundances at lower elevations, and *Artemisia* at higher elevations.

4.5. Zone SM-5 (144-225 cm; ca. 22.8-40 ka)

This zone is comprised of a sapropelic silt and clay layer with low percent organic carbon, increasing bulk density, and decreasing biogenic silica. *Nuphar* and algae present throughout most of this zone indicate the continued presence of a lake that was surrounded by wetland taxa (*Salix* and *Carex*). The forest surrounding the wetland was dominated by *Pinus* and *Picea* with both *Abies* and *Pseudotsuga/Larix*-type present as minor components of the forest, similar to the forest composition of SM-4. *Pinus* decreases towards the top of this zone as *Artemisia* and herbaceous taxa (Poaceae, *Ambrosia*-type, Tubuliflorae, and Chenopodiaceae) increase in abundance. These changes in the pollen assemblage indicate the establishment of an open environment, possibly marked by lowering of tree line and the expansion of *Artemisia* at higher elevation. The climate was likely becoming significantly colder and possibly drier (but not enough to greatly lower water depth at the core site) into the LGM.

4.6. Zone 6 (105-144 cm; ca. 14 – 22.8 ka)

This zone is marked by stiff silt and clay with very little organic material, low pollen concentration, and dominance of *Artemisia* pollen (>60%) in the one sample where pollen could be identified. This suggests the region had low tree cover and a very short growing season. This is consistent with a pollen record from Lost Trail Pass Bog in the Bitterroot Range (Mehringer et al., 1977) that was interpreted to reveal a vast treeless landscape during the late glacial period. These two records challenge the suggestion of the persistence of a mesic refugium existing in the region during the LGM.

4.7. Zone 7 (0-105 cm; ca. 14 ka to present)

Sufficient organic matter during the early Holocene period existed for a single pollen sample (99 cm; ca. 11.7 ka). A small lake occupied the site, as indicated by the presence of *Nuphar*, and the lake was productive enough for algae (*Pediastrum* and *Botryococcus*) to occur in high abundances. Cyperaceae and Typhaceae were the dominant wetland taxa surrounding the lake. A forest dominated by *Pinus*, with a few *Picea* and *Pseudotsuga/Larix*-type trees occurred around the lake with an understory containing high abundances of herbaceous taxa (Poaceae, *Ambrosia*-type and Tubuliflorae). The high abundances of herbaceous taxa (especially Poaceae) along with *Pinus* provide evidence of an open warm-dry habitat.

The pollen assemblages post-dating the Mazama tephra (ca. 7.63 ka) are very different from any previous assemblage. The absence of *Nuphar* and low algae abundances in this portion of zone SM-1, indicates that the lake dissipated and a wet sedge meadow established. This likely occurred due to the basin filling with sediment over time, which allowed only 20 cm of water to fill the basin before it overflows. Within the meadow, *Carex, Salix,* and *Comarum palustre* constitute the wetland vegetation. The forest surrounding the meadow is dominated by *Thuja plicata,* with minor amounts of *Pinus monticola, Picea engelmannii, Abies grandis*, *Pseudotsuga menziesii*, and *Alnus.* Cornaceae and Grossulariaceae (likely *Ribes*) also make their first appearance in the pollen record near the top of this zone. *Thuja plicata*, Cornaceae, and *Ribes* are currently associated with the warm and wet climate of the mesic forests.

4.8. Late-Holocene arrival of the mesic forests in northern Idaho

If a mesic forest environment persisted during the last glaciation within a refugium in the Clearwater drainage, as previous phylogenetic research has suggested (i.e. Brunsfeld and Sullivan, 2005; Brunsfeld et al., 2007; Carstens and Richards, 2007), then indicators of a mesic environment (i.e. mesic taxa) similar to the late-Holocene would be present prior to the onset of Holocene. Although much of the time the landscape around Star Meadows was forested, I found two periods during the late Pleistocene with very low forest cover, challenging the possibility that a mesic refugium could have existed in the broader region. Furthermore, the taxa most strongly associated with mesic climate, *Thuja plicata,* first appears in the pollen record only at ca. 6.3 ka. Below I discuss this history of *T. plicata* and its implications for understanding the existence of a mesic refugium in northern Idaho.

The mid-Holocene arrival of mesic taxa in northern Idaho is consistent with other paleorecords from glaciated areas in the Columbia Mountains of British Columbia. At

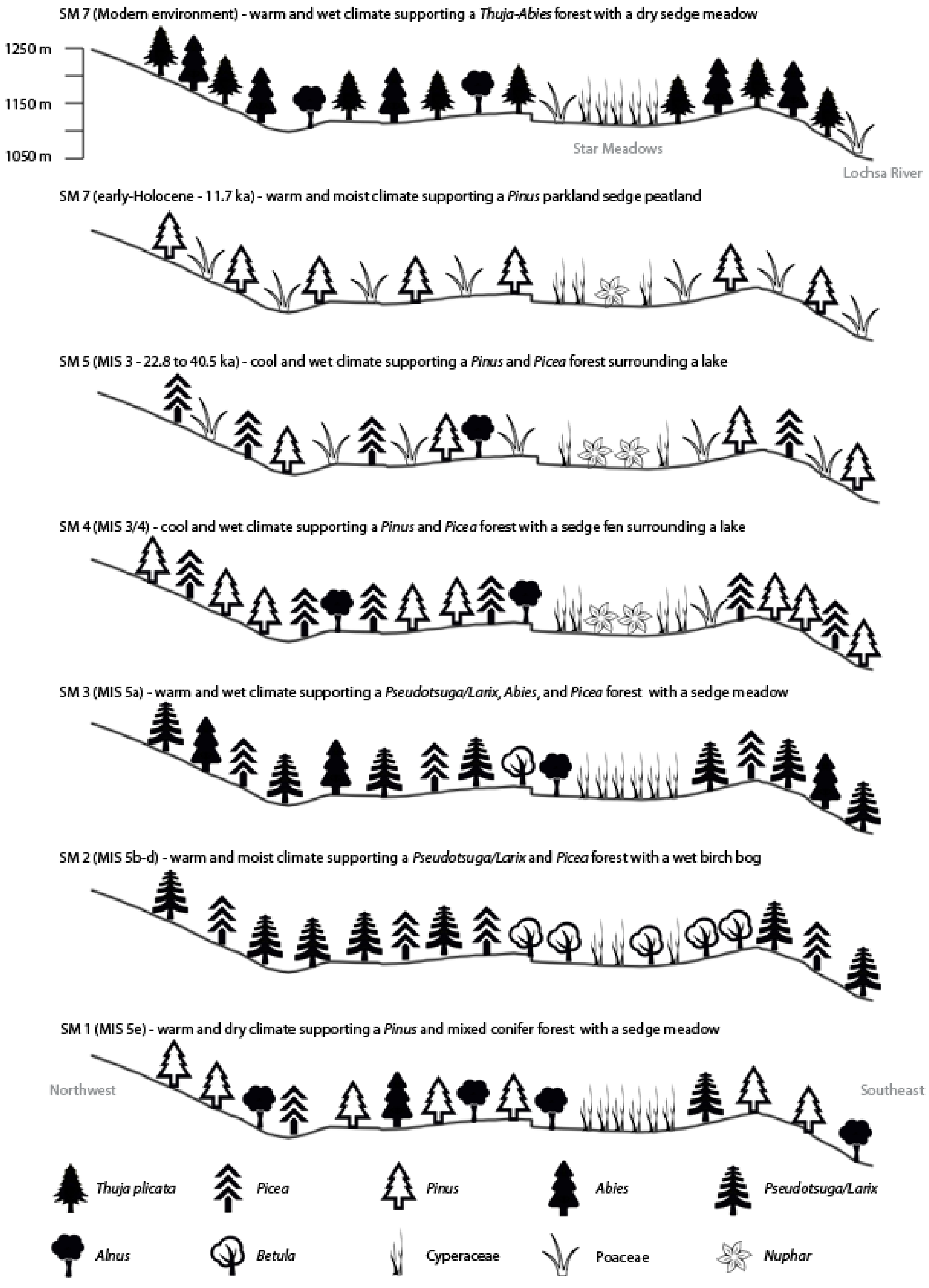


Figure 2.5. Schematic transects across Star Meadows showing the dominant vegetation, based on the pollen record, for each pollen zone with the exception of SM-6.

Lower Slocan Lake, *T. plicata* appears in the paleorecord approximately 5 ka (Hebda, 1995) and at Mirror Lake (Kaslo, BC) at 3 ka (Gavin, unpublished data). *Thuja plicata* can often be found in association with *Tsuga heterophylla* throughout most of its current distributions. However, the modern distribution of *T. heterophylla* does not extend south to the Lochsa River. Further north in Idaho and British Columbia, paleorecords provide evidence that *T. heterophylla,* like *T. plicata,* is a relatively recent arrival to the interior mesic forests. In northern Idaho near Priest Lake *Thuja-Tsuga* forests increased in abundance at 2.5 ka (Mehringer Jr, 1985; Mehringer, 1996), while farther north in British Columbia these species increased in abundance (>2%) after ca. 3.1 ka (Gavin et al., 2006).

The increase in abundance of *Thuja plicata* over the last ca. 6.3 ka shows that the forests during the late-Holocene were different than any other forest that existed in the Holocene and previous interglacial. What was different about the Holocene that enabled the establishment and later dominance of *T. plicata* and other mesic taxa in the region? I propose three main hypotheses for why mesic taxa, including *T. plicata,* did not establish in northern Idaho until the mid-Holocene. The relatively recent arrival of mesic taxa could have been limited by 1) dispersal, 2) climate, and/or 3) conditions for seedling establishment.

The first two explanations for the Holocene appearance of mesic taxa are that they were dispersal-limited due to a >100 km wide arid barrier between their main coastal populations and the northern Rocky Mountains, or that climate was not suitable for the mesic taxa prior to the Holocene. If dispersal was the only factor limiting the distribution of the mesic taxa during the Holocene, then it can be assumed the past climate could have supported other mesic taxa. Comparison within the core between MIS 1 (SM-7, modern environment) and MIS 5 (SM-1 through SM-3) shows that the vegetation and climate during these two time periods were not similar. Other than the recent occurrence of Cupressaceae, the most notable difference between the two time periods is the high abundances of *Betula* and *Pseudotsuga/Larix* during MIS 5, whereas both taxa are found in low abundances in the modern landscape (MIS 1). *Betula* and *T. plicata* can be found in association with one another today, but are always found in association with *T. heterophylla* and at higher latitudes in a cooler environment, such as at the north end of Priest Lake in the Selkirk Mountains. This is consistent with other records stating that MIS 5 is not a good analog for the current interglacial (Loutre & Berger, 2003; McManus et al., 2003). Instead, MIS 11 is a better analog for the Holocene because of its similar orbital configurations, carbon dioxide and other greenhouse gases concentrations, and because it represents the longest and warmest interglacial (similar to the Holocene) in the last 500 ka (Muller & MacDonald, 1997; Raynaud et al., 2005). The early Holocene was also likely too warm and dry for *T. plicata* forests, instead supporting a *Pinus* parkland (Figure 2.5). Modern climate is cooler and wetter than the early Holocene, suggesting that climate prior to the mid-Holocene was not ideal for mesic taxa expansion into the region. Thus, the regional vegetation history is more consistent with a climatic limitation, rather than dispersal limitation, affecting the Holocene establishment of *T. plicata* forests. Many other associated mesic-adapted taxa may have been affected similarly.

Although climate at Star Meadows may have been unsuitable for *T. plicata* (and possibly other mesic-adapted species) before the Holocene, the pollen data do not resolve whether most or all mesic-adapted taxa were restricted to the coast or whether they may have existed in the northern Rocky Mountains in small isolated refugia. The phylogeography of *Cardamine constancei*, an herbaceous species associated with *T. plicata* and endemic to northern Idaho, indicates small populations persisted within separate river canyons in unglaciated areas in northern Idaho (Brunsfeld & Sullivan, 2005). During the LGM (MIS 2), however, almost no pollen was recovered (SM-6). The climate of the LGM and late glacial was probably extremely challenging for mesic-adapted taxa in the region, as high levels of *Artemisia* suggest a very low tree line and a very short growing season. There are many canyons further south of Star Meadows in the mountains of Idaho. Perhaps a refugium for mesic-adapted species was able to exist on south facing slopes south of Star Meadows. The LGM period presents the largest hurdle for a persistence of mesic-adapted taxa in an interior refugium.

Species distribution models of several species (i.e. *Ascaphus montanus, Plethodon idahoensis, Microtus richardsoni, Salix melanopis, T. plicata*) residing within the interior mesic forests show that the LGM climate was too harsh for many of the species currently found in the region today (Carstens & Richards, 2007; Roberts, 2013). Both vegetation (subalpine *Pinus* and *Picea* forest with high abundances of *Artemisia*; SM-5) and sediment composition records (low percent organic carbon, decreasing biogenic silica, and increasing bulk density; SM-5 and SM-6) support climate simulations of a cool and dry LGM (Braconnot et al., 2007). In order to test if small isolated pockets of suitable climate could have existed in the region during the LGM, high-resolution climate variability needs to be assessed throughout the mountains.

A third possibility that may have promoted the Holocene arrival of *T. plicata* in northern Idaho was the tephra deposited from the eruption of Mt. Mazama. A total of 17 cm of ash was preserved in the Star Meadows core, which is consistent with other records in northern Idaho (e.g. Mehringer et al., 1977; Shipley and Sarna-Wojcicki, 1983; Matz, 1987; Brunelle and Whitlock, 2003; Kimsey et al., 2007). In paleorecords recovered in Oregon, the Mazama tephra has had a profound effect on vegetation by increasing the non-arboreal component in the ecosystem following ash deposition (Long et al., 2011, 2014). Similar to the sites in Oregon, the deposition of a thick Mazama ash at Star Meadows may have suppressed competing vegetation and mulched soils thereby increasing soil water capacity and enabling mesic taxa such as *T. plicata* to establish and increase in abundance fairly quickly. *Thuja plicata* is able to grow on nutrient-poor soils, and influences surrounding soils by raising pH and increasing soil cation capacities (Franklin et al., 2000). It is not known how well *T. plicata* germinates on ash relative to other species, but may have been able to outcompete other forest taxa that are not able to establish as easily on ash. In order to test this hypothesis, germination studies for *T. plicata* and other tree taxa need to be conducted on Mazama ash.

5. Conclusion

The Star Meadows core provides us our first glimpse of the long-term climate and vegetation history in northern Idaho over the last ca. 120 ka. Pollen recovered from the core suggests that the region underwent several major vegetation changes as a response to changes in climate at millennial scales. Pollen assemblages and sediment composition records can be linked to marine isotope stages, indicating global-scale climatic fluctuations were manifested as distinct vegetation changes in northern Idaho. At the base of the core (MIS 5e) a warm-dry climate existed enabling the establishment of a dry-mixed conifer forest around a dry sedge (*Carex*) meadow. During MIS 5b-5d the landscape became moister allowing a *Pseudotsuga/Larix* and *Picea* forest to develop on the slopes surrounding a wet birch (*Betula*) bog. Climate continued to warm which led to the establishment of a forest dominated by *Pseudotsuga/Larix*-type, *Picea,* and *Abies* to develop around a wet *Carex* meadow. During MIS 4 to MIS 2, a cool and wet climate developed in the region. An increase in available moisture enabled the meadow to fill with water and support *Nuphar,* while *Pinus* and *Picea* dominated the forest surrounding the lake. From ca. 22.8-40 ka, cooler and drier (than present) conditions prevailed, facilitating a subalpine parkland of *Pinus* and *Picea* to develop around a lake. Due to the low amounts of organic matter and poor preservation of pollen, pollen concentrations were extremely low that none could be analyzed during the LGM. Glaciers extended down-valley less than 10 km away from Star Meadows, providing evidence that vegetation was likely sparse in the immediate region (Dingler & Breckenridge, 1982). During the early Holocene (11.7 ka), climate warmed enabling the area surrounding Star Meadows to develop into a *Pinus* parkland dominated by Poaceae in the understory. The most dramatic change in vegetation occurred during the mid-Holocene with the appearance and then later dominance of *Thuja plicata* and other taxa associated with mesic forests in the region today.

