



Holocene fire and vegetation dynamics in a montane forest, North Cascade Range, Washington, USA

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ABSTRACT

We reconstructed a 10,500-yr fire and vegetation history of a montane site in the North Cascade Range, Washington State based on lake sediment charcoal, macrofossil and pollen records. High-resolution sampling and abundant macrofossils made it possible to analyze relationships between fire and vegetation. During the early Holocene (> 10,500 to ca. 8000 cal yr BP) forests were subalpine woodlands dominated by *Pinus contorta*. Around 8000 cal yr BP, *P. contorta* sharply declined in the macrofossil record. Shade tolerant, mesic species first appeared ca. 4500 cal yr BP. *Cupressus nootkatensis* appeared most recently at 2000 cal yr BP. Fire frequency varies throughout the record, with significantly shorter mean fire return intervals in the early Holocene than the mid and late Holocene. Charcoal peaks are significantly correlated with an initial increase in macrofossil accumulation rates followed by a decrease, likely corresponding to tree mortality following fire. Climate appears to be a key driver in vegetation and fire regimes over millennial time scales. Fire and other disturbances altered forest vegetation at shorter time scales, and vegetation may have mediated local fire regimes. For example, dominance of *P. contorta* in the early Holocene forests may have been reinforced by its susceptibility to frequent, stand-replacing fire events.

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Introduction

With their complex topography and steep environmental gradients, mountains support a wide range of vegetation assemblages and habitats. At high elevations, many species exist at altitudinal limits of their distribution and are particularly responsive to growth-limiting factors such as snow pack duration, growing degree days, site moisture, and local disturbance regimes (Körner, 2003). Rapid changes in climate associated with global warming may catalyze shifts in mountain environments and may restrict or eliminate available growing space of many species (Hansen et al., 2001; McKenzie et al., 2003). Fire regimes also may be responsive to changes in climate and in turn influence vegetation assemblages (Gedalof et al., 2005). Understanding how mountain environments responded to past changes in climate can help explain current patterns and drivers of vegetation assemblages and predict how these systems may respond to future climatic change (Jackson and Overpeck, 2000).

We reconstructed fire and vegetation history from a ca. 10,500-yr sediment record sampled from a small lake in the North Cascade Range, Washington State. The study area is located near the Cascade crest, and climate is transitional between the coastal and inland sides of the mountains. The montane forest surrounding our study site has 11 conifer species, an unusually high tree species diversity for Pacific Northwest forests. Given the transitional climate and montane forest type, we anticipated that vegetation might be particularly responsive to past and future climatic variability.

We used standard methods to reconstruct fire history, and then compared our charcoal record with high-resolution records from nearby sites to better understand the regional fire history. A number of variables potentially affect charcoal accumulation rates, including distance and position of the fire relative to the lake basin, wind direction at the time of individual fire events, fire severity, and fuel biomass (Cavin et al., 2007; Whitlock et al., 2008). Due to the uncertainty in lake sediment charcoal records, a secondary proxy is ideal to corroborate the interpretation of local fire events. Abundant macrofossils in our record made it possible to analyze the correspondence between lake sediment charcoal and macrofossil accumulation rates (MFAR) from the same high-resolution record.

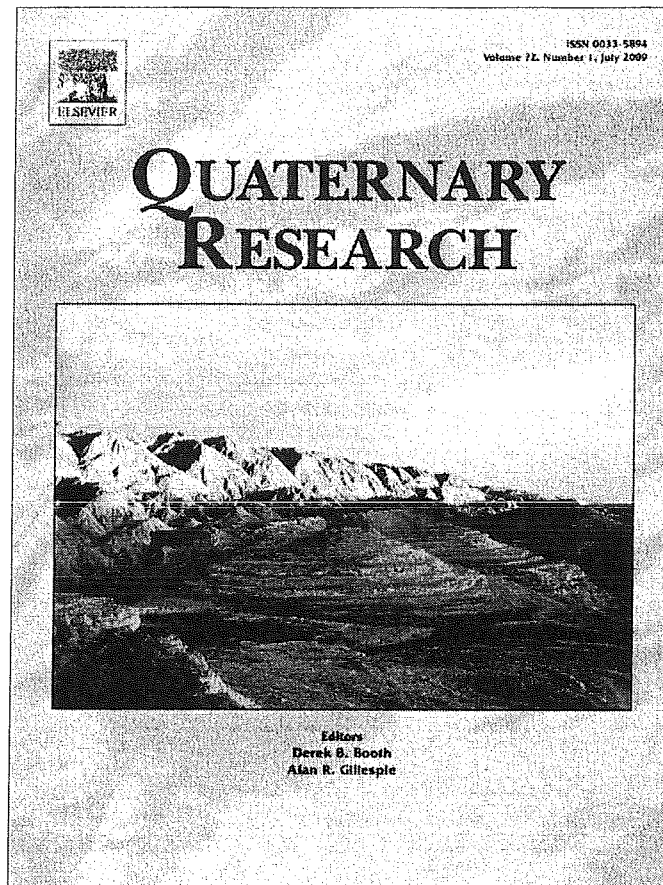
High-resolution lake sediment records are commonly used to evaluate dynamics between fire, vegetation, and climate, and inferences are generally made at millennial time scales. A number of

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studies have sampled fossil pollen at the same interval as charcoal and found a correspondence between charcoal peaks and distinct changes in pollen stratigraphy (Larsen and MacDonald, 1998; Timler *et al.*, 1999; Carcaillet *et al.*, 2001). A challenge with using pollen as an indicator of extra-local fires is that the spatial resolution is vague, and non-local pollen can mask the signal of local vegetation (Sugita, 1994). For example, correspondence between pollen accumulation rates and charcoal peaks could result from fires that were regionally widespread and/or local fire events (e.g., Carcaillet *et al.*, 2001). Plant macrofossils represent a much more localized signal of past vegetation than pollen (Dunwiddie, 1985) but are generally not sufficiently numerous in lake sediments to detect responses to fire events. In small lakes surrounded by coniferous forests macrofossils of conifer needles can be abundant (Dunwiddie, 1985) and can record local fire events through peaks in needle deposition associated with tree death and/or low needle deposition during forest regeneration following stand-replacing fire events. High-resolution macrofossil records also can be used to

evaluate the impacts of fire on vegetation assemblages and succession over long time periods.

Materials and methods

Study area

The study area is located in a mixed conifer forest on Fourth of July Pass, elevation 1100 m, near the center of North Cascades National Park (48°39'N, 121°02'W) (Fig. 1). Climate is transitional between the maritime west side and inland east side of the Cascades. Mean annual precipitation is estimated as 119 mm (December high 237 mm, July low 30 mm) and mean average annual temperature is estimated at 9.2°C (August high 18.7°C and January low 0.4°C). Approximately 90% of average annual precipitation falls between October and May.

