Millennial-scale changes in local vegetation and fire regimes on Mount Constitution, Orcas Island, Washington, USA, using small hollow sediments

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Abstract: We used pollen and charcoal records from small hollows plus a network of surface samples to reconstruct stand-level vegetation and fire history at three sites on the Mount Constitution plateau of Orcas Island, Washington, USA. One record (beginning ca. 7100 calibrated years BP) is from a xeric site on the northern plateau, and two (beginning 3800 and 7650 years BP, respectively) are from mesic sites on the central and south-central plateau. Before 5300 years BP, vegetation and fire regimes at both the northern and south-central sites resembled those of current Mount Constitution forests. Around 5300 years BP, *Alnus* increased and *Pinus* decreased at the mesic south-central site, suggesting a change to moister and (or) cooler conditions, but *Pinus* remained dominant at or near the more xeric northern site. At both sites, charcoal deposition decreased, suggesting a decrease in fire frequency and (or) severity consistent with wetter conditions. After 2000 years BP, charcoal deposition increased at all three sites, and *Pinus* increased in the central and south-central sites, suggesting a return to drier conditions. Thus, stands on different sites in close proximity responded individually to the same climate change, depending on local site conditions and the ecology of the dominant trees.

Résumé : Nous avons utilisé des données d'archives sur le pollen et le charbon de bois provenant de petites cuvettes ainsi qu'un réseau d'échantillons de surface pour reconstituer la végétation et l'historique des feux à l'échelle du peuplement dans trois stations sur le plateau du mont Constitution à l'île d'Orcas dans l'État de Washington, aux États-Unis d'Amérique. Dans un cas, les données d'archives (débutant il y a approximativement 7 100 ans calibré) proviennent d'une station xérique sur le plateau septentrional et, dans les deux autres cas (débutant respectivement il y a 3 800 et 7 650 ans), elles proviennent de stations mésiques sur le plateau central et le plateau méridional central. Il y a plus de 5 300 ans, la végétation et le régime des feux dans les stations du plateau septentrional et du plateau méridional central ressemblaient à ceux des forêts actuelles du mont Constitution. Il y a environ 5 300 ans, *Alnus* a pris de l'expansion et *Pinus* a régressé dans la station mésique du plateau méridional central, ce qui indique que les conditions sont devenues plus humides ou plus froides mais *Pinus* a continué de dominer dans ou près de la station plus xérique du plateau septentrional. Dans les deux stations, les dépôts de charbon de bois ont diminué, indiquant qu'il y a eu une diminution de la fréquence ou de la sévérité des feux en lien avec les conditions plus humides. Depuis 2 000 ans, les dépôts de charbon de bois ont augmenté dans les trois stations et *Pinus* a pris de l'expansion dans les stations du plateau central et du plateau méridional central, indiquant un retour à des conditions plus sèches. Les peuplements dans différentes stations situées à proximité les unes des autres ont par conséquent réagi individuellement au même changement climatique selon les conditions locales des stations et l'écologie des essences dominantes.

[Traduit par la Rédaction]

Introduction

The vegetation of any region is a conglomerate of many individual stands. In areas of high topographic or edaphic diversity, some stands may differ substantially from the regional mean. For example, low-elevation areas of western Washington are mainly dominated by mesic *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) – *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) forests, but sites that are unusually dry because of local rain shadows, exposed topography, or coarse soils may have more xeric vegetation dominated by *Pinus contorta* Dougl. ex Loud (lodgepole pine). Divergent stands in this and other regions almost certainly have different ecological histories and are likely to have different responses to future change compared with typical forests of the region. Understanding the diversity of forest responses to historical climatic changes is useful for anticipating potential variability in future forests.

Unfortunately, the traditional tools of paleoecological research have not shed much light on the history and dynamics of individual stands, because neither tree rings nor lake sediments provide the needed combination of long time span and small spatial resolution. Small hollows, wet forest depressions 5–20 m in diameter, have received attention in recent decades, because they potentially combine the fine spatial scale of tree rings with the long time span of lake