The Holocene is a unique period due to the appearance and dominance of *T. plicata* over the last ca. 6.3 ka in the Star Meadows region. The recent arrival of mesic forest taxa suggests that their range may have been limited by dispersal, climate, or a combination of both. Recent dispersal from the coast is in agreement with phylogenetic studies conducted on *T. plicata* populations (O’Connell et al., 2008). Pollen and sediment composition records from the core suggests that climate of the last interglacial (MIS 5) was substantially cooler than the modern environment, and that the LGM was regionally a very harsh climate. Thus, climate may have been the primary limiting factor for both the initial establishment of *T. plicata* at any location in the interior and its absence at Star Meadows until the late Holocene. Under this interpretation, long distance dispersal from the coast could have occurred one or more times over the last 100 ka, but *T. plicata* was not able to colonize until a suitable climate was established during the Holocene. Pollen records, however, are unable to rule out earlier colonization of microrefugia in the interior, though given the interpretation of LGM climate at Star Meadows such sites were likely located to the south by hundreds of km. In addition, the eruption of Mt. Mazama could have aided in the establishment of the modern mesic forest by reducing competition and providing a good substrate for seedling establishment.

Continuous records that extend back 120 ka are rare in western North America and are important for our understanding of long term vegetation-climate relationships. Star Meadows is the first paleorecord from the southern end of the interior mesic forest distribution in a putative glacial refugium. The mesic forests of northern Idaho are disjunct from the main population along the Pacific Northwest coast and contain many endemic taxa. Phylogenetic analysis on endemic and disjunct species in northern Idaho indicate that some species recently dispersed from coastal populations while others likely persisted during unfavorable climate conditions in a refugium in the Northern Rocky Mountains. The Star Meadows record challenges the notion that this region acted as a broad-scale mesic refugium during glacial conditions.

This chapter has focused on the long term climate and vegetation trends over the last ca. 125,000 years. From the research presented here, the mid-to late-Holocene was a unique period of time in which mesic taxa established in northern Idaho. Within this chapter I focused on one taxon, *T. plicata,* which dominates the region today at low elevations. In the following chapter, I expand on the conclusions presented here and explore the timing of *Tsuga mertensiana* arrival to the region at higher elevations in northern Idaho.

CHAPTER III

THE ECOLOGICAL HISTORY OF *TSUGA MERTENSIANA* IN THE INTERIOR MESIC FORESTS OF THE PACIFIC NORTHWEST

1. Introduction

A fundamental question in both ecology and paleoecology is whether vegetation is in equilibrium with climate (Webb, 1986; Peros et al., 2008; Prentice et al., 2011). Recent research on this subject has focused on estimating the degree to which modern distributions are in equilibrium with their climatically determined potential distribution (e.g., Svenning & Skov, 2004; Montoya et al., 2007). Paleoecological studies have a long history addressing vegetation equilibrium questions (Reid, 1899; Webb, 1986). Most recent studies have demonstrated a rapid response of plant communities to past climate changes (Williams et al., 2002; Shuman et al., 2011), but few studies have clearly addressed the biogeographic equilibrium of a specific taxa to Holocene climate change (e.g., Davis et al., 1986; Giesecke & Bennett, 2004; Magri et al., 2006; Willner et al., 2009). The studies that have focused on the range expansion patterns of individual taxa require the synthesis of many pollen records over large areas (e.g., Giesecke & Bennett, 2004; Giesecke, 2005; Kullman, 2008). In general, species that are in equilibrium with climate are those that are able to reproduce quickly and colonize the newly available climate space. Tree taxa that disperse slowly are more likely to appear in disequilibrium with climate due to migrational lags caused by the inability to reproduce and disperse rapidly. Barriers (climatic or geographic) may exacerbate the disequilibrium of vegetation and climate, depending on the dispersal ability of individual taxa (Davis et al., 1986).

In this study, we address climate versus dispersal limitations during the Holocene history of *T. mertensiana* expansion, a subalpine tree species of high-snow areas with a distribution characterized by major disjunctions. *Tsuga mertensiana* has a main distribution along the coast of the northwestern North America (from the central Sierra Nevada to south-central Alaska) and has several disjunct distributions in interior regions including those in: 1) eastern British Columbia, 2) northern Idaho, and 3) northeastern Oregon (e.g., Gavin et al., 2009; Björk, 2010). Of these three disjunctions, the interior mesic forest (IMF) of northern Idaho's Rocky Mountains are unique because they support over one hundred vascular plant species (including *Thuja plicata, Tsuga heterophylla,* and *T. mertensiana*) similarly disjunct from coastal distribution in the Pacific Northwest (PNW) (Lorain, 1988; Ally et al., 2000; Björk, 2010). Two hypotheses have been proposed regarding the history of the disjunct mesic forest populations: (1) they originated from a refugia south of the glacial limit (e.g., Nielson et al., 2001; Brunsfeld & Sullivan, 2005; Brunsfeld et al., 2007) , or (2) they originated from a recent dispersal from the coast (Brunsfeld et al., 2001; O'Connell et al., 2008). While the British Columbia disjunction of *T. mertensiana* is likely the result of a post-glacial dispersal because it lies >100 km north of the Cordilleran Ice Sheet maximum, the majority of the north Idaho population lies south of the glacial limit in a region assumed to be a glacial refugium (i.e., the Clearwater Refugium, Brunsfeld & Sullivan, 2005).

A basic assumption in pollen analysis is that there is a relationship between the abundance of pollen deposited in sediment and the abundance of the vegetation that produced it (MacDonald & Reid, 1989; Birks & Birks, 2000). In order to reconstruct the range history of an individual species, multiple sediment cores are needed to increase the chance of detecting small populations (Birks, 1989; Huntley et al., 1989). When estimating time of arrival of a species in a sediment record, the first appearance of that taxon's pollen may be problematic. Pollen percentages are dependent upon all other taxa deposited at that point in time, thus the complement of taxa can affect detection probabilities (Davis, 1969). In addition, some pollen types can travel long distances (e.g., Hyvärinen, 1975; Hicks, 1994) and some taxa produce more pollen than others (Davis et al., 1980; Ritchie, 1995), such that pollen presence may not necessarily reflect occurrence nearby. A network of modern surface samples is therefore essential to help guide the interpretation of fossil pollen record (Hicks & Hyvärinen, 1999; Bialozyt et al., 2012).

One problem that has been encountered when using *Tsuga mertensiana* pollen for paleoecological reconstruction is the inconsistent relationship between tree abundance in the pollen source area and pollen frequency in surface samples (Dunwiddie, 1987; Mathewes, 1993). Several studies have noticed a distinct underrepresentation of *T. mertensiana* in modern samples taken from the interior, even in samples taken in a near-pure stand of trees (Hebda, 1983, 1995; Mathewes, 1993; Rosenberg et al., 2003). Most studies show that *T. mertensiana* rarely represents over 1% of the total pollen assemblage in the interior distributions (Hazell, 1979; Rosenberg et al., 2003). The underrepresentation of *T. mertensiana* within the interior is likely due to the over representation of *Pinus* pollen. On the coast, where *Pinus* pollen is low, *T. mertensiana* abundance can be over 20% (Gavin et al., 2013). To date, no one has addressed pollen representation of *T. mertensiana* in the IMF.

Climate reconstructions and paleoclimatic simulations for the Pacific Northwest indicate significantly colder conditions prevailed during the glacial and late-glacial times, followed by warmer and drier climate in the early Holocene (Thompson et al., 1993; Bartlein et al., 1998; Hostetler & Bartlein, 1999). Species-distribution models indicate that it is unlikely that the cool-wet adapted *T. mertensiana* persisted in the Northern Rocky Mountains earlier than 5000 cal yr BP (Roberts, 2013). Paleoclimate records indicate increasing moisture, and cooler conditions, began in the middle-to-late Holocene, which facilitates an increase in *Tsuga heterophylla* and *Thuja plicata* (lower elevation dominate tree taxa) along the coast (Hebda, 1995; Heusser et al., 1999). Within the IMF , scattered paleoecological studies suggest these species have been components of the forests for less than 4000 cal yr BP (Mack et al., 1978; Hebda, 1995; Mehringer, 1996; Rosenberg et al., 2004; Hallett & Hills, 2006; Gavin et al., 2009). Since *T. heterophylla* and *T. plicata* appear to be recent components of the IMF, it is possible that the high-elevation *T. mertensiana* arrived recently to the region as well.

I present three new pollen records from northern Idaho and address the following questions: (1) how reliably does *T. mertensiana* pollen reflect the presence of *T. mertensiana*? (2) When did *T. mertensiana* become a dominant tree in the forests of Northern Rocky Mountains of Idaho? (3) Was *T. mertensiana* expansion into the interior limited by dispersal barriers and/or climate limitations?

2. Background

2.1. Geographical setting and climate

The uplift of the Cascade Range of western Oregon and Washington during the Miocene led to the development of a pronounced rain shadow to their east. This dry environment extends eastward until it meets the Rocky Mountains where orographic precipitation supports a separate interior mesic climate (Daubenmire, 1975; Thackray et al., 2004). On the west side of the Rocky Mountains in Idaho, most precipitation falls during the winter and spring months and at higher elevations in the form of snow.

The disjunct IMF extends from the Columbia Mountains of British Columbia southward to the Lochsa and Selway rivers of northern Idaho (Figure 3.1). The IMF has been of long interest to biogeographers (Daubenmire, 1975, 1980; Gavin et al., 2009; Björk, 2010). At low-to-mid elevations these forests are dominated by *Tsuga heterophylla* (western hemlock) and *Thuja plicata* (western redcedar). *Picea engelmannii* (Engelmann spruce), *Abies lasiocarpa* (subalpine fir), *Pseudotsuga menziesii* (Douglas-fir), *Larix occidentalis* (western larch), *Abies grandis* (grand fir), *Pinus monticola* (western white pine), *Pinus contorta* (lodgepole pine), and *Alnus rubra* (red alder) constitute the remainder of the tree taxa. At higher elevations within the mesic forest, the dominant tree transitions from *T. heterophylla* to *T. mertensiana* (mountain hemlock) with similar associated tree taxa. Daubenmire (1975) and Björk (2010) have completed extensive vegetation surveys across the IMF.

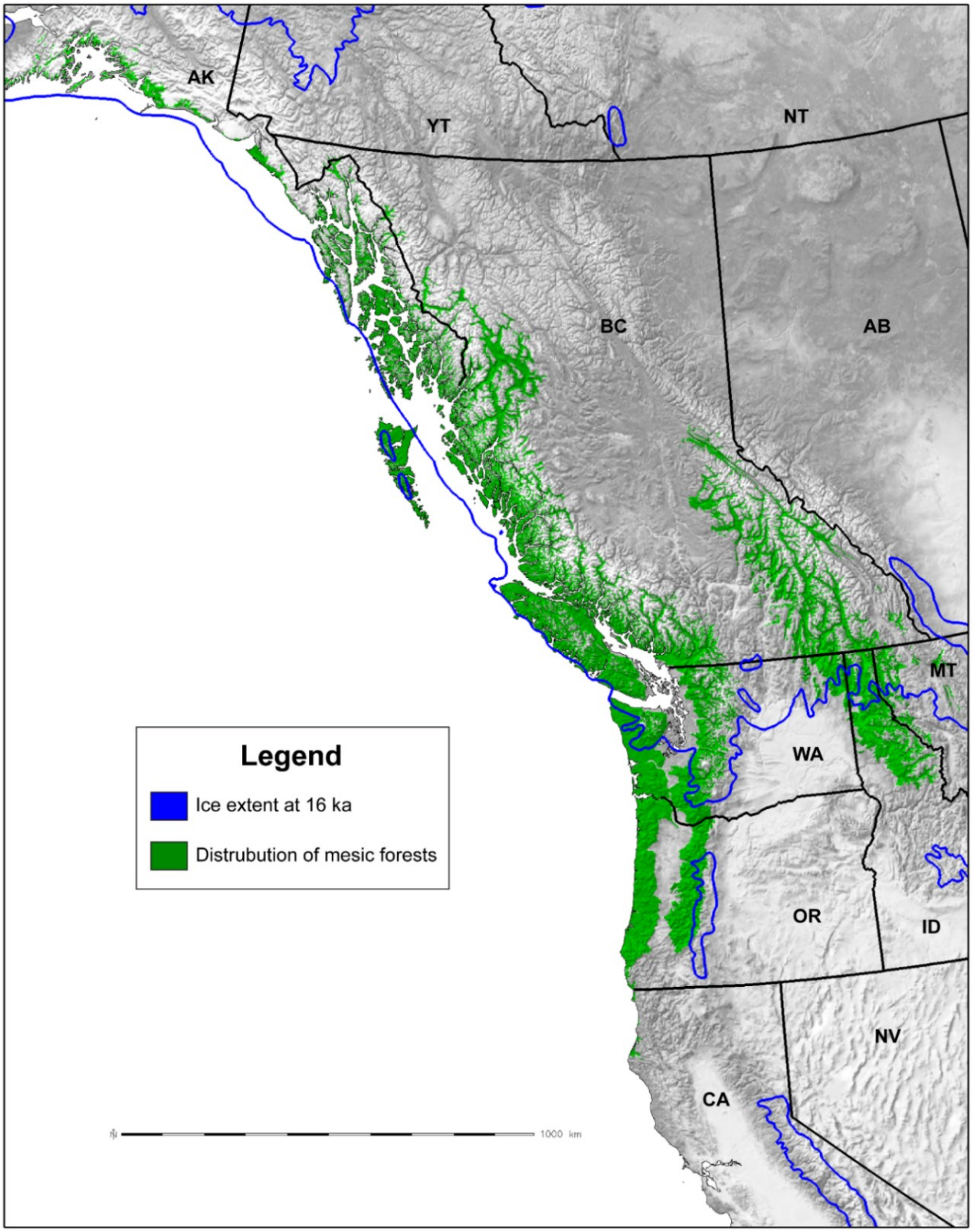


Figure 3.1. Digital elevation map of the Pacific Northwest. The distribution map of the mesic forests, showing the disjunction between the coastal and interior populations (*Thuja plicata* and *Tsuga heterophylla*), based on ecosystem classifications (see Gavin & Hu, 2006) and the reconstructed ice extent at 16 ka.

2.2. Ecology of *Tsuga mertensiana*

Tsuga mertensiana is a shade tolerant, late-successional subalpine species that can live up to 700 years or more (Clausen, 1965; Lowery, 1973; Means, 1990; Edwards & El-Kassaby, 1996; Peterson & Peterson, 2001). *Tsuga mertensiana* growth is mainly limited by abotic factors such as temperature, length of growing season, snow pack depth and timing of melt, and soil temperature (Gedalof & Smith, 2001; Peterson & Peterson, 2001; Albright & Peterson, 2013). The physiological advantage the species has under high snowpack remains unclear, though it is able to maintain root cold-hardiness for longer periods than other conifers (Coleman et al., 1992).

Like most conifers, *T. mertensiana* pollen is wind dispersed and pollen release occurs between mid-May to mid-July throughout most of its distribution (Ebell & Schmidt, 1964; Owens & Molder, 1975). The pollen is saccate and relatively large in size, averaging 60 µm in length (Bassett et al., 1978; Owens & Blake, 1983; Kapp, 2000). Timing of pollen release appears to be dependent on daytime temperature with increased pollen released during warm, dry days (Ebell & Schmidt, 1964; Means, 1990). Trees are able to start bearing cones as young as 20 years. Cones ripen and open from late September to November and produce large crops every three years (Franklin et al., 1974; Eyre, 1980; Means, 1990). *Tsuga mertensiana* cones are larger than most other *Tsuga* species (approx. 2.5 cm in length), ranging from 4 to 8 cm at maturity (Arno, 2007). *Tsuga mertensiana* seeds are dispersed by wind and 47% to 75% of each crop is able to germinate (Schuller, 1977). The winged seeds of *T. mertensiana* are relatively light, averaging 250,000 per kg (Arno, 2007). The seed wing is 2.67 times the size of the seed itself enabling it to be carried long distances (Owens & Molder, 1975; Ally & Ritland, 2007). Approximately 25% of the weight of *T. mertensiana* seeds are made up of the seed coat, which increases the longevity of the seed during suboptimal conditions (Kandya & Ogino, 1986). Temperature appears to be the largest factor in the ability of seeds to form, germinate, and disperse (Edwards & El-Kassaby, 1996). Due to their large wings and light weight, *T. mertensiana* seeds have the potential to travel long distances.

3. Materials and methods

3.1. Current distribution and analysis of modern pollen assemblages

Distribution data for *T. mertensiana* was compiled from 7480 observations obtained from several data sources. A detailed list of all methods and sources used to construct the modern distribution map of *T. mertensiana* can be found in Appendix B. The map was created using a 6-km buffer around each point of tree observation. In order to assess the accuracy of pollen in detecting the range limit of *T. mertensiana,* I compared the presence and percentage of *T. mertensiana* pollen in sediment-surface samples of lakes to the distance to the nearest tree in the mapped distribution. I analyzed 299 sites from the (Whitmore et al., 2005) pollen surface-sample database that occur within 200 km of a *T. mertensiana* observation. Within this data set, no *T. mertensiana* pollen was observed at distances over 200 km from an observed *T. mertensiana* tree location.