Two parallel sediment cores were extracted from one of the Panther Potholes, a set of lakes situated on Fourth of July Pass. The

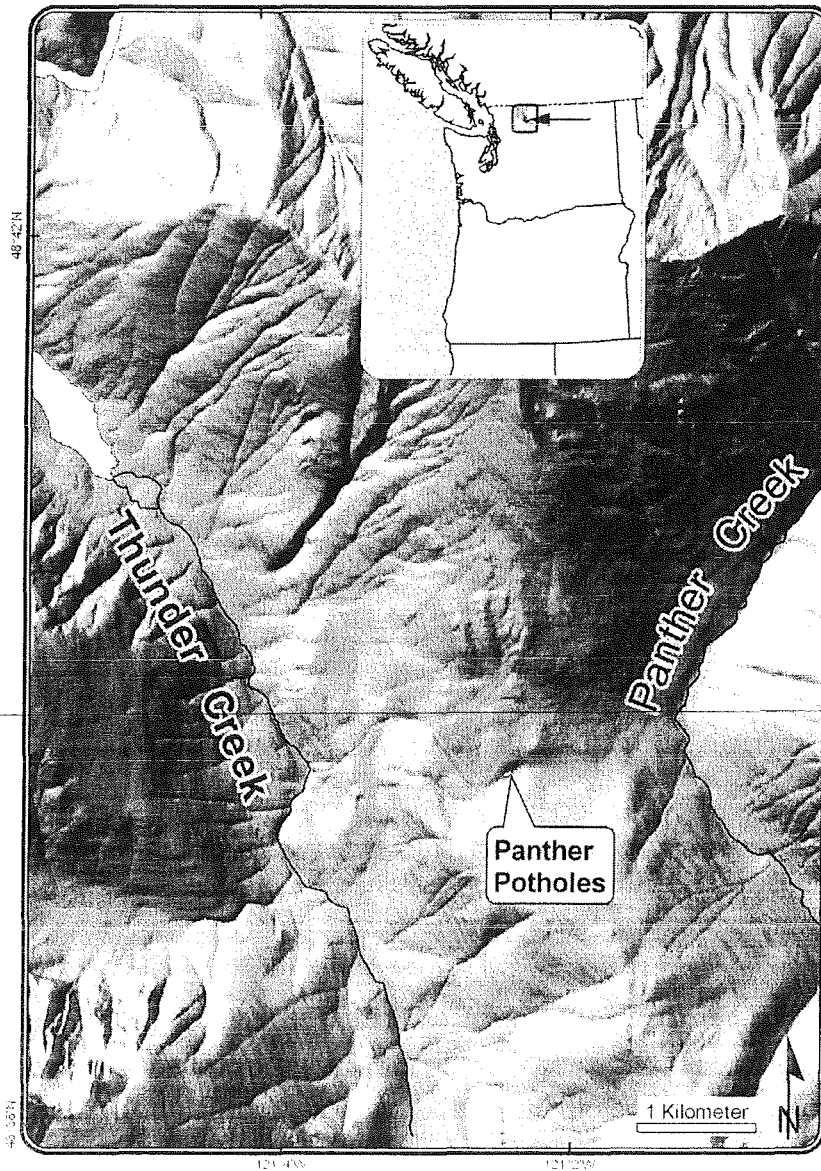


Figure 1. Location of the Panther Potholes in North Cascades National Park.

mountain pass was carved by alpine glaciers during the Fraser glaciation, and local site geology is part of the Skagit Gneiss Complex (Tabor and Haugerud, 1999). The lake is <0.4 ha, shallow (1 to 5 m), fed by an intermittent stream that connects the two lakes, and has a small outlet. The lake basin is mostly forested and has steep side slopes, interspersed with talus fields and cliffs.

The montane forest surrounding the Panther Potholes is transitional between low-elevation assemblages of *Pseudotsuga menziesii*, *Thuja plicata*, and *Tsuga heterophylla*, and high-elevation assemblages of *Abies amabilis*, *A. lasiocarpa*, *Chamaecyparis nootkatensis*, *Picea engelmannii*, *Pinus monticola*, and *Tsuga mertensiana*. *A. lasiocarpa* is common along the lakeshore, and *A. amabilis*, *P. menziesii*, *T. heterophylla*, and *T. plicata* are common associates in upland forests. Numerous snags of *P. monticola*, associated with a white pine blister rust outbreak, indicate that this species was until recently a common stand associate. *Pinus contorta* is uncommon within the immediate study area but is locally abundant within 0.5 km of the study site along a glacially carved ridgeline with shallow soils. *Alnus sinuata* is present on the lakeshore but is absent in upland forests.

The fire regime surrounding our study area is generally of mixed severity. Agee et al. (1990) reconstructed a fire history of Desolation Peak, approximately 25 km north of our study area. They reported mean fire return intervals of 75 yr for *P. contorta*-*P. menziesii* forests, 137 yr for *P. menziesii*-*T. heterophylla* forests, 107 yr for *P. contorta*-*A. lasiocarpa* forests, and 137 yr for *T. mertensiana*-*A. amabilis* forests. Desolation Peak has a drier climate than our study area, and mean fire return intervals may be somewhat longer at our site.

Lake sediment sampling and analysis

At the deepest location of the lake, two parallel sediment cores were extracted approximately 1 m apart with a 5-cm-diameter modified Livingston piston sampler (Wright et al., 1984). The top 0.5 m of sediment, including the mud-water interface, was sampled with a clear plastic, 7.6-cm-diameter tube, held vertically and immediately sectioned into 1-cm intervals. The remainder of the cores were extruded horizontally in the field, wrapped in plastic wrap and aluminum foil, and encased in PVC piping. Cores were air lifted out of the backcountry via helicopter and transported to cold storage (4 °C). The longer of the two sediment cores (978 cm) was selected for further analysis. The sediment core was sectioned into 1-cm contiguous samples, and 1 cm³ from each sample was archived for pollen analysis.

A sediment chronology was created using Accelerator Mass Spectrometry (AMS) radiocarbon, ²¹⁰Pb and tephra dates. Three tephra layers were identified using glass chemistry analysis (N. Foit, Washington State University Electron Microbeam and X-ray Analysis Labs, Pullman, WA). Radiocarbon dates were obtained for six macrofossils (conifer needles and seeds) using AMS and were calibrated using a 2 σ calibration (95% probability) (Talrn and Vogel, 1993). ²¹⁰Pb activity was measured on 7 samples in the upper 35 cm of the mud-water interface, and sedimentation rates were modeled using slope regression model and constant rate of supply (CRS) models, both of which yielded similar results (Flett Research Ltd, Manitoba, Canada). A locally weighted regression model was fit to known tephra and AMS radiocarbon dates and ²¹⁰Pb dates ($r^2 > 0.99$).

