POSTGLACIAL VEGETATION AND FIRE HISTORY OF THE SOUTHERN MISSION VALLEY, MONTANA

by

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ABSTRACT

Ecosystems shaped by mixed-severity fire regimes cover a large area of the Northern Rocky Mountains, yet relatively little is known about the historical variability and drivers of these ecosystems. The low- and mid- elevations of the Mission Range, Montana, are dominated by mixed conifer forests, and the area has been occupied by humans for at least 10,000 years, making it an ideal location for investigating how climate and humans may have affected vegetation and fire regimes during the late-glacial period through the Holocene. Pollen and charcoal records from lake sediment cores from a small closed-basin lake (Twin Lake) were used to reconstruct the vegetation and fire history of the southern Mission Valley, Montana, and compared to other sites in the region. During the late-glacial period, data show an abundance of *Pinus (P. albicaulis* or *monticola*) *Artemisia,* and Poaceae pollen prior to 13,000 cal yr BP, suggesting the site was dominated by an open landscape with shrubs and grass, cold relatively dry conditions, and minimal fire activity. Increased percentages of *Pinus* (*P. Ponderosa* or *contorta*), *Picea,* and *Abies* pollen at 13,000 cal yr BP mark the onset of a closed conifer forest, relatively cool and wet conditions and an increase in fire activity accompanying an increase in biomass. Large increases in *Pseudotsuga/Larix* and *Artemisia* pollen between 10,000-6000 cal yr BP suggest warmer and drier climatic conditions developed during this interval, consistent with other records from the northwestern U.S. Charcoal influx show this interval of warm and dry conditions led to low severity fires followed by high severity fires as forests of *P. contorta or P. ponderosa* became more dense between 7000 and 5000 cal yr BP. The mixed-conifer forests that dominate the site today began to develop ca. 6000 cal yr BP when fire frequency and severity became highly variable. Surprisingly, fire activity from ca. 5000 cal yr BP to present remained relatively high despite a cooling and wetting trend in the region. This departure of fire activity from climatic controls suggests other local factors influenced fire activity, and may suggest a greater role of human influence during the late Holocene.

INTRODUCTION

Fire activity has increased in the western US over recent decades, likely as a result of drier-than-average summers, earlier spring onset, and longer fire seasons (Westerling et al., 2006, Abotzoglou and Williams 2016). Additionally, gradual accumulation of fuels from decades of successful fire suppression has increased fire intensity in some areas (Schoennagel et al., 2004). Investigations into the controls on fire activity in the western US have demonstrated that both natural and anthropogenic factors have caused changes in fire dynamics in recent decades; therefore, it is of interest to evaluate the relative role of climate and humans on fire activity throughout the Holocene.

Of key interest are the mixed-severity fire regimes that affect low-to-mid-elevation mixed-conifer forests. Of the three fire regime classifications/types (low, mixed, and high), the least is known about mixed-severity fire regimes, especially in the Northern Rocky Mountains. Unanswered questions include the degree to which climate and fuel load influence fire severity and frequency in these systems, as well as their historical dynamics (Schoennagel et al., 2004). In forests with long-lived trees (>200 years), separating climate, vegetation, and human influences on fire regimes is difficult based on recent observations alone, thus using paleoecological methods to research fire and vegetation histories of specific regions provides essential information about natural and human influenced fire variability over long timescales.

There is a scarcity of vegetation and charcoal records in the Northern Rocky Mountains (NRM), where mixed-conifer forests are a dominant ecosystem type. The Mission Valley and surrounding Mission Range in central Montana is located within the NRM, but also contains Pacific Northwest (PNW) forest taxa; hence, it is important to compare the vegetation and fire history of this area to sites that span both regions. The Mission Valley also has a long history of human occupation, making it an ideal location to study climate-human-vegetation interactions over time. The objectives of this study are as follows:

- To determine the vegetation and fire history of the Twin Lakes region, and assess how its history compares with other parts of the PNW and NRM.
- To determine how fire activity responded to climate and vegetation changes, and human interaction on millennial time scales.

Site Description

The Mission Range is a north-south trending mountain range in western Montana, bordered on the west by Flathead Lake and the Mission Valley, and on the east by Swan Valley. The axis of the range is 88.5 km in length, and the highest peak, McDonald Peak, is 2990 m elevation. The mountains consist of Precambrian sedimentary and metasedimentary rocks from the Belt Supergroup, and the lower slopes and valleys are mantled by late-Pleistocene glacial deposits (USGS mineral Resources On-Line Spatial Data; Harrison et al., 1969). Pleistocene glaciation is responsible for the jagged peaks, cirque basins and U-shaped valleys (Davis, 1916).

During the Last Glacial Maximum (26,000-19,000 cal yr BP), the Flathead lobe of the Cordilleran Ice Sheet extended to the northern tip of the Mission Range and alpine glaciers existed throughout the range (Alden, 1953; Davis, 1916). Small glaciers, such as Gray Wolf Glacier and McDonald Glacier, still remain in the higher elevation cirques in the middle-to-south end of the range.

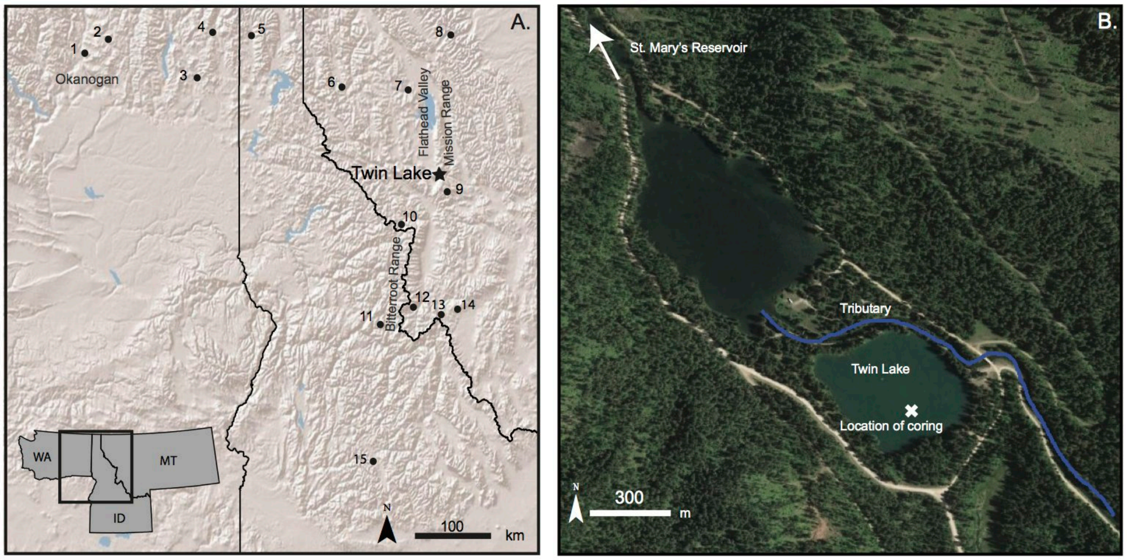

Figure 1. A) Map of Twin Lake and regional study sites in the Northern Rocky Mountains and Pacific Northwest: 1. Mud Lake (Mack et al., 1979) 2. Bonaparte Meadows (Mack et al., 1979) 3. Waits Lake (Mack et al., 1978a) 4. Big Meadow (Mack et al., 1978) 5. Hager Pond (Mack et al., 1978b) 6. Tepee Lake (Mack et al., 1983) 7. Foy Lake (Power et al., 2006) 8. Johns Lake (Whitlock et al., 1992) 9. Sheep Mountain Bog (Mehringer et al., 1984) 10. Pintler Lake (Brunelle et al., 2004) 11. Hoodoo Lake (Brunelle et al., 2004) 12. Burnt Knob (Brunelle et al., 2004) 13. Lost Trail Pass Bog, (Mehringer et al., 1977) 14. Baker Lake (Brunelle et al., 2004) 15. Decker Lake (Whitlock et al., 2011) (Map source, ESRI). B) Close up of Twin Lake, including location of coring and the tributary around the lake is highlighted in blue (Map source Google Earth).

The Twin Lakes are two small (4-5 ha) lakes located at the southwestern end of the Mission Range (47.24°N, 113.91°W, 1261 masl) (Fig. 1). This study focuses on the eastern of two adjoining lakes (hereafter referred to as Twin Lake) that are presently separated by a late-glacial recessional moraine or post-glacial landslide that created the two basins. In 1930, Tabor dam was built on St. Mary's Lake, located approximately 2.5 km northeast of Twin Lake (Parrett and Jarret, 2000), and a tributary canal was routed from Grizzly Creek (which meets the North Fork of the Jocko River) to bypass eastern Twin Lake and flow directly into St. Mary's Lake. As a result of this diversion, the northern lake shoreline and surrounding hydrology was altered.

Present-day Climate

Today the Mission Range is influenced by air masses from the Pacific maritime climate region and continental polar air masses from the north. Mean annual temperature of valley sites (~1200 masl) is 7°C, average maximum summer temperature (JJA) is 25°C, and the minimum summer temperature is 9°C. Mean minimum winter (DJF) temperature is -8°C and the maximum is 0°C (all climate data are 30-year averages from 1981-2010, PRISM Climate Group, 2015). Precipitation primarily arrives from Pacific storm systems in winter, and while the northeastern Pacific subtropical high-pressure system suppresses precipitation in summer, local convectional storms bring modest precipitation to the range in spring and summer. Average annual precipitation is 38 cm in the Mission Valley lowlands and 150 cm at higher elevations (Parrett, 1997). Twin Lake receives an annual average of 71 cm of precipitation, with 21 cm arriving in the winter (DJF), 14 cm in the summer (JJA) (ratio of summer/winter precipitation (JJA/DJF)=.67), an additional 20 cm falling in spring (MAM), and the remaining 16 cm in fall (SON) (PRISM Climate Group) (Fig 2). Storms originating in the Gulf of Mexico do not typically affect the west side of the Mission Range (Parrett and Jarrett, 2000), but can provide additional atmospheric moisture to the region influencing local convective activity.

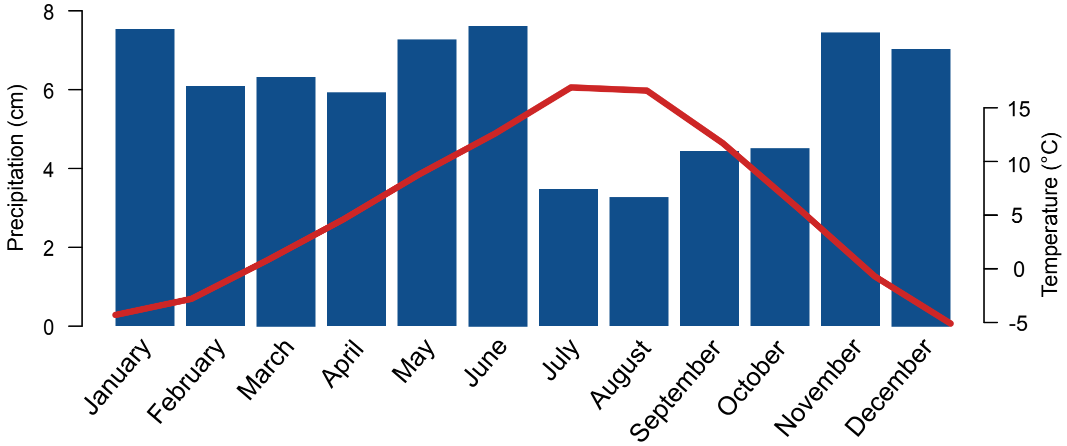

Figure 2. Average monthly precipitation and average monthly temperature from 1981-2010 for Twin Lake, MT (PRISM Climate Group, 2015).

Present-day Vegetation

The Mission Range lies at climatic and biogeographic boundaries that have influenced the distribution of plant taxa for millennia. The position of the Mission Valley at this intersection leads to the presence of a diverse array of taxa associated with both coastal PNW and interior NRM vegetation. Plant communities are strongly associated with biophysical controls linked to elevation as a result of upslope decreases in temperature and increases in moisture (Fig. 3). Lower treeline is located ca. 1060 masl, below which are valley grasslands with perennial grasses and forbs. *Pinus ponderosa* and *Pseudotsuga menziesii* forests dominate lower elevations (1060-1500 masl), while mesic settings, such as north-facing low-elevation slopes, contain *Larix occidentalis, Picea engelmannii, Pinus contorta,* as well as *Thuja plicata, Abies grandis,* and *Pinus monticola* (Swaney, 2005; Arno, 1979; Burns and Honkala, 1990). *Picea engelmannii* and *Abies lasiocarpa* forests are found at higher elevations (1700-2400 m), and *Pinus albicaulis* and *Larix lyallii* grow in subalpine parklands, just below upper treeline (2700 m), above which is alpine tundra (Pfister et al., 1977)(Fig. 3).

Twin Lake is surrounded by mixed-conifer forests dominated by *Pinus ponderosa* and *Pseudotsuga menziesii.* Other present conifer species are *Picea engelmannii, Abies grandis, Pinus contorta, Larix occidentalis,* and *Thuja plicata.* Riparian deciduous trees include *Populus tremuloides*, *Populus balsamifera* ssp. *trichocarpa,* and *Salix scouleriana.* Common understory plants surrounding the lake include *Acer glabrum, Holodiscus discolor, Prunus virginiana, Rosa woodsii, Physocarpus malvaceus, Xerophyllum tenax,* and *Vaccinium globulare*. Aquatic plants include *Potomogeton spp, Nuphar luteum*, and *Myriophyllum*. *Polygonum amphibium* and species of Poaceae, *Carex,* Isoetes, *Scirpus*, and *Typha* occupy lake margins.

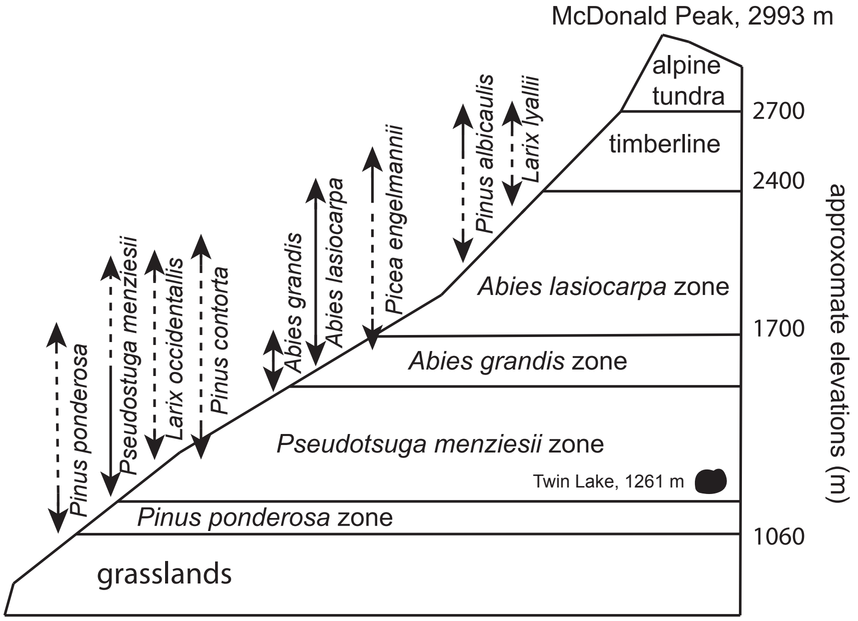

Figure 3. Generalized vegetation zones of mountains in west-central Montana. Vertical arrows represent the elevational range of each species; solid lines indicate where species is potential climax, and dashed lines indicate where it is seral (adapted from Arno, 1979; Pfister, 1977).

Modern Fire Regime

Currently, low-, mid-, and high-severity fire regimes coincide with elevation and microclimatic gradients in forests of the Mission Range. Low-severity fires consist of frequent non-lethal surface fires that occur in lowland valleys and on south-to-west aspects in dry *Pseudotsuga* and *Pinus ponderosa* forests (Swaney, 2005). At higher elevations and in more fuel-rich subalpine forests, infrequent high-severity stand-replacement fire regimes occur, including in stands of *Pseudotsuga, A. grandis, T. plicata,* and *P. engelmannii* (Swaney, 2005). Because of the topographic complexity and microclimates of the Mission Range, dry and fire-prone forests often lie in close proximity to fire-inhibiting mesic forests. This leads to diverse mixed-conifer forests that support both frequent low-severity ground fires and occasional high-severity stand-replacing or partial stand-replacing fires. This mixed-severity fire regime characterizes the forest around Twin Lake.

METHODS

Core Collection

Two 50-mm diameter cores were obtained from a platform anchored in the deepest part of Twin Lake (4 m) in October 2014: a 120-cm-long core (core A) with a 7.5-cm diameter polycarbonate tube (Klein corer) and a 564-cm-long core (core B) with a modified Livingstone square-rod-piston coring device (Wright et al., 1983). A second 391-cm-long core (core C) was extracted in September 2015, with the modified Livingstone square-rod-piston corer. Core C began 450 cm below the mud-water interface, and extended to glacial clays. Core A was sealed at the site, and the two other cores were extruded at the site and wrapped in plastic wrap and aluminum foil to avoid contamination and oxidation. All cores were transported to the cold storage room at Montana State University, where they were refrigerated until analysis.

Laboratory

Cores A and B were transported to the National Lacustrine Core Facility (LacCore) at the University of Minnesota, where they were split longitudinally. A working half was analyzed for lithological changes, photographed, and measured for magnetic susceptibility (MS) at 0.5-cm contiguous intervals. Core C was split longitudinally and analyzed for lithological changes at the Paleoecology Laboratory at Montana State University. The archival half of all cores were sealed with plastic wrap and stored in plastic tubes in the cold room at Montana State University, and the working half was analyzed for macrofossils, charcoal, and pollen.