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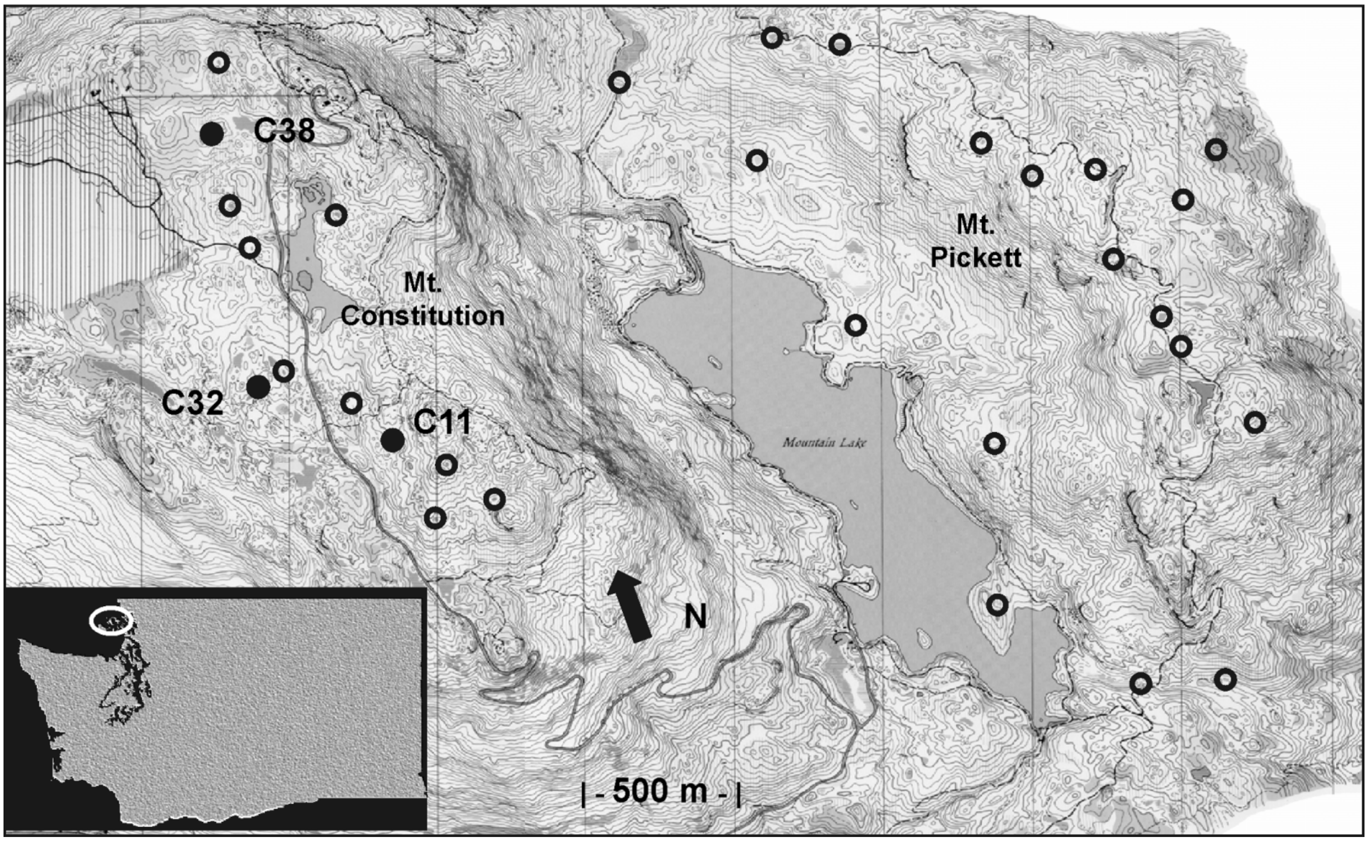
Fig. 1. Study sites (○) in Moran State Park, Orcas Island, Washington (48°30′N; 122°50′W). Surface samples were taken from all sites, and three sites (●) were also used for long-term reconstructions.



sediments (Bradshaw 1988; Davis et al. 1998; Parshall 2002). Source-area calibration studies indicate that pollen and charcoal records from these basins reflect stand-level forest composition (Sugita 1994; Calcote 1995, 1998) and fire events (Higuera et al. 2005), providing information on patch dynamics and site-specific controls (Davis et al. 1998; Greenwald and Brubaker 2001). Thus, small-hollow sediments have the potential to resolve stand-level histories of both vegetation and fire, providing unique, long-term (10^4 years) ecological records that can resolve disturbance and vegetation histories on individual sites.