A total of 58 1-cm³ subsamples at roughly 15-cm depth increments were selected for pollen analysis. Pollen samples were prepared for analysis using standard methods (Faegri and Iversen, 1975). Tablets containing *Lycopodium* spores were added to allow measurement of pollen concentrations and estimation of pollen accumulation rates (Stockmarr, 1971). Pollen residues were mounted in silicone oil, and pollen grains and spores were counted at 400x or 1000x magnification. At least 300 pollen grains of terrestrial taxa were counted for each sample, and all pollen and spore percentages are expressed as a

percentage of the sum of identified and unidentified pollen grains. Based on 25–30 pollen grains per sample, *A. sinuata*-type and *A. rubra*-type pollen grains were separated by pore morphology, and *Pinus* pollen was separated into *Pinus* subgenus *Pinus* and *Pinus* subgenus *Strobus* (McAndrews et al., 1973).

Charcoal and macrofossil analysis was conducted on the remainder of each 1-cm core section. Bulk samples were soaked for 72 h in a known volume of 10% sodium metaphosphate solution to aid in sediment dispersal. Prior to sieving, the total volume of sediment in solution was measured to calculate the actual sediment volume (i.e., total volume minus known volume of dispersal agent). Sediments were then gently washed through nested 500- and 150- μ m sieves. Prior to charcoal counting, the 150- to 500- μ m sieve fraction was bleached with an 8% hydrogen peroxide solution for 8 h and re-washed to terminate the bleaching process. Charcoal fragments were identified and tallied for each 1-cm section using a stereomicroscope at 10–40x magnification. Because charcoal fragments in the >500- μ m fraction were rare, they were combined with the 150- to 500- μ m fraction for subsequent analyses. Charcoal concentrations were high throughout the sediment core, with a mean of 14 fragments per cm³.

Macrofossils of conifer needles were collected from the > 500- μ m fraction and identified to species using a published key (Dunwiddie, 1985) and a modern reference collection. Needle fragments were tallied as needle equivalents (i.e., 1 tip and 1 base equals a needle equivalent) and identified to species with the following exceptions. Needle fragments of *P. contorta* and *P. monticola* were too numerous to reconstruct needle equivalents. Instead, fascicles were tallied as needle equivalents (Dunwiddie, 1987). Branchlets (i.e., clusters of two or more scales) of *C. nootkatensis* and *T. plicata* were tallied as needle equivalents. *A. amabilis* and *A. grandis* are indistinguishable by needle morphology and were classified to genus.

Sedimentation rates based on the sediment chronology (cm yr⁻¹) were multiplied by charcoal and macrofossil concentrations (pieces or needles equivalents cm⁻³) to calculate accumulation rates (CHAR=charcoal pieces cm⁻² yr⁻¹, MFAR=macrofossil needle equivalents cm⁻² yr⁻¹). Macrofossil accumulation rates were calculated by species and total needle equivalents. Accumulation rates were interpolated to evenly spaced 12.5-yr intervals, which approximates the mean sedimentation rate of the core.

A standard method for detecting fire events from lake sediment charcoal is to decompose the record into background and peak components (Clark et al., 1996; Gavin et al., 2007; Whitlock et al., 2008). In our analysis, charcoal peaks likely caused by local fires (i.e., within 500–1000 m of the lake) were identified using methods described in Gavin et al. (2006). Background CHAR was delineated using a locally-weighted regression (Cleveland, 1979) with a window width of 500 yr. The peak component was defined as the difference between CHAR and background CHAR. To identify local fire events within the peak component, we then considered two subpopulations: a noise subpopulation, caused by distant fires and other variations in charcoal deposition, and local fire events representing the uppermost range of the peak. The noise subpopulation was assumed to be

Table 1a

Tephra dates based on glass chemistry analysis (F. Foit, Washington State University Electron Microbeam and X-ray Analysis Labs, Pullman, WA).

Tephra depth (cm)	Probable correlation	Similarity coefficient	Measured date (¹⁴ C yr BP)	Calibrated date (years before 1950)	Lab ID
303–308	Mount St. Helens P	0.99	2500–3000 ¹⁴ C yr BP	2590–3184 cal yr BP	Prichard PPBHC
396–406	Mount St. Helens Y	0.97	2930–3510 ¹⁴ C yr BP	4000–3300 cal yr BP	Prichard PPBHD
623–639	Mazama Climactic	0.99	6850 ¹⁴ C yr BP	7690–7610 cal yr BP	Prichard PPBHG

Table 1b
AMS radiocarbon dates; samples were analyzed and calibrated by Beta Analytic, Inca.

Depth (cm)	Measured radiocarbon date (^{14}C yr BP)	2 σ Calibrated date (yr before 1950)	Laboratory no.	Sample type
219	1950 (± 50)	1800–1990 cal yr BP	Beta-172005	Conifer seed
378	3260 (± 40)	3470–3350 cal yr BP	Beta-169623	Seed
404	3520 (± 40)	3880–3680 cal yr BP	Beta-169624	Pollen cone
504	4500 (± 40)	5320–5050 cal yr BP	Beta-169207	Pollen cone
756	7330 (± 40)	8350–8170 cal yr BP	Beta-169208	Seed
972	9370 (± 40)	10,660–10,430 cal yr BP	Beta-169625	Needle fragments (<i>Pinus contorta</i>)

normally distributed around zero and was calculated as all peak component values ≤ 0 and their absolute values. To identify local fire events, we explored three threshold values calculated as the 95th, 99th and 99.9th percentile of the noise subpopulation. The two most recent charcoal peaks at 36 cal yr BP and 456 cal yr BP, identified under all three thresholds, correspond to documented stand-age distributions (Prichard, 2003). Estimated fire return intervals are reported for the 99th percentile threshold.

Fire frequency was summarized by calculating a locally weighted mean fire frequency from a binary time series (1 = fire event, 0 = no fire event) and smoothing to 1000-yr window widths. Fire intervals were calculated as the years between identified charcoal peaks. Mean fire return intervals (MFRI) were summarized by Early Holocene (EH), Mid Holocene (MH), and Late Holocene (LH) vegetation zones. Differences in fire return interval distributions between zones were tested using Kolmogorov-Smirnov goodness of fit tests between periods at $\alpha = 0.05$.