Charcoal

The top 20 cm of core A and top 50 cm of core B were subsampled at 0.5-cm contiguous intervals, and the remainder of core B and all of core C were subsampled at 1-cm contiguous intervals for charcoal analysis. Following procedures outlined by Whitlock and Larsen (2001), 2 cm^3 samples at each interval were soaked in a mixture of bleach and sodium metaphosphate ($NaPO3$) for 24 hours to deflocculate the sediment. The remnants were gently wet-screened through a 125-μm sieve, and charcoal particles > 125 μm in diameter were counted using a stereomicroscope. This size fraction was chosen because previous studies show that particles larger than this size reflect a local fire (Whitlock and Larsen, 2001). Tephra layers and distinctive charcoal peaks were used to correlate the three cores and create one continuous record.

CharAnalysis program (https://sites.google.com/site/charanalysis/) was used to perform a statistical analysis of the charcoal counts and reconstruct a fire history for Twin Lake according to the methods described by Higuera et al. (2009). Charcoal counts were converted into charcoal accumulation rates (CHAR; particles $cm^{-2}yr^{-1}$) and the time series was interpolated to 17-yr time steps (the median deposition time per sample) to minimize differences in charcoal accumulation due to changes in deposition rate. A 750-yr lowess smoother, robust to outliers, was used to distinguish the long-term background trends (BCHAR), and positive deviations from BCHAR were counted as both fire peaks and noise. A 750-year window was chosen because it produced the least amount of insignificant peaks (peaks with a signal-to-noise index of <3). Fire peaks were distinguished from noise by crossing a set threshold, and the time in between fire episodes was smoothed with a 1000-yr window to produce a fire frequency record (fire 1000 yrs^{-1}). The fire frequency record was also smoothed within R- Statistical Program (http://www.r-project.org/) with a smoothing spline = 0.8 to evaluate trends.

Pollen

Samples of 0.5 cm^3 and 1 cm^3 volume were taken at approximate 10 cm intervals for pollen analysis resulting in a mean sample resolution of 200 years. Pollen was processed following procedures outlined by Bennet and Willis (2001), and a *Lycopodium* tablet of known concentration was added to each sample in order to calculate the concentration of pollen per sample (grains cm^{-3}) and pollen accumulation rates (PAR; grains cm^{-3} yr^{-1}). Pollen residues were mounted onto slides with silicon oil, and a minimum of 300 terrestrial pollen grains were counted per slide at magnifications of 400 to 1000x. Grains were identified to the lowest taxonomic level possible, using reference slides and pollen identification books (Faegri and Iverson, 1989; Kapp et al., 2000; McAndrews et al., 1973). Terrestrial pollen counts were converted into percentages based on the terrestrial pollen sum, and aquatic pollen counts were converted based on the total terrestrial and aquatic pollen sum.

Several species of *Pinus* grow in the Mission Range, and their pollen grains were separated into haploxylon-type and diploxylon-type *Pinus.* Haploxylon-type *Pinus* grains (identified by the presence of verrucae on the distal membrane) were attributed to *P. albicaulis, P. monticola* and/or *P. flexilis,* and diploxylon-type *Pinus* grains were likely from *P. ponderosa* and/or *P. contorta*. *Pinus* grains that had missing distal membranes were counted as undifferentiated *Pinus*. *Abies* grains were attributed to *A. grandis* and/or *A. lasiocarpa*, and Cupressaceae pollen was likely from *Juniperus communis, J. scopulorum* and/or *Thuja plicata. Pseudotsuga menziesii, Larix occidentalis,* and *L. lyallii* are all found within the Mission Range, and their grains are undistinguishable; therefore, they were identified as *Pseudotsuga/Larix.*

Terrestrial taxa were split into "forest" and "non-forest" or open landscape categories to better understand shifts in the ecological structure of the watershed. The "Rosaceae" group includes *Spiraea*, *Sorbus*, and *Prunus*-type pollen grains. "Other Trees and Shrubs" contains *Quercus, Cornus, Corylus, Shepherdia,* and *Arceuthobium,* and Ericaceae pollen grains, and the "Other Herbs" category contains Liguliflorae, Brassicaceae, Campanulaceae, Saxifragaceae, Onagraceae, Ranunculaceae, Caprifolaceae, Fabaceae, Primulaceae, *Lycopus virginicus*-type*, Galium, Actea rubra, Rumex,* and *Thalictrum*. Cyperaceae was included in the "Riparian and Aquatic Taxa" category, with Carex as the likely dominant contributor.

The “Other Aquatics” category included *Polygonum amphibium, Menyanthes, Myriophyllum,* and *Typha.* Pollen grains that were unidentifiable were counted as “Unknown,” and damaged or hidden grains were counted as “Indeterminate.” Arboreal taxa included all tree and shrub species other than *Artemisia,* and non-arboreal taxa included *Artemisia,* herbs, and grasses.

Regional Analysis

The Twin Lake record is one of few records from mixed-conifer forests in the PNW and NRM. To evaluate similarities and differences between the Twin Lake record and regional sites, the Twin Lake record was compared with twelve pollen records from sites in the PNW and NRM. Because many of these sites were analyzed in the late 1970s to early 1980s, and the chronologies were based on uncalibrated ^{14}C dates, new age-depth models were created using CLAM software v. 2.2 within an R framework (http://chrono.qub.ac.uk/blaauw/clam.html; https://www.r-project.org). Original radiocarbon dates were characterized as high or low quality based on their relation to tephra layers of known age, magnitude of error, and whether error was suspected in the original analysis. Low-quality radiocarbon dates were not used in the new age-depth model estimates.

Similarly, for the regional fire history, we examined charcoal data from six other sites in the NRM. These records were analyzed with CharAnalysis, using a 500-yr lowess smooth robust to outliers and a 1000-year smoothing window to obtain CHAR and fire frequency (fires per 1000 yrs^{-1}) for every site. In order to assess regional trends in CHAR over time, a generalized additive model (GAM) was created with equation $char_{(t,s)} = s(time)+site+\varepsilon_{(t,s)}$ with s(time)=smoothed function of time; ε=error$\sim N(\mu,\partial)$. The GAM was created within an R framework.

RESULTS

Lithology

Sediment cores were primarily composed of brown gyttja (Fig. 4). Core A was entirely brown fine detritus gyttja. Core B consisted of fine detritus gyttja from 0-336 cm depth, and coarse detritus gyttja/peat from 336-564 cm depth, other than 10 cm of tephra from 514-524 cm depth identified to be from the eruption of Mount Mazama at 7,633 ± 49 cal yr BP (Egan et al., 2015). Core C was composed of coarse detritus gyttja from 425 to 672 cm depth, other than light gray tephra from 437-447 cm depth, also identified as the Mazama ash. Another gray layer of possible ash or silt was at 672-673 cm depth, overlying fine detritus gyttja from 673 to 703 cm depth, other than 2 cm of ash at 682-684 cm, which corresponds to the Glacier Peak eruption at 11,600 ± 50 ^{14}C year (Keuhn et al., 2009). From 703 to 816 cm depth was gray-pink inorganic clay, and 796-816 cm depth was inorganic clay with pebbles that ranged in diameter from 0.5 to 3 cm. Peaks in the MS are assigned to the Mount Mazama ash, although geochemical identification of the tephra was not undertaken.

Chronology

A single chronology for the three cores was created based on eleven accelerator mass spectrometry (AMS) ^{14}C dates and two known-age tephra-layers, Mazama Ash and Glacier Peak Ash (Fig. 5)(Table 1). Charcoal peaks were used to match cores A and B, and Mazama Ash for cores B and C (Fig. 4). The ^{14}C dates were converted to calendar years in CLAM software version 2.2 in R software using the IntCal13 calibration curve (Reimer et al., 2013), and an age-depth model was created with a smoothing spline of .25 (http://chrono.qub.ac.uk/blaauw/clam.html, https://www.r-project.org).

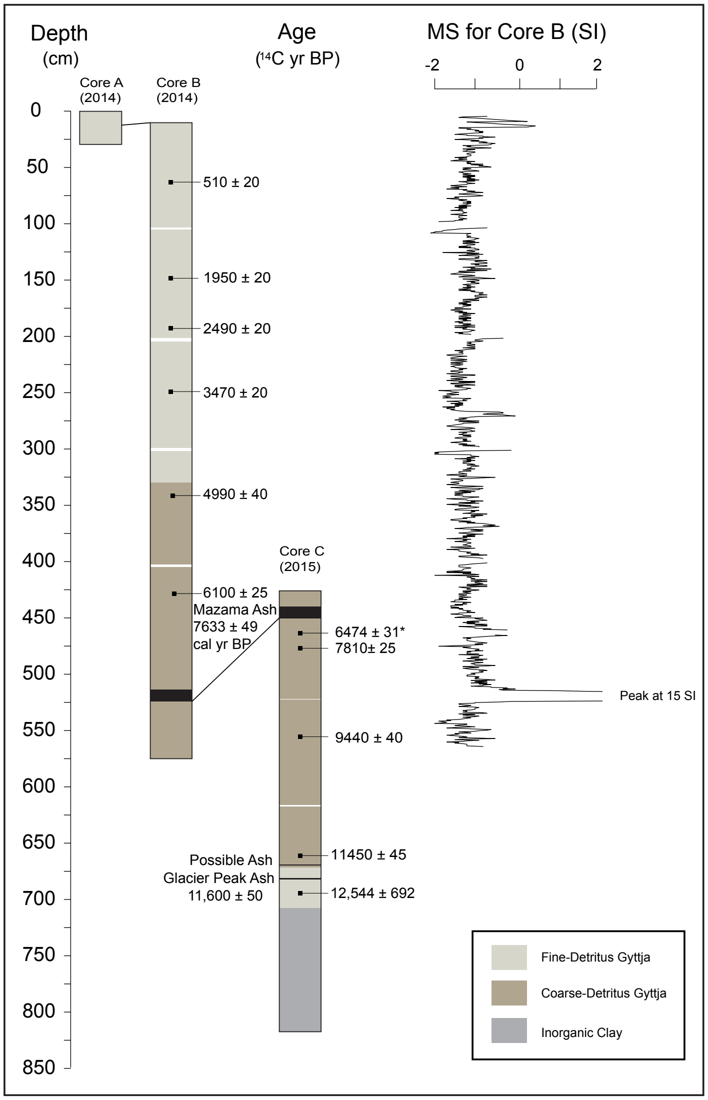

Figure 4. Lithology diagram of the three cores from Twin Lake, the location of uncalibrated radiocarbon dates, and magnetic susceptibility profile for core A. * denotes rejected date.

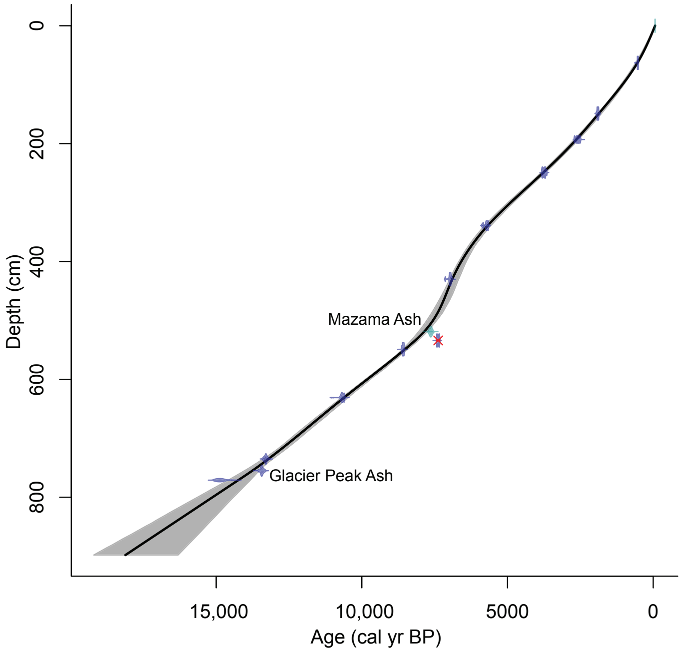

Figure 5. Age-depth model of Twin Lake. The black line shows the interpolated age for each depth of the core, and the grey shading represents the 95% confidence interval. The dots are the calibrated radiocarbon dates and the horizontal bars show their error. The two ash layers are identified, and the one rejected date is crossed out in red.

Table 1. Radiocarbon dates for Twin Lake.

Core	Master Depth (cm)	Lab Number/ Reference	Material Dated	Uncalibrated Age (C yr BP)		Calibrated Age Range (Cal yr BP)
B	63	128398	Terrestrial plant debris	510	± 20	512-544
B	154	20141	Bulk sediment	1950	± 20	1864-1947
B	193	128407	Douglas fir needle	2490	± 20	2490-2644
B	249	128408	Charcoal	3470	± 25	3688-3829
B	344	20142	Charcoal	4990	± 40	5639-5763
B	435	20143	Bulk sediment	6100	± 25	6891-7021
B	519	Egan et al., 2015	Mazama Ash			7537-7728
C	534	D-AMS 014427	Terrestrial plant debris	6474	± 31	7321-7434
C	549	20152	Bulk sediment	7810	± 25	8546-8630
C	631	20153	Bulk sediment	9440	± 40	10,570-10,768
C	735	20151	Bulk sediment	11,450	± 45	13,184-13,415
C	755	Keuhn et al., 2009	Glacier Peak Ash	11,600	± 50	13,410-13,710
C	771	D-AMS 014439	Bulk sediment	12,544	± 50	14,479-15,123

Pollen and Charcoal Data

Pollen percentage data from Twin Lake were divided into four pollen zones based on CONISS cluster analysis and visual inspection (Grimm, 1987)(Fig. 6):

Zone TL-1: 896-730 cm depth; >14,000-13,000 cal yr BP

Zone TL-1 was dominated by taxa associated with open shrub-steppe or parkland environment. Shrubs and grasses had high pollen percentages at the base of the zone and decreased towards the top: *Artemisia* decreased from 13 to 5%, and *Alnus, Salix*, and Poaceae decreased from 4%, 5% and 6% respectively to <1%. Total *Pinus* had the highest percentage of pollen (between 55 and 69%), and haploxylon-type *Pinus* values remained stable with an average of 29%, while diploxylon-type *Pinus* increased from 13 to 25%. *Pinus* PAR (not shown) was fairly high (between 1200 and 2000 grains $cm^{-2}yr^{-1}$) suggesting that pine was growing near the lake. *Picea,* and *Abies* pollen were present at an average of 5% and 2%, respectively, and Cupressaceae percentages were 4% at the base but decreased to 1% at the top. Of the aquatic and riparian taxa, only percentages of *Isoetes* spores were high*.* Total PAR ranged from 1637 to 2677 grains $cm^{-2}yr^{-1}$, which matches well with studies modern PAR from forest-tundra vegetation (Davis et al., 1973), and the arboreal/nonarboreal (AP:NAP) ratio increased through the zone. CHAR and BCHAR were very low before 13,000 cal yr BP. Charcoal peaks increased to 5 fires 1000 yrs^{-1} at the top of the zone (Figure 7).

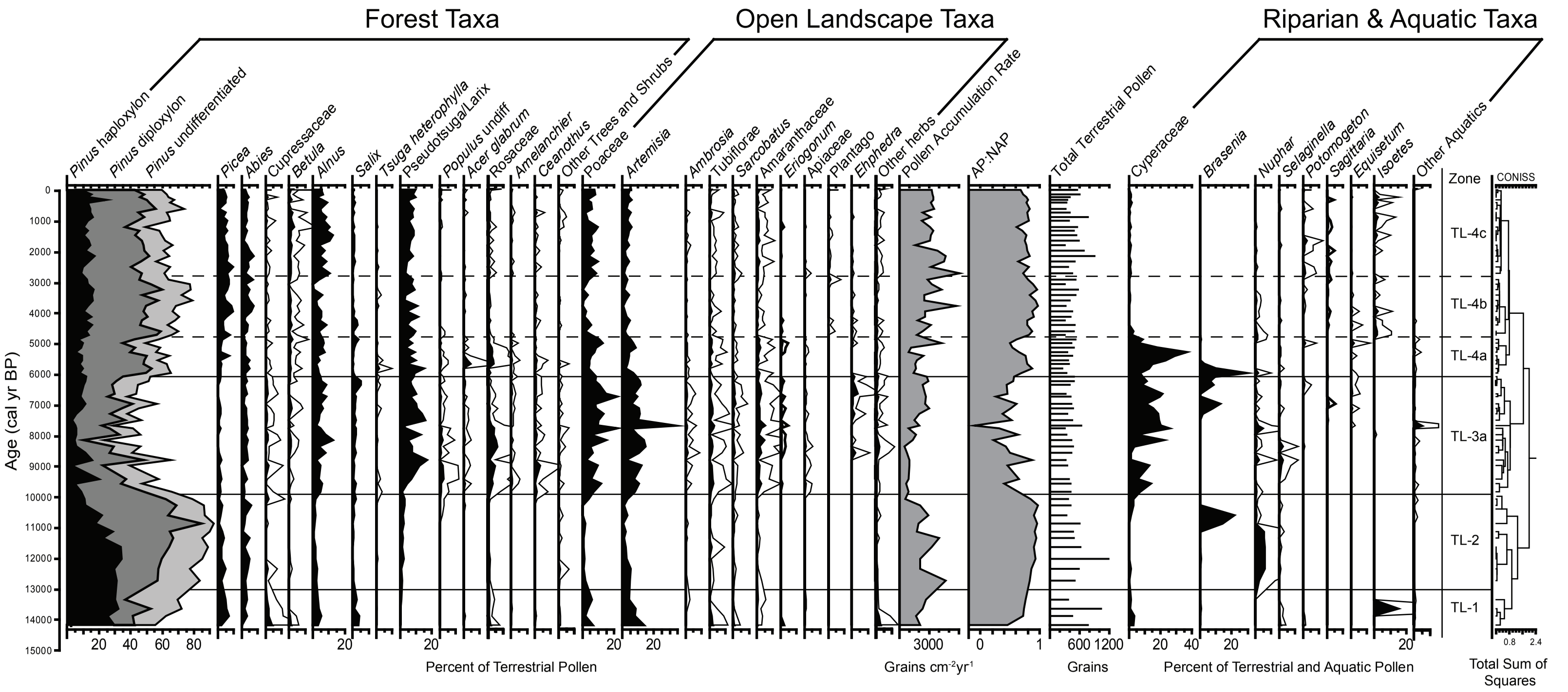

Figure 6. Pollen percentage diagram showing selected taxa from Twin Lake, Montana. Terrestrial pollen percentages based on terrestrial pollen sums, and aquatic pollen percentages are of aquatic and terrestrial pollen sums. Outlines represent 5x exaggeration.