3.2. Study sites

The Clearwater drainage basin occupies a ca. 27,000 km^2 area, 200 km south of the southernmost extent of the Cordilleran ice sheet. No paleoecological studies having been conducted in this drainage basin or in the St. Joe drainage basin to the north (Figure

3.2). The three lakes used in this study are small, mid-to-high elevation lakes that reside within cirque basins in the St. Joe and Clearwater Mountains (Table 3.1). These sites were chosen because they all reside near the southernmost extent of the modern distribution of *T. mertensiana*. Two lakes (Rocky Ridge and Horseshoe lakes) are located near the proposed refugium for several other taxa as determined by phylogeogrpahic studies (Brunsfeld et al., 2001; Carstens & Richards, 2007).

Table 3.1. Site details for the three new coring locations from northern Idaho.

Site Name	**Elevation (m a.s.l.)**	**Coordinates**	**Size (max. water depth)**	**Surrounding dominant vegetation**
Dismal Lake	1630	47°07’0’’N 115°38’0’’W	2.9 ha (20 m)	*Tsuga mertensiana* and *Picea engelmannii* surround the lake with *Larix occidentalis* and *Abies lasiocarpa* on the hillsides
Rocky Ridge Lake	1750	46°26’31’’N 115°29’35’’W	1.1 ha (13 m)	*Tsuga mertensiana* and *Pinus contorta* surround the lake with *Abies lasiocarpa*
Horseshoe Lake	1920	46°32’59’’N 115°04’06’’W	1.1 ha (3m)	*Abies lasiocarpa, Picea engelmannii, Pinus contorta,* and *Tsuga mertensiana* surround the lake

3.3. Sampling and analysis

All sites were accessed by road. Two parallel sediment cores were taken at each lake from the deepest point using a modified Livingstone corer. Coring continued until reaching impenetrable rock. Surface cores were taken using a clear plastic tube fitted with a piston to preserve the mud-water interface of the upper-most sediments. The surface cores were subsampled at 1-cm intervals in the field.

I sectioned the cores longitudinally and described the sediment stratigraphy by visual inspection. The two parallel cores were correlated with each other by visual inspection. Accelerator mass spectrometry (AMS) radiocarbon dates were obtained on macrofossils recovered from each sediment core (Table 3.2). Radiocarbon dates were calibrated to calendar years BP, and rounded to the nearest decade using CALIB 5.0 (Stuiver & Reimer, 1993; Reimer et al., 2004). I created age-depth models using a modified version of CLAM (Blaauw, 2010) that fits a monotonic spline to calibrated radiocarbon dates, the Mt. Saint Helen's tephra from the 1980 eruption, and the Mazama tephra layer (Zdanowicz et al., 1999).

I processed 62 (0.5 cm^3) samples for pollen analysis across the three cores. Fifty pollen samples were extracted from Dismal and Horseshoe Lakes (25 samples from each site) above the Mazama tephra. An additional 20 samples from Dismal Lake and 10 samples from Horseshoe Lake were examined below the Mazama tephra, but no *T. mertensiana* pollen was present. Since *T. mertensiana* was not found in any sample prior to the Mazama tephra, I decided to present only the post-Mazama vegetation record at Dismal and Horseshoe Lakes. Based on the late arrival of *T. mertensiana* at Dismal and Horseshoe lakes, only 12 samples from the top 62 cm were analyzed for pollen from

Rocky Ridge Lake. Subsamples were chemically processed for pollen analysis following standard methods (Krzywinski et al., 2000). Processed samples were stained and pollen was examined at 400X magnification. I identified pollen to the lowest taxonomic level possible using published keys (Kapp, 2000; Krzywinski et al., 2000) and the modern pollen reference collection at the Paleoecology and Biogeography Laboratory at the University of Oregon. *Pinus* (pine) grains were differentiated into *Pinus* and *Strobus* subgenera-types based upon the presence or absence of verrucae on the leptoma. At Rocky Ridge Lake, *Alnus* was differentiated between *A. rubra* and *A. sinuata* based on the pore structure and arci thickness (Leopold et al., 2012; May & Lacourse, 2012). *Alnus* grains were not differentiated at Dismal or Horseshoe lakes. I identified a minimum of 350 terrestrial pollen grains in each sample. Pollen concentration was determined by adding known quantities of a *Lycopodium* tracer and pollen accumulation rates were calculated using the sedimentation rates from the modeled age-depth relationship. For the purposes of this study, only the dominant tree taxa are presented.

4. Results

4.1. Current distribution and analysis of modern pollen assemblages

In order to understand the association between *T. mertensiana* pollen abundance in modern surface samples (Whitmore et al., 2005) and its relationship to distance from an observed *T. mertensiana* tree location, I created box plots of distance-to-nearest observations for a range of pollen percentage values (Figure 3.3). In general, trace pollen percentages (0-1%) occur mainly within 140 km of the nearest observed *T. mertensiana* location observations, while pollen percentages above 1% occur mainly within 36 km.

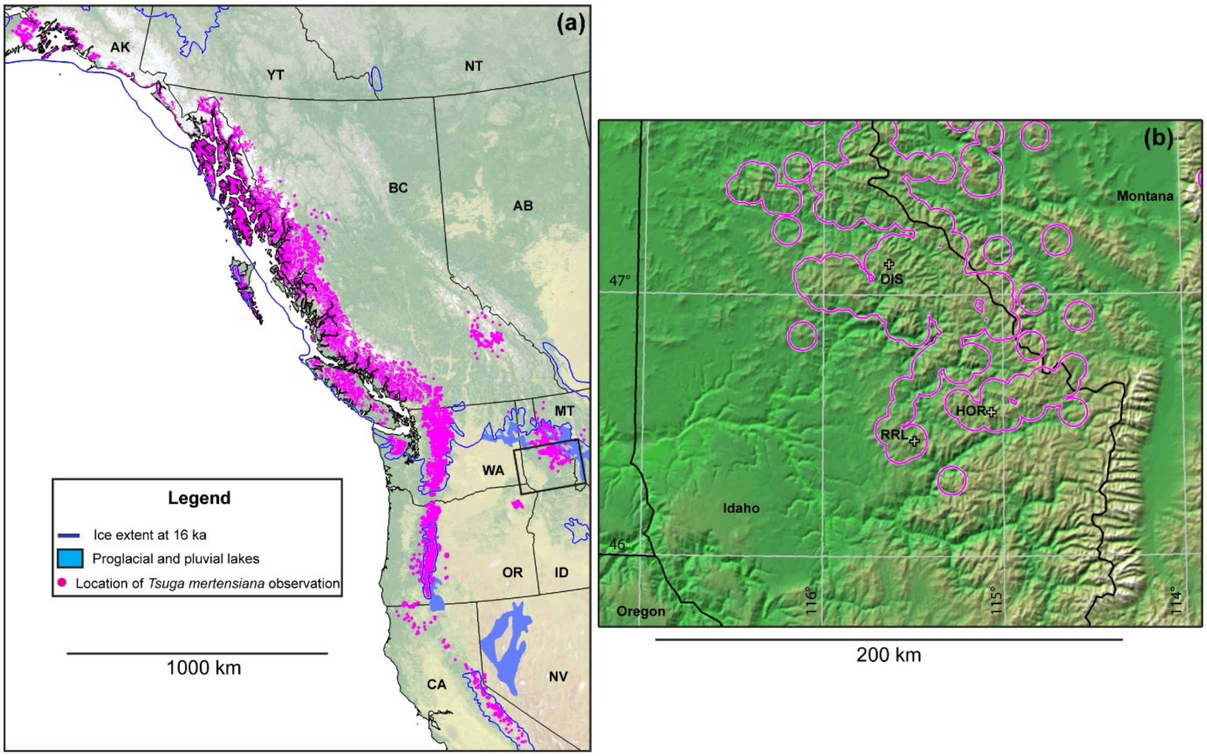


Figure 3.2. (a) Distribution map of *Tsuga mertensiana*. Square indicates the area enlarged for the map in (b). (b) Shaded relief map of all three lakes (DIS – Dismal Lake, RRL – Rocky Ridge Lake, and HOR – Horseshoe Lake) in northern Idaho within the distribution of *T. mertensiana.*

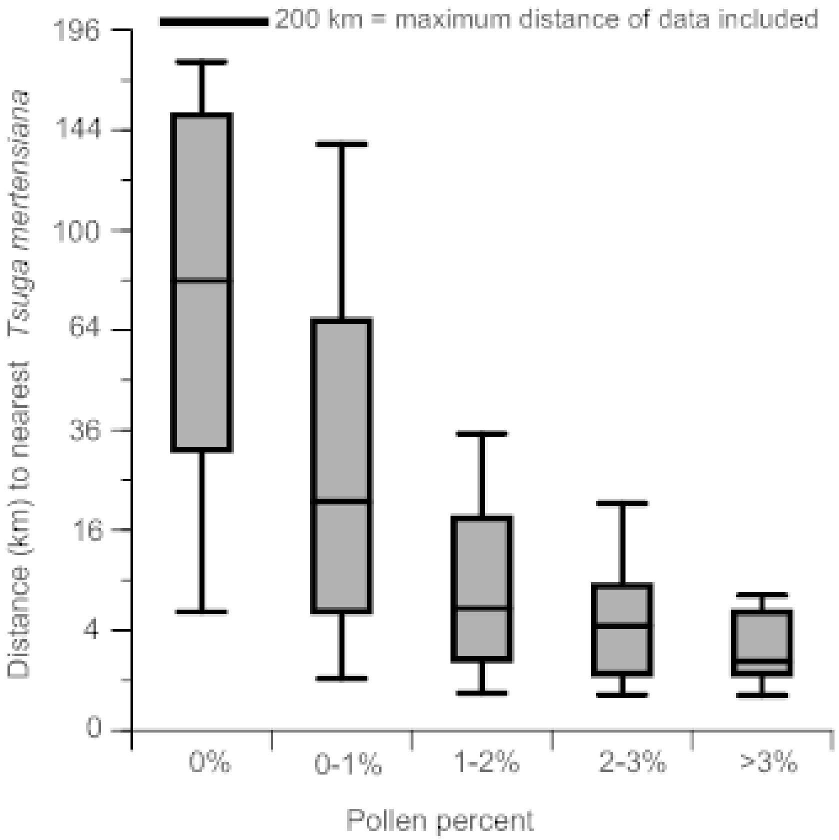


Figure 3.3. Box plots of distance to nearest observed *Tsuga mertensiana* tree as a function of percent class of pollen using a square-root transformation of distance. N= 299 pollen surface sample sites that are within 200 km of *T. mertensiana* observations. Data are from the Whitmore et al. (2005) surface sample pollen database.

4.2. Chronology and sediment characteristics

A sediment chronology for each lake was constructed from AMS radiocarbon dates and two tephras (Table 3.2, Figure 3.4). 1000-cm of sediment was recovered from Dismal Lake, of which 593 cm occurs above the Mazama tephra. Six AMS dates and two tephra layers were used to construct the Dismal Lake age model above the Mazama tephra (Table 3.2; Figure 3.4). The Dismal Lake sediment core is comprised of three lithologic components: massive gyttja (0 to7 cm), finely laminated gyttja (8 to 593 cm), and tephra (7 to 8 and 593 to 734 cm; Figure 3.4).

A total of 729 m of sediment was recovered from Rocky Ridge Lake. The chronology for Rocky Ridge Lake was determined from two AMS dates and two tephras. Massive gyttja extends from 0 to278 cm with several dense vegetation mats of *Elodea canadensis* occurring within this layer (Figure 3.4). Tephra from Mt. St. Helens 1980 eruption was preserved in the sediment record from 7 to 7.5 cm, while the tephra from Mazama extended from 278 to 439 cm.

The core from Horseshoe Lake yielded a 389 cm record. The chronology for Horseshoe Lake was determined from two AMS dates and one tephra layer. More sediment was recovered below the Mazama tephra, but correlation between the two parallel cores could not be made below the tephra layer. Laminated gyttja extends from 0 to178 cm, while tephra from the Mazama eruption extends from 178 to389 cm.

4.3. Pollen

At Dismal Lake, *Pinus* occurs at its lowest relative abundance (22%) directly above the Mazama tephra (Figure 3.5). *Pinus* then increases towards the mid-Holocene and remains fairly constant throughout the remainder of the core (averaging 51%). *Picea* is absent directly above the Mazama tephra, but increases at approximately 5500 cal yr BP and remains fairly constant throughout the rest of the core (averaging 9%). From 700 to present *Picea* decreases to 8% at the top of the record. *Abies* is low following Mazama (8%) and increases steadily until approx. 3300 cal yr BP. The highest abundance of this taxa occurs between 700 and 2700 cal yr BP (averaging 19%). *Pseudotsuga/Larix*-type

Table 3.2. AMS ^{14}C and tephra layers used to construct of the chronology results for all three sites. AMS ^{14}C samples were analyzed at Lawrence Livermore National Laboratory (CAMS) and Woods Hole (NOSAMS). * At Dismal Lake, the date at 68-69 cm was not used.

Site	**Depth (cm)**	**Lab numbers**	**^{14}C age (yr BP)**	**Calibrated age (median cal yr BP and 2 σ range)**	**Item dated (or reference for tephras)**
Dismal Lake	7-8	Mt. St. Helens tephra		-30	1980 Mt. St. Helens tephra
	67-68	CAMS-165327	1390±80	1300 (1150-1480)	3 *Larix occidentalis* needles
	68-69*	CAMS-151028	1500±35	1370 (1310-1420)	Charcoal
	142-143	NOSAMS-74113	1670±25	1580 (1530-1680)	wood
	331-332	NOSAMS-74114	3340±30	3580 (3480-3670)	wood
	378-379	CAMS-156040	3675±30	4010 (3920-4110)	wood
	473-474	CAMS-156041	5210±35	5970 (5920-6140)	wood
	504-505	NOSAMS-74115	5640±40	6420 (6320-6500)	wood
	593-734	Mazama tephra		7630 (7480-7780)	Zdanowicz et al., 1999
Rocky Ridge Lake	7-7.5	Mt. St. Helens tephra		-30	1980 Mt. St. Helens tephra
	61-62	CAMS-159526	2090±35	2060 (1970-2180)	Terrestrial plant part
	140-141	CAMS-151037	2965±30	3140 (3030-3250)	1 *Abies lasiocarpa* stem
	278-439	Mazama tephra		7630 (7480-7780)	Zdanowicz et al., 1999
Horseshoe Lake	16-17	CAMS-159525	1460±30	1370 (1310-1400)	Aquatic plant (*Elodea canadensis*)
	68-69	CAMS-151033	3980±30	4460 (4370-4520)	*Pinus contorta* needle
	178-389	Mazama tephra		7630 (7480-7780)	Zdanowicz et al., 1999

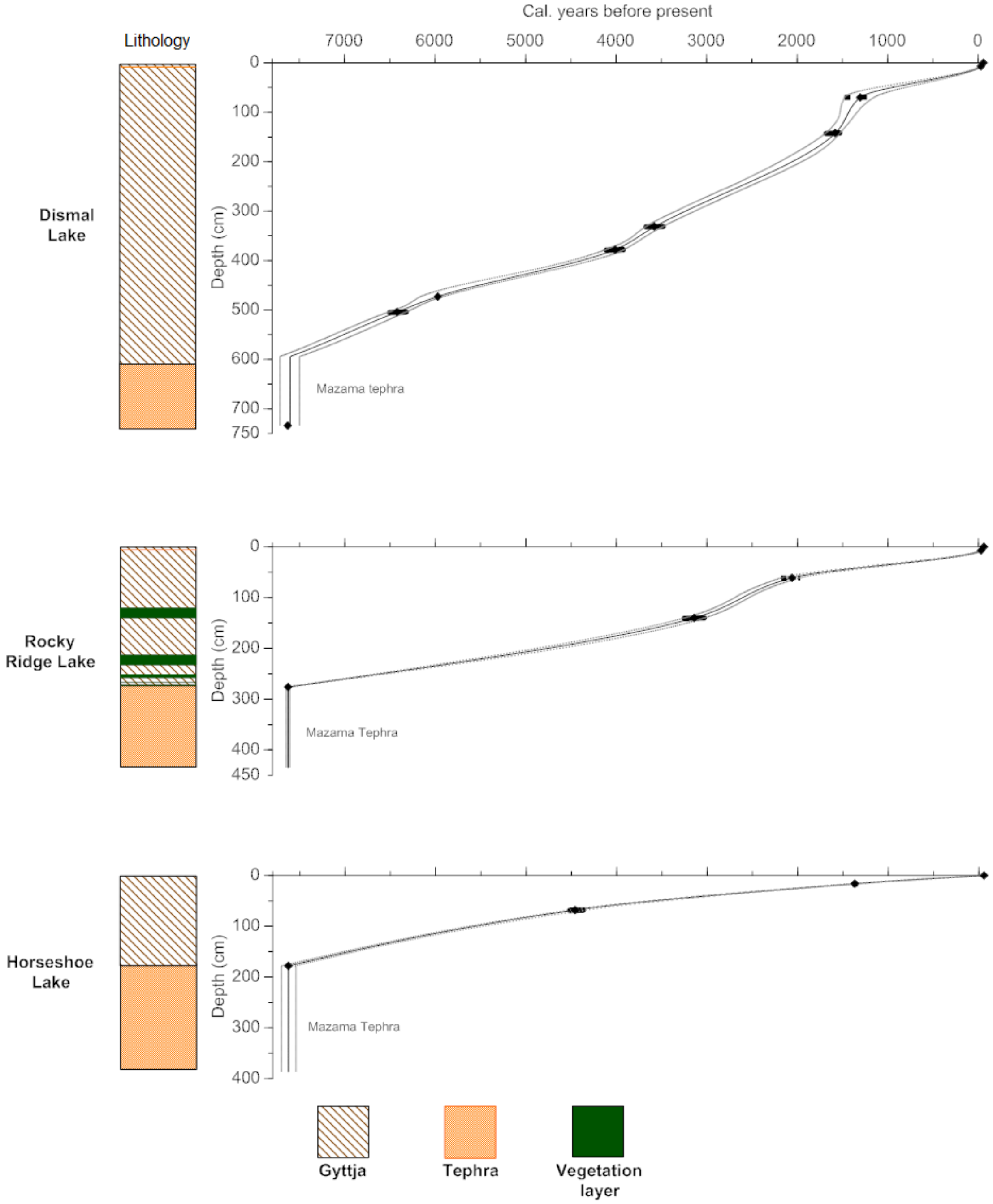


Figure 3.4. Age-depth models using a constrained spline curve fit to radiocarbon dates and tephras at three lakes in northern Idaho, USA. Error bars for calibrated radiocarbon dates are shown. Low and high age estimates (dashed gray lines) are based on resampling of calibrated radiocarbon dates using CLAM software.