This study utilized small-hollow sediments to reconstruct vegetation and fire histories over the past 7600 years in stands on the Mount Constitution plateau in the San Juan Islands of Washington, USA (Fig. 1). This area has several advantages for revealing site-level variations in forest responses to regional climate change. Although Puget Lowland lake records show little vegetation change over this period (Barnosky 1981; Tsukada and Sugita 1982; McLachlan and Brubaker 1995), the San Juan Islands have a substantially drier climate than the rest of the Puget Lowlands, resulting in distinctive vegetation that we hypothesized might be more responsive than regional forests to climate change. In addition, the Mount Constitution plateau of Orcas Island has local variation in soil characteristics that leads to further small-scale variation in vegetation and is richly dotted with small hollows that may record vegetation changes (Fig. 1). Finally, the forests on Mount Constitution and nearby Mount Pickett have never been logged, making them valuable as modern analogues for interpreting late-Holocene forest composition and disturbance regimes. Thus, the small hollows on Mount Constitution allowed us to study long-term variation in vegetation composition and fire regimes across a range of site conditions, showing how site factors influence vegetation and fire-regime responses to changing regional climate.

Study area

The study area is an 800 ha region of Moran State Park on Orcas Island, in northwestern Washington, USA (48°39′N, 122°50′W) (Fig. 1). Mean annual precipitation at Olga, Washington (approximately 6 km south of the study site; elevation 8 m), is 74 cm (71% falling between October and March), and mean January and July temperatures are 4 °C and 15 °C, respectively (Western Regional Climate Center 2007). Orcas Island is in the rain shadows of mountain ranges on the Olympic Peninsula and Vancouver Island and receives about 30% less precipitation than the Puget Sound Basin (Western Regional Climate Center 2007).

Moran State Park includes two upland areas with different elevations, soils, and vegetation types. Mount Constitution, the location of sediment cores described here, is a southeast-sloping plateau with a maximum elevation of 735 m above sea level (asl). Mount Pickett, used for vegetation and pollen assemblage comparisons, is slightly lower at 300–500 m asl. The soils of both Mount Constitution and Mount Pickett are classified as Pickett-Rock outcrop complex, a moderately productive soil consisting of well-drained to imperfectly drained upland soils underlain by dense, weakly to strongly cemented glacial till or bedrock (Schlots 1962). Mount Constitution soils are weathered from parent graywacke or arkose sandstone rock (Schlots 1962) and are typically thin and coarse, especially at the northern and southern ends of the plateau. Mount Pickett soils are generally deeper and richer and are weathered from igneous porphyrite, gabbrodiorite, quartz, diorite, and serpentine (Schlots 1962). Forest hollows 5–20 m in diameter are common throughout the study area, retain standing water from approximately October to July, and remain moist in August and September.

Moran State Park has never been logged, and current forests in both upland areas fall in the *Tsuga heterophylla* Zone as defined by Franklin and Dyrness (1988). The Mount Constitution plateau is mostly dominated by mixed stands of *Pseudotsuga menziesii* var. *menziesii*, *Tsuga heterophylla*, and *Pinus contorta* var. *murrayana*. Elsewhere in the Puget Lowlands, *Pinus contorta* is largely restricted to dry or boggy areas, but it is found throughout the forest on Mount Constitution and is dominant (although slow growing and stunted) on shallow soils at the northern and southern ends of the plateau. Mount Pickett has a more mesic species composition, dominated by *Pseudotsuga menziesii* and, to a lesser extent, *Tsuga heterophylla*, with occasional *Pinus contorta*, *Alnus rubra* Bong. (red alder), and *Thuja plicata* Donn. (western redcedar). *Pinus monticola* Dougl. (western white pine) and *Picea sitchensis* (Bong.) Carr. (Sitka spruce) are present but uncommon in both study areas. The current fire regime throughout Moran State Park is similar to that of mesic to dry *Tsuga heterophylla* Zone forests, with high- and mixed-severity fires occurring once every 100–200 years (Agee 1993; Higuera et al. 2005).

Methods

Field methods

To document the modern pollen rain on Mount Constitution and Mount Pickett, the top ~2 cm of sediment was collected from each of 30 small hollows, selected on the basis of basin morphology and distance from other hollows using a detailed topographic map (Cascade Orienteering Club, Seattle, Washington) (Fig. 1). Three sites on different parts of the Mount Constitution plateau were selected for fire and vegetation reconstruction (Fig. 1). Soil depth and local topography were similar at all sites. Sites C11 and C32 (both 660 m asl) are located in relatively mesic areas of the south-central and central plateau, respectively. The basal area of the modern C11 stand is 59% *Tsuga heterophylla*, 24% *Pinus contorta*, and 17% *Pseudotsuga menziesii*, whereas site C32 is codominated by *Pseudotsuga menziesii* and *Tsuga heterophylla* (52% and 48%, respectively) (Higuera 2002, appendix C). Site C38 (685 m asl) is at the northern end of the plateau and is also codominated by *Pseudotsuga menziesii* and *Tsuga heterophylla* (46% each), with 7% *Pinus contorta* and <1% *Pinus monticola* (Higuera 2002, appendix C). However, site C38 is close to and downwind from slow-growing *Pinus contorta* stands that occupy large areas of rocky outcrops and scoured ridgelines (690–735 m asl, about 500 m to the northwest) close to the summit of Mount Constitution.