Zone TL-2: 730-604 cm depth; 13,000-9,900 cal yr BP

In Zone TL-2, pollen of shrubs, grasses, and herbs decreased to their lowest percentages of the record, and diploxylon-type *Pinus* increased to a high of 67%. AP:NAP also increased and PAR averaged 2740 grains cm^{-2}yr^{-1}, which is typical of modern forest-tundra environments or closed boreal forest (Davis et al., 1973). Haploxylon–type *Pinus* decreased after 11,300 cal yr BP, but *Picea* and *Abies* remained constant at 2% and 3% respectively. Aquatic and riparian taxa remained low other than *Nuphar* (at 5% from 12,000-10,000 cal yr BP) and a surge in *Brasenia* percentages between 11,000 and 10,000 cal yr. BP. CHAR and BCHAR increased to a maximum at 11,400 cal yr BP, fire frequency remained around 4-5 fires 1000 yrs^{-1}.

Zone TL-3: 604-374 cm depth; 9900-6100 cal yr BP

Pollen of haploxylon- and diploxylon-type *Pinus, Picea,* and *Abies* decreased to their lowest percentages of the record (2%, 6%, <1%, 2%, respectively), and *Pseudotsuga/Larix* increased to its highest point in the record (18%). Poaceae and *Artemisia* also increased in abundance (both averaged at 10%), along with percentages of Rosaceae, Amaranthaceae, Tubuliflorae, *Alnus, Ceanothus*-type, *Eriogonum,* and *Sarcobatus*. Cyperaceae pollen percentages increased to a high of 25%. AP:NAP decreased to its lowest values, and PAR reached a low of 503 grains cm^{-2}yr$^{-1.}$ The low PAR is consistent with modern tundra vegetation PAR (David et al., 1973), but the high percentages of *Artemisia* and Poaceae are typical of modern day steppe vegetation (Whitlock, 1993), signifying a shrub-steppe environment.

Pseudotsuga/Larix pollen is poorly represented even in places where the conifers are abundant (Sugita, 1994), and an average of 9% pollen suggests that one or both conifers was locally present. The high values of *Artemisia* and Poaceae are evidence of landscape openings. Following the eruption of Mt Mazama, *Pseudotsuga/Larix* percentages decreased by 10% and *Artemisia* rose to 32%, and within 200 years of the eruption, both returned to pre-Mazama levels. CHAR and BCHAR decreased during the first half of the zone, but increased at about 7300 cal yr BP. Peak frequency data indicate an increase from 4 to 5 fires 1000 yrs^{-1} at 8000 cal yr BP, followed by a decreased to 4 fires 1000 yrs^{-1} at the end of this zone.

Zone TL-4a, b, c, 374-0 cm depth; 6100-0 cal yr BP

This zone was dominated by pollen of conifer taxa. Subtle shifts in pollen percentage data are noted in three subzones. Zone TL-4a (374-324 cm depth, 6100-4800 cal yr BP), featured drops in *Artemisia* and Poaceae percentages, and a large rise in diploxylon-type *Pinus* (from 20 to 42%). *Picea* values increased from the previous zone (1 to 2%), and percentages of haploxylon-type *Pinus* (12%), *Abies* (2%), and *Pseudotsuga/Larix* (7%) were low. Cyperaceae values initially rose to 38% but dropped to 1% at the top of the subzone and remained low for the rest of the record. PAR increased towards the top of the subzone to a high of 4200 grains cm^{-2}yr^{-1}, which matches values from modern boreal forest (Davis et al., 1973). AP:NAP also increased towards the top of the subzone. Subzone 4a had the highest CHAR and BCHAR of the record, although charcoal peak frequency still remained the same as the previous zone, between 3-5 fires 1000 yrs^{-1}.

High amounts of *Picea* and *Abies* pollen (6 and 4% respectively) and *Pinus* (78%) characterized Zone TL- 4b (324-202 cm depth, 4800-2800 cal yr BP). *Pseudotsuga/Larix* pollen continued to fluctuate between 3 and 10%, and haploxylon-type *Pinus* pollen remained between 15 and 12%. Poaceae and *Artemisia* pollen both decreased to an average of 2% and 3%, respectively, and other shrubs and herbs decreased as well (*Alnus,* Rosaceae, *Ceanothus*-type, *Acer glabrum*-type, and Amaranthaceae). PAR and AP:NAP increased, consistent with a closed forest. Biomass burning and peak magnitude decreased, but fire frequency increased to 8 fires 1000 yrs^{-1}.

Subzone 4c (202-0 cm depth, 2800 cal yr BP-present day) marks the establishment of the present-day forest. Conifer pollen percentages decreased (*Pinus*, *Picea,* and *Abies* fell to averages of 61%, 5%, and 3% respectively), and pollen of shrubs and grasses increased in abundance (Poaceae and *Alnus* increased to 6%, and other herbs and shrubs such as *Betula*, Rosaceae, and Amaranthaceae, increased to slightly over 1%). PAR and AP:NAP fell slightly from their subzone 4b levels, consistent with a more open forest. *Potomogeton, Sagittaria, Equisetum,* and *Isoetes* increased throughout Subzone 4c. CHAR and BCHAR values were similar levels to the preceding subzone, but increased CHAR occurred at 1000 cal yr BP. Charcoal peak frequency reached the highest point of the record at 2000 cal yr BP, then decreased from 9 to 6.5 fires 1000 yrs^{-1} at present day.

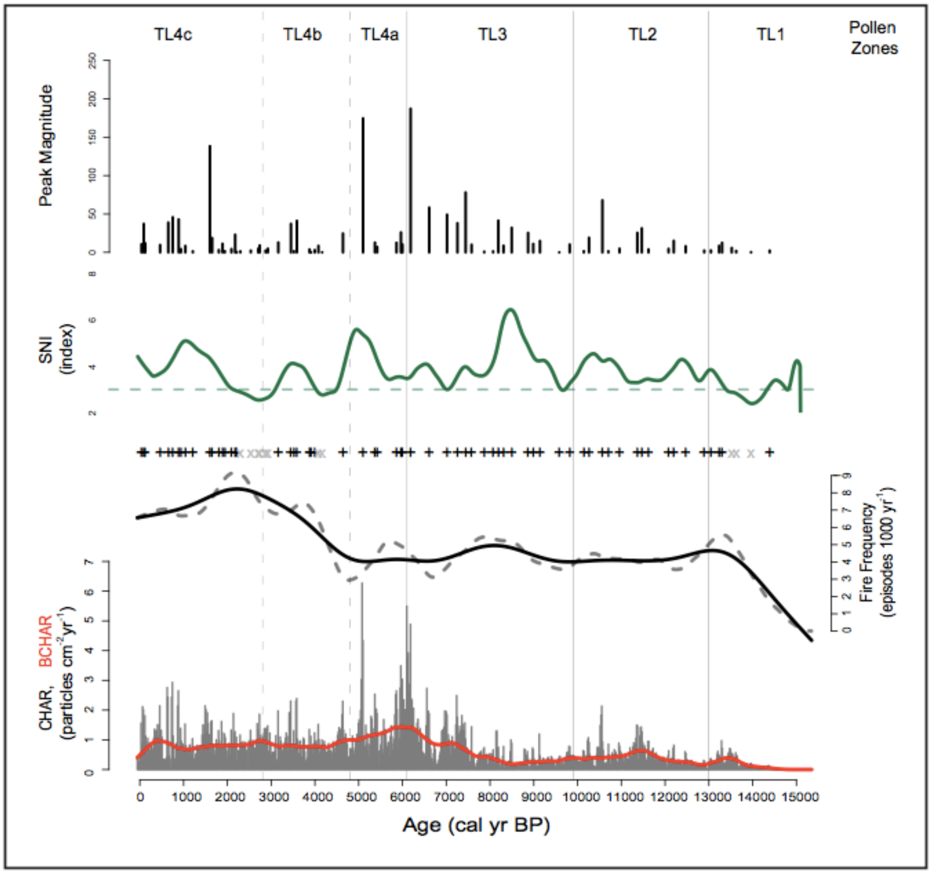

Figure 7. Charcoal diagram from Twin Lake, Montana.

DISCUSSION

The reconstruction of paleoenvironmental change at Twin Lake highlights a strong relationship between millennial-scale variations in climate, fire activity, and vegetation prior to the late Holocene when fire activity departs from trends in climatic drivers. Paleoclimate model simulations of the western United States (Bartlein et al., 1998; Kutzbach et al., 1998; Thompson et al., 1993) provide a paleoclimatic context for the interpretations of our results. The Twin Lake vegetation record is compared with twelve other low-to-mid elevation lake and wetland sites in the PNW and NRM to understand how vegetation changed across the region. Low- and middle- elevation sites were chosen because of their potential sensitivity to changes in both temperature and precipitation. Similarly, the fire record was compared with eight charcoal records from sites in the NRM to evaluate whether changes in fire activity at Twin Lake reflected regional or more local patterns.

The twelve sites in the PNW and RNM were separated based on their locations (see Fig. 1 for site locations): seven sites lie on a west-east transect from the Okanogan region of Washington to the Twin Lake area of the NRM in Montana (Mud Lake, Bonaparte Meadow, Waits Lake, Big Meadow, Hager Pond, Tepee Lake, and Foy Lake) (Fig. 8) and four comprise a north-south transect in the NRM from the Glacier National Park region to the Bitterroot Range in Montana and the Sawtooth Range in Idaho (Johns Lake, Sheep Mountain Bog, Pintler Bog, Lost Trail Pass Bog, and Decker Lake) (Fig. 9). The west-east sites lie along a climate gradient from the drier interior Washington state to the wetter NRM in Montana, while the north-south sites receive different amounts of moisture with no north-south trend (Table 2). Information about present-day forests can be found in Table 2.

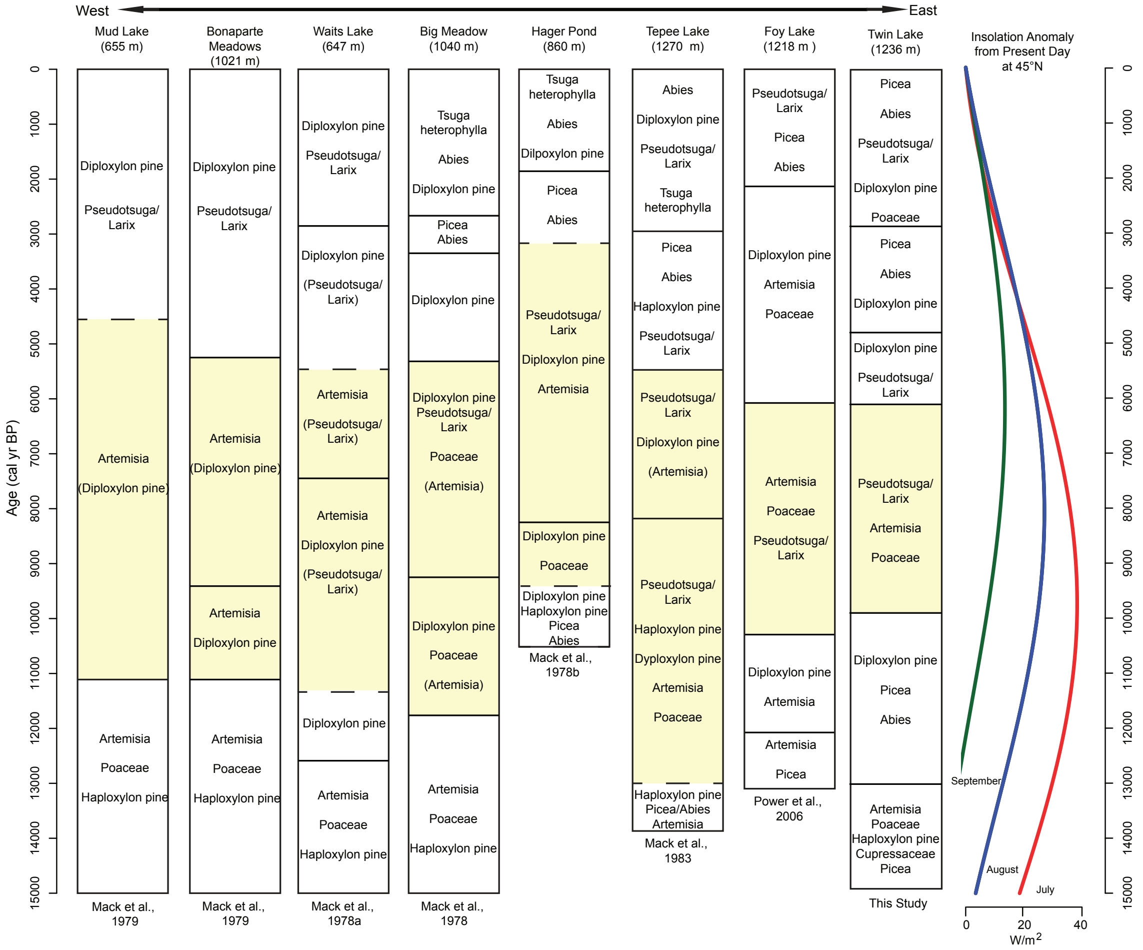

Figure 8. Vegetation history of study sites on a west-east transect from Okanogan region, WA, to Mission Range, MT. Yellow shading represents intervals of warm, effectively dry conditions. Dashed lines denote vegetation changes in which timing of change was uncertain due to low quality radiocarbon dates. Parentheses () indicate taxa that were not dominant, but their presence on the landscape is worth noting for comparisons. The insolation anomalies for different months is provided by P.J. Bartlein, and based on Berger (1978).

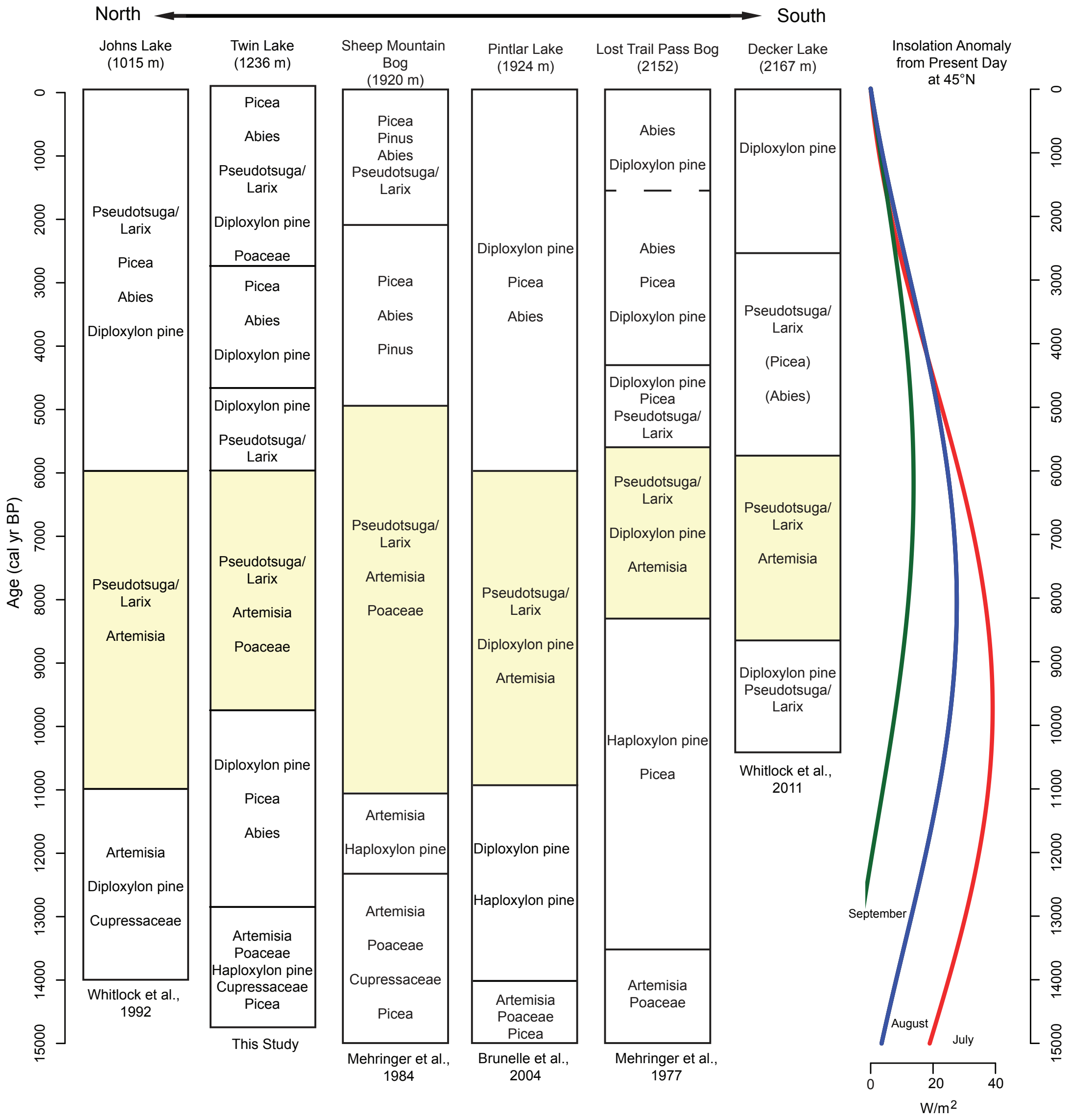

Figure 9. Vegetation history of study sites on a north-south transect from Glacier National Park, MT to the Sawtooth Range, ID. Yellow shading represents intervals of warm, effectively dry conditions. Dashed lines denote vegetation changes in which timing of change was uncertain due to low quality radiocarbon dates. Parentheses () indicate taxa that were not dominant, but their presence on the landscape is worth noting for comparisons. The insolation anomalies for different months is provided by P.J. Bartlein, and based on Berger (1978).