varies from 4% to 9%, with the highest abundance occurring at 4400 cal yr BP. *Alnus* is highest above Mazama (21%) and near the top of the record (averaging 14%), and lowest at 4400 cal yr BP (5%). *Betula* occurs at low levels (<1%) from 200 cal yr BP to present. *Tsuga mertensiana* pollen is first detected at Dismal Lake around 1300 cal yr BP, but does not occur at > 1% until 960 cal yr BP. PAR shows that plant abundance around the lake increases dramatically above the Mazama tephra. A large increase in PAR at 1500 cal yr BP reflects a sharp increase in sedimentation rate but is not matched by a change in the pollen assemblages. Increased efficiency of sediment delivery from littoral areas to the core location may explain this period of high PAR.

At Rocky Ridge Lake, *Pinus* and *Picea* pollen remain fairly constant throughout the length of this short record (averaging 44% and 7% respectively). *Abies* abundance varies from 4% to 17% over the last 2100 cal yr BP. *Pseudotsuga/Larix*-type is present in very low abundance varying from <1% at the base and increases throughout the record to 4% near the top of the core. *Alnus rubra* has an abundance of <1% in all samples except the uppermost sample which increases to a 2% abundance. *Alnus viridis* var. *sinuata* is highest in abundance prior to 1000 cal yr BP (averaging 25%), and decreases in abundance towards the top of the record (averaging 11% in the uppermost samples). *Betula* is present throughout most of the record but in abundances of <1%. *Tsuga mertensiana* pollen first appears at Rocky Ridge Lake at ca. 1600 cal yr BP, but does not become consistently above 1% until 730 cal yr BP. *Tsuga mertensiana* reaches its highest abundance (averaging 12%) between 40 and 210 cal yr BP. PAR is only high at the base and top of the record. PAR remains steady through the arrival and increase in abundance of *T. mertensiana* pollen.

At Horseshoe Lake, *Picea* (0-10%), *Abies* (1-19%), and *Alnus* (5-25%) increase in abundance to approximately 3500 cal yr BP. From 3500 cal yr BP to present, *Picea* (4-9%), *Abies* (4-9%), and *Alnus* (4-8%) decrease in abundance. *Pinus, Pseudotsuga/Larix*-type, and *Betula* are fairly constant throughout the length of the core (averaging 69%, <1%, and <1% respectively). *Tsuga mertensiana* pollen first appears at Horseshoe Lake around 4100 cal yr BP, but does not become consistently above 1% until 330 cal yr BP. Above the Mazama ash, PAR increases to its highest level at ca. 7000 cal yr BP, but is low compared to PAR at Dismal and Rocky Ridge Lakes. From 6000 cal yr BP to present, PAR decreases and remains unchanged through the arrival and increased abundance of *T. mertensiana.*

5. Discussion

Paleoenvironments and Tsuga mertensiana expansion in interior forests

During the period following the Mazama ash, disturbance-adapted taxa such as *Pinus* (likely *Pinus contorta*) and *Alnus* dominated the forest surrounding Dismal and Horseshoe Lakes. The forest composition subsequently changed to reflect a cooling climate. By 5000 cal yr BP, a mixed conifer forest, consisting of *Pinus, Picea, Abies*, and *Pseudotsuga/Larix*, was able to establish. For the remainder of the Holocene (5000 cal yr BP to present), the climate continued to cool and available moisture increased in the Northern Rocky Mountains (Power et al., 2011). The changing climate conditions reduced the severity and frequency of regional fires, enabled the forests to become denser, and new species to migrate into the region (Mehringer et al., 1977; Brunelle & Whitlock, 2003; Brunelle et al., 2005).

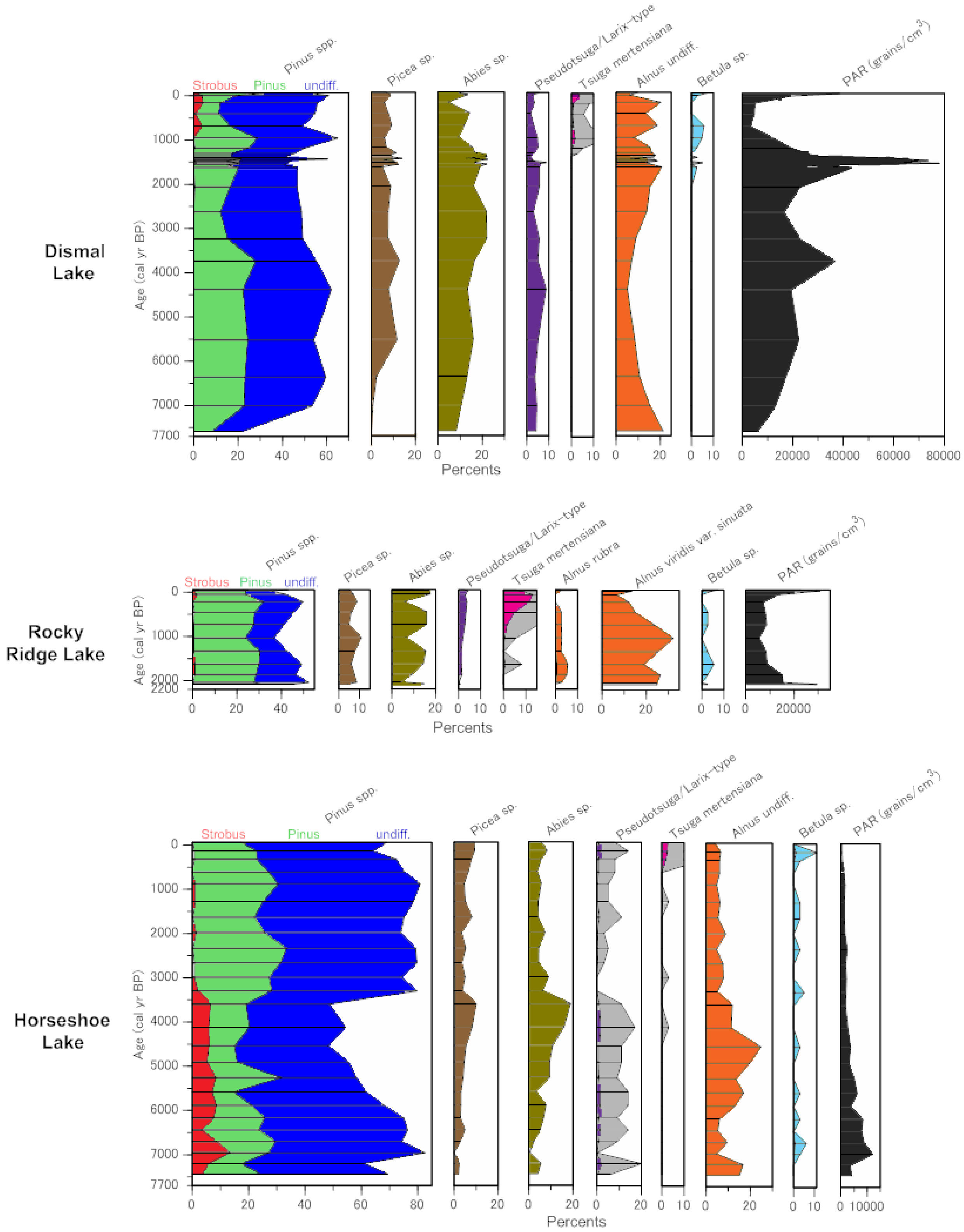


Figure 3.5. Summary pollen diagrams and pollen accumulation rate (PAR) from the three lakes in northern Idaho.

In northern Idaho, *T. mertensiana* pollen first appeared at the highest elevation site (Horseshoe Lake) 4100 cal yr BP (Figure 3.5). This timing corresponds with regional cooling and regionally advancing glaciers (Menounos et al., 2009; Gavin et al., 2011). However, *T. mertensiana* pollen at this site is rare (one grain, <1%) and inconsistent (only found at three depths). It is unlikely that these three grains were dispersed from the coast since *T. mertensiana* has not been observed to travel distances greater than 200 km (Fig. 3.2). The low abundance at Horseshoe Lake likely indicates that the grains were dispersed from distant populations within the IMF (>36 km) or they were detected in low abundance due to over representation of other pollen types such as *Pinus* (e.g., Heusser, 1983; Macdonald, 1989; Walanus & Nalepka, 2013). *Tsuga mertensiana* pollen did not increase in abundance above 1% (detection of populations within 36 km of lake) or remain a constant component of the sediment record until ca. 960 cal yr BP at Dismal Lake, ca. 730 cal yr BP at Rocky Ridge Lake, and ca. 330 cal yr BP at Horseshoe Lake.

Because my new records do not extend back to the LGM, I cannot provide evidence to support or refute the presence of this taxa in a glacial refugium. No *T. mertensiana* was found pre-LGM at Star Meadows, a much longer sediment record in northern Idaho, under colder climates of the late-Pleistocene (Chapter II). Even if such pollen data were available, *Tsuga mertensiana*'s low pollen representation (Hebda, 1983, 1995; Mathewes, 1993; Rosenberg et al., 2003) and small populations result in it being difficult to detect in the paleorecord when it is at low abundance. Thus, it may be impossible for fossil evidence to support the presence of this taxa within a glacial refugia.

Even though the pollen data does not extend back to the LGM, the inferred timing of *T. mertensiana* expansion in the pollen records is consistent with a recent dispersal from the coast. It is instructive to compare the history of *T. mertensiana* in Idaho with its record from its interior British Columbia distribution where it occurs >300 km north of the Cordilleran Ice extent and therefore had to be colonized following ice sheet retreat. A pollen record from Revelstoke, British Columbia, shows *T. mertensiana* increased abruptly at ca. 2500 cal yr BP. Given that climate had become sufficiently cool and moist by 4200 cal yr BP for establishment of another mesic-adapted species, *Tsuga heterophylla* (Gavin et al. 2011), it is possible that the later detection of *T. mertensiana* in British Columbia represents a dispersal lag. In Idaho, the earliest pollen appearance appears closer in time to the neoglacial climates beginning at 4200 cal yr BP. Thus, the initial detection, at 4200 cal yr BP, of *T. mertensiana* in Idaho may represent its initial colonization. However, expansion of *T. mertensiana* within the interior distributions did not occur in the region until recently. The pollen data are also consistent with *Tsuga mertensiana* arriving first at the highest elevation site and then expanding its range downslope as the neoglacial cooling in the region progressed. Consistent with this interpretation is the increase in *T. mertensiana* pollen to modern levels from 700 to 300 cal yr BP during the coolest neoglacial climate associated with the Little Ice Age (Luckman, 2000).

The very broadly similar timing of the increase of *T. mertensiana* among the three Idaho sites and the disjunct British Columbia site is consistent with a regional climate control on the establishment of interior distributions of this species, though the establishment at any one site may be affected by migration lags due to limited dispersal and/or competition with established forests. *Tsuga mertensiana* seeds are light weight can have relatively large wings which enables them to disperse long distances. Mountain updrafts can aid in seed dispersal over great distances (>100 km) (Tackenberg, 2003). Phylogenetic studies also indicate that the interior populations in British Columbia are genetically similar to coastal populations, adding further support for recent long-distance dispersal (Benowicz & El-Kassaby, 1999; Benowicz et al., 2001).

Dispersal and establishment is slow to proceed and there is evidence that this fairly recent (last few millennia) colonization of the IMF is continuing to this day. Specifically, the large region between the Idaho and British Columbia distributions contains extensive regions of suitable habitat (as suggested by climate data from in the region and occurrence of high snowpack normally associated with *T. mertensian*a) in which this species could persist. Outlier populations around the centers of abundance in Idaho and British Columbia are consistent with its continued spread (Figure 3.2).The spatial pattern of *T. mertensiana* point observations near the southern edge of the British Columbia population, and at the northern edge of the Idaho population, are consistent with continued diffusion of populations into the unoccupied areas of southeast British Columbia (Figure 3.2). Competition among other forest taxa is likely impeding its dispersal into areas with suitable habitat.

6. Conclusion

The results of this study have clarified the history and provided explanations for the population disjunctions of *T. mertensiana.* Distribution of *T. mertensiana* in the interior is split into three distinct populations in northeast corner of Oregon, southeastern British Columbia, and northern Idaho. Several outlier populations are present in eastern Washington and northwestern Montana. Using modern surface samples of *T. mertensiana*

I was able to determine that pollen abundances >1% originated from a population located within 36 km of the sample location. *Tsuga mertensiana* is a relatively recent component of the IMF of British Columbia, arriving ca. 2500 cal yr BP.

Similar to the IMF in British Columbia, *T. mertensiana* in northern Idaho is also a recent component of the forest. *Tsuga mertensiana* first appeared in the pollen record (ca. 4100 cal yr BP) at the highest elevation site (Horseshoe Lake) in very low abundance. Based on pollen abundance, *T. mertensiana* has becomes a more dominant component of the forests of northern Idaho only over the last 400 years. The light, winged, *T. mertensiana* seeds have the capacity to disperse over large distances. Considering that pollen data are unlikely to detect the earliest presence of a species within several km of a lake, *T. mertensiana* initial occurrence in the region is consistent with arrival close in time to the onset of neoglacial cool and wet climate at 4200 cal yr BP. Climate was thus likely limiting the expansion of *T. mertensiana* into the IMF from the coast, but within the IMF a slow expansion due to interspecific competition, was just as important in the past as they are in the present. Further neoglacial cooling was required to accelerate range infilling in northern Idaho. However, suitable habitat and similar climates to where *T. mertensiana* currently exists can be found between the British Columbia and northern Idaho populations. This indicates that *T. mertensiana* is not in equilibrium with climate and range expansion is still occurring. Together, the paleoecological data indicate the large dispersal barriers were relatively insignificant at slowing migration, and that *T. mertensiana* spread within Idaho for millennia at low abundances until Little Ice Age climate promoted its recent increase in forest ecosystems. However, the infilling of potential range since the Little Ice Age has likely been impeded by competition among other forest taxa.

In this chapter, I discussed the timing of regional arrival of *T. mertensiana* to the interior populations. In all three sediment cores used for this chapter, only the sediment above the Mt. Mazama tephra was used. The previous two studies found that the vegetation before and after the deposition of the Mt. Mazama tephra was different from one another. In this next chapter I explore the impacts of tephra deposits on vegetation at the Dismal Lake site.