Superposed epoch analysis was used to evaluate relationships between macrofossil accumulation rates (MFAR) and fire events delineated from CHAR peaks (Swetnam, 1993). To induce stationarity in the MFAR record, the chronology was log-transformed (after adding 10 to allow for values of zero), and then detrended using a fifth-order polynomial fit. MFAR anomalies were then standardized for a mean of zero. The MFAR departure from zero was calculated over the eight samples preceding and following identified charcoal peaks in addition to the sample corresponding to the fire. Because needle equivalents are uncommon relative to the total number of macrofossils found in the record, total macrofossil accumulation rates and macrofossil needle accumulation rates were included in this analysis. We also evaluated individual species response to fire. At each 12.5-yr lead/lag,

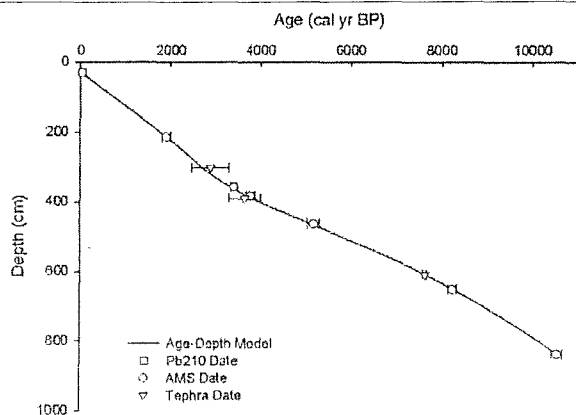


Figure 2. Age-depth model with AMS radiocarbon, tephra, and ^{210}Pb dates. Error bars indicate one standard deviation. The age-depth regression equation is $8.727x - 183.6$ ($r^2=0.9966$).

Table 1c
 ^{210}Pb dates based on CRS age–depth model (Flett Research Ltd., Winnipeg, Canada).

Depth (cm)	Total activity (DPM/g)	Error (1 σ)	Modeled date
3	29.69	2.87	na
7	32.55	3.47	12.3
14	8.30	1.15	40
21	2.68	0.72	61
28	3.22	0.74	70
35	3.76	0.77	85

Total activity and standard error are expressed in ^{210}Pb disintegration per minute per gram of dry weight material.

90% confidence limits were calculated on the MFAR anomaly. This analysis describes the mean macrofossil (MFAR) response to a peak in charcoal, or the "canonical" response to fire. To determine whether this canonical response is an artefact of a subset of the fire events, we calculated the correlation between individual fire events and the canonical fire over the interval with significant relationships identified in the canonical fire event described above. This analysis provides a measure of how strongly each individual fire event resembles the overall mean response, as well as providing insight into the time stability of the response.

Results

Core stratigraphy and chronology

The sediment core consists almost entirely of uniform fine detritus gyttja with a sedimentation rate of 0.078 cm yr^{-1} (12.8 yr cm^{-1}). Three tephra layers are present and were identified as Mount Saint Helens set P at 303–308 cm (2590–3184 cal yr BP), Mount St. Helens set Y at 396–406 cm (3300–4000 cal yr BP), and Mazama Climactic at 623–639 cm (7610–7690 cal yr BP) (Table 1a). All tephras match known standards with high similarity coefficients (r^2 0.99, 0.97 and 0.99, respectively). The six AMS radiocarbon dates (Table 1b) range from the basal date of $10,545 \pm 115$ cal yr BP at 864 cm to the most recent date of 1895 ± 95 cal yr BP at 214 cm. All AMS radiocarbon dates and two of the tephras fall on a virtually straight line (Fig. 2). The oldest modeled ^{210}Pb date (Table 1c) is 85 yr at 35 cm.

Vegetation history

Four major vegetation zones (Table 2) were delineated based on broad changes in macrofossil assemblages (Fig. 3).

Early Holocene (EH) (ca. 10,500 to 8000 cal yr BP)

P. contorta dominates the EH macrofossil record. *A. lasiocarpa*, *P. menziesii*, and *P. monticola* are less important but have higher macrofossil accumulation rates than at any other time in the Holocene. Species composition varied through this zone with a pulse of *A. lasiocarpa* and simultaneous drop in *P. monticola* between

Table 2
Major vegetation types and mean fire return intervals.

Vegetation zone	Years before 1950 (cal yr BP)	Vegetation type	Mean fire return interval (years, SD)
Early Holocene (EH)	ca. 10,500 to 8000	Dry montane conifer forest	119 \pm 67 yr
Mid Holocene (MH)	ca. 8000 to 4500	Dry montane conifer forest (likely open stand structure)	267 \pm 156 yr
Late Holocene (LHa)	ca. 4500 to 2000	Moist montane conifer forest	175 \pm 106 yr
Late Holocene (LHb)	ca. 2000 to present	Moist montane conifer forest with increase in subalpine species	197 \pm 167 yr