Table 2. Data for regional sites in the study. Asterix denotes sites used only in regional charcoal comparison.

Site Name	Latitude/Longitude	Elevation (m)	JJA ppt (cm)	DJF ppt (cm)	Present-day Vegetation	Reference
Mud Lake	48.355 N/119.376 W	655	7.2	11.5	*Pseudotsuga, P.ponderosa*	Mack et al., 1979
Bonapartes Meadow	48.413 N/ 119.105 W	1021	12	15	*Pseudotsuga, P.ponderosa, P. contora, L. occidentalis*	Mack et al., 1979
Waits Lake	48.112 N/117.473 W	647	9	17.5	*Pseudotsuga, P.ponderosa*	Mack et al., 1978a
Big Meadow Lake	48.433 N/117.335 W	1040	9.5	26	*Tsuga, A. grandis, Picea, Pseudotsuga*	Mack et al., 1978
Hager Pond	48.355 N/116.581 W	860	11.5	25.5	*Tsuga, A. grandis , P. contorta, P. monticola, L. occidentalis*	Mack et al., 1978b
Tepee Lake	48.714 N/ 115.420 W	1270	14	24	*A. grandis, P. contorta P. monticola, L. occidentalis*	Mack et al., 1983
Foy Lake	48.165 N/114.359 W	1006	13.5	10	*P. ponderosa, Pseudotsuga L. occidentalis, Picea*	Power et al., 2011
Johns Lake	48.637 N/ 113.867 W	1015	16	21	*A. grandis, Tsuga, Pseudotsuga L. occidentalis,*	Whitlock et al., 1992
Twin Lake	47.241 N/113.911 W	1236	14	21	*Pseudotsuga, P. ponderosa L. occidentalis, A. grandis*	This study
Sheep Mountain Bog	46.571 N/113.484 W	1920	16.5	36	*Picea, A. lasiocarpa, P. contorta*	Mehringer et al., 1984
Lost Trail Pass Bog	45.421 N/113.565 W	2152	15	31	*A. lasiocarpa, Picea, P. contorta*	Mehringer et al., 1977
Pintlar Lake	45.841 N/113.440 W	1921	13	14.5	*P. contorta, Picea Pseudotsuga*	Brunelle et al., 2004
Decker Lake	44.014 N/ 114.533 W	2167	8	17	*P. contorta*	Whitlock et al., 2011
Baker Lake*	45.892 N/114.262 W	1183	23	66.5	*A. bifolia, P. albicaulis L. lyallii*	Brunelle et al., 2004
Burnt Knob Lake*	45.700 N/114.990 W	2250	18	31	*A. bifolia, P. albicaulis P. contorta*	Brunelle et al., 2004
Hoodoo Lake*	46.320 N/ 114.652 W	1770	20	67	*P. contorta, Picea*	Brunelle et al., 2004

Because only a few of the transect sites had charcoal records, additional sites in the NRM were used for a fire history comparison, resulting in a total of eight charcoal records from all elevations in western Montana and central Idaho (Foy Lake, Sheep Mountain Bog, Lost Trail Pass Bog, Hoodoo Lake, Burn Knob Lake, Baker Lake, Decker Lake, and Pintler Lake). Six of the sites used high-resolution charcoal analysis similar to that employed at Twin Lake, while the fire history reconstructions from Lost Trail Pass Bog and Sheep Mountain Bog are based on discontinuous pollen slide microscopic (<100 microns) charcoal and observation of charcoal in the sediment cores.

Late-glacial Period (>14,000-11,000 cal yr BP)

The recession of large North American ice sheets in the late glacial led to a major climatic transition from cold, dry glacial conditions to warmer, and effectively wetter conditions across most of the western US. Climate simulations show that during full-glacial conditions, high pressure over the ice sheet promoted the establishment of a large persistent glacial anticyclone, which directed the jet stream approximately 20° south of its present location over northwestern North America (Thompson et al., 1993). Between 16,000 and 11,000 cal yr BP, summer insolation levels rose from 4% to 8% above present day, and the ice sheet retreated from 85% to 30% of its full-glacial size (Kutzbach et al., 1998). The melting of the ice sheet caused the glacial anticyclone to weaken, which resulted in a northerly shift of the jet stream and associated storm tracks toward their present-day location (Bartlein et al., 1998; Kutzbach et al., 1998; Thompson et al., 1993).

The record from Twin Lake registers this transition from cold and dry conditions in the late-glacial period to warmer and effectively wetter conditions in the early Holocene. Prior to 14,000 cal yr BP, pollen of *Artemisia, Juniper* (attributed to *J. communis),* haploxylon-type *Pinus,* and minor amounts of *Picea* suggest a shrub-steppe vegetation or parkland environment. *Artemisia* and *Juniper* are both xerophytic taxa, *Picea* is currently more common in elevations higher than Twin Lake (Arno, 1979; Pfister, 1977), and the haploxylon-type *Pinus* pollen is likely representative of *P. monticola* or *P. albicaulis (*both found at higher elevations in the Mission Range today)*. P. flexilis,* which tolerates a wide range of climate conditions, may also have been present near the site, although it is uncommon in the region today (Burns and Honkala, 1990). The presence of taxa well adapted to alpine and tundra conditions suggest conditions were cold and dry.

Low CHAR are also consistent with cool conditions and limited availability of woody fuels at Twin Lake prior to 14,000 cal yr BP. An increase in fire frequency from 0 to 4 fires 1000 yr^{-1} between 15,000 and 13,000 cal yr BP corresponds with pollen evidence indicating an increase in woody vegetative cover. Fire frequencies of 0-4 fires 1000 yr^{-1} are consistent with modern fire regime estimates for subalpine parkland in the PNW and NRM (Agee, 1993; Arno, 1980). Following 13,000 cal yr BP, a large increase in diploxylon-type *Pinus* and decline in *Artemisia* and Poaceae suggest the forest became more closed. Fire frequency remained stable from 13,000 to 11,000 cal yr BP, although an increase in biomass burned (inferred by levels of CHAR) implies increased fire severity with the forest closing. These vegetation changes suggest that climate was becoming progressively warmer and wetter after 13,000 cal yr BP although still colder than today.

The network of pollen records show that during the late-glacial period, tundra/steppe/subalpine parkland was widespread across both the PNW and NRM. The pollen data from the Washington sites (Mud Lake, Bonaparte Meadow, Waits Lake, and Big Meadow) and Tepee Lake, in northwestern Montana, were dominated by tundra or parkland taxa, and P. *albicaulis* or P. *monticola* was the dominant conifer (although it was likely present in small numbers). Of the Montana sites, Foy Lake and Pintler Lake supported *Picea* parkland prior to 12,500 cal yr BP and

14,000 cal yr BP respectively, and Twin Lake, Johns Lake, and Sheep Mountain Bog featured an open vegetation of *Juniper* and *Pinus* prior to 13,000 cal yr BP (14,000 cal yr BP for Twin Lake). Only the high-elevation site, Lost Trail Pass Bog in the Bitterroot Mountains, records a largely treeless alpine tundra environment prior to ca. 13,500 cal yr BP after which *Picea* and haploxylon-type *Pinus* pollen increased.

The pollen records are consistent with a late-glacial climate that was overall cooler than present, but levels of moisture are less clear (Alder and Hostetler, 2015). In the Okanogan region, Mack et al. (1978) conclude that the presence of *Typha* and haploxylon-type *Pinus* pollen was evidence of wetter-than-present conditions. Foy Lake in the NRM also suggests mesophytic vegetation and higher moisture levels. In contrast, Twin Lake, Sheep Mountain Bog, Johns Lake, and Lost Trail Pass Bog supported more xerophytic taxa before 13,000-14,000 cal yr BP implying relatively dry conditions. Power et al. (2011) propose that the vegetation differences between wet and dry sites in the late-glacial is related to their proximity to continental and alpine glaciers. This interpretation does not explain the broader patterns evident in the west-to-east transect, since the Washington sites were adjacent to the retreating Cordilleran ice sheet, yet had mesophytic vegetation. The differences between the postglacial assemblages could alternatively be a biogeographical response to deglaciation, with taxa existing in certain areas not because conditions were more suitable than other areas, but rather due to mechanisms related to dispersal as well as proximity to source populations. Regardless of these differences, by 13,000 cal yr BP, the pollen data suggest that most sites supported conifers, and many, including

Twin Lake, had parkland or forest vegetation dominated by *Picea, Abies,* and *Pinus*. The regional vegetation is consistent with increasing effective moisture across the region. Low CHAR and fire frequencies are likely related to sparse fuels and cold conditions, and all sites (other than Pintler lake, which is poorly dated) show an increase of fire frequency into the early Holocene in response to increasing fuel availability associated with the shift from subalpine parkland to closed forest (fig. 10).

The Younger Dryas Chronozone (YDC) is not marked by a widespread and distinctive vegetation change in these sites, although some sites exhibit changes that could reflect an abrupt cooling between 12,900-11,500 cal yr BP (Alley et al., 2000). At Sheep Mountain Bog, haploxylon-type *Pinus* reached a maximum at 12,450-11,320 cal yr BP, suggesting an expansion of high-elevation *P. albicaulis* during YDC. Low-elevation Foy Lake, however, registered low lake levels during the YDC (Shuman et al., 2009), during the time when a shift from *Picea* parkland to *P. contorta* forests and open grasslands suggests drying and most likely warming. Other sites do not register marked vegetation changes associated with the YDC, suggesting that if there was a climate change during this period it was too short or muted to trigger changes in all of the pollen record.

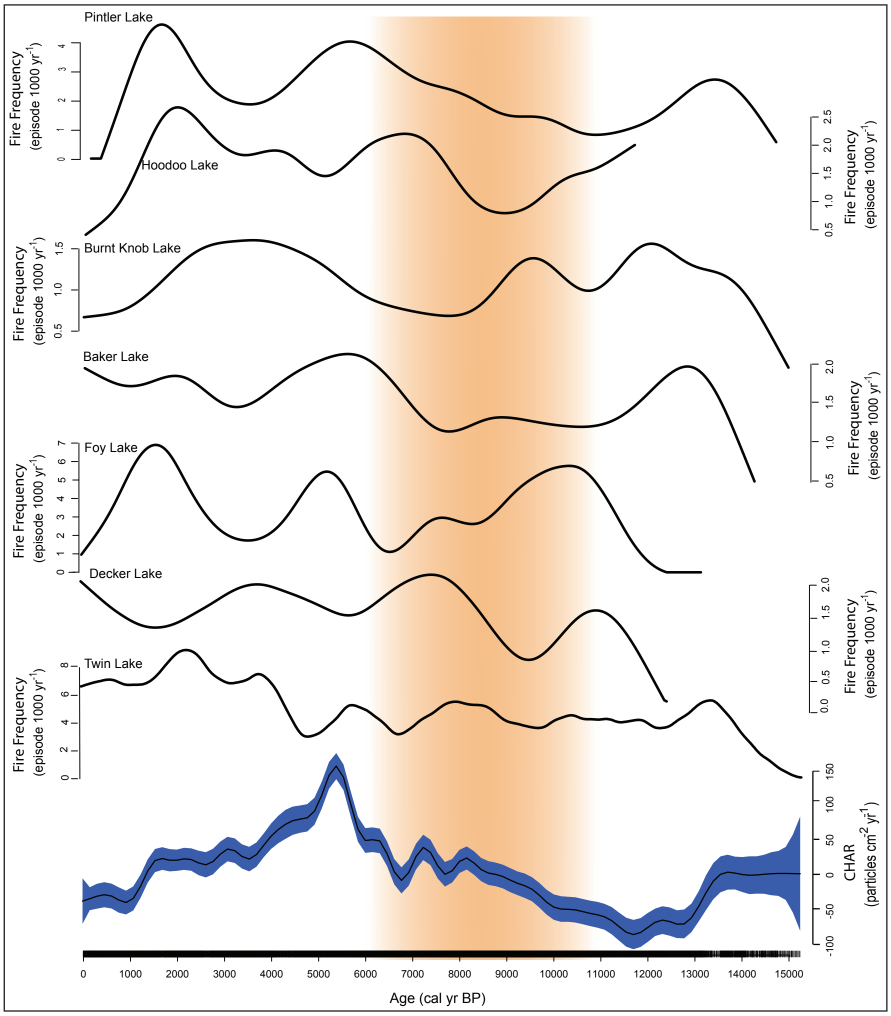

Figure 10. Composite CHAR (from seven sites in the Northern Rocky Mountains, and the fire frequency per 1000 years for all sites. (Generalized Additive Model (GAM) formula: char$_{(t,s)}$ = s(time)+site+$\varepsilon_{(t,s)}$ with s(time)=smoothed function of time; ε=error~N(μ,∂). 29.2% deviance was explained). Yellow shading indicates interval of warm, effectively dry conditions.

Early Holocene (11,000-6,000 cal yr BP)

Summer insolation reached a maximum at ca. 11,000 cal yr BP (8% higher than present day) resulting in higher summer temperatures and increased evapotranspiration (Kutzbach et al., 1998; Berger, 1978, Alder and Hostettler 2015).

Climate simulations also show a strengthened subtropical high-pressure system during the summer insolation maximum, which suppressed summer precipitation in northwestern North America. Therefore, summers were warmer and drier than at present or before (Kutzbach et al., 1998; Bartlein et al., 1998; Thompson et al., 1993).

Warm and dry conditions help explain the substantial drop in *Pinus* and other mesophytic conifers (*Picea* and *Abies*) between 10,000 and 6000 cal yr BP and the increase of *Pseudotsuga/Larix, Artemisia,* Poaceae, and other shrubs and herbs in the Twin Lake pollen record. Although *Pseudotsuga* and *Larix* pollen grains are unable to be differentiated, it is likely the forest was primarily composed of *Pseudotsuga* rather than *Larix,* based on the presence of *Pseudotsuga* macrofossils at Johns Lake located 150 km to the north in Glacier National Park (Whitlock, 1992), and at Sheep Meadow Bog, 34 km to the southeast (Mehringer, 1985). *Pseudotsuga* pollen is often underrepresented in pollen records because it does not produce much pollen, nor does the pollen disperse far from the tree (Sugita, 1994); therefore, high percentages of *Pseudotsuga/Larix* at Twin Lake during this time suggest that *Pseudotsuga* and possibly *Larix occidentalis* were abundant.

The pollen data provide evidence of an open *Pseudotsuga* parkland with *Artemisia* and Poaceae. Pollen of xerophyte *Ephedra* was wind-deposited from some distance, also indicating an open landscape. Additionally, isolated pollen grains of *Tsuga heterophylla* appear in the record during this period, which were either transported from mesic forests in the PNW or from small stands in wet habitats in the NRM. The increase of Cyperaceae during this time also implies a shallow lake environment with wetland margins, indicating dry conditions.

The charcoal data at Twin Lake are consistent with a low-severity fire regime, typical of present-day *Pseudotsuga* parkland. Fire frequency remained at four fires 1000 yr^{-1} between 11,000-7500 cal yr. BP, and charcoal influx was low, indicating small surface fires. *Pseudotsuga* trees are well adapted to fire and are often associated with low- and mixed-severity fire regimes, which reduce competition from other conifers (Agee, 1993; Whitlock et al., 2015).

Other pollen records in the region indicate either an open *Pseudotsuga/Larix* environment, or solely an *Artemisia* steppe environment in the early and middle Holocene. Mud Lake and Bonaparte Meadows had an increase in *Artemisia* at the expense of conifers (Mack et al., 1979), which was likely due to their location in the relatively dry Okanogan region. Moving eastward towards Montana, *Pseudotsuga/Larix* pollen becomes more prominent, suggesting increasing forest density to the east.

The majority of the sites register an onset of warm dry conditions at ca. 11,000 cal yr BP, including the three sites closest to Twin Lake (Foy Lake, Johns Lake, and Sheep Mountain Bog). Warming at Twin Lake, however, was approximately 1000 yrs later (at 10,000 cal yr BP), and two of the eastern sites (Lost Trail Pass Bog and Decker Lake) had vegetation changes reflective of a warm climate between 9000-8000 cal yr BP. The pollen record from Rock Lake in the Mission Range at a higher elevation (1888 m) did not contain a strong warm/dry signal at any time (Gerloff et al., 1995). The asynchronous timing of the onset of the warm period may be related to site differences in elevation, topography, and/or edaphic factors. Rock Lake, for example, is located within the middle of the *Picea-Abies* subalpine forest zone, and the pollen may not have been sensitive to changes at upper or lower treeline (Gerloff et al., 1995). Lost Trail Pass Bog and Decker Lake are located at significantly higher elevations in relatively cold settings, which may have been less sensitive to regional warming. Regardless of the timing of the onset and duration of this warm period, changes in insolation appear to have had broad consequences on vegetation across the western US during the early and middle Holocene.

Regional charcoal records show a slow increase in CHAR in the early Holocene (fig. 10), and very little change in fire frequency between 11,000 and 9000 cal yr BP and the late glacial. The low levels of CHAR could be the result of low-severity fires occurring in open *Pseudotsuga* forests at the lower elevation sites; fires which do not contribute significant amounts of charcoal influx to the record. The two sites that show high fire frequency (Foy Lake and Burnt Knob Lake) did so despite having low levels of CHAR. Similar to Twin Lake, fires at Foy Lake were likely low severity fires associated with open *Pseudotsuga* forest. The presence of *Pinus* forest at Burnt Knob Lake from 11,000-10,000 cal yr BP suggests that fires increased in response to rising fuel biomass during increasingly warmer and drier conditions, although low CHAR levels at Burnt Knob Lake indicate that fires were small. An increase in fire activity at Decker Lake at 9500-7500 cal yr BP occurred during a transition into the establishment of open *Pseudotsuga* forest from *Pinus contorta* and *Pseudotsuga* forest. This shift implies increased fire activity and warm conditions facilitated the transition into a more open landscape.