CHAPTER IV

TEPHRA-MEDIATED VEGETATION CHANGE OBSERVED IN A 13,600-YEAR RECORD FROM THE NORTHERN ROCKY MOUNTAINS, IDAHO

1. Introduction

Vegetation composition in the Pacific Northwest (PNW) has been influenced by climate and natural disturbances. The relationship between climate, fire, and vegetation has been the focus of many paleoecological studies (Mehringer Jr, 1985; Whitlock, 1992; Whitlock et al., 2000; Power et al., 2011). Other natural disturbances such as volcanic eruptions have the potential to significantly influence vegetation trajectories but have been less studied. For example, there has been little research on the effects of Holocene ash deposit effects on vegetation at locations far from the source of the eruption (Lotter & Birks, 1993; Dwyer & Mitchell, 1997), instead most research has focused on more recent eruptions and the short-term effects within heavily impacted areas close to the vent (Moral, 1983; Zobel & Antos, 1991, 1997). Recent studies have demonstrated how the deposition of tephra can alter soil properties and affect vegetation (Wada & Aomine, 1973; Shoji et al., 1994; Vitousek & Farrington, 1997; Ugolini & Dahlgren, 2002). For example, the effects of tephra deposition vary depending on the type of vegetation (e.g., herbaceous versus woody taxa), the thickness of tephra deposited, and the size of the ash particles (Rees, 1970; Blong, 1984; Giles et al., 1999; Dale et al., 2005a). In general, the deposition of thick tephra layers, 20-50 cm, can kill much of the understory forest taxa, but may have little effect on trees (Antos & Zobel, 2005; Dale et al., 2005a, 2005b).

Volcanic eruptions not only influence the environment close to the volcano, but tephra ejected from major Plinian (one large catastrophic event) eruptions can affect environments tens to hundreds of kilometers away (del Moral & Grishin, 1999; Dale et al., 2005b). Studies of recent eruptions have shown that tephra has influenced ecosystems and facilitated vegetation shifts (del Moral & Grishin, 1999; Antos & Zobel, 2005), and some modern vegetation patterns are attributable to thick Holocene tephra deposits (e.g., the Pumice Plateau of southern Oregon; (Dyrness & Youngberg, 1966; Franklin & Dyrness, 1988; Hagmann et al., 2013). Therefore, it is reasonable to expect a major vegetation response to thick tephra deposition during postglacial vegetation succession.

In the PNW, the two largest volcanic eruptions during the late-Quaternary were Glacier Peak occurring ca. 13,400 cal yr BP (Kuehn et al., 2009) and Mt. Mazama occurring ca. 7600 cal yr BP (Figure 4.1) (Zdanowicz et al., 1999). Thick (>10 cm) tephra from these eruptions have been found in sediment records over broad areas (Mehringer et al., 1977; Hammer et al., 1980; Hallett et al., 1997; Gavin et al., 2006; Long et al., 2014). The eruption of Glacier Peak in the late-Pleistocene (ca. 13,400-13,700 cal yr BP) was not a single event (Zdanowicz et al., 1999; Kuehn et al., 2009). Instead, there was a Plinian eruption followed by several smaller eruptions (Porter, 1978; Westgate & Evans, 1978). Tephra from the eruptions of Glacier Peak was dispersed eastward covering vast areas of Washington, Oregon, Idaho and Montana, and even extended into portions of Wyoming, Alberta, and Saskatchewan (Figure 4.1; Zdanowicz et al., 1999; Kuehn et al., 2009). The mid-Holocene eruption of Mt. Mazama (ca. 7627 cal yr BP) was the largest volcanic eruption of the Holocene in North America (Zdanowicz et al., 1999; Long et al., 2014). The eruption of Mt. Mazama was similar to the eruption of Glacier Peak, with a Plinian eruption followed by several smaller eruptions (Bacon, 1983; Sarna-Wojcicki et al., 1983; Shipley & Sarna-Wojcicki, 1983). The tephra from the eruption of Mt. Mazama covered a much greater area (1,700,000 km^2; (Sarna-Wojcicki et al., 1983) than tephra from Glacier Peak G (covering 550,000 km^2) and B (covering 250,000 km^2; (Kuehn et al., 2009); Figure 4.1). Mt. Mazama tephra greater than 15 cm in thickness extended over 800 km to the northeast into Idaho and British Columbia (Matz, 1987).

The effects of the tephra from Mt. Mazama on fire and vegetation have been the focus of recent paleoecological studies in the PNW (Long et al., 2011, 2014). Long et al. (2011, 2014) recovered 14 to 50 cm of Mt. Mazama tephra from four lake sites in the Cascade Range in Oregon. At each of these sites, the tephra deposited from the Mt. Mazama eruption appeared to only be one event. The deposition had a higher impact on the understory herbaceous taxa than on arboreal taxa, but there were no abrupt shifts in vegetation. All vegetation communities returned to their pre-depositional abundances within 50 to 100 years. At Lost Trail Pass, Idaho, Meheringer et al.'s (1977) core contained 8 cm of tephra from the Mt. Mazama eruption and 5 cm of tephra from Glacier Peak. No changes in the pollen record were attributed to the deposition of tephra on the landscape (Mehringer et al., 1977). Tephra thickness varied greatly across the PNW, especially for the Mt. Mazama tephra, and therefore likely produced different responses among vegetation types (e.g., dry pine forests of eastern Oregon versus mesic forests of northern Idaho) and over time (e.g., during the cool-wet climate of the late Glacial or the warm-dry climate of the early Holocene). Unlike the previous work in the Pacific Northwest, cores from Ireland show that vegetation in the past, including trees, was impacted by large amounts of ash fall (Lotter & Birks, 1993; Hall, 2003).

In this study, I present a high-resolution pollen record of vegetation response to the deposition of two thick tephras in mesic forests in northern Idaho to 1) examine the long-term relationship between climate and vegetation, 2) examine the effect of tephra deposition on postglacial vegetation change.

2. Site description

Dismal Lake is a small (2.9 ha), deep (20.9 m) closed cirque basin at 1630 m elevation, (47°07'N, 115°38'W) in the St. Joe National Forest of northern Idaho (Figure 4.1). The surrounding watershed is small (20 ha), and varies only 130 m in elevation. The lake is located on a steep mountainside (slopes up to 75% within the watershed) with rocky shallow soils (Figure 4.1). The lake is south of the maximum extent of the Cordilleran Ice Sheet, but alpine glaciers were common in the surrounding mountains until ca. 14,000 years ago (Thackray et al., 2004; Brunelle et al., 2005). Bedrock consists of Cretaceous granite and Paleozoic metasedimentary rock (Thackray et al., 2004).

Mesic climates currently exist on the coast of the western North America and in the western ranges of the northern Rocky Mountains. A dry environment extends from the Cascade Range eastward until the Rocky Mountains of northern Idaho and southeast British Columbia provide orographic precipitation from moist Pacific air masses, resulting in a separate interior mesic climate. Thus, Dismal Lake experiences a maritime west-coast climate with snowy winters. Mean annual precipitation is greater than one meter, with most falling during the winter months and approximately 41% as snow. In July the daily maximum and minimum temperatures are 20.3°C and 8.6°C, respectively (average=14.5°C). In December the daily maximum and minimum temperatures are -2.2°C and -7.4°C, respectively (average=-4.8°C) (Wang et al., 2012).

The forest surrounding Dismal Lake is dominated by *Tsuga mertensiana* (mountain hemlock) and *Picea engelmannii* (Engelmann spruce) with minor amounts of *Abies lasiocarpa* (subalpine fir). Infrequent tree species near the lake include *Pinus monticola* (western white pine), *Larix occidentalis* (western larch), and *Pinus contorta* (lodgepole pine). Shrubs include *Sambucus* sp. (elderberry), *Menziesia ferruginea* (false huckleberry), *Rhododendron albiflorum* (Cascade azalea), *Vaccinium* spp., *Lonicera utahensis* (Utah honeysuckle), *Sorbus sitchensis* (Sitka mountain-ash), and *Spirea* sp. Herbs found in the understory include *Xerophyllum tenax* (bear grass), *Lupinus* sp., *Anaphalis* sp., *Ranunculus* sp. (buttercup), and *Viola* sp. Two ferns *Polystichum munitum* (sword fern) and *Adiantum pedatum* (maidenhair fern) are scattered in the forest understory. Aquatic vegetation at the lake margin is dominated by *Menyanthes trifoliata* (bogbean). Other aquatic plants include *Carex* sp. (sedge) and *Potentilla palustris* (marsh cinquefoil).

3. Methods

3.1. Field and laboratory methods

In August 2008, two parallel sediment cores were taken one meter apart from the deepest point at Dismal Lake using a modified square-rod Livingstone piston corer (Figure 4.1c; (Wright et al., 1984). I extruded and wrapped each core section in the field. A surface core was also taken using a clear plastic tube fitted with a piston within a meter

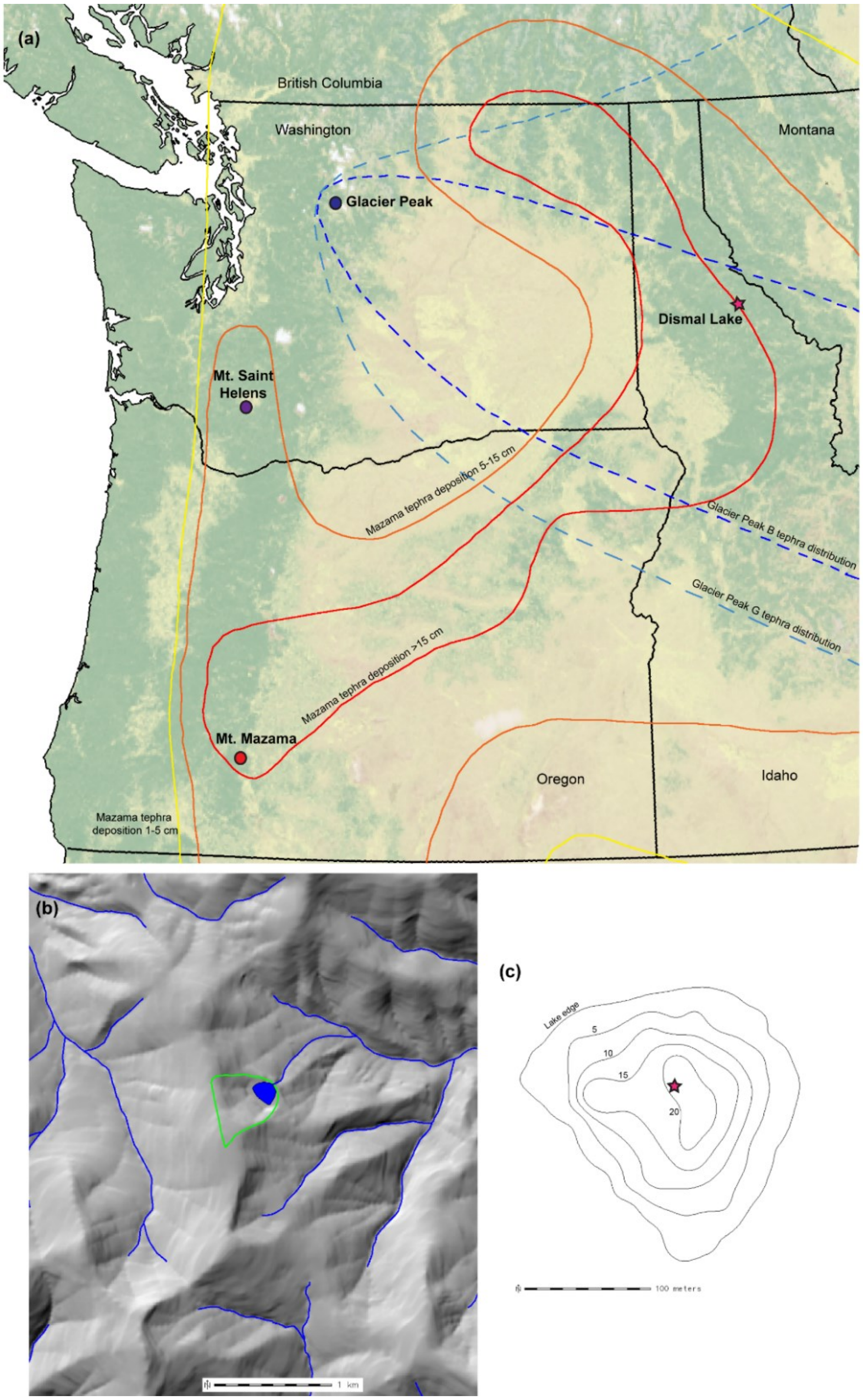


Figure 4.1. (a) The distribution of tephra from the eruptions of Glacier Peak (Kuehn et al., 2009) and Mt. Mazama (ca. 7600 cal yr BP; (Matz, 1987; Zdanowicz et al., 1999) in the Pacific Northwest. Estimates of ash-fall thickness from the eruption of Mt. Mazama are included (Matz, 1987). (b) Detailed view of Dismal Lake showing the surrounding topography and watershed. (c) Bathymetric map showing the location of the core taken from Dismal Lake. The star indicates the location the sediment core was taken.

of the long sediment core. The surface core was subsampled at 1-cm intervals in the field. To construct a bathymetric map, water depths were measured at 64 locations using a depth sounder. I transported all sediment to the Paleoecology and Biogeography Laboratory at University of Oregon and stored the core at 4°C.

I sectioned the cores longitudinally and described the sediment stratigraphy by visual inspection. The two parallel cores were correlated with one another by visual inspection, and the Livingstone core was correlated with the surface core using the 1980 AD Mount St. Helens tephra at 8 cm depth. Twelve terrestrial plant macrofossils (needles, wood, or charcoal) were extracted, identified and used for accelerator mass spectrometry (AMS) radiocarbon dates. Radiocarbon dates were calibrated to calendar years BP, and rounded to the nearest decade using CALIB 5.0 (Stuiver & Reimer, 1993; Reimer et al., 2004). I created an age model using CLAM (Blaauw, 2010); version 2.2) with monotonic spline interpolation between the AMS dates, the Mt. St. Helen's 1980 tephra, the Mt. Mazama tephra (Zdanowicz et al., 1999), and the Glacier Peak tephra (Kuehn et al., 2009).

Organic content, measured by loss-on-ignition at 550°C, was measured on 516 1-cm^3 subsamples at 1-cm or 2-cm intervals. I measured magnetic susceptibility using a Sapphire Instruments magnetic cup meter at continuous 1-cm intervals using 3 cm^3 subsamples. After the magnetic susceptibility data was obtained, the same subsamples were analyzed for macrofossils. Macrofossil samples were soaked in a 5% sodium hexametaphosphate solution for a minimum of 24 hours. Samples were wet sieved into 125-250 µm and >250 µm size fractions. The >250 µm size fraction was examined for macrofossils, which were identified using published keys for conifer foliage (Dunwiddie,

1985) and the reference collection at the University of Oregon.

Pollen analysis was conducted on 45 0.5-cm^3 subsamples following standard methods (Krzywinski et al., 2000). Processed samples were stained and pollen was examined at 400X magnification. I identified pollen to the lowest taxonomic level possible based on published keys (Krzywinski et al., 2000; Kapp, 2000) and the modern pollen reference collection at the Paleoecology and Biogeography Laboratory at the University of Oregon. Asteraceae pollen types were differentiated into four categories: Tubuliflorae-type (sunflower); *Ambrosia*-type (bursage); Liguliflorae-type (lettuce subfamily), and *Artemisia* (sagebrush). *Pinus* (pine) grains were differentiated into *Pinus* and *Strobus* subgenera-types based upon the presence or absence of verrucae on the leptoma. I identified a minimum of 350 terrestrial pollen grains in the total pollen sum. Pollen zones are based on a constrained cluster analysis on the pollen record and variations in the sediment properties (CONISS; Grimm, 1987). Pollen accumulation rates (PAR) was calculated from the product of the pollen concentration (cm^3) and the sediment accumulation rate ($cm\ yr^{-1}$) at each site (Bennett & Willis, 2002). Variation in pollen assemblages was scaled to two axes by using nonmetric multidimensional scaling (MDS) using the Bray-Curtis dissimilarity index on the 17 most abundant pollen types using square-root transformed pollen percentages (Prentice, 1980; Faith et al., 1987; Gavin et al., 2013).

4. Results

4.1. Lithology and chronology

A total of 10 m of sediment was recovered from Dismal Lake. The sediment core is composed of three major lithologic components: gyttja, tephra, and clay (Figure 4.2). Tephras were identified from their position in the stratigraphy and the extent of mapped tephra distributions (Table 4.1). Massive gyttja dominates the core extending from 0 to 7 cm. Finely laminated gyttja extends from 8 to 593 cm. Mt. Mazama tephra extends from 593 to 734 cm, with a 20 cm organic segment (640-660 cm) separating the two airfall events. From 734 to 908 cm the lithology consists of laminated gyttja. Glacier Peak tephra extends from 908 to 932 cm. A silt and clay unit, most likely from glacial run off, is present at the base of the core extending from 932 to 1000 cm. Both major tephras, the 141-cm Mt. Mazama tephra and the 24-cm Glacier Peak tephra, may be substantially thicker than the actual airfall input, due to slopewash from the steep-sided watershed and sediment focusing within the small deep lake.