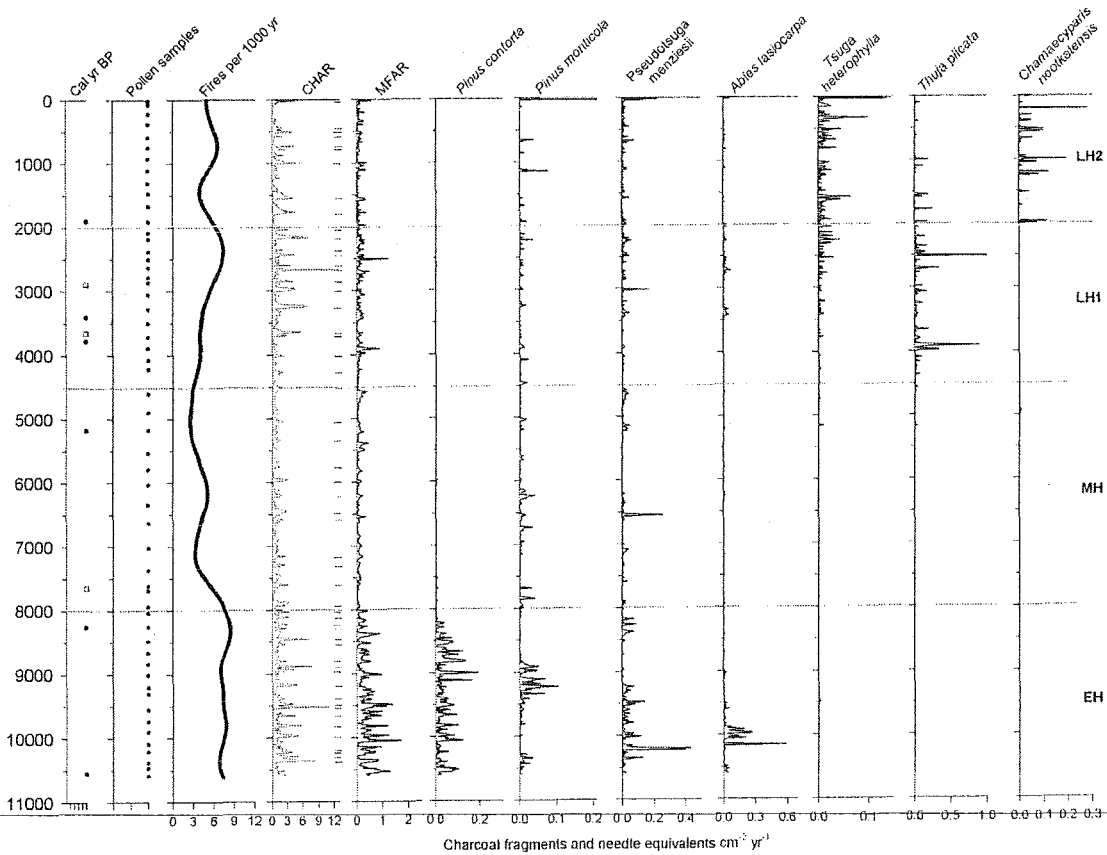


Figure 3. Macrofossil and charcoal records of the entire Holocene. Charcoal (CHAR), macrofossil (MFAR) and macrofossil accumulation rate by species. Fire frequency (number of fires per 1000 yr) is shown to the left of the CHAR diagram. Fire events are indicated by a horizontal line next to identified CHAR peaks.

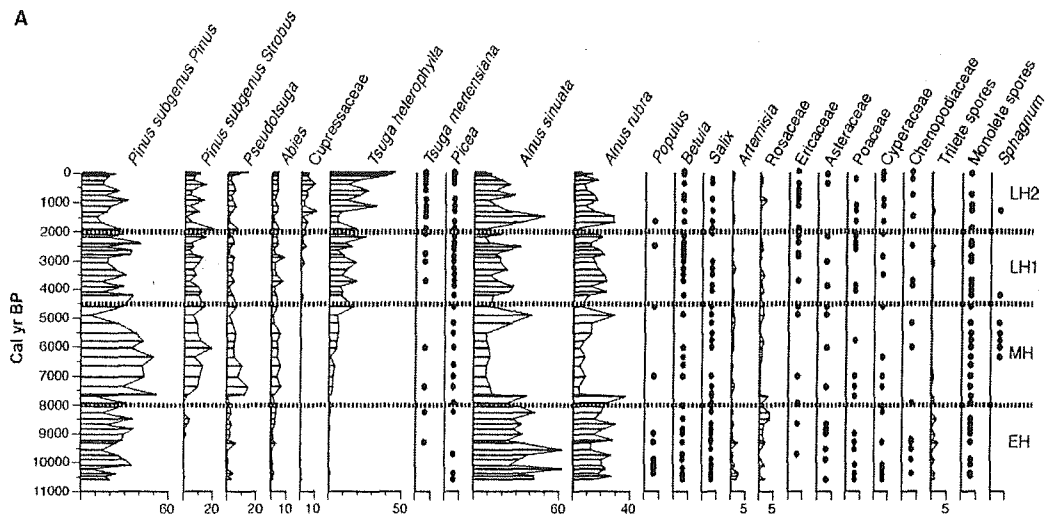


Figure 4. a: Pollen percentage diagram. Dots indicate the presence of species with trace pollen percentages. b: Pollen influx diagram of tree species.

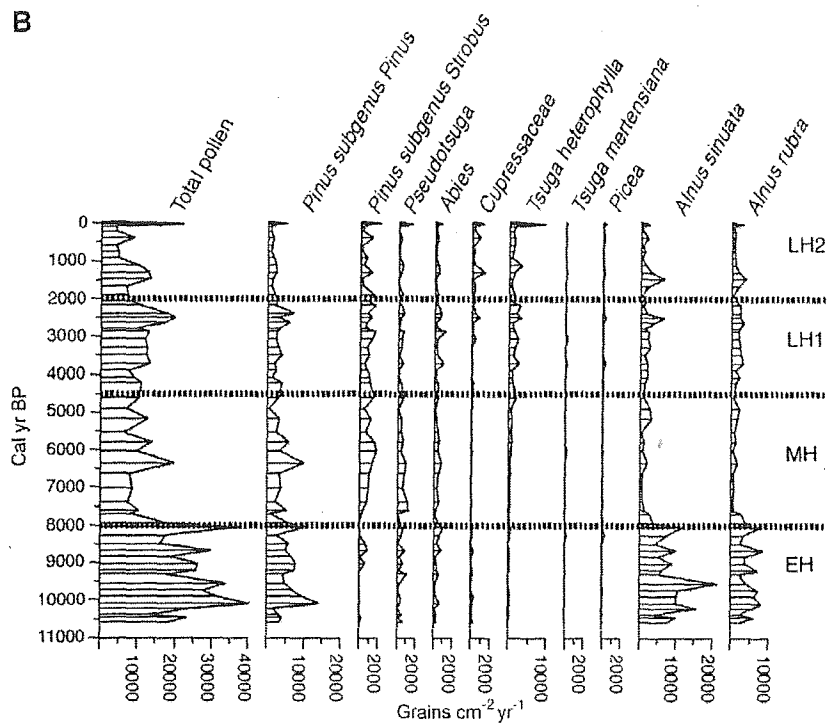


Figure 4 (continued).

ca. 10,200 to 9800 cal yr BP. *P. menziesii* was rare or absent from 9100 and 8500 BP. Macrofossils of *P. engelmannii*, *T. mertensiana* and *Abies* spp. other than *A. lasiocarpa* are present but uncommon.

Pollen percentages and influx rates of *Pinus* subgenus *Pinus* are high in this zone, corroborating the dominance of *P. contorta*. (figs. 4A, B). *Abies* and *Pseudotsuga*-type pollen percentages are low (5–10% respectively); *Abies* spp. and *P. menziesii* are low pollen producers and are typically underrepresented in pollen records (Pellatt et al., 1997). Although *P. monticola* was common in the macrofossil record, *Pinus* subgenus *Strobus* pollen percentages and influx rates are low throughout much of this zone. *Alnus* pollen percentages are high (30–60%) with a greater contribution from *A. sinuata* than *A. rubra*. Of the nonarborescent taxa, the relative abundance of *Rosaceae* and *Artemisia* pollen is highest in this zone.

Mid Holocene (MH) (ca. 8000 to 4500 cal yr BP)

The start of the MH ca. 8000 cal yr BP is marked by an abrupt decline in MFAR (fig. 3). *P. contorta* sharply declines around 8100 cal yr BP and is rare or absent throughout the remainder of the Holocene. Macrofossil accumulation rates of all species are substantially lower than in the EH, and *A. lasiocarpa*, *P. monticola*, and *P. menziesii* are the major tree species. There is a pronounced decrease in both CHAR and MFAR from ca. 7500 cal yr BP to ca. 4000 cal yr BP (Fig. 3). The core chronology indicates no major change in sedimentation rates that would explain this change in accumulation rates. The decrease is initially associated with the Mazama tephra layer, but CHAR and MFAR remain low for several millennia.