Sediment cores were collected from the three hollows in August and September 2000, using a 7.62 cm diameter, 1 m long modified Gavin sampler (Gavin et al. 2003). The cores were 61.5 cm long at site C11, 28 cm long at site C32, and 71 cm long at C38. Cores were extruded and described in the field, wrapped in polyvinylidene chloride film (Saran Wrap™) and aluminum foil, transported in polyvinyl chloride (PVC) tubes, and stored at the University of Washington at 3–4 °C.

Laboratory methods

Sediment cores were sectioned contiguously at 0.25 cm increments, and samples were kept in cold storage. The resolution (no. of samples per depth interval) of charcoal and pollen analyses varied among cores because of time constraints for analysis, with the highest resolution towards the top of each core. In the C11 core, charcoal content was analyzed for every 0.25 cm section from the top to the base of the core. Pollen was analyzed for every section to a depth of 32.25 cm, then for every fourth section (every 1 cm) to the base of the core. The C32 core was analyzed for charcoal in every sample to a depth of 20 cm, then every 0.5 cm to the base of the core. Pollen was analyzed every 1 cm to a depth of 20 cm, then every 2 cm to a depth of 28 cm. The C38 core was analyzed for charcoal every 0.5 cm throughout the entire core, with 0.25 cm resolution around peaks in the top 20 cm (1–2.5 cm and 7–15.5 cm). Pollen in the C38 core was analyzed every 2 cm except between 7 and 16 cm in depth, which was analyzed every 1 cm. Loss on ignition (LOI), the percentage of mass lost after heating approximately 1 cm^3 of dried sediment at 500 °C for 4 hours, was analyzed approximately every centimeter for all cores.

For charcoal analysis, 3 cm^3 subsamples were disaggregated in a 10% sodium metaphosphate solution for 72 h and then gently washed with water through 500 and 150 µm sieves. To aid in charcoal identification, samples were bleached in ~8% hydrogen peroxide for 8 h (Rhodes 1998) and then rewashed through the sieves to remove the hydrogen peroxide. Charcoal pieces were counted with a stereomicroscope at 10–40× magnification. The 150–500 µm and >500 µm size fractions were counted separately but combined for analysis, because the pooled size fraction (everything >150 µm) yields the most accurate information on past fire occurrence in our study area (Higuera et al. 2005).

For pollen analyses, 1 cm^3 samples were prepared using standard digestion methods (Faegri and Iversen 1989), and grains were examined at 400 and 1000×. Tablets containing *Lycopodium clavatum* L. spores were added to the subsamples to allow estimation of pollen concentrations and pollen accumulation rates (Stockmarr 1971). In most cases, modern samples were counted to at least 300 pollen grains (mean 388). Pollen counts for fossil samples were somewhat lower (mean 263) but were deemed sufficient to resolve long-term temporal trends of the major taxa. Cupressaceae pollen in both modern and fossil assemblages is assumed to be *Thuja plicata*, because no other Cupressaceae are common in the region. Similarly, all *Pseudotsuga*-type and *Alnus* pollen is assumed to be *Pseudotsuga menziesii* and *Alnus rubra*, respectively. All pollen data are presented as percentages or ratios relative to the sum of all terrestrial pollen types except sedge (Cyperaceae) and grass (Poaceae), which potentially occupy hollow surfaces. Spore percentages are relative to

Table 1. Calibrated ^{14}C and tephra dates from each small hollow site, with median probability dates and 95% confidence intervals.