Loss-on-ignition (LOI) varies from 1.93 to 54.74% (Figure 4.3). The highest values occur from 2630 cal yr BP to present (top 250 cm of the core) after steadily increasing above the Mt. Mazama tephra. The lowest LOI values occur at the base of the core (13,500-13,600 cal yr BP; 940-1000 cm). LOI decreases after the deposition of Mt. Mazama and Glacier Peak tephra. MS varies from -6×10^{-6} to 5.95×10^{-4} SI. Peaks in MS correspond to the locations of tephra deposition.

The chronology is based on eleven AMS dates and the tephra layers that fell in stratigraphic order (Table 1). One AMS date at 68-69 cm was anomalously old, and replaced by a date on *Larix* needles. The omitted date determined from a piece of charcoal that may have been secondarily deposited and/or inherited an older age from the age of the burned wood, resulting in an older age than the adjacent sediment. Sedimentation rates were generally low below the Mt. Mazama tephra (average 0.04

cm/yr) and increased greatly above the tephra (average 0.09 cm/yr). Two periods of relatively high sedimentation rate exist. First, the silt and clay sediments at the base of the core (928-100cm) were deposited rapidly until the Glacier Peak tephra (0.5 cm/yr). Second, a period of fast sedimentation rates was constrained by radiocarbon dates from 68 to 143 cm (0.29 cm/yr). A small peak in MS suggests that the latter segment of high sedimentation rate may be erosional in origin. Before fitting the age model, the tephra thicknesses were removed from the stratigraphic column and the depths were adjusted.

4.2. Pollen

Zone DIS-1 (13,400 to 13,600 cal yr BP; 928 to 1000 cm)

This zone consists of two pollen samples (Figure 4.3). This zone is distinguished by having the highest percentages of *Picea* (44-62%) in the core. The remainder of the arboreal taxa in this section consists of *Pinus* (7-8%), *Abies* (2%), *Pseudotsuga/Larix*-type (1-4%), and *Alnus* (2%). Other minor components of the ecosystem include Rosaceae (1-2%) and *Artemisia* (12-21%). The herbaceous taxa in the understory consists of Poaceae (5-11%) and very minor amounts of members of the Asteraceae family (*Ambrosia*-type 1% and Tubuliflorae-type 1-2%), *Chenopodium*-type (0-0.3%), and Ranunculaceae 0-1%). *Selaginella* and *Pteridium* are present at the base of this section. Needles of *Pinus monticola, Picea engelmannii*, *Abies lasiocarpa*, and *Larix occidentalis* were found. PAR was very high due to high sedimentation in this zone, and increased from 21,000 to 25,000 grains/cm^2/yr at the top of the zone.

Table 4.1. AMS ^{14}C and tephra layers used to construct of the chronology results for Dismal Lake. AMS ^{14}C samples were analyzed at Lawrence Livermore National Laboratory (CAMS) and Woods Hole (NOSAMS). * The date at 68-69 cm was not used.

Depth (cm)	Lab number	^{14}C age (yr BP)	Calibrated age (median cal yr BP and 2 σ range)	Item dated (or reference for tephras)
7-8	Mt. St. Helens tephra		-30	1980 Mt. St. Helens tephra
67-68	CAMS-165327	1390±80	1300 (1150-1480)	3 *Larix occidentalis* needles
68-69*	CAMS-151028	1500±35	1370 (1310-1420)	Charcoal
142-143	NOSAMS-74113	1670±25	1580 (1530-1680)	wood
331-332	NOSAMS-74114	3340±30	3580 (3480-3670)	wood
378-379	CAMS-156040	3675±30	4010 (3920-4110)	wood
473-474	CAMS-156041	5210±35	5970 (5920-6140)	wood
504-505	NOSAMS-74115	5640±40	6420 (6320-6500)	wood
593-734	Mazama tephra		7627 (7480-7699)	Zdanowicz et al., 1999
773-774	CAMS-151029	7460±40	8280 (8190-8370)	2 *Pseudotsuga menziesii* needles
786-787	CAMS-151030	7980±90	8840 (8610-9080)	wood
840-841	NOSAMS-74116	8900±40	10,040 (9860-10,180)	wood
881-882	CAMS-151031	10,250±100	12,000 (11,580-12,400)	2 *Abies lasiocarpa* needles
908-928	Glacier Peak tephra	11,600±50	13,400 (13,300-13,550)	Kuehn et al., 2009
978-982	CAMS-151032	11,675±45	13,450 (13,300-13,600)	Charcoal pieces

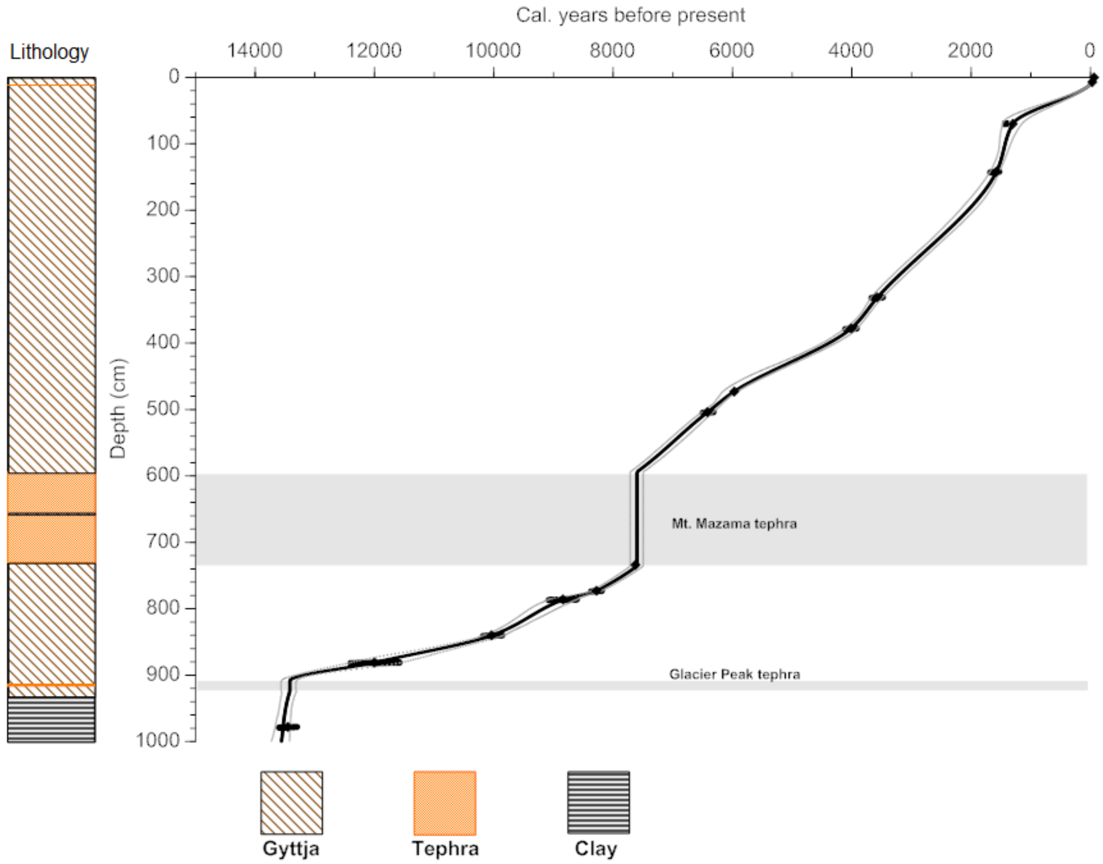


Figure 4.2. Age-depth model using a constrained spline based on radiocarbon dates and ash layers (tephra) for Dismal Lake. Error bars for each radiocarbon date are included.

Zone DIS-2 (11,600 to 13,400 cal yr BP; 873 to 908 cm)

Six samples comprise this pollen zone. This zone has a large peak in *Pinus* (46-67%) and *Abies* (6-17%). The rest of the tree taxa consists of *Picea* (2-8%), *Pseudotsuga/Larix*-type (1-4%), and *Alnus* (8-22%). Other components of the ecosystem include Ericaceae (present), Rosaceae (0-0.2%), and *Artemisia* (2-9%). The herbaceous taxa in the understory consists of Poaceae (1-4%) and very minor amounts of members of the Asteraceae family (*Ambrosia*-type 0-0.2% and Tubuliflorae-type 0-1%), *Chenopodium*-type (0-2%), and Ranunculaceae 0-1%). *Selaginella* is not present in this zone. Needles of *Picea engelmannii* and *Abies lasiocarpa* were found. PAR decreased from 81,000 grains/cm^2/yr at the base to 4000 grains/cm^2/yr at the top of the zone.

Zone DIS-3 (7,600 to 11,600 cal yr BP; 734 to 874 cm)

This zone consists of eleven pollen samples. This zone is distinguished by having the highest percentages of *Pseudotsuga/Larix*-type (7-34%) in the core. The remainder of the arboreal taxa consist of amounts of *Pinus* (19-69%), *Picea* (0-3%), *Abies* (5-17%), and *Alnus* (5-17%). Other woody taxa include Rosaceae (1-2%; occurring in the highest abundance in the core) and *Artemisia* (3-10%). Ericaceae is present only in the top of the section. The understory taxa consists of Poaceae (1-8%), members of the Asteraceae family (*Ambrosia*-type, 0-3% and Tubuliflorae-type, 0-1%), and *Chenopodium*-type (1-6%), Ranunculaceae (0-2%). *Selaginella* is present in only one sample near the top of this section. Three fern taxa, *Pteridium* (0-8%), *Polystichum* (0-7%), and *Dryopteris* (0-3%) are present in this section and reach their highest percentages in the upper half of this section. Macrofossils consisting of needles of *Abies grandis, Abies lasiocarpa*, and *Pseudotsuga menziesii* were found throughout this zone. PAR remains low varying from 4500 to 12,000 grains/cm^2/yr.

Zone DIS-4 (6,300 to 7,600 cal yr BP; 496 to 594 cm)

This zone consists of four pollen samples, one of which is from the organic layer between the two Mt. Mazama ash-fall events. Within the organic layer (650 cm) *Pinus* (65%) and *Abies* (14%) remain high with low amounts of *Pseudotsuga/Larix*-type (3%) and one grain of *Picea*. The rest of this sample is comprised of *Alnus* (5%), one grain of

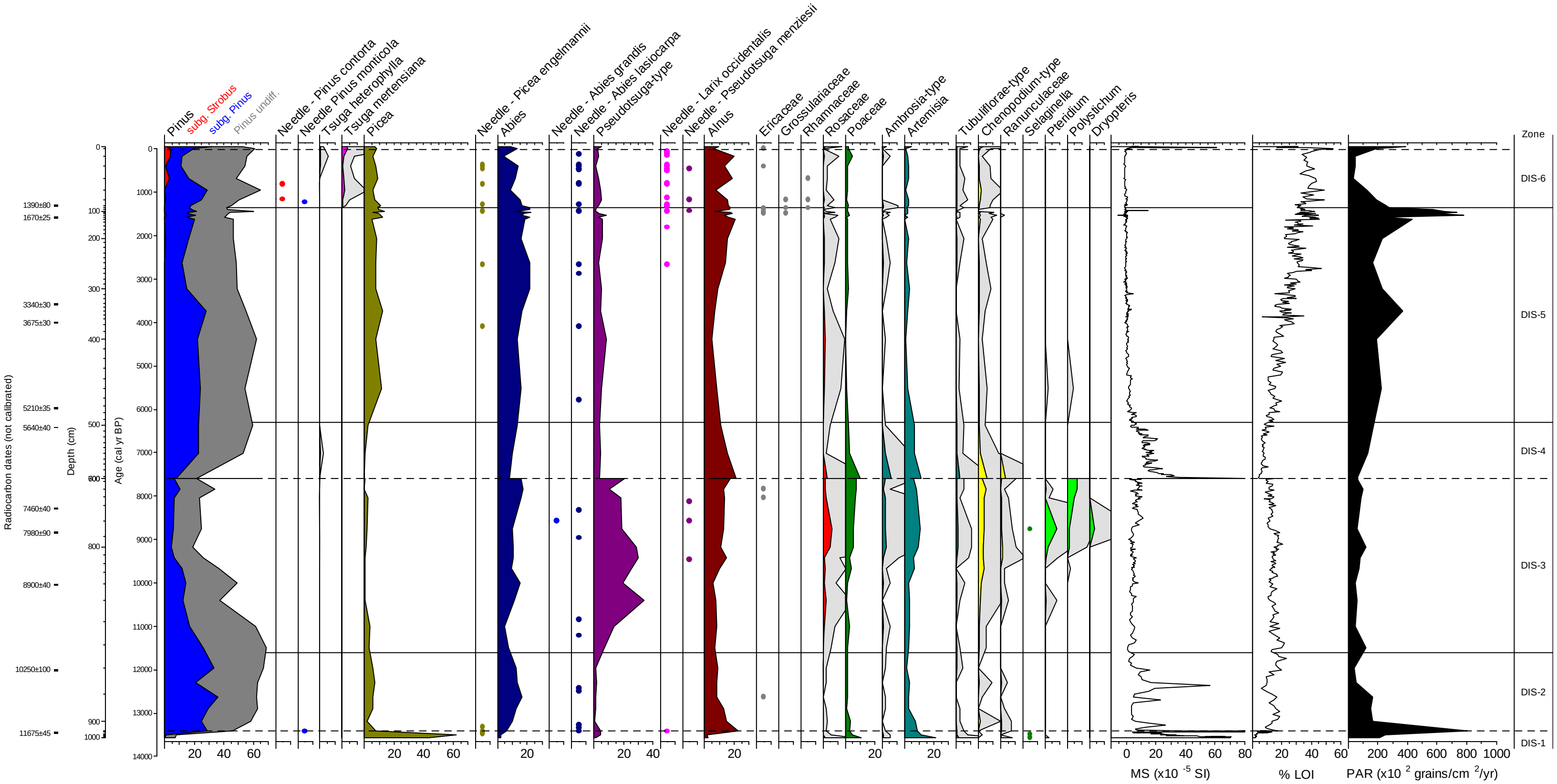


Figure 4.3. Pollen, macrofossil diagram, magnetic susceptibility (MS), % loss-on-ignition (LOI), and pollen accumulation rate (PAR) from Dismal Lake. Identified macrofossils and select rare pollen types (Ericaceae, Grossulariaceae, Rhamnaceae, and *Seleginella*) are show as presence only. The patterned lines for *Tsuga heterophylla, Tsuga mertensiana*, Rosaceae, *Ambrosia*-type, Tubuliflorae-type, *Chenopodium*-type, Ranunculaceae, *Pteridium*, *Polystichum*, and *Dryopteris* indicate 10x exaggeration. Horizontal dashed lines indicate tephra layers. Since tephra layers were deposited instantaneously, their thicknesses are not shown in this diagram.

Rosaceae, Poaceae (5%), *Ambrosia*-type (1%), *Artemisia* (5%), Tubuliflorae-type (1%), and *Chenopodium*-type (1%). Above the Mt. Mazama tephra, there is an abrupt change in pollen assemblages. The abundance of *Pinus* (22-50%), *Picea* (0-2%), Abi*es* (8-13%) increases towards the top of this section, while *Alnus* (21-10%), Rosaceae (3-1%), Poaceae (10-3%), *Ambrosia*-type (6-0%), *Artemisia* (12-7%), Tubuliflorae-type (3-1%), *Chenopodium*-type (6-1%), Ranunculaceae (3-0%) abundance all decrease. Abundance of *Pseudotsuga/Larix*-type (4%) remains low, while one grain of *Tsuga heterophylla* is present. *Selaginella* and the three fern species were not present in this zone. No macrofossils were recovered from this section. PAR increased from 6,000 grains/cm^2/yr to 17,000 grains/cm^2/yr.

Zone DIS-5 (1,350 to 6,300 cal yr BP; 79 to 495 cm)

This zone consists of fourteen pollen samples. This zone has relatively high abundances of *Pinus* (41-62%), *Picea* (5-13%), and *Abies* (13-22%), with the latter two increasing abundance through most of the zone. The remainder of the forest canopy is made up of *Pseudotsuga/Larix*-type (1-9%) and *Alnus* (5-21%). Ericaceae, Grossilariaceae, and Rhamnaceae make their first appearance near the top of this zone. Rosaceae (0-1%) and *Artemisia* (0-3%) make up the rest of the woody vegetation of the region. The rest of the understory taxa is comprised of Poaceae (0-3%) members of the Asteraceae family (*Ambrosia*-type, 0-1% and Tubuliflorae-type, 0-1%), *Chenopodium*-type (0-1%), and Ranunculaceae (0-1%). *Selaginella* is not present in this zone. Two fern taxa, *Pteridium* (0-1%) and *Polystichum* (0-1%), are found in very low abundances near the base of this zone. Within this zone, needles of *Picea engelmannii, Abies lasiocarpa,* *Larix occidentalis*, and *Pseudotsuga menziesii* were recovered. PAR varies around 20,000 grains/cm^2/yr for the majority of the zone and increases to 78,000 grains/cm^2/yr during a period of high sedimentation rate at the top of the zone.