Pollen data indicate an ecological response to the eruption of Mount Mazama at ca. 7633 cal yr BP. A marked increase in *Artemisia* pollen percentages and PAR, and a modest drop in conifer pollen percentages immediately following ash deposition at Twin Lake suggest post-eruption conditions promoted *Artemisia* growth (i.e. ash, climate, or other factors). Increases in *Artemisia* percentages were also noted in pollen records from nearby sites (Sheep Mountain Bog, Lost Trail Pass Bog, Hager Pond, and Tepee Lake, Foy Lake), and it is possible that the ashfall damaged and/or killed conifers by burial or by the desiccation/modification of soils (Zobel and Antos, 1985). Increased shrub and herbaceous cover also occurred in tephra-covered landscapes following the 1980 eruption of Mount Saint Helens (Zobel and Antos, 1997). However, Brunelle and Whitlock (2003) noted a decrease in conifer pollen and increase in herbaceous pollen types but not *Artemisia* following the Mazama eruption, and Long et al. (2010) found an increase in arboreal taxa at the expense of herbs. These varying responses show that post-eruption vegetation growth is likely dependent on a number of environmental factors, including ash depth and the timing/duration of ash deposition (Zobel and Antos, 1997), as well as ecological conditions prior to the eruption. Regardless of the short-term effect, pre-Mazama pollen percentages returned to all sites within 100-200 years of the eruption.

Late Holocene (6000-Present day)

After 6000 cal yr BP, summer insolation levels steadily declined towards present-day levels resulting in general cooling. Paleoclimate model simulations show cooler summers than before and winters that were warmer and wetter at 6000 and 3000 cal yr BP. Additionally, attenuation of the subtropical high-pressure system in the late Holocene reduced summer drought in the region (Alder and Hostetler, 2015; Thompson et al., 1999; Bartlein et al., 1998).

The vegetation history at Twin Lake shows a decrease in xerophytic taxa (most notably *Artemisia* and Poaceae), and an increase in mesophytic taxa (such as *Picea*), beginning at 6000 cal yr BP, suggesting cooler and wetter conditions. Diploxylon-type *Pinus* (*P. contorta* and/or *P. ponderosa*), increased significantly relative to values in the early Holocene, coinciding with a large increase in CHAR. Despite the increase in CHAR, fire frequency remained at approximately 4 fires 1000 yr^{-1}, which suggests a shift from low-severity to high-severity fires. The increase in BCHAR to its highest level in the record ca. 6000 cal yr BP suggests woody fuels were abundant (Marlon et al., 2006), consistent with a transition from an open-steppe/parkland to closed conifer forest.

Between 5000 and 3000 cal yr BP, high levels of *Picea* and *Abies,* increases in haploxylon-type *Pinus,* and high AP:NAP values suggest a closed forest and cooler and wetter conditions. Pollen of diploxylon-type *Pinus* additionally suggests the presence of *P. contorta* or *P. ponderosa.* Although less abundant than during the early Holocene, the presence of *Pseudotsuga/Larix* suggests low severity fires still occurred. Decreases in Cyperaceae and increases in other aquatic taxa (*Potomogeton,* Isoetes, and *Sagittaria*) suggest water levels rose during this time.

Interestingly, fire frequency increased significantly during this period despite the onset of cooler and wetter conditions (Shuman and Marsicek 2016). This could be the result of an increase in convective storms and ignitions, intensification of annual to decadal droughts, or anthropogenic burning (discussed below). CHAR at Twin Lake decreased from its highest levels at 6000-5000 cal yr BP, but values remained higher than during the late-glacial and early Holocene period. The increase in fire frequency from 4 to 7 fires 1000 yr^{-1} at 3000 cal yr BP is slightly less than the 10-13 fires 1000 yr^{-1} associated with mixed-severity fire regimes in the NRM today (Arno et al., 2000), but charcoal data does not always detect low-severity surface fires (Whitlock and Larsen, 2001). The increase in fires and more variable CHAR levels from 5000 cal yr BP to present suggest a mixed-severity fire regime at this time.

At ca. 2800 cal yr BP, increases in Poaceae and open vegetation taxa coincided with a decrease of conifer percentages, notably *Picea, Abies*, and *Pinus.* The shift suggests a change from closed to slightly more open forest. Fire frequency continued to increase from the previous period to its maximum at ca. 2000 cal yr BP (9 fires 1000 yr^{-1}), although CHAR and BCHAR remained unchanged from the previous period, implying that the severity of fires did not increase.

Across the region, cooler wetter conditions during the late Holocene led to a decrease in *Artemisia* and other shrubs, herbs, and grasses, and an increase in conifers (*Pinus, Picea,* and *Abies)* at the expense of *Pseudotsuga/Larix.* Other than Hager Pond and Foy Lake, all sites show cooler conditions beginning at 6000 and 5000 cal yr BP. The warm period at Foy Lake ended ca. 1000 years earlier than other sites in the transect, and Hager Pond registered a warm period until ca. 3000 cal yr BP. As noted earlier, the Twin Lake record showed evidence of a colder wetter period between ca. 5000-3000 cal yr BP, and Big Meadow, Hager Pond, Tepee Lake, and Sheep Mountain Bog, all record distinct increases then decreases of *Picea* and *Abies,* which could reflect a brief cool period. At Tepee Lake, the *Picea-Abies* period lasts from ca. 5300-3000 cal yr BP, at Sheep Mountain Bog, it is from ca. 5500-2500 cal yr BP, while at Big Meadow, it occurs from ca. 3200-2800 cal yr BP, and it takes place at ca. 3200-2000 cal yr BP at Hager Pond. There is no documented evidence of renewed glaciation in the mountain ranges closest to these sites, but there were glacial readvances in British Columbia between ca. 4800-3900 cal yr BP and 3200-2800 cal yr BP (Menounos, 2008), overlapping with the cold periods recorded in the pollen records.

Present-day vegetation was established in the late Holocene, and at most sites, this transition occurred between 3000 and 2000 cal yr BP. The three western most Washington sites (Mud Lake, Bonaparte Meadows and Waits Lake) developed forests of *P. ponderosa* and/or *P. contorta* and *Pseudotsuga* and/or *Larix,* and the three sites to the east (Big Meadow, Hager Pond, and Tepee Lake) show the establishment of mesic *Tsuga heterophylla* forests between 3000-2000 cal yr BP. Foy Lake, Johns Lake, Sheep Mountain Bog, Lost Trail Pass Bog, and Pintler Lake developed a mixed-conifer forest consisting of primarily *P. ponderosa* and/or *P. contorta, Picea, Abies, Pseudotsuga,* and *Larix.* Pollen data from Decker Lake in the Sawtooth Range show the development of *P. contorta* forest at 2650 cal yr BP.

Most sites indicate a closing of forests during the late Holocene, except at Twin Lake (which became more open after 2800 cal yr BP) and Foy Lake, which opened at ca. 750 cal yr BP and then again at 1880 AD. The first forest opening at Foy Lake was attributed to changes in climate or Native American burning, and the second was attributed to Euro-American settlement (Power et al., 2006). While the forest at Twin Lake was not as open as in the early Holocene, the increase in Poaceae suggests an open understory. This forest structure developed during a time when fire frequency was increasing and could also be the result of Native American land use. Humans were known to burn at low elevations to open forest and grasslands (discussed below), and Twin Lake could have been in a location where native land use was prevalent.

During the middle and late Holocene, the regional fire history was similar to that at Twin Lake in that all sites register an increase in fire frequency after 6000 cal yr BP, despite the expansion of mesophytic vegetation, suggesting cool and wet conditions. The exact period of high fire frequency varied across sites (fig. 11), however, and did not correspond with increased levels of CHAR (fig. 10). CHAR increased across the region at ca. 5000 cal yr BP, reflecting regional increases in forest biomass as a result of wetter conditions. Fire records from sites can be separated into two groups: those that show a peak in fire activity at ca. 2000 cal yr

BP and a slight decrease to present day (Twin Lake, Pintlar Lake, Hoodoo Lake, and Foy Lake), and those that register a decline in fire frequency prior to 2000 cal yr BP, followed by an increase in fires from 2000 cal yr BP to present day (Decker Lake, Baker Lake, Sheep Mountain Bog, Lost Trail Pass Bog) (Fig. 10). Burnt Knob is the exception with a period of high fire activity from 5000-3000 cal yr BP, and Decker Lake and Sheep Mountain Bog also show a period of increased fire activity from ca. 5500 to 4500 cal yr BP (Fig. 10).

A number of proxy data show that climate during the late Holocene was highly variable in the NRM and PNW. Diatom records from Foy Lake suggest a climate change at ca. 4500 cal yr BP followed by periods of unpredictable drought (Stone and Fritz, 2006), and lake oxygen-isotope records from across the NRM and PNW suggest greater climate variability after at ca. 4000 cal yr BP (Anderson et al., 2016). The Medieval Climate Anomaly (MCA, a period of unusual warmth and summer aridity at ca. 1200-700 cal yr BP, (Mann et al., 2009; Cook et al., 2004)) is not strongly evident in the pollen records in either transect, suggesting periods of drought may have been too short to show any ecological response detectable in the pollen record. Whitlock et al. (2011) suggests that levels of fuel biomass would have increased in prolonged wet periods allowing large fires to occur during severe, punctuated droughts or summers with extreme hot and dry conditions.

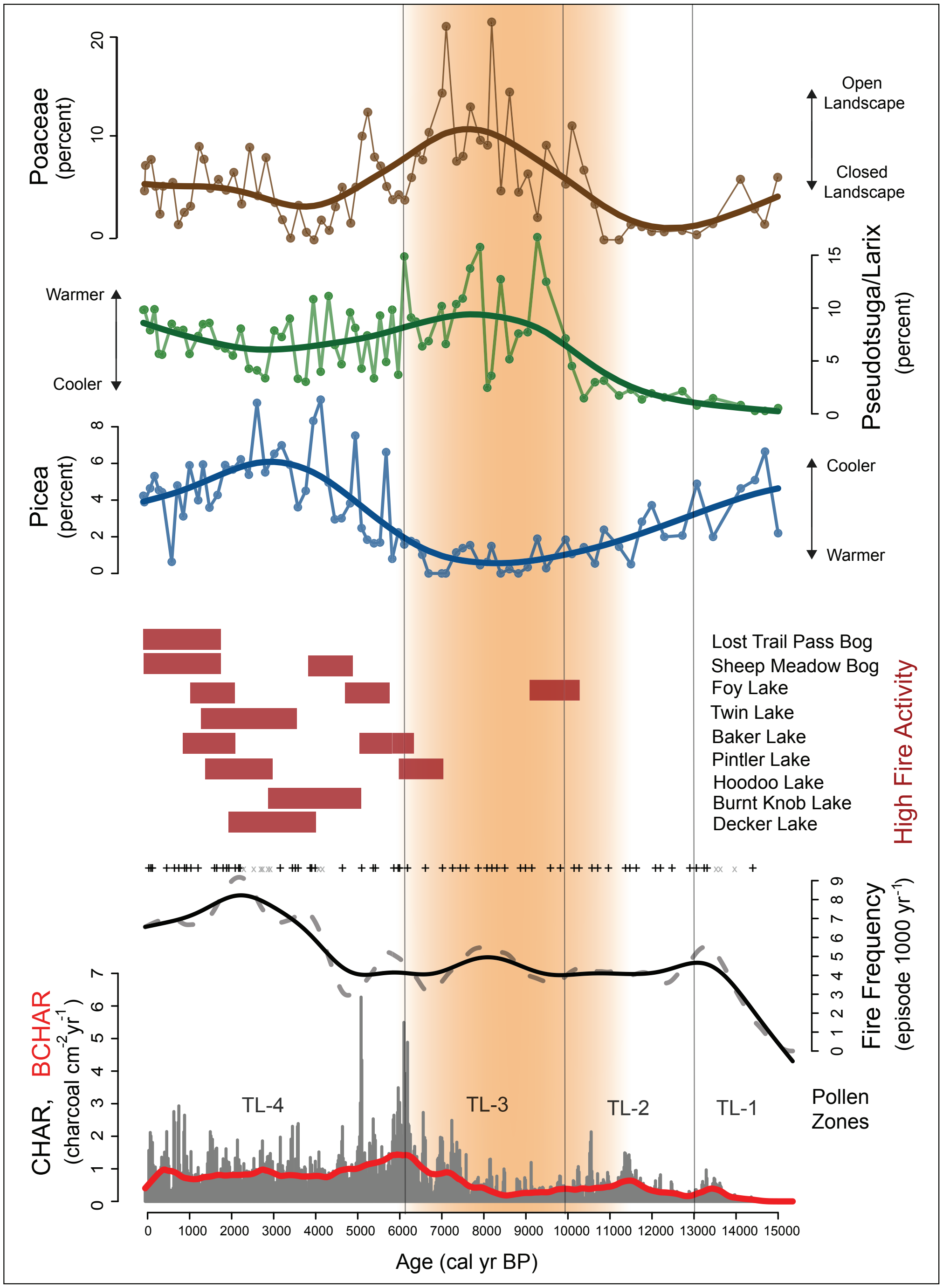

Figure 11. Selected pollen and charcoal data from Twin Lake compared with times of high fire activity (red rectangles) at other sites from the region. Yellow shading indicates interval of warm, effectively dry conditions.

The MCA caused an increase in fire activity at many sites in the Rocky Mountains (Calder et al., 2015), and while it did not promote any notable increase in fire activity at the sites in this study, anomalously warm dry conditions have been shown to contribute to regional fires in the PNW and NRM. The Great Fire of 1910 burned approximately three million acres of northeast Washington, northern Idaho, and western Montana (including the Twin Lake watershed (Swaney, 2005; Historical Research Associates, 1977)). Diaz and Swetnam (2013) analyzed climate conditions surrounding this fire, and suggest that extreme warm conditions in March of 1910 helped set the stage for the immense August burn. The warm spring extended into a warm summer, which desiccated the soil and woody fuel, and this in combination with anomalously high winds produced conditions perfect for a large regional fires. Similarly, the increase in fire activity at some of the sites in this study ca. 2000 cal yr BP coincides with a period of drought noted in tree-ring studies in the region (Cook and Krusic, 2004, Grid 69). However, the 2000 cal yr BP drought was not more severe than recent droughts in the tree-ring record.

Human Influence

The Mission Range is located in the Flathead Indian Reservation, which is home to the confederated Salish (Bitterroot Salish and Pend d'Oreille tribes) and Kootenai tribes. These tribes have occupied areas of the NRM and PNW for over ten thousand years (Malouf, 1969), and used fire for a number of purposes including communication, hunting, native food plant production, and travel (Boyd, 1999;

Barrett, 1981). Additionally, Native Americans throughout the interior PNW and NRM maintained and expanded grasslands through frequent burning (Barrett, 1981).

Human populations are thought to have increased after ca. 2500-2000 cal yr BP across the western US (Aikens, 1983), when they established more permanent settlements throughout the late Holocene up until the time of European arrival (Ubelaker, 1992). Two studies highlight population increases in the Rocky Mountains and Pacific Northwest. A study in the Bighorn Basin, Wyoming, suggests that human populations expanded during cooler wetter intervals, ca. 5500-4500 and ca. 2000-1200 cal yr BP (Kelly et al., 2013). In coastal British Canada, paleoecology studies describe an increase in xerophytic *Quercus* (oak) at the expense of *Tsuga heterophylla*, despite late-Holocene wet conditions. The oak expansion coincides with an increase in the number of Coast Salish archaeological sites suggesting increases in population at 3400 and 2000 cal yr BP (McCune et al., 2013; Pellatt et al., 2001). Fire activity increased in the late Holocene (most notably around ca. 2000 cal yr BP) at the sites in this study from the NRM, as well as some other sites farther north in British Columbia, Canada (Hallett and Hills, 2006). Since this period coincides with human population expansion in the northwestern US, anthropogenic burning may well have contributed to the increase in charcoal abundance at most sites.

Other studies investigating the significance of anthropogenic burning produced similar results. Arno (1976) collected fire scars in the Bitterroot Range and found that fire frequency was higher in areas of human settlement than in adjacent valleys, suggesting that Native Americans were using fire locally. Walsh et al. (2015) looked at a number of sites in Oregon, Washington, and southern British Columbia and also found a rise of charcoal levels during the mid-to-late Holocene despite pollen evidence of cold wet conditions. They suggest a possible correlation between the frequency of the El Niño Southern Oscillation (ENSO) and fire frequency, and also suggest that the rise in human populations during this period was a contributor to increased fires.

Arguing against a significant pre-Euro-American human influence on fire activity, Baker (2002) notes that there are very few accounts by early explorers and settlers that actually describe Native Americans setting fires and the perceptions of early Euro-Americans may have been biased toward anthropogenic burning based on their experiences in places where natural fires were rare. Baker (2002) suggests that the number of human-set fires was likely an insignificant contribution to the fire regime of the Rocky Mountains, which was (and still is) predominantly controlled by lightning-induced fires. However, he does note that Native American ignitions would have been more significant in low-elevation areas in the NRM, where lightning strikes are rare. These opposing views on the relative contribution of humans versus climate in explaining the late Holocene increases in fire activity are difficult to reconcile completely.

Future studies coupling charcoal records with tree-ring and fire-scar data in the same watershed might help better identify the occurrence of anthropogenic fires, and would add information on the spatial distribution and extent of past fires and fire severity. Charcoal records are limited in their ability to accurately detect low-severity fires, which are often frequent small events that produce little charcoal. At sites, like Twin Lake, where the fire regime includes both frequent low-severity fires in some areas and infrequent high-severity fires in others, charcoal records likely underrepresent fire activity and overemphasize the importance of high-severity events. Generating spatially explicit reconstructions of past fires would help our understanding of how this mixed-conifer forest evolved and maintained its species composition. Additionally, reconstructing fire histories from high-resolution charcoal data at other low-elevation sites in the region would improve our understanding of local-versus-regional fire history patterns by identifying broad patterns related to climate and local patterns that might human derived. Within the same region, it would be worthwhile to compare charcoal records from areas with documented human occupation and areas where it is likely that humans did not settle (which could be determined through archaeological evidence and oral histories) to gain a better understanding of differences in fire activity related to location.