Core identification No.	CAMS No.	Sample depth (cm)	^{14}C age (years BP)	Calibrated age (years BP)	Minimum age (years BP)	Maximum age (years BP)	Sample material
C11	85901	18.25	780	701	663	769	Pollen
	83110	29.75	2110	2077	2000	2273	Pollen
	85902	36.75	3330	3558	3451	3681	Pollen
	84915	43.5	4705	5417	5326	5574	Pollen
		61.5	6800	7650	7570	7730	Tephra (Mazama)
C32	82474	22.25	2630	2755	2504	2855	Pollen
C38	82475	28.75	2405	2445	2352	2701	Pollen
	85903	47.0	4020	4486	4394	4771	Pollen
	82476	53.0	4500	5162	4990	5294	Pollen
	82009	70.25	4920	5667*	5345	5917	Charcoal

Note: The tephra layer was analyzed at Washington State University, Pullman, Wash. CAMS, Center for Accelerator Mass Spectrometry.
*The 70.25 cm sample in C38 was not used in fitting age–depth curves.

the same pollen sum. Pollen accumulation rates (PARs, grains·cm^{-2}·year^{-1}) were calculated from pollen concentrations (grains·cm^{-3}) and sediment accumulation rates established by age–depth curves (described below).

Accelerator mass spectrometry (AMS) ^{14}C radiocarbon dates, tephra-layer identification, and ^{210}Pb techniques provide dating control for the three sediment cores (Table 1). At sites C11 and C32, AMS samples were taken close to prominent changes in *Pinus* pollen percentages. One radiocarbon date, at the base of C38, was obtained from large (>0.5 cm) charcoal pieces. The other eight dates were obtained from purified pollen extracts, prepared according to protocols used at the University of Alaska, Fairbanks, Alaska (Fujikawa 2002). Sediment samples were washed in KOH and soaked in heavy liquid (sodium polytungstate) to separate pollen grains from clastic material. Microscopic charcoal fragments were removed with prolonged centrifuging and subsequent pipetting. Each sample was scanned under a light microscope at 400× to ensure that pollen grains comprised most of the dated material. At C32, the lowest depth with sufficient pollen to date was 22.25 cm. Radiocarbon dates (^{14}C BP) were converted to calibrated years BP (cal BP) using the median of the probability distribution in CALIB, version 4.3 (Stuiver and Reimer 1993). The tephra layer at the base of core C11 was identified as Mazama ash (6800 ^{14}C years BP; 7650 cal BP) by microprobe and chemical analysis (Dr. Nick Foit, Washington State University, Pullman, Wash.). Upper core sediments (<200 years) were aged by ^{210}Pb techniques as reported in Higuera et al. (2005).

Sediment age assignments were based on ^{210}Pb, tephra, and AMS C^{14} chronologies. In each core, a polynomial curve was fit to the ^{210}Pb data to describe the marked increase in sedimentation rates near hollow surfaces (Higuera et al. 2005). The basal date of the polynomial curve was used as the uppermost date of age–depth curve for lower sediments, which was based on individual considerations for each core. Linear interpolation was chosen for C11 and C32, because this approach preserved the AMS ages of pollen changes without causing unrealistic changes in sedimentation rates. The lowest AMS date for C38 was not used, because it implies a sharp increase in sedimentation rates that is not supported by other sediment features (such as a decrease in pollen concentration or LOI). Linear interpolation and linear regression produced indistinguishable curves for the remaining C38 dates, and linear regression was chosen for ease of estimating ages of lowest sediments.

Interpretation of charcoal records

Charcoal concentrations were converted into charcoal accumulation rates (CHARs, pieces·cm^{-2}·year^{-1}) based on sediment accumulation rates established by age–depth curves. No attempt was made to identify individual fires, because the low sediment accumulation rates prevented separation of all charcoal peaks and because low- and mixed-severity fires are inconsistently recorded in small-hollow sediments of this area (Higuera et al. 2005).

Interpretation of pollen records

The interpretation of stand-scale forest histories was aided by comparisons between fossil and modern pollen assemblages using discriminant analysis (DA) (StatSoft Inc. 1984–2003; Liu and Lam 1985). DA of the seven major arboreal pollen taxa in modern and fossil assemblages (*Alnus*, *Thuja*, *Pseudotsuga*, *Abies*, *Tsuga heterophylla*, *Pinus*, and *Picea*) was first applied to test whether Mount Constitution and Mount Pickett sites could be differentiated based on their pollen assemblages (Liu and Lam 1985; Oswald et al. 2003). A cross-validation test assessed the classification accuracy, and DA loadings determined which taxa were most important for distinguishing between Mount Constitution and Mount Pickett pollen assemblages (Liu and Lam 1985). Second, the "posterior probability" (SPSS Inc. 1999) determined the probability that a fossil sample belonged to modern Mount Constitution or Mount Pickett pollen assemblages, providing a basis for interpreting the similarity between past and present forest composition (Liu and Lam 1985; Oswald et al. 2003).