Although *Pinus* subgenus *Pinus* percentages remain high throughout this zone (Fig. 4A), lodgepole pine-type pollen influxes markedly decline ca. 8000 cal yr BP (Fig. 4B). Around 7700 cal yr BP, alder pollen percentages sharply decline from approximately 40% to 10–15%. Percentages of *Pseudotsuga*-type, *Abies*, and *Pinus* subgenus *Strobus* pollen are high relative to the EH throughout the MH. *T. heterophylla* gradually increases in the pollen record starting ca. 7700 cal yr BP but is absent from the macrofossil record until ca. 5200 cal yr BP.

Late Holocene a (LHa) (ca. 4500 to 2000 cal yr BP)

T. plicata and *T. heterophylla* macrofossils appear nearly synchronously at the start of the LH (Fig. 3). *T. plicata* appears to have rapidly established whereas *T. heterophylla* gradually increased in importance from 4500 to 3000 cal yr BP. Accumulation rates of *A. lasiocarpa* and *P. monticola* are similar to those of the MH, whereas *P. contorta* macrofossils are rare and *P. menziesii* accumulation rates are slightly higher than the MH.

T. heterophylla pollen percentages increase markedly ca. 4800 cal yr BP, supporting macrofossil evidence that populations established near the Panther Potholes around this time (Fig. 4A). *Cupressaceae* pollen gradually increases and corresponds with increasing abundances of *T. plicata* macrofossils. *Pinus* subgenus *Pinus* pollen generally decreases throughout this zone, corresponding with the near absence of *P. contorta* macrofossils.

Late Holocene b (LHb) (ca. 2000 cal yr BP to present)

Alaska yellow-cedar first appears in the macrofossil record ca. 2000 cal yr BP (Fig. 3) and generally increases to the present, coincident with a decline in *T. plicata* accumulation rates. A small cluster of Alaska yellow-cedar branch lets was identified ca. 5000 cal yr BP but probably represents a rare individual.

Cupressaceae and *T. heterophylla* pollen generally increase over the last 2000 yr while pine and alder pollen generally decrease (Figs. 4A, B). *T. heterophylla* markedly increases in both macrofossil and pollen records around 500 cal yr BP. Although macrofossil evidence of *T. mertensiana* is scarce, there is a slight increase of *T. mertensiana* pollen percentages throughout this zone. There is also an increase in the occurrence of *Ericaceae* pollen in the last 1000 yr.

Fire history

Fifty-nine fire events were detected throughout the sediment record (Fig. 3). Recent CHAR-based fire events correspond to fire dates inferred from nearby tree and stand-age distributions. The closest

stands to the Panther Potholes contain a 500–520 yr cohort of dominant *P. menziesii* trees. Approximately 0.25 km west of the Panther Potholes, stand ages range from 80–100 yr. Further west and at lower elevations, stand ages range from 160–170 yr. The 80–100 yr and 500–520 yr stand establishment dates corresponds to the ages of the two most recent charcoal peaks. The 160 to 170 yr establishment date has no corresponding peak in the lake sediment record.

Fire frequency varies throughout the Holocene record, with frequent fires in the EH and the highest fire frequency (9 fires per 1000 yr) ca. 8500 cal yr BP. Fire frequency markedly declines ca. 8000 cal yr BP and remains low throughout the MH. Fires again became more frequent in the LH with high fire frequency between 3000 and 2000 cal yr BP and 1000 and 500 cal yr BP. Calculated fire return intervals differ by Holocene zone (EH, MH, and LH, Table 2). The EH has the lowest mean fire return interval (MFRI) of 119 ± 67 yr, and the fire interval distribution significantly differs from the MH (MFRI 256 ± 67 yr; $p < 0.0001$) and LH (MFRI 185 ± 133 yr; $p = 0.0079$). Fire interval distributions are not significantly different between the MH and LH ($p = 0.1474$) or between LHa (MFRI 175 ± 106) and LHb (MFRI 197 ± 167) ($p = 0.9384$).

Macrofossil response to fire events

There is a clear macrofossil response to fire events delineated from CHAR peaks (Fig. 5). When all macrofossil fragments are included in the MFAR, there is a significant increase in MFAR anomalies at the time of the fire (Fig. 5). In the decades following the fire, MFAR are significantly below normal, with significant reductions seen at 24, 36, 60 and 84 yr following the fire. The correlation between individual fires and the canonical event was calculated over the interval from 0 to 84 yr following the fire event. Of the 57 CHAR peaks included in this analysis, 37 of the events have MFAR responses that are positively correlated with the canonical macrofossil response to fire, and there is no obvious clustering in time. SEA results are weaker when only

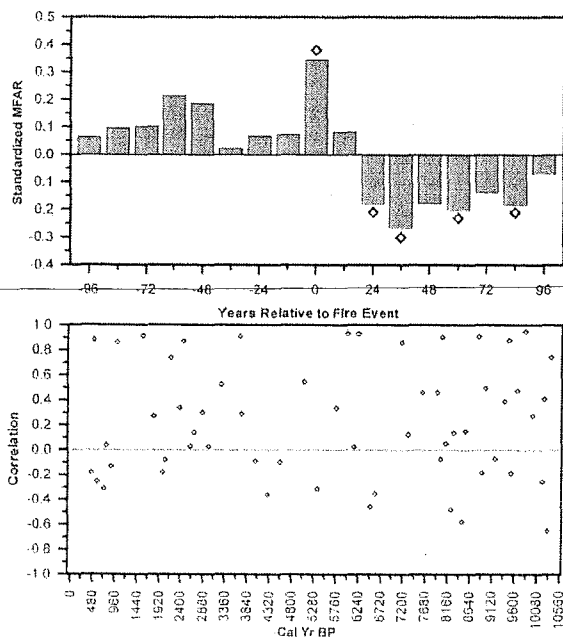


Figure 5. (Upper panel) Results of the superposed epoch analysis (SEA). Significant departures in MFAR are indicated by a diamond. (Lower panel) Covariance between individual fires and the "canonical" response identified by the significant relationships in the SEA. The covariance coefficients are scaled; positive values indicate fire events whose MFAR response resembles the canonical fire event. Negative values indicate individual fire events whose MFAR response is, on average, opposite to the canonical event.

needle equivalents are considered, with a single significant reduction in MFAR 24 yr following the fire. No significant findings were found in SEA analysis by individual species.