CONCLUSIONS AND BROADER IMPLICATIONS

The paleoenvironmental reconstruction at Twin Lake and other sites in the Pacific Northwest and Northern Rocky Mountains highlight important shifts in past vegetation and fire activity in response to millennial-scale climate variability (from changes in the seasonal cycle of insolation), human land-use, and local topographical and climate factors. Four major transitions are noted in the regional vegetation history:

- Following deglaciation, open forest parkland and tundra vegetation established during the cold conditions of the late glacial. Sparse fuels and cold conditions limited fire activity at Twin Lake and at sites throughout the NRM. Forests became more closed after ca. 13,000 cal yr BP, indicating increasing temperatures and moisture.
- Between 11,000 and 10,000 cal yr BP, an increase in *Pseudotsuga/Larix, Artemisia,* and Poaceae marks a transition from closed forests to open *Pseudotsuga* forests at most sites coincident with a regional trend towards warming and dry conditions. The climate and associated open vegetation promoted low-severity fires until ca. 6000 cal yr BP.
- During the late mid-to-late Holocene, conditions became cooler and wetter than before and modern forests were established across the region. At Twin Lake, mixed-conifer forests of *Pinus, Pseudotsuga/Larix, Abies,* and *Picea* developed along with a mixed-severity fire regime. An increase in CHAR

beginning at ca. 5000 cal yr BP across the region reflects high levels of available fuels associated with a transition to closed forests.

- Late-Holocene fire activity remained high despite significantly cooler and wetter conditions, suggested by the expansion of mesophytic conifers. The decoupling of fire and climate trends suggests that human-set fires or increased intensity of interannual climatic variability were responsible.

The pollen record from Twin Lake suggests that the vegetation has changed little in composition over the last ca. 5000 yrs. Historical photographs and modern records, however, show that the density and forest composition in the Mission Range has changed since the introduction of fire suppression in the 1940s (Confederated Salish & Kootenai Tribes Div. of Fire Mgmt, 2006). The lack of fires has increased both dead and living ladder fuels, leading to denser forests, and an increase in species such as *Pseudotsuga* at the expense of less-shade-tolerant *P. ponderosa* in lower elevations (Swaney, 2005). While it is assumed that Native Americans used fire in this region for millennia, their fires were likely low-severity surface fires. Restoring surface fires through prescription burns and other fuel treatments around Twin Lake may help recreate a more-open forest structure typical of forests prior to mid-20th century fire suppression. It also might mitigate the chance of severe crown fires in low-to-mid elevation forests that seldom experience such events.

Fire regimes in many NRM forests have already shifted away from historical low-severity or mixed-severity regimes with the occurrence of more stand-replacement fires due to the increase of dead and living ladder fuels (Arno et al. 2000). The Mission Range is no exception. Recent anomalously dry and warm summers, such as the summer of 2003, resulted in a number of large stand-replacing fires at low- and mid-elevations (Confederated Salish & Kootenai Tribes Div. of Fire Mgmt, 2006). If this trend of warm dry summers and high-severity fires continues, it could potentially cause the decline of low-elevation species such as *Pseudotsuga* and *P. ponderosa* that are adapted to low-severity fires. Alternatively, if fuels are reduced over time, warm dry conditions and low-severity fires could benefit fire-adapted species at the expense of less-adapted species, such as *A. grandis,* and *Picea.* Through the direct or indirect effects of climate, the forests are likely to change.

Temperatures have been increasing in western Montana over the past century, and are likely to continue into the future (Pederson et al., 2010). Depending on the amount of greenhouse gas emissions, climate projections for Lake County (where Twin Lake is located) show a 2-2.5°C increase in maximum temperature by 2050, as well as decreases in summer precipitation levels (Alder and Hostetler, 2013). Regardless of the role of fire, this level of warming will likely change forest composition and shift the distribution of plant species. *Picea* and *Abies* may thrive at higher elevations due to longer growing seasons, while their presence in low-elevation mixed-conifer forests might decline due to moisture stress (Halofsky et al., 2017). Predicting future successional dynamics is further complicated by considering plant-community responses to changing fire regimes as a result of warming and/or decades of fire suppression.

Efforts to conserve the mixed-conifer forests in the Mission Range must thus consider the effects of both future climate change and past land management. These forests have been sensitive to climate change in the past; thus, warming temperatures and an extended fire season are likely to alter their structure and function as well as the disturbance regime significantly. For example, during the early Holocene, warming temperatures caused a change in forest composition from mixed-conifer forest to open *Pseudotsuga* parkland. However, forests have shown little change in composition despite increases in fires, possibly set by Native Americans. The paleoecological perspective gained from this study of Twin Lake, along with the acquisition of new records from other low-elevation settings, can help inform and guide natural resource management plans that seek to maintain naturally diverse forests at low elevations, which have been present for millennia.

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APPENDICES

APPENDIX A

RAW CHARCOAL COUNTS

Age (cal yr BP)	**Sediment Depth (cm)**	**Charcoal Counts (# particles)**	**Sediment volume (cm^3)**
-64	0	6	2
-63	0.5	7	2
-58	1	7	2
-54	1.5	3	2
-49	2	6	2
-45	2.5	2	2
-40	3	2	2
-36	3.5	2	2
-31	4	2	2
-27	4.5	5	2
-22	5	6	2
-18	5.5	5	2
-13	6	2	2
-9	6.5	6	2
-4	7	12	2
0	7.5	5	2
5	8	7	2
9	8.5	7	2
14	9	12	2
18	9.5	18	2
23	10	18	2
27	10.5	28	2
32	11	52	2
36	11.5	10	2
41	12	18	2
46	12.5	21	2
50	13	15	2
55	13.5	21	2
59	14	25	2
64	14.5	44	1.5
68	15	50	2
73	15.5	30	2
77	16	57	2
82	16.5	30	2
87	17	11	2
91	17.5	16	2
96	18	17	2

Age (cal yr BP)	**Sediment Depth (cm)**	**Charcoal Counts (# particles)**	**Sediment volume (cm^3)**
100	18.5	16	2
105	19	26	2
110	19.5	30	2
114	20	18	2
119	20.5	12	2
124	21		2
128	21.5	15	2
133	22	34	2
138	22.5	19	2
142	23	22	2
147	23.5	19	2
152	24	11	2
156	24.5	4	2
161	25	8	2
166	25.5	15	2
170	26	14	2
175	26.5	27	2
180	27	24	2
185	27.5	14	2
189	28	7	2
194	28.5	12	2
199	29	12	2
204	29.5	26	2
209	30	9	2
213	30.5	24	2
218	31	13	2
223	31.5	19	2
228	32	13	2
233	32.5	6	2
238	33	13	2
243	33.5	18	2
247	34	13	2
252	34.5	10	2
257	35	6	2
262	35.5	25	2
267	36	16	2
272	36.5	11	2

Age (cal yr BP)	Sediment Depth (cm)	Charcoal Counts (# particles)	Sediment volume (cm^3)
277	37	3	2
282	37.5	8	2
287	38	30	2
292	38.5	24	2
297	39	11	2
302	39.5	5	2
307	40	11	2
312	40.5	26	2
317	41	13	2
322	41.5	32	2
328	42	28	2
333	42.5	15	2
338	43	35	2
343	43.5	44	2
348	44	21	2
353	44.5	26	2
359	45	16	2
364	45.5	23	2
369	46	27	2
374	46.5	29	2
379	47	31	2
385	47.5	27	2
390	48	24	2
395	48.5	35	2
401	49	40	2
406	49.5	23	2
411	50	27	2
417	50.5	24	2
422	51	23	2
428	51.5	20	2
433	52	29	2
439	52.5	49	2
444	53	25	2
450	53.5	54	2
455	54	57	2
461	54.5	48	2
466	55	10	2

Age (cal yr BP)	Sediment Depth (cm)	Charcoal Counts (# particles)	Sediment volume (cm^3)
477	56	37	2
489	57	23	2
500	58	28	2
511	59	12	2
523	60	4	2
535	61	9	2
546	62	9	2
558	63	7	2
570	64	6	2
582	65	8	2
594	66	8	2
606	67	11	2
618	68	72	2
630	69	85	2
643	70	27	2
655	71	18	2
668	72	10	2
681	73	16	2
693	74	0	2
706	75	2	2
719	76	57	2
732	77	110	2
745	78	28	2
758	79	30	2
771	80	23	2
785	81	7	2
798	82	15	2
811	83	4	2
825	84	33	2
839	85	17	2
852	86	33	2
866	87	124	2
880	88	18	2
894	89	17	2
908	90	9	2
922	91	40	2
936	92	33	2

Age (cal yr BP)	**Sediment Depth (cm)**	**Charcoal Counts (# particles)**	**Sediment volume (cm^3)**
950	93	17	2
965	94	11	2
979	95	31	2
993	96	13	2
1008	97	15	2
1022	98	52	2
1037	99	26	2
1052	100	21	2
1067	101	14	2
1141	106	27	2
1157	107	22	2
1172	108	6	2
1187	109	27	2
1202	110	37	2
1218	111	15	2
1233	112	8	2
1249	113	12	2
1264	114	17	2
1280	115	15	2
1296	116	26	2
1312	117	24	2
1327	118	22	2
1343	119	20	2
1359	120	21	2
1375	121	34	2
1391	122	14	2
1407	123	20	2
1424	124	59	2
1440	125	38	2
1456	126	36	2
1472	127	57	2
1489	128	77	2
1505	129	63	2
1522	130	31	2
1538	131	74	2
1555	132	43	2
1571	133	39	2

Age (cal yr BP)	**Sediment Depth (cm)**	**Charcoal Counts (# particles)**	**Sediment volume (cm^3)**
1588	134	39	2
1605	135	12	2
1621	136	60	2
1638	137	55	2
1655	138	21	2
1672	139	26	2
1689	140	20	2
1706	141	16	2
1723	142	26	2
1740	143	35	2
1757	144	20	2
1774	145	30	2
1791	146	49	2
1809	147	30	2
1826	148	28	2
1843	149	22	2
1861	150	66	2
1878	151	35	2
1895	152	27	2
1913	153	17	2
1930	154	53	2
1948	155	28	2
1965	156	23	2
1983	157	21	2
2001	158	4	2
2018	159	45	2
2036	160	17	2
2054	161	15	2
2072	162	56	2
2089	163	28	2
2107	164	18	2
2125	165	73	2
2143	166	44	2
2161	167	47	2
2179	168	31	2
2197	169	39	2
2215	170	8	2

Age (cal yr BP)	Sediment Depth (cm)	Charcoal Counts (# particles)	Sediment volume (cm^3)
2233	171	25	2
2251	172	22	2
2269	173	22	2
2287	174	50	2
2305	175	23	2
2323	176	28	2
2341	177	35	2
2359	178	32	2
2377	179	27	2
2396	180	37	2
2414	181	19	2
2432	182	26	2
2450	183	4	2
2469	184	27	2
2487	185	35	2
2505	186	32	2
2524	187	53	2
2542	188	22	2
2560	189	34	2
2579	190	38	2
2597	191	22	2
2615	192	29	2
2634	193	21	2
2652	194	35	2
2671	195	56	2
2689	196	51	2
2708	197	36	2
2726	198	71	2
2744	199	28	2
2763	200	48	2
2781	201	32	2
2855	205	54	2
2874	206	43	2
2892	207	53	2
2911	208	53	2
2929	209	20	2
2947	210	14	2

Age (cal yr BP)	Sediment Depth (cm)	Charcoal Counts (# particles)	Sediment volume (cm^3)
2966	211	54	2
2984	212	20	2
3003	213	17	2
3021	214	24	2
3039	215	18	2
3058	216	19	2
3076	217	26	2
3094	218	47	2
3113	219	12	2
3131	220	6	2
3149	221	71	2
3167	222	24	2
3186	223	28	2
3204	224	43	2
3222	225	30	2
3240	226	19	2
3258	227	25	2
3276	228	24	2
3294	229	34	2
3312	230	31	2
3330	231	51	2
3348	232	28	2
3366	233	20	2
3384	234	36	2
3402	235	70	2
3420	236	46	2
3437	237	83	2
3455	238	31	2
3473	239	22	2
3490	240	26	2
3508	241	47	2
3525	242	26	2
3543	243	30	2
3560	244	93	2
3578	245	79	2
3595	246	21	2
3612	247	13	2

Age (cal yr BP)	**Sediment Depth (cm)**	**Charcoal Counts (# particles)**	**Sediment volume (cm^3)**
3630	248	20	2
3647	249	37	2
3664	250	31	2
3681	251	24	2
3698	252	10	2
3715	253	14	2
3732	254	43	2
3748	255	31	2
3765	256	17	2
3782	257	6	2
3799	258	11	2
3815	259	13	2
3832	260	29	2
3848	261	24	2
3865	262	46	2
3881	263	19	2
3897	264	38	2
3914	265	21	2
3930	266	28	2
3946	267	15	2
3962	268	23	2
3978	269	43	2
3994	270	31	2
4010	271	29	2
4026	272	23	2
4042	273	24	2
4058	274	38	2
4074	275	56	2
4090	276	17	2
4105	277	16	2
4121	278	20	2
4137	279	25	2
4152	280	32	2
4168	281	27	2
4183	282	20	2
4199	283	26	2
4214	284	35	2

Age (cal yr BP)	Sediment Depth (cm)	Charcoal Counts (# particles)	Sediment volume (cm^3)
4230	285	13	2
4245	286	17	2
4260	287	19	2
4276	288	13	2
4291	289	21	2
4306	290	27	2
4321	291	20	2
4336	292	15	2
4351	293	21	2
4366	294	17	2
4381	295	4	2
4396	296	24	2
4411	297	29	2
4426	298	22	2
4441	299	15	2
4529	305	38	2
4544	306	41	2
4558	307	34	2
4573	308	34	2
4588	309	49	2
4602	310	29	2
4617	311	66	2
4631	312	64	2
4645	313	42	2
4660	314	20	2
4674	315	40	2
4688	316	22	2
4703	317	43	2
4717	318	23	2
4731	319	27	2
4745	320	5	2
4760	321	14	2
4774	322	8	2
4788	323	15	2
4802	324	21	2
4816	325	19	2
4830	326	14	2

Age (cal yr BP)	Sediment Depth (cm)	Charcoal Counts (# particles)	Sediment volume (cm^3)
4844	327	32	2
4858	328	31	2
4872	329	14	2
4886	330	14	2
4900	331	14	2
4914	332	33	2
4928	333	19	2
4942	334	32	2
4956	335	33	2
4970	336	33	2
4984	337	40	2
4998	338	54	2
5012	339	33	2
5025	340	31	2
5039	341	61	2
5053	342	79	2
5067	343	105	2
5080	344	258	2
5094	345	26	2
5108	346	32	2
5122	347	13	2
5135	348	17	2
5149	349	29	2
5163	350	50	2
5176	351	16	2
5190	352	38	2
5204	353	9	2
5217	354	31	2
5231	355	15	2
5244	356	10	2
5258	357	33	2
5272	358	28	2
5285	359	84	2
5299	360	12	2
5312	361	39	2
5326	362	32	2
5340	363	26	2

Age (cal yr BP)	**Sediment Depth (cm)**	**Charcoal Counts (# particles)**	**Sediment volume (cm^3)**
5353	364	56	2
5367	365	79	2
5380	366	34	2
5394	367	54	2
5407	368	59	2
5421	369	37	2
5434	370	30	2
5448	371	12	2
5461	372	2	2
5475	373	14	2
5489	374	23	2
5502	375	22	2
5516	376	36	2
5529	377	20	2
5543	378	13	2
5556	379	15	2
5570	380	66	2
5583	381	31	2
5597	382	37	2
5610	383	30	2
5624	384	33	2
5637	385	15	2
5651	386	21	2
5665	387	21	2
5678	388	34	2
5692	389	11	2
5705	390	13	2
5719	391	32	2
5732	392	43	2
5746	393	35	2
5760	394	22	2
5773	395	15	2
5787	396	26	2
5801	397	22	2
5814	398	42	2
5828	399	65	2
5842	400	69	2

Age (cal yr BP)	Sediment Depth (cm)	Charcoal Counts (# particles)	Sediment volume (cm^3)
5855	401	74	2
5910	405	12	2
5924	406	34	2
5938	407	64	2
5951	408	121	2
5965	409	55	2
5979	410	42	2
5993	411	103	2
6007	412	53	2
6020	413	68	2
6034	414	60	2
6048	415	44	2
6062	416	63	2
6076	417	49	2
6090	418	165	2
6104	419	102	2
6118	420	111	2
6132	421	109	2
6146	422	57	2
6160	423	78	2
6174	424	161	2
6188	425	58	2
6202	426	79	2
6216	427	60	2
6231	428	53	2
6245	429	60	2
6259	430	35	2
6273	431	44	2
6288	432	32	2
6302	433	38	2
6316	434	30	2
6331	435	47	2
6345	436	53	2
6359	437	24	2
6374	438	30	2
6388	439	22	2
6403	440	52	2

Age (cal yr BP)	**Sediment Depth (cm)**	**Charcoal Counts (# particles)**	**Sediment volume (cm^3)**
6417	441	25	2
6432	442	30	2
6446	443	18	2
6461	444	16	2
6476	445	16	2
6490	446	15	2
6505	447	13	2
6520	448	11	2
6534	449	48	2
6549	450	85	2
6564	451	59	2
6579	452	44	2
6594	453	86	2
6609	454	23	2
6624	455	35	2
6639	456	15	2
6654	457	10	2
6669	458	11	2
6684	459	6	2
6699	460	11	2
6714	461	29	2
6730	462	26	2
6745	463	14	2
6760	464	5	2
6776	465	5	2
6791	466	3	2
6838	469	14	2
6853	470	18	2
6869	471	22	2
6884	472	39	2
6900	473	45	2
6916	474	39	2
6932	475	29	2
6948	476	57	2
6963	477	64	2
6979	478	44	2
6995	479	68	2