Zone DIS- 6 (-58 to 1,350 cal yr BP; 0 to 78 cm)

This zone consists of eight pollen samples. This zone contains the first appearance of *Tsuga mertensiana* (0-4%). The rest of the forest taxa consists of *Pinus* (45-61%), *Tsuga heterophylla* (0-1%), *Picea* (6-11%), *Abies* (4-17%), *Pseudotsuga/Larix*-type (2-6%), and *Alnus* (6-20%). The regional taxa consists of Ericaceae (present throughout the zone), Grossilariaceae (present at the base of this zone), and Rhamnaceae (present in the lower half of this zone), Rosaceae (0-1%), Poaceae (1-5%), Asteraceae (*Ambrosia*-type, 0-1%, *Artemisia*, 1-5%, and Tubuliflorae-type, 0-1%), and *Chenopodium*-type (0-3%). *Selaginella* is not present in this zone. None of the fern species are present in this zone. Needles of *Pinus monticola, Pinus contorta, Picea engelmannii, Abies lasiocarpa, Larix occidentalis*, and *Pseudotsuga menziesii* were recovered. PAR is high at the base (38,000 grains/cm^2/yr) and the top of this zone, and declines to values as low as 3,000 grains/cm^2/yr.

NMDS ordination of pollen assemblages

The nonmetric multidimensional scaling produced two independently varying axes of variation (Figure 4.4). Axis 1 positively correlated with *Pinus* and negatively correlated with Poaceae and *Artemisia*. *Pinus* had peak abundances prior to the start of the Holocene and after the deposition of Mt. Mazama tephra while Poaceae and

Artemisia had peak abundances during the early Holocene. Axis 2 positively correlated with *Picea* and *Chenopodium*-type, and correlated negatively with *Pseudotsuga/Larix*-type. These three pollen types had high abundances prior to the deposition of tephra layers from Glacier Peak and Mt. Mazama (*Picea, Pseudotsuga/Larix*-type, and *Chenopodium*-type). Comparison between the two axes show that after each of the two tephra events, there was a large change in pollen assemblages towards decreasing followed by increasing values on axis 1 (Mt. Mazama tephra) or increasing on both axes (Glacier Peak tephra). Despite the fact that the vegetation composition varied before each tephra deposit, the vegetation changed to a similar composition after each tephra deposition.

5. Discussion

5.1. Late Pleistocene [DIS-1 (13,400 to 13,600 cal yr BP; 928 to 1000 cm)]

As the alpine glaciers began to recede due to increasing temperatures, glacier-derived clay was deposited into the newly formed Dismal Lake. MS is high, while organic content is low throughout this section. Low vegetation cover and the steep, freshly deglaciated basin resulted in the very high sedimentation rate of inorganic sediment. The vegetation surrounding the lake was dominated by an open *Picea engelmannii* forest with lower amounts of *Pinus monticola, Abies lasiocarpa,* and *Larix occidentalis* and herbaceous taxa (Poaceae, Tubuliflorae-type) dominated meadows. The high *Artemisia* abundance suggests that the climate of the region was cool and dry. The area surrounding Dismal Lake was an open subalpine/alpine forest dominated by taxa adapted to cool and dry conditions. The top of this zone is delimited by 20 cm of Glacier

Peak ash (Figure 4.3).

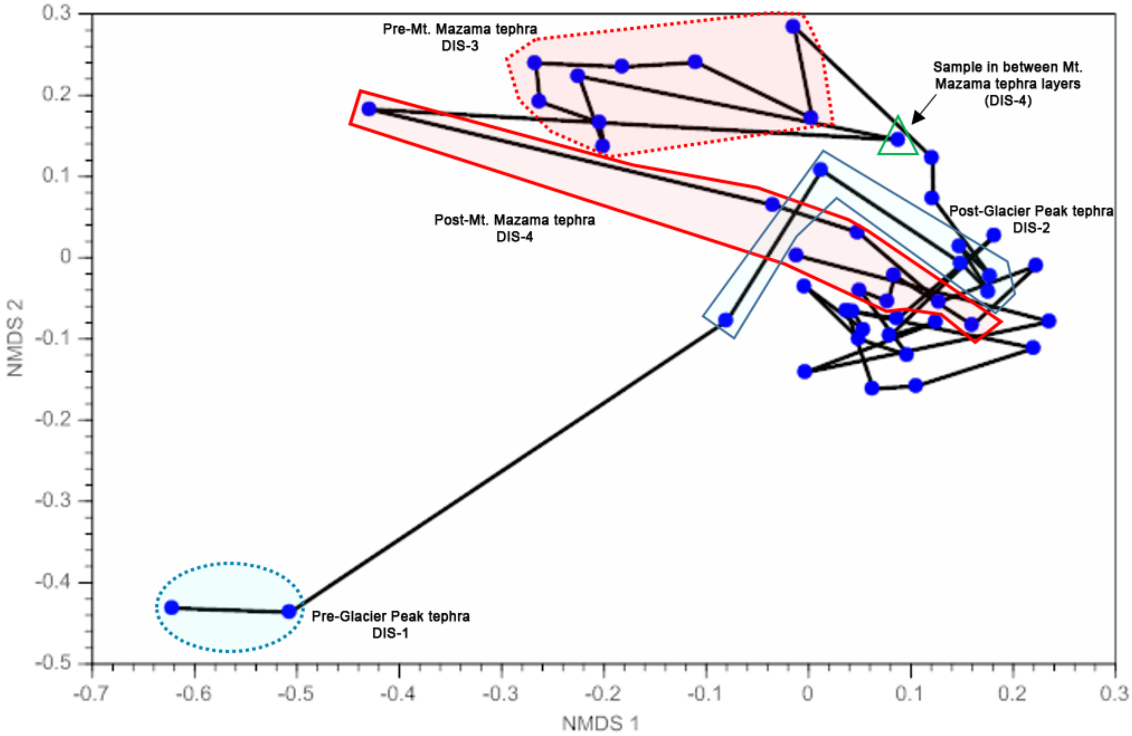


Figure 4.4. Comparison of pollen assemblages before and after each tephra deposition using nonmetric multidimensional scaling (NMDS).

5.2. Late Pleistocene to Holocene [DIS-2 (11,600 to 13,400 cal yr BP; 874 to 908cm)]

The deposition of the Glacier Peak ash (13,400 cal yr BP) marks the first large shift in the vegetation (Figures 4.3 and 4.4). Above the ash layer, MS is variable with several large peaks occurring from 12,000 to 12,800 cal yr BP. The timing of the MS peaks is consistent with the Younger Dryas climate reversal. The peaks in MS could be evidence of the landscape response to the abrupt cooling during Younger Dryas, or remobilization of the tephra, but more precise dating and another climate proxy would be needed to confirm this. As climate continued to warm, and the Pleistocene transitions into the Holocene, LOI increased suggesting increased organic matter production. Sedimentation and PAR were low in this zone, which suggests that much of the surrounding landscape was barren and soils were thin. Dense forest may have only existed at lower elevations with deeper soils.

After the deposition of ash from the eruption of Glacier Peak, the vegetation surrounding Dismal Lake underwent a complete change. *Picea engelmannii* dropped from 62 to 6% and remained at low abundance while *Pinus* (possibly both *Pinus monticola and Pinus contorta*) became the dominate tree species. *Alnus* also increases rapidly after the ash was deposited, likely due to its ability to colonize disturbed areas. *Artemisia* decreases at the beginning of this section, and occurs in low abundance throughout the remainder of the zone as a response to warming climate conditions. *Pseudotsuga/Larix*-type (*Larix occidentals*) remains at low abundance. Overall, the remarkably rapid change in vegetation following the tephra deposition, involving regionally dispersed pollen types (*Pinus* and *Picea*), suggests a regionally synchronous and rapid change in vegetation incited by the tephra deposition.

5.3. Early to middle Holocene [Zone DIS-3 (7,600 to 11,600 cal yr BP; 734 to 873 cm)]

During the early Holocene, organic content and MS remained relatively stable. PAR remains relatively low, suggesting that forest density was not greatly increasing, and that soil development was limited. Trees were likely sparse on the surrounding steep slopes, with pollen likely being transported from lower elevations. The early Holocene in the region is marked by warm and dry summers (Whitlock, 1992; Brunelle et al., 2005;

Power et al., 2011). This warmer climate facilitated the establishment of a *Pseudotsuga menziesii* forest with minor components of *Pinus, Picea, Abies* (both *Abies lasiocarpa* and *Abies grandis*), and *Alnus.* Because *Pseudotsuga* is rare at the elevation of Dismal Lake today, the early Holocene was likely a period of upslope range extension of this species. At ca. 10,000 cal yr BP *Pseudotsuga menziesii* abundance began to decrease, while *Artemesia, Ambrosia*-type, Rosaceae and Poaceae abundances increase. The forest understory was rich in diversity, containing Ericaceae, Tubuliflorae-type, *Chenopodium*-type, Ranunculaceae, *Pteridium*, *Polystichum,* and *Dryopteris*, taxa which are all found together today in the interior mesic forests of northern Idaho. This forest composition suggests a warm and sufficiently moist climate was able to support these species through the early Holocene.

5.4. Middle Holocene [Zone DIS-4 (6300 to 7600 cal yr BP; 496 to 734 cm)]

The base of this zone contains a 141 cm (593-734 cm) thick ash layer from the eruption of Mt. Mazama. The deposition of this layer had profound effects on the ecosystem surrounding Dismal Lake. A single pollen sample from an organic layer deposited between the two episodes of tephra was very high in *Pinus*, suggesting the first ash deposition had already greatly affected the vegetation. Following the second episode of tephra, MS decreases while LOI and PAR increase, consistent with a slow stabilization of tephra and increasing vegetation cover (Figure 4.3). Vegetation change within this zone is marked by two phases of change suggestive of primary succession. First, the abrupt decrease in *Pseudotsuga* and *Abies* and subsequent increase in disturbance-related taxa. Herbaceous taxa (Poaceae, *Ambrosia*-type, Tubuliflorae-type, *Chenopodium*-type, Ranunculaceae) and *Alnus* all experienced an increase in abundance directly above the tephra layer and then decreased throughout the rest of the zone. All conifer species (*Pinus, Picea, Abies*, and *Pseudotsuga/Larix*-type) were marked by low pollen percentages. Second, *Pinus* increased shortly after the increase in disturbance-related taxa, while *Picea* and *Pseudotsuga/Larix*-type remained relatively low and constant in abundance (Figure 4.3). *Abies* increases slightly in abundance through the zone, consistent with a succession from pine to true fir species. I note the presence of the single *Tsuga heterophylla* grain is likely long-distance transport from coastal populations (Rosenberg et al., 2003). Overall, the vegetation changes in this zone are consistent with a direct response to a thick deposition of Mt. Mazama tephra and not a result of climate induced change.

5.5. Middle to late Holocene [Zone DIS-5 (1350 to 6300 cal yr BP; 79 to 495 cm)]

Within this zone, MS remains stable while LOI has a general increasing trend. At about 5000 cal yr BP, LOI starts to increase at a faster rate. PAR continues to increase and peaks ca. 1400 cal yr BP. This suggests that soil development on the previous rocky sites continued to increase after the deposition of Mt Mazama tephra, resulting in increased terrestrial organic matter to the lake basin. The deposition of the Mt. Mazama tephra could have initiated the development of soils on previously rocky sites. Most components of the modern subalpine forest reach their modern proportions, including *Pinus, Picea engelmannii, Abies lasiocarpa, Larix occidentalis*, and *Alnus*. The understory has a similar composition to DIS-3, with the exception of lower fern abundances. Ericaceae, Grossulariaceae, Rhamnaceae, and *Pseudotsuga menziesii* are all present in the uppermost samples of this section. Vegetation records throughout the PNW show a shift to more mesic adapted vegetation occurring at the end of the HTM (Barnosky, 1981, 1985; Whitlock, 1992; Gavin et al., 2009, 2011, 2013). The only notable change within this zone is the establishment of *Picea engelmannii* suggestive of increased mesic conditions and an increase in abundance in *Abies* suggesting an increase in late-successional forests, the forest ecosystem.

5.6. Late Holocene [Zone DIS-6 (-58 to 1350 cal yr BP; 0 to 78 cm)]

The MS record remains stable throughout this section, with one large peak occurring near the top of the core at the Mt. St. Helens ash deposit. The LOI curve fluctuates greatly throughout this zone, likely as a response to either small shifts in climate or terrestrial inputs into the watershed. *Pinus* (both *Pinus monticola* and *Pinus contorta*), *Tsuga mertensiana, Picea engelmannii*, *Pseudotsuga menziesii, Larix occidentalis,* and *Alnus* are the dominant taxa within the zone. *Tsuga mertensiana*, a dominant tree at the lake today, is first detected at the base of this zone and remains at ca. 1%.

The recent appearance of *Tsuga mertensiana* (ca. 1300 cal yr BP) pollen is consistent with other paleorecords recovered from the interior mesic forest indicating that the mesic taxa are recent components of the Northern Rocky Mountains (Mehringer Jr, 1985; Rosenberg et al., 2003; Gavin, 2009). *Tsuga mertensiana* arrival post-dates the period of rapid sedimentation, and coincides with a peak in *Pinus*; and thus could be a response to disturbance.

5.7. Impact of ash deposition on vegetation

Tephra deposition from volcanic eruptions may affect forested ecosystems in various ways. The magnitude of a tephra effect on vegetation depends on the amount of tephra deposited and its chemical composition (Westgate & Evans, 1978; Lotter & Birks, 1993; van den Bogaard et al., 2002; Antos & Zobel, 2005; Sumita & Schmincke, 2013). Plants can be damaged by airfall tephra in four main ways: 1) complete burial of the plant, 2) restriction of oxygen access to roots by partial burial, 3) defoliation and prolonged absence of leaves, and 4) inhibition or decreased gas exchange due to tephra covering photosynthetic surfaces of plants (Rees, 1970; Blong, 1984). Limbs on trees could also be damaged due to tephra loading (similar to snow loading) from large amounts of tephra (Rees, 1970). Analysis of the effects of tephra deposition from recent eruptions on agricultural crops provides evidence that the amount of damage an ecosystem can sustain is dependent on both the amount of tephra deposited and the type of vegetation (herbaceous vs. woody taxa) (Blong, 1984). Vegetation that is tall (trees) are less likely to be buried by ash, and therefore the likelihood of survival increases (Eggler, 1948; Means & Winjun, 1983; Giles et al., 1999). However, when a very thick layer (≥1 m) of tephra is deposited on vegetation, most vegetation (including trees) is killed, and recovery (return to a state of vegetation prior to tephra deposition) is difficult (Blong, 1984; Dale et al., 2005a). Plant mortality (especially of herbaceous taxa) and decreased growth can occur when only a few centimeters of tephra is deposited (Eggler, 1948; Wilcox & Coats, 1959).

The deposition of Glacier Peak ash caused an abrupt and persistent change in vegetation in the region surrounding Dismal Lake. Prior to the deposition of 20 cm Glacier Peak ash, *Picea engelmannii* dominated the landscape probably with few other conifer taxa present. With an ash thickness of 5-15 cm, there was likely a loss of plant biomass. Low-growing herbaceous taxa may have been killed by burial or by the inhibition of root oxygen exchange by partial burial (Antos & Zobel, 2005; Hotes et al., 2006; Millar et al., 2006). Taller, woody vegetation likely suffered from loss of foliage and limbs. *Picea engelmannii* roots do not penetrate deep into soil layers and are sensitive to changes in temperature and gas exchange (Delucia, 1986; Sowell & Spomer, 1986; Day et al., 1990). Even thin layers of ash could alter the ability of the roots of *P. engelmannii* to undergo gas exchange, causing the tree to slowly die. After the deposition of Glacier Peak ash, *Pinus* and *Abies lasiocarpa* became the dominant conifer taxa with high abundances of *Alnus*. Herbaceous and *Alnus* taxa likely colonized the area within a few years after the eruption.