Discussion

Fire and vegetation dynamics

Early Holocene (EH) (ca. 10,500 to 8000 cal yr BP)

At the Panther Potholes, the EH is distinguished by a mixed conifer assemblage more similar to subalpine communities currently found in the eastern Cascade Range than to the modern forest assemblage at Panther Potholes. The relatively high percentages of *Artemisia* and Rosaceae pollen throughout this zone suggest forest canopies were open and supported understories of these taxa (Fig. 4A). *A. lasiocarpa* may have been localized, as it is currently, in the cold air drainage of the Panther Potholes watershed. Alternatively, *A. lasiocarpa* is known to be underrepresented in the pollen record (Heinrichs et al., 2002), and high macrofossil accumulation rates of this species may indicate the importance of this species during the EH, particularly ca. 10,200 to 9800 cal yr BP. High levels of alder pollen may have originated from avalanche tracks dominated by *A. sinuata*. Heine (1998) reports evidence of glacial advances from ca. 10,900 to 9950 cal yr BP at Mount Rainier, indicating greater snow accumulations during this period. Snow avalanches may have been more common in the EH and supported large patches of *A. sinuata* at high-elevation sites (Gavin et al., 2001).

Pollen from deciduous taxa, including *Alnus rubra*, *Populus*, and *Betula*, may have originated from riparian forests at lower elevations along Thunder Creek, which is today a large drainage with an extensive riparian forest approximately 3 km west of the Panther Potholes. Although *A. rubra*-type and *Betula* pollen are present in the uppermost sediments at Panther Potholes, the nearest current populations of *A. rubra* and *B. papyrifera* are located at lower elevations near Thunder Creek (S.J. Prichard, personal observation).

During the EH, summers were likely warmer than present, while winters were colder due to differences in seasonal insolation (Thompson et al., 1993). Warm, dry summers probably perpetuated a dry, montane forest assemblage dominated by *P. contorta*. Fires were the most frequent during the EH with a peak in fire frequency coinciding with a pine-dominated forest from 9200 to 8200 cal yr BP.

A warm period is distinct in most interpretations of EH vegetation in high- and low-elevation sites throughout western Washington and southern British Columbia. Most low-elevation EH records have a high relative abundance of *P. menziesii* associated with high accumulations of lake sediment charcoal in the EH. A common interpretation is that short-fire intervals perpetuated the dominance of early seral species,

including *P. menziesii* on the lowland landscape (Cwynar, 1987; Brown and Hebdada, 2002). Holocene reconstructions at subalpine sites in the Pacific Northwest demonstrate vegetation responses to the EH warm period, but patterns of vegetation change are more site-specific. At a subalpine site in southwestern interior British Columbia, Pellatt et al. (2000) describe the replacement of alpine tundra with a subalpine parkland of *A. lasiocarpa*, *P. engelmannii*, and whitebark pine (*Pinus albicaulis*) ca. 11,500 to 7800 cal yr BP. They also note high levels of *A. sinuata*-type pollen and maximum lake sediment charcoal concentrations during this period. Over a similar time period, Heinrichs et al. (2002) report the emergence of open pine parkland at a subalpine site in southern interior British Columbia. At a subalpine site in the northeastern Olympic Mountains, Gavin et al. (2001) report an expansion of subalpine forest into alpine tundra, high levels of alder pollen, and an increase in charcoal concentrations between ca. 13,000 and 8500 cal yr BP. In contrast, a subalpine site in the central Olympics remained dominated by alpine tundra, possibly due to high snow accumulations and shorter growing seasons (Gavin et al., 2001). At a subalpine site in southwestern British Columbia, Hallett et al. (2003)

report frequent fires between 11,000 and 8800 cal yr BP. Although vegetation composition differed among these sites, the timing of the EH warm period with more frequent fires is markedly similar to our record.

Mid Holocene (MH) (ca. 8000 to 4500 cal yr BP)

Around 8000 cal yr BP, the forest assemblage at the Panther Potholes underwent a major transition from a dry forest dominated by *P. contorta* to mixed conifer forest with a relatively small component of *P. contorta*. Although *T. heterophylla* does not appear in the macrofossil record until around 5000 cal yr BP, its gradual increase in the pollen record starting around 7000 cal yr BP suggests it became more important regionally, likely at lower elevations. The decrease in alder pollen suggests a decline in *A. sinuata* populations.

Prior to the MH, *P. contorta* was likely perpetuated by frequent, stand-replacing fire events, favoring *P. contorta* and in turn, characteristics of *P. contorta* (e.g., retention of fine, dead branches and downed woody fuel recruitment) contributed to frequent fire (Agee, 1993). Gradual changes in climate, accompanied by a shift in species composition towards short-needled conifers and increased fire return intervals may have altered this feedback and resulted in the decline of *P. contorta*. A reduction in MFAR during the MH might be attributed to a change in needle composition, from long, rigid *Pinus* needles, to short needles that are more susceptible to decomposition.

Gradual changes in regional climate may have triggered shifts in fire regimes and vegetation during the MH. In our record, vegetation composition and fire frequency dramatically change starting ca. 8000 cal yr BP with a rapid decline in *P. contorta*, a significant increase in fire return intervals, and overall decline in CHAR and MFAR. Pollen records in northern Washington and southern British Columbia document a major shift in vegetation around 7800 cal yr BP (Lepofsky et al., 2005). At low-elevation sites, pollen of late-successional species, including *T. plicata* and *T. heterophylla*, increased while *P. menziesii* and red alder-type pollen and lake sediment charcoal accumulation rates declined (Cwynar, 1987; Brown and Hebda, 2002). At a subalpine site in interior British Columbia, Pellatt et al. (2000) documented an increase in conifer abundance starting ca. 7800 cal yr BP, indicating more closed canopy conditions, which they attribute to warmer and moister climatic conditions than present. In the northeastern and central Olympic Mountains Gavin et al. (2001) described a gradual decrease in *Alnus* and an increase in conifer species including Cupressaceae (likely *C. nootkatensis*) ca. 8500 cal yr BP and an increase in pine, *T. heterophylla*, and *T. mertensiana* ca. 7800 cal yr BP. Climatic conditions east of the Cascades may have remained relatively warm and dry for a few millennia longer (Mack et al., 1979). In the Okanogan Valley east of the North Cascade Range, Mack et al. (1979) report that xeric *Artemisia* shrub-steppe was not replaced by modern forests dominated by *P. menziesii* until ca. 5700 cal yr BP.