Age (cal yr BP)	Sediment Depth (cm)	Charcoal Counts (# particles)	Sediment volume (cm^3)
7011	480	57	2
7027	481	27	2
7044	482	39	2
7060	483	31	2
7076	484	30	2
7092	485	16	2
7109	486	26	2
7125	487	39	2
7141	488	21	2
7158	489	31	2
7174	490	23	2
7191	491	21	2
7208	492	32	2
7224	493	89	2
7241	494	74	2
7258	495	26	2
7275	496	37	2
7292	497	49	2
7309	498	50	2
7326	499	30	2
7343	500	65	2
7360	501	54	2
7377	502	46	2
7394	503	43	2
7412	504	58	2
7429	505	38	2
7446	506	26	2
7464	507	25	2
7481	508	24	2
7499	509	22	2
7517	510	5	2
7534	511	9	2
7552	512	16	2
7570	513	54	2
7588	514	5	2
7606	515	17	2
7624	516	14	2

Age (cal yr BP)	Sediment Depth (cm)	Charcoal Counts (# particles)	Sediment volume (cm^3)
7642	517	4	2
7660	518	1	2
7697	520	9	2
7715	521	13	2
7734	522	19	2
7752	523	21	2
7771	524	21	2
7789	525	23	2
7808	526	16	2
7827	527	14	2
7846	528	31	2
7865	529	26	2
7884	530	9	2
7903	531	18	2
7922	532	21	2
7941	533	6	2
7960	534	5	2
7979	535	22	2
7999	536	20	2
8018	537	9	2
8038	538	17	2
8057	539	28	2
8077	540	13	2
8096	541	9	2
8116	542	10	2
8136	543	74	2
8156	544	27	2
8176	545	32	2
8196	546	15	2
8216	547	6	2
8236	548	1	2
8256	549	8	2
8276	550	16	2
8297	551	31	2
8317	552	1	2
8337	553	10	2
8358	554	7	2

Age (cal yr BP)	Sediment Depth (cm)	Charcoal Counts (# particles)	Sediment volume (cm^3)
8379	555	6	2
8399	556	7	2
8420	557	12	2
8441	558	4	2
8461	559	43	2
8482	560	39	2
8503	561	7	2
8524	562	6	2
8545	563	9	2
8566	564	5	2
8588	565	9	2
8609	566	5	2
8630	567	5	2
8652	568	6	2
8673	569	3	2
8695	570	13	2
8716	571	7	2
8738	572	6	2
8760	573	8	2
8781	574	39	2
8803	575	15	2
8825	576	21	2
8847	577	28	2
8869	578	6	2
8891	579	0	2
8913	580	4	2
8935	581	9	2
8958	582	32	2
8980	583	29	2
9002	584	11	2
9025	585	10	2
9047	586	6	2
9070	587	1	2
9093	588	12	2
9115	589	55	2
9138	590	7	2
9161	591	9	2

Age (cal yr BP)	Sediment Depth (cm)	Charcoal Counts (# particles)	Sediment volume (cm^3)
9184	592	12	2
9207	593	20	2
9230	594	8	2
9322	598	20	2
9346	599	8	2
9369	600	13	2
9392	601	23	2
9416	602	12	2
9439	603	13	2
9463	604	6	2
9487	605	2	2
9510	606	15	2
9534	607	12	2
9558	608	17	2
9582	609	24	2
9606	610	8	2
9630	611	10	2
9654	612	13	2
9678	613	6	2
9703	614	12	2
9727	615	21	2
9751	616	31	2
9776	617	21	2
9800	618	44	2
9825	619	23	2
9849	620	24	2
9874	621	17	2
9898	622	24	2
9923	623	20	2
9948	624	17	2
9973	625	15	2
9998	626	14	2
10023	627	12	2
10048	628	14	2
10073	629	11	2
10098	630	19	2
10123	631	37	2

Age (cal yr BP)	**Sediment Depth (cm)**	**Charcoal Counts (# particles)**	**Sediment volume (cm^3)**
10149	632	14	2
10174	633	23	2
10199	634	23	2
10225	635	57	2
10250	636	47	2
10276	637	20	2
10302	638	14	2
10327	639	21	2
10353	640	6	2
10379	641	5	2
10405	642	4	2
10431	643	38	2
10457	644	39	2
10483	645	34	2
10509	646	77	2
10535	647	111	2
10561	648	50	2
10588	649	12	2
10614	650	11	2
10640	651	9	2
10667	652	14	2
10693	653	46	2
10720	654	16	2
10747	655	8	2
10773	656	30	2
10800	657	21	2
10827	658	36	2
10854	659	32	2
10881	660	21	2
10908	661	7	2
10935	662	48	2
10962	663	33	2
10989	664	29	2
11016	665	20	2
11043	666	12	2
11071	667	24	2
11098	668	22	2

Age (cal yr BP)	**Sediment Depth (cm)**	**Charcoal Counts (# particles)**	**Sediment volume (cm^3)**
11125	669	19	2
11153	670	18	2
11180	671	41	2
11208	672	25	2
11236	673	22	2
11263	674	51	2
11291	675	40	2
11319	676	59	2
11347	677	91	2
11375	678	18	2
11403	679	63	2
11431	680	82	2
11459	681	71	2
11487	682	33	2
11515	683	49	2
11544	684	12	2
11572	685	21	2
11600	686	59	2
11629	687	35	2
11657	688	19	2
11686	689	37	2
11715	690	40	2
11743	691	16	2
11772	692	33	2
11801	693	18	2
11946	698	24	2
11975	699	17	2
12004	700	14	2
12033	701	3	2
12062	702	38	2
12092	703	10	2
12121	704	20	2
12151	705	23	2
12180	706	49	2
12210	707	13	2
12239	708	8	2
12269	709	18	2

Age (cal yr BP)	**Sediment Depth (cm)**	**Charcoal Counts (# particles)**	**Sediment volume (cm^3)**
12299	710	18	2
12328	711	14	2
12358	712	10	2
12388	713	9	2
12418	714	18	2
12448	715	36	2
12478	716	20	2
12508	717	18	2
12538	718	6	2
12568	719	19	2
12599	720	17	2
12629	721	13	2
12659	722	8	2
12690	723	12	2
12720	724	12	2
12751	725	8	2
12781	726	5	2
12812	727	7	2
12843	728	6	2
12873	729	19	2
12904	730	10	2
12935	731	2	2
12966	732	2	2
12997	733	16	2
13028	734	23	2
13059	735	10	2
13090	736	14	2
13121	737	13	2
13153	738	17	2
13184	739	38	2
13215	740	30	2
13246	741	8	2
13278	742	60	2
13309	743	16	2
13341	744	9	2
13404	746	25	2
13436	747	36	2

Age (cal yr BP)	Sediment Depth (cm)	Charcoal Counts (# particles)	Sediment volume (cm^3)
13468	748	44	2
13499	749	35	2
13531	750	32	2
13563	751	15	2
13595	752	36	2
13627	753	28	2
13659	754	2	2
13723	756	12	2
13756	757	5	2
13788	758	15	2
13820	759	6	2
13852	760	13	2
13885	761	3	2
13917	762	12	2
13950	763	13	2
13982	764	4	2
14015	765	7	2
14047	766	4	2
14080	767	3	2
14112	768	6	2
14145	769	7	2
14177	770	6	2
14210	771	3	2
14242	772	7	2
14275	773	2	2
14307	774	3	2
14340	775	9	2
14373	776	5	2
14405	777	1	2
14438	778	2	2
14470	779	3	2
14503	780	2	2
14535	781	2	2
14568	782	1	2
14600	783	0	2
14633	784	0	2
14665	785	0	2

Age (cal yr BP)	**Sediment Depth (cm)**	**Charcoal Counts (# particles)**	**Sediment volume (cm^3)**
14698	786	0	2
14731	787	0	2
14763	788	1	2
14796	789	0	2
14828	790	0	2
14861	791	0	2
14893	792	0	2
14926	793	0	2
14958	794	0	2
14991	795	0	2
15023	796	0	2
15056	797	0	2
15089	798	0	2
15121	799	0	2
15154	800	0	2
15186	801	0	2
15219	802	0	2
15251	803	0	2
15284	804	0	2
15316	805	0	2
15349	806	0	2
15381	807	0	2
15414	808	0	2
15447	809	0	2
15479	810	0	2
15512	811	0	2
15544	812	0	2
15577	813	0	2
15609	814	0	2
15642	815	0	2
15674	816	0	2
15707	817	0	2
15740	818	0	2
15772	819	0	2
15805	820	0	2
15837	821	0	2
15870	822	0	2

Age (cal yr BP)	**Sediment Depth (cm)**	**Charcoal Counts (# particles)**	**Sediment volume (cm^3)**
15902	823	0	2
15935	824	0	2
15967	825	0	2
16000	826	0	2
16032	827	0	2
16065	828	0	2
16098	829	0	2
16130	830	0	2
16163	831	0	2
16195	832	0	2
16228	833	0	2
16260	834	0	2
16293	835	0	2
16325	836	0	2
16358	837	0	2
16390	838	0	2
16423	839	0	2
16456	840	0	2
16488	841	0	2
16521	842	0	2
16553	843	0	2
16586	844	0	2
16618	845	0	2
16651	846	0	2
16683	847	0	2
16716	848	0	2
16748	849	0	2
16781	850	0	2
16814	851	0	2
16846	852	0	2
16879	853	1	2
16911	854	0	2
16944	855	0	2
16976	856	0	2
17009	857	0	2
17041	858	0	2
17074	859	0	2

Age (cal yr BP)	**Sediment Depth (cm)**	**Charcoal Counts (# particles)**	**Sediment volume (cm^3)**
17106	860	0	2
17139	861	0	2
17172	862	0	2
17204	863	0	2
17237	864	0	2
17269	865	0	2
17302	866	0	2
17334	867	0	2
17367	868	0	2
17399	869	0	2
17432	870	0	2
17465	871	0	2
17497	872	0	2
17530	873	0	2
17562	874	0	2
17595	875	0	2
17627	876	0	2
17660	877	0	2
17692	878	0	2
17725	879	0	2
17757	880	0	2
17790	881	0	2
17823	882	0	2
17855	883	0	2
17888	884	0	2
17920	885	0	2
17953	886	0	2
17985	887	0	2

APPENDIX B

POLLEN KEY

HAPLOXYLON	H
DIPLOXYLON	D
PINUS UNDIFF	P
PICEA	PI
ABIES	AB
PSEUDOTSUGA/LARIX	PL
TSUGA	TS
CUPRESSACEAE	CU
ALNUS	AL
SALIX	SA
POPULUS	PO
QUERCUS	QU
AMELANCHIER	AM
ACER GLABRUM	AC
CEANOTHUS	CE
ARCEUTHOBIUM	AR
SARCOBATUS	SA
POACEAE	POA
ARTEMESIA	ART
TUBIFLORAE	TUB
LIGULIFLORAE	LIG
AMARANTHACEAE	AMT
ERIOGONUM	ERI
POLYGONUM BISTORTOIDES	PB
BRASSICACEAE	BR
CAMPANULACEAE	CA
CORNUS	CO
ROSACEAE	ROS
SORBUS	SO
SPIREA	SP
LYCOPUS VIRGINICUS	LV
ERICACEAE	ER
AMBROSIA	AMB
SAXIFRAGACEAE	SAX
EPHEDRA	EPH
BETLUACEAE	BET
CORYLUS	CY
GALIUM	GA

ONAGRACEAE	OG
ACTEA RUBRA	ARB
RANUNCULACEAE	RAN
CAPRIFOLIACEAE	CAP
CARYOPHYLLACEAE	CAR
FABACEAE	FA
THALICTRUM	TH
PRIMULACEAE	DOD
PTERIDIUM UNDIFF	PTE
INDETERMINATE	IND
UNKNOWN	UNK
PLANTAGO	PLA
RUMEX	RU
APIACEAE	AP
PRUNUS VIRGINIANA	PV
SHEPHERDIA CANADENSIS	SC
DRYOPTERIS	DRY
MENYANTHES	MEN
CYPERACEAE	CYP
POLYGONUM AMPHIBIUM	PGA
ISOETES	ISO
MYRIOPHYLLUM	MYR
POTOMOGETON	POT
SAGITTARIA	SAG
EQUISETUM	EQU
BRASENIA	BRA
SELAGINELLA	SEL
TYPHA	TYP
NUPHAR	NUP
LYCOPODIUM	LY

APPENDIX C

RAW POLLEN COUNTS

Age (cal yr BP)	Depth (cm)	H	D	P	PI
-47	2.25	55	162	66	23.5
-25	4.75	41	173	84	19.5
103	18.75	88	205	86	28
202	29.25	49	133.5	69	21
300	39.25	83	94	60	16
372	46.25	44	132	43.5	15
588	65.5	46	131	56	2
713	75.5	56	122	70	19
846	85.5	123	251	122	24
986	95.5	49	124	80	23
1180	108.5	57	145	70	22
1288	115.5	61	161	60	29
1432	124.5	54	174	87	19
1613	135.5	79	195	87	25
1783	145.5	43.5	103	55	18
1957	155.5	76	260	82	39
2134	165.5	150	314	116	56
2314	175.5	66	168	47	27
2496	185.5	36	111.5	89	34
2680	195.5	38.5	174	64	25
2883	206.5	62	173	93	33.5
3049	215.5	39	119.5	74	21
3231	225.5	95	251	99	34
3411	235.5	81.5	170	129	19
3587	245.5	64	166	84.5	18
3757	255.5	40	116	57.5	26
3922	265.5	47.5	174	82	43.5
4098	276.5	62	153	84	21
4238	285.5	32	111	64	9
4389	295.5	76	153	87	15
4581	308.5	56	229	54	18.5
4696	316.5	40	133	29	23
4837	326.5	33	190	80	13
4963	335.5	42.5	110	61	8
5115	346.5	41	168	75	8
5251	356.5	18	124	56	6

5387	366.5	42.5	185	65	30
5523	376.5	34	149	31	3
5658	386.5	29.5	153	55	8.5
5794	396.5	24	111.5	26	4
5945	407.5	26	143	53	6
6055	415.5	56	114	84	8
6195	425.5	55.5	97	99	5
6338	435.5	39	72	65	0
6632	455.5	28	68.5	44.5	0
6722	461.5	32.5	73	50.5	0
6956	476.5	49	131	66	5
7101	485.5	44	119	50	6.5
7267	495.5	20	77	38	5.5
7490	508.5	13	151	43	2
7651	517.5	32	109	45	4
7743	522.5	16	64	44	4.5
7951	533.5	17.5	91	43	0
8146	543.5	19	28	52	1
8348	553.5	26	111	78	0
8556	563.5	49	69	63	1.5
8771	573.5	48	106	53	6
8969	582.5	8	71	60	1
9404	601.5	75	67	77	7
9546	607.5	19	125	55	4.5
9813	618.5	37	167.5	71	6
10061	628.5	39	191	61	2
10263	636.5	47.5	242	71	10
10601	649.5	73.5	146	79	5
10868	659.5	103	403	44	3
11112	668.5	131	168	116	13
11333	676.5	106	217	88	18
11615	686.5	212	190	154	12.5
12019	700.5	402	302	305	24.5
12343	711.5	175	166	116	29
12705	723.5	155	130	133	10
13325	743.5	109	25	120	17
13643	753.5	331	221	197	53
13869	760.5	114	72	94	30
14161	769.5	226	102	100	17

AB	PL	TS	CU	AL	SA
13.5	53	0	4	33	9
10	48	0	0	26	3
18	46	0	0	37	0
17	38	0	6	8	3
9	19	0	0	19	2
13	18	0	1	30	4
10	26	0	1	14	0
10	30	0	0	20	3
21.5	59	0	3	65	0
13	21	0	5	25	0
8	39	1	2	58	4
15	40	0	0	39	0
11	44	0	0	64	4
6	36	0	3	59	4
10	18	0	0	11	3
33	36	1	5	50	7
67	70	0	0	35	4
17.5	20	0	1	42	8
15	14	1	2	16	2
10	14	0	2	47	0
34	39	0	0	17	2
7	21	0	1	0	0
27	50	1	0	2	0
17.5	16	3	2	30	0
20	11	0	2	8	1
23	33	1	0	7	0
26	17	0	0	24	4
9.5	46	0	0	21	1
5	19	0	2	13	8
19.5	22	0	1	41	16
16	45	0	2	18	2
3	24	0	0	14	1
8	21	0	1	31	19
11	31	1	4	29	9
10	15	0	1	26	5
7	32	0	0	25	1

11	21	1	0	10	2
17.5	36	3	2	15	0
13	13	1	2	7	2
12	37	5	2	7	0
8	30	0	1	12	1
11	41	2	4	22	8
16	30	1	5	25	26
7	26	2	4	32	20
11	32	0	5	15	3
7	26	0	5	34	8
5	44	0	0	20	6
13	50	3	3	29	7
10	48	1	4	15	4
13.5	69	0	5	15	8
20	14	0	6	12	6
11.5	10	0	0	14	6
7	41	0	5	26	6
16	21	1	8	52	7
12	34	0	2	17	5
14	33	0	2	35	9
12.5	52	0	1	6	1
1	43	0	8	16	3
12	26	2	1	14	1
4	18	1	0	23	9
6	5	3	4	19	4
5	10	1	9	5	7
24	12	0	0	3	1
7	5	0	0	5	3
8.5	12	0	2	6	0
4	5	0	0	2	1
24	8	0	0	3	1
10	8	0	0	8	0
59	22	2	1	17	0
22	3	0	9	15	2
10.5	6	0	2	10	1
12.5	2	0	5	10	9
17	0	1	22	35	10
14.5	0	0	10	23	19
0	2	0	35	24	25

PO	QU	AM	AC	CE	AR
8	0	1	1	0	1
1	1	1	2	0	2
1	1	0	0	0	1
0	0	0	0	1	0
1	0	0	1	0	0
0	0	0	0	0	0
0	0	1	0	0	0
0	2	2	2	5	1
0	4	1	0	1	0
1	0	1	0	0	2
2	2	0	0	2	1
0	0	0	0	0	0
0	0	0	0	2	0
0	2	1	0	1	0
0	0	0	0	0	0
0	0	0	1	4	0
1	0	0	0	1	0
0	0	2	0	0	0
0	0	0	1	3	0
1	0	1	0	0	0
1	0	0	1	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	2	2	0
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0	0	0	0	1	0
0	0	0	1	1	0
0	0	0	0	0	0
0	0	0	0	2	0
0	2	0	0	2	0
3	0	0	0	0	0
2	0	1	0	0	0
0	0	0	3	1	0
1	0	4	0	0	0
0	0	0	3	1	0
2	0	1	0	0	0