The Mt. Mazama tephra had a significant and persistent effect on vegetation at Dismal Lake. Although the tephra thickness at Dismal was likely affected by secondary deposition and sediment focusing, Matz (1987) mapped the region to have 15-100 cm of tephra deposition (Figure 4.1). Prior to the deposition of ash from the Mt. Mazama eruption, the conifer component of the forest was dominated by *Pseudotsuga menziesii* and *Abies* (*Abies grandis* and *Abies lasiocarpa*). Deposition of up to 100 cm of ash would have caused a large loss of vegetation over broad areas. The deposition of such a thick layer of ash would have likely killed low growing vegetation by complete or partial burial. Trees would also be greatly damaged or killed due to limb brakeage, foliage loss, and the inhibition of gas exchange. Reestablishment of vegetation on the ash would be difficult because of the low water-holding capacity of coarse ash and possibly due to the lack of available nutrients (Blong, 1984). Recovery back to a forest ecosystem could have taken many decades as organic soils developed on the ash surface. The forest underwent an abrupt and persistent change above the tephra layer. *Pseudotsuga/Larix*-type pollen decreases drastically and never recovered to pre-Mt. Mazama levels through the rest of the record. Disturbance-related and herbaceous taxa (*Alnus*, Poaceae, *Ambrosia*-type, *Artemisia, Tubuliflorae*-type, *Chenopodium*-type, and Ranunculaceae) all show an initial increase in abundance right above the ash layer, and decrease once other tree taxa become more abundant in the pollen record. *Pinus* and *Abies* show an initial decrease in abundance, but *Pinus* eventually benefits the most in the decades to centuries following the deposition Mt. Mazama tephra. Some of the patterns of post-tephra vegetation change could be the result of sampling resolution. In order to understand the impact of thick tephra deposits higher resolution sampling methods need to be conducted on this core.

The increase in sediment organic matter through the Holocene, after the deposition of Mt. Mazama tephra, may reflect an increase in soil depth. Without the deposition of thick tephra layers, tree rooting may have been limited by soil depth. Once tephra was emplaced, a 5000-year trajectory of increasing organic matter could be the result of deep organic horizons developing on the tephra parent material. Other sites in drier climates (Long et al., 2014) do not show such a dramatic response to Mt. Mazama tephra deposition. Perhaps the mesic environment that surrounds Dismal Lake may not have had the proper parent material or soil depth to support mesic taxa prior to the deposition of tephra (Chapter III). The thick deposition of tephra in the region may have facilitated the development of thicker soil layers when enabled the modern diverse mesic forest to establish.

6. Conclusion

This is the first record, to my knowledge, that demonstrates the role of tephra at inciting abrupt vegetation change and modifying long-term vegetation trajectories in Pacific Northwest forests. Most paleorecords recovered from the PNW have focused on climate and vegetation changes since deglaciation. There have been very few studies that have demonstrated a long-lasting impact of tephra deposition, especially at sites far from the source of eruption. The Dismal Lake record contains two thick ash deposits from the eruptions of Glacier Peak (20 cm) and Mt. Mazama (141 cm). Comparison between the vegetation before and after each ash layer shows a large change in vegetation which was likely caused by the deposition of thick ash layers. Tephra depositions occurred alongside other factors forcing vegetation change, especially climate and fire disturbances. Thus a further understanding of the marginal roles of tephra, climate change, and disturbance, in the Holocene development of modern forests of northern Idaho will require additional paleoecological research.

CHAPTER V

SUMMARY

In this dissertation I examined the climate and vegetation history of the mesic forests in the Northern Rocky Mountains by analyzing pollen and sediment composition (biogenic silica and measures of inorganic and organic matter). Paleoecological records were evaluated from four study sites at different elevations, located near the southern edge of the interior mesic forests in northern Idaho. The overarching goal of this research was to provide information on the environmental history of these forests that are disjunct from the main population along the Pacific Northwest coast. The dominant trees currently found in the mesic forests, *Thuja plicata* and *Tsuga mertensiana*, are likely recent arrivals to their interior distributions and did not persist in a refugium. Shifts in vegetation composition in the region are a response to both millennial scale climate changes and tephra deposition.

The Star Meadows core, presented in Chapter II, provides our first glimpse of the long term climate and vegetation history in northern Idaho over the last ca. 120 ka (thousand years ago). This pollen record revealed several major vegetation changes as a response to changes in climate at millennial scales. The changes in pollen assemblages were able to be linked to marine isotope stages, indicating global-scale climatic fluctuations were manifested as distinct vegetation changes in northern Idaho. During MIS 5e (marine isotope stage; ca. 116 to 125 ka) the region was warmer and drier than today and was dominated by *Pinus* (likely *P. contorta*) mixed conifer forest surrounding a *Carex* meadow. A warm-moist climate (MIS 5b-5d; ca. 84 to 116 ka) soon developed, and the site was inundated with deep water. Pollen indicated bog vegetation (*Betula glandulosa,* Typhaceae, and *Salix*) developed around a lake with a *Pseudotsuga/Larix* and *Picea* forest on the surrounding slopes. During MIS 5a (ca. 71 to 84 ka), a slightly warmer climate, than MIS 5b-MIS 5e, that supported a *Pseudotsuga/Larix, Abies,* and *Picea* forest on the surrounding hillsides and a *Carex*-dominated environment within a dry meadow. From MIS 4 to MIS 3 (ca. 40 to 71 ka), a cool and wet *Pinus* and *Picea* forest predominated. Water levels rose, enabling *Nuphar* to persist within a perennial lake while a sedge fen established along the lake margin. As climate transitioned into MIS 2 (ca. 22.8-40 ka), a cooler and drier, than MIS 3, climate supported a *Pinus* and *Picea* subalpine parkland, though water levels remained high enough to support *Nuphar*. During the Last Glacial Maximum the sediment was mainly silt and clay with high *Artemisia* and very poor pollen preservation. Glaciers descended to 500 m elevation above Star Meadows in adjacent drainages suggesting a periglacial environment occurred at Star Meadows. The lake level decreased through the Pleistocene-Holocene transition (ca. 11.7 ka) and the site returned to a sedge peatland surrounded by an open *Pinus* forest. The most dramatic change in vegetation occurred during the mid-Holocene with the appearance and then later dominance of *Thuja plicata* and other taxa associated with mesic forests in the region today. The recent arrival of *T. plicata* and other mesic forest taxa suggests that their range may have been limited by dispersal, climate, or a combination of both into northern Idaho. The fossil pollen evidence from this core is in agreement with a phylogenetic study (O’Connell et al., 2008) indicating that *T. plicata* may have recently dispersed from the coast.

In Chapter III, I examined the ecological history of *Tsuga mertensiana* in the interior mesic forests of the Pacific Northwest. *Tsuga mertensiana* occurs in three distinct interior populations (separated by more than 100 km) in British Columbia, northern Idaho, and northeast Oregon. Examination of modern surface samples of *T. mertensiana* and distance to a known *T. mertensiana* population shows that if *T. mertensiana* abundance is >1%, the stand from which the pollen originated is likely within 36 km of the location of the modern sample.

Using pollen recovered from three sediment cores from northern Idaho across different elevations suggests that *T. mertensiana* is a recent component to the interior mesic forests of northern Idaho appearing in the pollen record 4100 cal yr BP, but not a dominant component (relative abundance >1%) until 330 cal yr BP. Evidence from the three pollen records and climate reconstructions from the broader region suggest that climate rather than dispersal was a greater limiting factor in its dispersal into the interior distribution in northern Idaho. *Tsuga mertensiana* was able to disperse into Idaho and exist for millennia at low abundances. It was not until Little Ice Age climate promoted its recent increase in importance in the mesic forests. Suitable habitat exists between the two interior populations in northern Idaho and southeastern British Columbia for *T. mertensiana*. However, dispersal and species competition are likely limiting the infilling of these gaps.

Chapter IV focused on the impact that thick layers of ash-fall have on vegetation. A 13,600-year, 10-m, high-resolution multi proxy (pollen, plant macrofossil, loss-on-ignition, and magnetic susceptibility) sediment record recovered from Dismal Lake in northern Idaho is presented. At the start of this record (ca. 13.6-13.4 ka), *Picea* *engelmanni* parkland established in the region as climate was warming and glaciers were receding. A 20 cm-thick tephra layer from the eruption of Glacier Peak (13.4 ka; (Kuehn et al., 2009), marked an abrupt loss of *Picea, Artemisia*, and *Selaginella*. Following the tephra, the forest composition consisted of *Pinus contorta, Abies lasiocarpa* and *Alnus,* which remained common to the present. As climate warmed with the onset of the Holocene, *Pseudotsuga menziesii* increased abundance and expanded its range to higher elevations eventually becoming the dominant tree species of the forest.

The pollen assemblages again changed abruptly with a sharp decrease of *Pseudotsuga menziesii* and corresponding increases of *Pinus, Picea,* and *Abies* following 141 cm-thick tephra from Mt. Mazama (7.6 ka; (Zdanowicz et al., 1999). The forest composition remained similar until 1.3 ka, when *Tsuga mertensiana,* one of the co-dominant taxa of the modern forest, was first detected in the pollen record. The record from Dismal Lake shows that the three major postglacial vegetation changes are consistent with regional climate change, but two were abrupt and persistent changes that were mediated by tephra deposition. Tephra likely contributed to tree mortality and overcame the inertia of vegetation response to climate change, and provided a substrate that supported development of deep soils and denser forests than would otherwise occur.

This dissertation provides the first comprehensive reconstruction of the vegetation history of an important biodiversity region in the northern Rocky Mountains. Continuous records that extend back 120,000 years are rare in western North America and are important for our understanding of long term vegetation-climate relationships. Star Meadows is the first paleorecord from the southern end of the interior mesic forest distribution in a putative glacial refugium and one of nine records that extend back to the last interglacial in the western US. Each sediment record presented in this study show a dynamic environment that has been highly influenced climate and tephra events. The fossil pollen records all suggest the dominant mesic forest taxa that currently exist in the Northern Rocky Mountains of Idaho are recent arrivals to the area and did not persist in a refugium during glacial conditions. Expansion into the region was likely from coastal populations, and their expansion in the interior was limited by climate and species competition.

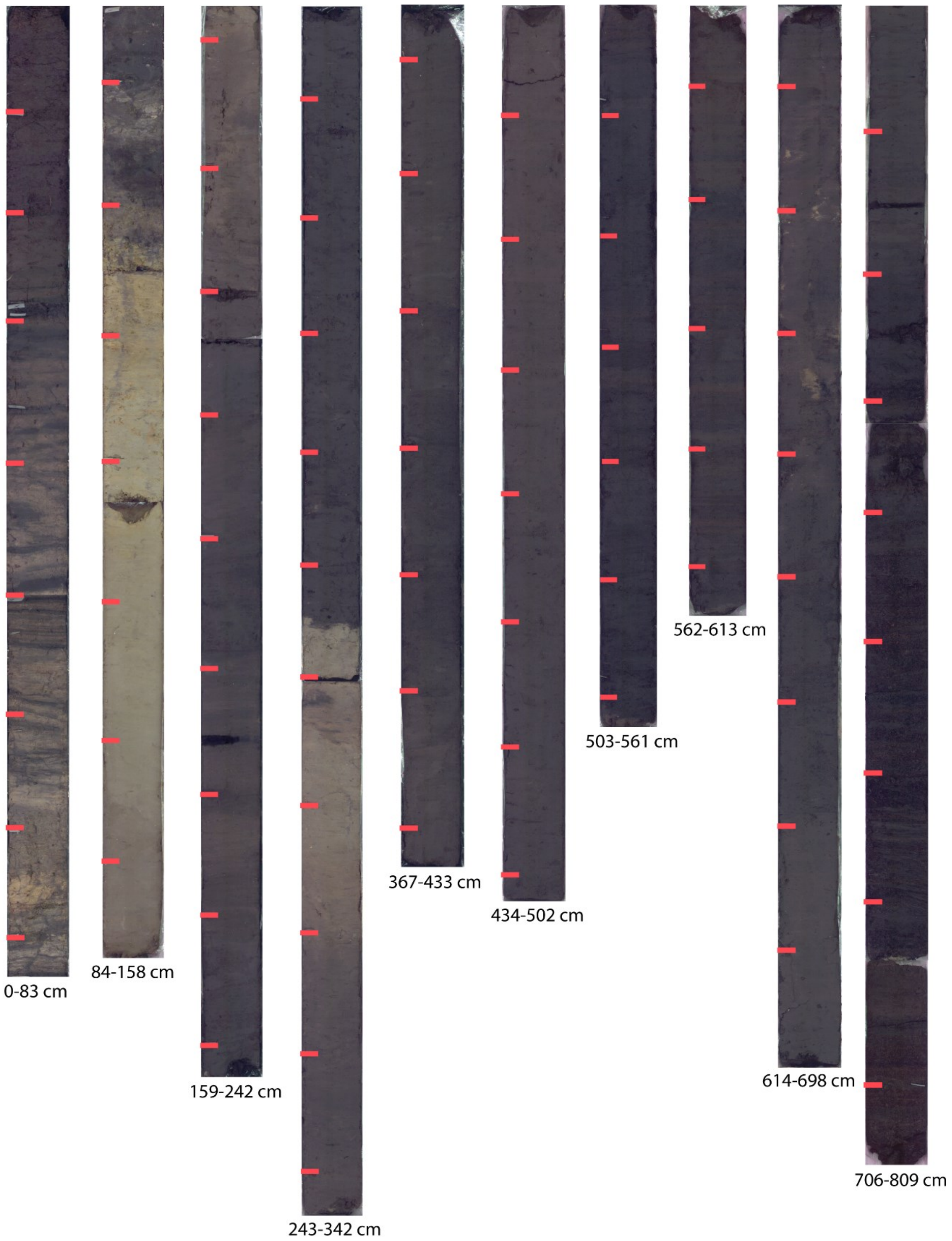
APPENDIX A

SUPPLEMENTARY MATERIAL FOR CHAPTER II

Species list of taxa surrounding Star Meadows

Taxon	**Type**	**Habitat**
Abies grandis	Tree	Forest
Adiantum pedatum	Fern	Forest
Anaphalis margaritaceae	Herb	Forest
Asarum caudatum	Herb	Forest
Capsella bursa-pastoris	Herb	Forest
Carex aquatilis	Sedge	Meadow
Carex spp.	Sedge	Meadow
Ceanothus	Shrub	Forest
Centaurea stoebe	Herb	Forest
Chimaphila umbellata	Herb	Forest
Circaea alpina	Herb	Forest
Clintonia uniflora	Herb	Forest
Comarum palustre	Shrub	Meadow
Coptis occidentalis	Herb	Forest
Disporum hookeri	Herb	Forest
Fragaria virginiana	Herb	Forest
Galium triflorum	Herb	Forest
Goodyera oblongifolia	Herb	Forest
Gymnocarpium dryopteris	Fern	Forest
Linnaea borealis	Herb	Forest
Osmorhiza chilensis	Herb	Forest
Picea engelmannii	Tree	Forest
Pinus monticola	Tree	Forest
Pseudotsuga menziesii	Tree	Forest
Pterospora andromedea	Fungi	Forest
Pyrola asarifolia	Herb	Forest
Rosa gymnocarpa	Shrub	Forest
Smilacina stellate	Herb	Forest
Solidago canadensis	Herb	Meadow edge
Sphagnum	Moss	Meadow
Thuja plicata	Tree	Forest
Tiarella trifoliata	Herb	Forest
Tiarella trifoliate	Herb	Forest
Trillium ovatum	Herb	Forest
Veratrum viride	Herb	Forest
Viola orbiculata	Herb	Forest
Xerophyllum tenax	Grass	Forest

Core photos with depths. Red marks are placed every 10 cm throughout the core.



APPENDIX B

SUPPLEMENTARY MATERIAL FOR CHAPTER III

Data sources for *Tsuga mertensiana* map

Point locations were obtained from various databases yielding a total of 7480 unique locations. Large unverified outliers were checked against aerial photographs; if the location appeared unreliable (e.g., occurring in a non-forested area) or was not verified by two data sources, then it was discarded. We used Google Earth to locate or verify several verbal descriptions of locations in herbaria databases or suspicious coordinates (e.g. rounded to one decimal place) that date to before availability of GPS. Locations of 158 herbaria specimens were not pursued because verbal descriptions indicated they occurred near existing observations. A 6-km buffer was placed around each point on the *T. mertensiana* map.

Major data sources include the United States Forest Inventory and Analysis (n=3487), United States Forest Service Ecology plot database (n=2960), the British Columbia Biogeoclimatic Ecosystem Classification system (BEC) plot database (n=672), VegBank (n=307), Pacific Northwest Herbaria database (n=232), Arctos database (n=29), the International Tree-ring Data Bank (n=15), CalFlora (n=37), georeferenced photographs on panoramio.com (n=14), and the publications listed below. In British Columbia, sparse observations in the Coast Range were supplemented by adding the Biogeoclimatic Ecosystem Classification for the Mountain Hemlock Zone (Meidinger & Pojar 1991).

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