Late Holocene a (LHa) (ca. 4500 to 2000 cal yr BP)

During the past 4500 yr the forest assemblage at the Panther Potholes assimilated its modern species composition, suggesting a change toward an even cooler, moister climate. *T. plicata* and *T. heterophylla* first appeared at the site ca. 5000 cal yr BP and gradually increased in relative abundance until the present. *T. plicata* appears to have become locally established nearly 1000 yr prior to *T. heterophylla*. Based on the increase in late-successional tree species and low representation of nonarborescent taxa, LH forests were likely denser than the MH. Macrofossil accumulation rates are also considerably higher in the LH than the MH.

Despite evidence of a moist forest assemblage, fire frequency increased in the LH. Fuel accumulations from denser, more productive forests could have contributed to increased incidence of high-severity, large fire events. Other possible explanations include an increase in local lightning ignitions related to the onset of unstable air masses associated with a cooler, moister regional climate (Rorig and

ferguson, 1999), an increase in anthropogenic ignitions during this time period (Lepofsky et al., 2005), and possibly an increase in the frequency of summer drought conditions, despite the overall shift to cooler, moister climatic conditions (Carcailler et al., 2001; Hallett et al., 2003).

Late Holocene b (LHb) (ca. 2000 cal yr BP to present)

The most recent arrival of tree species at the Panther Potholes was Alaska yellow-cedar at ca. 2000 cal yr BP. *T. mertensiana* has never been abundant at the Panther Potholes, but its increase in the pollen record in the last 2000 yr along with the increase in Alaska yellow-cedar macrofossils indicate that the last two millennia have been particularly cool and moist. Both species are typically found at high elevations, on moist sites, in the Pacific Northwest. The greater occurrence of Ericaceae pollen in the last millennium also suggests cooler, moister climatic conditions. The modern forest assemblage has the highest diversity of tree species of any time in the Holocene. The recent influx of species that compete well in cool, moist environments may be the result of neoglacial cooling over the last 2000 yr (Pellatt et al., 2000; Sugimura et al., 2008).

The onset of cooler, moister climatic conditions in the LH is commonly interpreted from pollen records of LH vegetation change in western Washington and southern British Columbia. At the Panther Potholes, vegetation appears to have gradually shifted, starting ca. 4500 cal yr BP with the arrival and establishment of *T. heterophylla*, *T. plicata* and finally Alaska yellow-cedar ca. 2000 cal yr BP. The ca. 4500 cal yr BP transition to modern vegetation is also documented in studies by Pellatt et al. (1998, 2000) at subalpine sites in southwestern British Columbia and by Mack et al. (1978) in the Okanogan Valley, Washington. Gavin et al. (2001) describe the Mid and late Holocene as a gradual transition to modern assemblages. Others note a shift to even more mesic, late-successional forest assemblages in the LH beginning ca. 3800 cal yr BP (Dunwiddie, 1986; Pellatt et al., 2000) and ca. 2000 cal yr BP (Sugimura et al., 2008).

Fire and vegetation change

Although regional climatic forcing appears to have been responsible for major changes in both vegetation composition and fire frequency at the Panther Potholes, there undoubtedly were interactions between vegetation and fire. Most CHAR peaks are associated with a canonical response in the macrofossil record (Fig. 5). This association corroborates our interpretation that delineated CHAR peaks represent local fire events (i.e., fire events occurring at or within 100 m of the lake basin). A peak in macrofossils associated with CHAR peaks suggests high needle influx following high-severity fires. The subsequent decrease in MFAR may reflect young, regenerating forests and their relatively small leaf area density.

It is difficult to determine whether changes in fire frequency are driven solely by climate or are also influenced by vegetation assemblages (Carcailler et al., 2001). In the case of the Panther Potholes, there may be evidence of both. For example, in the EH, warm, dry summers likely supported a frequent fire regime and dominance of *P. contorta* dominated forests. This vegetation assemblage regenerates readily following fire, and with increasing fire hazard over time, likely perpetuated a frequent fire regime. The concurrent decline in fire frequency and *P. contorta* at the start of the MH may have been triggered by a shift in regional climate to cooler, moister conditions, establishment of other conifer species, and a corresponding reduction in fire frequency.

The increase in fire frequency during the LH is somewhat unexpected in a moister forest assemblage. Increases in available fuels, short-term periods of summer drought, anthropogenic burning, and/or lightning ignitions are all plausible explanations for this increase. Agee et al. (1900) estimated fire return intervals from stand-age mapping and fire scars at Desolation Peak, approximately 25 km

north of our site and characterized the fire regime as mixed severity, with a range of fire sizes, severity classes, and return intervals. Even with fire return intervals of < 100 yr, mixed conifer forests with some component of late-successional species, including *T heterophylla* and *T plicata*, are supported under the current climate and are not excluded by the mixed severity fire regime. It is possible that as regional climate became cooler and moister, a more mesic assemblage formed even as fires became more frequent.

Conclusions

Temporal variation in vegetation and fire regimes in the North Cascade Range correspond to region-wide patterns of variation, and climate appears to be a key driver over broad time scales. Over the past ca. 10,500 yr, vegetation has varied considerably at the Panther Potholes, and these vegetation patterns correspond to millennial-scale variation of climate and vegetation in the Pacific Northwest. Fire and other disturbances were important agents of change at decadal and centennial time scales, and there were likely interactions between vegetation and fire.

Long-term records of vegetation at high elevations are site-specific, whereas at low elevations more broad generalizations about regional vegetation change are possible. In this study, we found evidence of neoglaciation cooling in the last 2000 yr, which, due to differences in species assemblages, may not be detectable at lower-elevation sites. The Pacific Northwest is dominated by topographically complex mountain systems. Any analysis of the effects of climatic change on vegetation, past or present, must acknowledge the variability of sites and growing conditions of mountain systems.

We found strong correspondence between fires detected by standard CHAR decomposition techniques and responses in the macrofossil record. Macrofossil evidence indicates that most peaks in the charcoal record represent local fire events. Fire-return intervals vary throughout the record and suggest that MFRIs alone would not adequately characterize the temporal dynamics of fire. To estimate the historic range of variability of fire in the North Cascade Range, records that extend beyond the scale of tree-ring reconstructions are necessary.

Paleoecological reconstructions demonstrate that vegetation has varied dynamically with changing climatic and disturbance regimes over the Holocene. Climate itself varies continuously, and it is important to consider longer time scales to appreciate the range of variability in ecosystem dynamics, including changing vegetation assemblages, forest structure and disturbance regimes. Future climatic change may cause ecosystems and fire regimes to shift outside of their historical range of variability (Hansen et al., 2001). Simulations from General Circulation Models for the Pacific Northwest predict warmer temperatures throughout the year as well as wetter winters over the next 50–100 yr (Mote et al., 2008), a combination that is not analogous to the broad-scale climatic regimes over the Holocene. A rapid climatic shift, coupled with stand-replacing fires and other disturbances, could result in new vegetation assemblages with no historic analogues.

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