2	0	2	4	2	0
4	0	4	10	6	0
4	0	1	18	4	0
1	0	1	0	2	0
0	0	1	0	0	0
2	2	4	0	4	0
3	0	0	1	4	0
0	1	1	1	3	0
2	0	2	0	3	0
4	0	2	2	1	0
2	2	1	0	1	0
3	0	2	3	4	0
2	1	1	2	0	0
2	0	1	3	1	0
0	0	2	3	5	0
4	1	0	1	1	0
3	0	0	2	4	0
8	0	1	4	4	1
2	0	0	0	0	0
5	0	2	0	3	0
0	0	1	2	1	0
8	0	0	3	12	0
9	0	4	0	4	0
4	2	4	4	2	0
5	0	0	0	7	0
2	0	0	0	1	0
2	0	0	1	0	0
1	0	0	0	0	1
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0	0	0	0	0	1
0	0	0	0	0	3
0	0	0	0	0	1
0	0	0	0	0	0
0	0	1	0	1	0
0	0	0	1	1	0
0	0	0	0	0	0

SA	POA	ART	TUB	LIG	AMT
1	27	35	5	0	6
2	37	23	6	0	9
4	48	22	2	0	4
0	21	16	1	0	4
1	9	20	1	0	4
1	18	13	1	0	5
0	18	9	0	0	0
0	6	20	7	0	4
2	21	27	10	0	8
1	13	13	1	0	5
4	51	33	3	0	7
0	39	20	3	0	7
2	27	20	3	0	5
1	35	15	5	0	13
2	15	13	2	0	2
1	46	12	6	1	4
5	32	21	3	0	6
1	46	22	5	0	11
1	16	7	3	1	3
5	37	6	4	0	4
3	19	17	1	0	4
0	6	7	0	0	2
1	1	5	1	0	1
0	18	21	3	0	3
1	3	8	1	0	1
0	0	2	2	0	0
1	9	8	7	0	4
0	4	12	2	0	3
0	10	14	1	0	2
2	26	17	0	0	5
1	8	9	4	1	0
0	16	8	1	1	0
1	54	28	9	0	10
2	55	30	7	0	6
2	40	41	7	0	11
2	26	15	8	0	5

1	24	18	4	0	4
2	15	14	3	0	5
0	17	13	6	0	1
0	10	5	0	0	0
1	21	23	1	0	7
3	42	44	2	0	7
1	39	53	5	0	5
4	42	45	6	1	8
4	47	23	2	0	10
4	87	38	4	0	11
8	34	26	7	1	7
2	39	48	10	0	10
3	47	40	9	0	7
2	44	45	3	0	8
5	60	209	20	6	36
0	65	18	9	0	9
3	16	31	1	1	4
2	63	59	8	0	22
4	22	68	10	4	10
6	29	46	7	1	13
0	7	7	1	0	1
2	33	43	6	0	7
2	21	27	8	0	6
2	48	44	12	0	13
1	29	33	5	0	4
1	13	12	2	0	0
0	0	5	1	0	0
2	0	11	1	0	1
1	9	2	0	0	0
1	6	10	1	0	1
0	4	5	2	0	2
0	5	12	12	0	2
1	11	29	3	0	0
2	3	31	3	0	1
1	8	25	3	0	3
0	22	16	0	0	4
2	32	85	10	0	5
2	7	35	8	2	3
7	48	105	18	0	5

ERI	PB	BR	CA	CO	ROS
1	0	1	0	0	9
0	0	0	0	0	2
0	1	0	0	0	1
0	2	0	0	0	1
0	0	0	0	0	1
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	1
0	0	0	0	0	2
0	0	2	0	0	1
2	0	0	0	0	5
0	0	0	0	0	2
0	0	0	0	0	0
0	0	0	0	0	4
0	0	0	0	0	0
0	0	0	0	0	3
1	0	0	0	0	1
0	0	1	0	0	4
0	0	0	0	0	0
0	0	0	0	0	5
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	1
0	1	0	0	0	1
0	0	0	0	0	1
0	0	0	0	0	0
0	0	0	0	0	0
1	0	0	0	0	1
0	0	0	0	0	0
1	1	0	0	0	0
0	0	0	0	0	1
0	0	0	0	0	1
4	0	0	0	0	3
3	2	0	0	0	12
2	0	0	0	0	5

0	0	0	0	0	12
0	0	0	0	0	13
0	0	0	0	0	13
0	0	0	0	0	0
0	0	0	0	0	1
0	0	0	0	0	0
2	0	1	0	0	2
1	1	0	0	0	1
0	0	0	0	0	3
2	0	1	0	0	4
0	1	0	0	0	2
3	0	0	0	0	3
1	0	0	0	0	2
0	0	0	0	0	4
6	0	0	0	0	12
0	0	0	0	2	8
2	0	0	0	0	8
2	1	0	0	0	18
3	1	0	0	4	29
2	3	0	0	1	11
0	1	0	0	0	3
0	0	0	0	1	13
0	0	0	0	0	9
1	1	0	0	0	7
0	1	0	0	0	3
0	0	0	0	0	1
0	0	0	0	0	0
0	0	0	0	1	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	3
0	0	0	0	0	1
0	0	0	0	0	1
0	1	0	0	0	3
0	0	0	0	0	6
0	0	0	0	0	2
3	1	0	2	0	12

SO	SP	LV	ER	AMB	SAX
0	1	0	0	3	0
0	0	0	0	1	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	1	0	0
0	0	0	0	2	0
0	0	0	2	1	0
0	0	0	0	1	0
0	1	0	0	0	0
0	0	0	0	0	0
0	0	0	0	2	0
0	0	0	0	1	1
0	0	0	0	2	0
1	0	0	0	2	1
0	0	0	0	1	0
0	0	0	0	1	0
0	1	0	0	0	0
0	0	0	0	0	2
0	0	0	0	1	0
0	0	0	0	0	0
0	0	0	0	1	0
0	0	0	0	0	0
0	0	0	0	1	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	1	0
0	0	0	0	0	0
0	0	0	0	0	0
0	1	0	0	0	0
0	0	0	0	1	0
0	3	0	0	0	0
0	0	0	0	1	0
0	0	0	0	1	0
1	4	0	0	1	0

0	0	0	0	1	0
0	0	0	0	2	0
0	2	0	0	0	0
0	0	0	0	1	1
0	0	0	0	1	0
0	0	2	0	2	0
0	0	0	0	0	1
0	0	0	0	2	0
0	0	0	0	4	0
0	0	1	0	4	0
0	0	0	0	3	0
2	1	0	0	1	1
0	0	0	0	3	0
0	0	0	0	1	0
0	2	0	0	9	0
0	4	0	1	3	0
0	5	0	0	1	0
0	5	0	0	4	0
0	0	0	0	2	0
3	3	0	0	8	0
0	0	0	0	0	0
0	4	0	0	3	0
0	1	0	0	0	0
2	5	0	0	3	0
1	3	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	2	0
0	0	0	0	0	0
0	0	0	0	1	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	4	0	0
0	0	0	0	1	0
0	0	0	0	2	0
0	0	0	1	2	0
0	0	0	0	0	1
0	0	0	0	0	1

EPH	BET	CY	GA	OG	ARB
0	19	0	0	0	0
0	6	0	0	0	0
0	3	0	0	0	0
0	4	0	0	0	0
0	6	0	0	0	0
0	0	0	0	0	0
0	1	0	0	0	0
0	9	0	0	0	0
2	9	0	1	0	0
0	8	0	0	0	0
0	19	0	2	0	0
0	6	0	0	0	0
0	7	0	0	0	0
0	5	0	0	0	0
0	6	0	0	0	0
1	9	0	0	0	0
0	5	0	0	0	0
1	6	0	0	0	0
0	4	0	0	0	0
1	6	0	0	0	0
0	5	0	0	0	0
0	0	0	0	0	0
0	2	0	0	0	0
2	5	0	0	0	0
0	6	0	0	0	0
0	3	0	0	0	0
1	6	0	0	0	0
0	3	0	0	0	0
2	3	0	0	1	0
0	9	0	0	0	0
3	2	0	0	0	0
1	3	0	0	0	0
1	13	0	0	0	0
3	4	0	0	0	0
0	3	0	0	0	0
0	5	0	0	0	0

0	4	0	1	0	0
0	3	0	0	0	0
0	3	0	0	0	0
0	4	0	0	0	0
0	2	0	0	0	0
9	3	0	0	0	0
4	5	1	0	0	0
7	0	1	0	0	0
13	0	0	0	0	0
4	1	0	2	0	1
3	6	0	0	0	0
2	8	0	0	0	0
6	3	1	0	0	0
2	0	0	0	0	0
0	4	0	0	0	0
0	0	0	0	0	0
0	2	0	0	0	0
2	5	0	1	1	0
0	5	0	0	0	0
10	3	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	2	0	0	1	0
0	1	0	0	0	0
0	0	0	1	0	0
0	1	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	1	0	0	0	0
0	2	0	0	1	0
0	0	0	1	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	4	0	0	1	0
0	9	0	1	0	0

RAN	**CAP**	**CAR**	**FA**	**TH**	**DOD**
1	0	0	0	0	1
0	0	0	0	0	1
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	1	0
0	0	0	0	0	1
1	0	0	0	0	0
0	0	0	0	3	1
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	1	0	1
0	0	0	0	1	1
0	0	0	0	1	1
2	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	1
0	0	0	0	1	1
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	2
0	0	0	0	0	1
0	0	0	0	2	0
0	0	0	0	1	0
0	0	0	0	1	0
0	0	0	0	1	0
1	0	0	0	1	0
0	1	0	1	0	0

0	0	1	0	0	0
0	1	1	0	0	0
0	0	1	0	0	1
0	0	0	0	0	0
0	0	0	0	0	0
1	0	0	0	2	2
0	0	0	0	2	1
0	0	0	0	1	1
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	1
1	0	0	0	2	0
0	0	0	0	1	0
0	0	0	0	3	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	1	1	0
2	0	2	0	0	2
0	0	0	0	0	0
0	0	0	0	0	0
0	0	1	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	1	1
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	1	1
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
1	0	0	0	0	1
3	0	1	0	0	5

PTE	PLA	RU	AP	PV	SC
1	7	3	0	0	0
0	0	1	0	0	0
1	0	3	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	4	0	0	0
0	3	4	0	1	1
0	0	0	0	0	0
0	1	0	1	1	0
0	2	0	0	0	0
0	3	0	0	0	0
0	1	1	0	0	0
0	0	0	0	0	0
0	2	1	0	0	1
0	3	5	0	0	0
0	1	0	1	0	0
0	1	0	0	0	0
0	0	0	4	0	0
0	8	0	0	0	0
0	1	0	0	0	0
0	0	0	0	0	0
0	0	0	1	0	0
0	0	0	0	1	0
0	0	0	0	0	0
2	0	0	0	0	0
1	0	0	0	0	0
1	2	0	0	0	0
1	1	0	0	0	0
0	4	0	0	0	0
0	0	0	0	0	0
2	0	0	1	0	0
0	0	2	0	0	0
2	0	1	2	0	0
1	0	0	2	0	0

0	0	0	1	0	0
0	0	0	0	0	0
1	0	0	1	5	0
0	0	0	0	0	0
1	0	0	0	0	0
3	0	0	1	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	1	0	0
0	0	1	1	0	0
1	0	0	1	0	0
1	0	0	0	0	0
1	0	0	2	0	0
0	0	0	1	0	0
0	0	0	0	0	0
0	0	0	0	0	0
1	0	0	1	0	2
0	0	0	2	0	0
0	0	0	5	0	0
0	0	3	0	0	0
0	0	0	2	0	0
0	0	0	3	0	0
2	0	0	0	0	0
1	0	1	4	0	1
1	0	0	3	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
2	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	1	0	1
0	0	0	0	0	0
0	0	0	1	0	0
0	0	3	2	0	1
0	0	2	0	0	1
3	0	8	0	0	2

DRY	IND	UNK	MEN	CYP	PGA
1	0	3	0	4	0
0	2	0	0	1	0
0	3	0	0	8	0
0	1	0	0	5	0
0	5	1	0	2	0
0	0	0	0	7	0
0	0	0	0	0	0
0	0	1	0	2	0
0	2	0	0	1	0
0	0	1	0	1	0
1	4	2	0	6	0
0	1	2	0	1	0
0	0	0	0	4	0
0	0	0	0	3	0
0	0	1	0	4	0
0	2	1	0	7	0
0	1	0	0	4	0
0	1	0	0	6	0
0	1	1	0	2	0
0	0	1	0	7	0
0	0	0	0	0	0
0	1	0	0	0	0
0	0	0	0	0	0
0	0	0	0	4	0
0	1	0	0	3	0
0	0	0	0	0	0
0	0	1	0	0	0
0	0	0	0	1	0
0	0	0	0	0	0
0	0	2	0	0	0
0	3	0	0	14	0
0	1	2	0	5	0
0	0	1	0	49	0
0	3	2	0	30	0
0	4	1	0	108	0
0	4	0	1	203	0

0	2	3	0	186	0
0	0	3	0	115	0
0	4	1	0	68	0
0	0	0	0	42	0
0	0	1	0	40	0
0	1	0	0	51	0
0	2	0	0	69	0
0	0	0	0	38	0
0	2	0	0	89	0
0	0	0	0	102	0
0	1	3	0	63	0
0	1	1	0	95	0
0	0	0	0	83	0
3	4	1	0	104	0
0	4	5	0	178	22
0	1	4	0	108	0
0	5	1	0	16	0
0	6	4	0	121	0
1	2	2	0	17	0
0	8	1	0	6	0
0	3	2	0	4	0
0	0	2	0	53	0
0	2	0	0	23	0
0	4	0	0	69	0
0	0	0	0	33	0
2	4	0	0	11	0
0	0	0	0	13	0
0	0	0	0	5	0
0	0	0	0	0	0
0	0	0	0	0	0
0	1	0	0	0	0
0	0	1	0	2	0
0	0	0	0	0	0
1	2	0	0	7	0
0	0	0	0	1	0
0	0	8	0	4	0
0	1	2	0	12	0
2	0	1	0	15	0
7	0	2	0	21	0

ISO	MYR	POT	SAG	EQU	BRA
0	1	6	0	0	1
0	0	1	0	0	0
4	0	0	0	0	0
13	0	0	0	1	0
1	0	0	3	0	0
8	0	1	0	0	0
0	0	4	0	0	0
0	0	0	0	0	0
21	0	3	1	0	0
6	0	1	2	0	0
5	0	0	4	1	0
1	0	0	2	0	0
11	0	0	0	0	0
3	0	15	0	0	0
0	0	4	0	0	0
7	0	9	7	1	0
0	0	0	0	0	0
0	0	0	3	0	0
0	0	5	1	0	0
0	0	8	1	1	0
7	0	0	3	0	0
0	0	0	0	0	0
0	0	3	1	0	0
4	0	0	1	2	0
0	0	1	0	0	0
0	0	1	0	0	0
11	0	1	2	5	0
0	0	0	1	0	0
3	0	0	0	0	0
5	0	0	1	8	0
11	0	0	0	0	0
7	0	0	0	0	0
0	0	0	0	0	2
0	0	8	0	12	0
0	0	0	0	0	0
0	0	0	0	1	0

0	0	0	0	5	0
0	0	0	0	0	1
0	0	0	0	0	11
0	0	0	0	0	33
0	0	0	0	4	157
0	1	1	1	6	58
0	0	2	0	5	37
0	0	5	0	3	41
0	0	1	0	5	0
0	0	0	0	0	0
0	0	0	6	0	73
0	1	0	0	7	49
0	0	0	0	0	6
0	0	0	1	0	1
0	0	0	0	5	2
0	0	0	0	0	0
1	0	0	0	0	0
0	0	0	0	0	0
0	0	1	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	1
0	0	0	0	0	0
0	0	0	0	0	1
0	0	0	0	0	1
0	0	0	0	0	96
0	0	0	0	0	97
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	4
0	0	0	0	0	1
0	0	0	0	0	0
0	0	0	0	0	0
200	1	0	1	0	4
0	0	1	0	0	0
0	0	3	0	0	0

SEL	**TYP**	**NUP**	**LY**
1	2	0	239
0	0	0	241
0	0	0	283
0	0	0	112
0	0	0	101
0	0	0	150
1	0	0	73
0	0	0	181
0	0	0	254
0	0	0	119
0	0	1	165
0	0	0	124
0	0	0	141
0	0	0	111
1	0	0	111
0	0	1	142
0	0	0	150
0	0	0	87
0	0	1	62
0	0	0	56
0	0	0	96
0	0	0	48
0	0	0	72
0	0	3	112
1	0	3	129
0	0	2	32
0	0	2	105
0	0	2	102
1	1	0	106
0	0	2	103
0	0	5	132
0	0	5	115
0	4	8	123
0	1	0	102
1	1	0	283
1	4	0	269

1	0	0	136
0	0	0	154
0	1	0	167
2	1	0	105
0	1	11	178
0	0	0	179
1	1	3	168
1	1	0	165
0	0	1	80
0	0	4	141
0	0	0	150
4	0	3	131
1	0	0	146
0	0	2	161
0	29	18	174
0	0	22	173
0	0	0	103
1	4	4	158
12	0	4	436
0	1	0	264
8	0	9	4
6	1	0	149
3	0	0	169
0	3	1	251
0	0	4	180
0	2	1	260
2	0	1	77
0	2	3	43
0	0	2	113
3	0	27	95
0	0	30	42
2	0	40	65
0	0	75	191
1	0	41	94
0	0	13	34
0	1	0	42
6	0	0	135
2	1	0	82
7	0	0	113