Results

Modern pollen samples

Modern pollen assemblages on Mount Constitution differ from those on Mount Pickett (Fig. 2). In general, Mount Constitution hollows exhibit high *Pinus* (52% ± 16%; mean ± SD) and low *Pseudotsuga* (4% ± 2%) and *Alnus* percentages (22% ± 9%). Mount Pickett assemblages have lower *Pinus* (18% ± 15%) and higher *Pseudotsuga* and *Al-*

Fig. 2. Box plots of pollen percentages from modern surface samples on Mount Constitution and Mount Pickett, showing the median (horizontal lines; not visible for *Pseudotsuga* and *Thuja* at Mount Constitution), 25th to 75th percentiles (shaded boxes), and 10th to 90th percentiles (error bars). *Pseud*, *Pseudotsuga*. Mount Constitution samples contain more *Pinus*, and Mount Pickett samples contain more *Alnus* and *Pseudotsuga*.

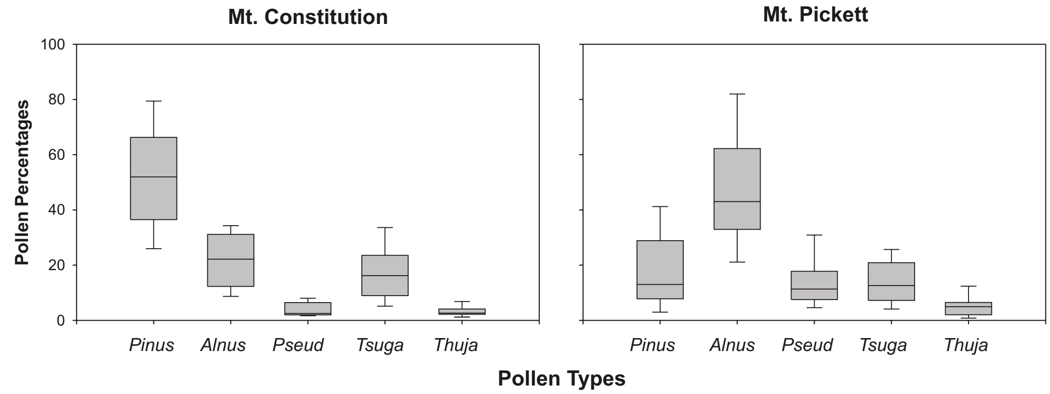
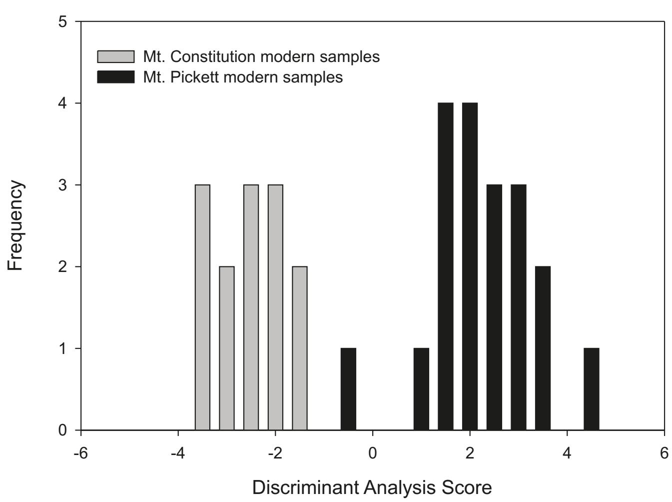


Table 2. Classification and cross-validation results for discriminant analysis of the modern pollen samples from Mount Constitution and Mount Pickett.

	Predicted surface	
Actual surface	Mount Constitution	Mount Pickett
Classification		
Mount Constitution	13 (100)	0 (0)
Mount Pickett	1 (5)	18 (95)
Cross-validation		
Mount Constitution	13 (100)	0 (0)
Mount Pickett	1 (5)	18 (95)

Note: Percentages of samples classified as that land surface are given in parentheses. Cross-validation results indicate that the analysis is robust.

Fig. 3. Histogram of discriminant scores for modern pollen samples from Mount Constitution and Mount Pickett small hollows.



nus percentages (12% ± 7% and 50% ± 20%, respectively). DA classifies 95% of the hollows correctly (Table 2) with only one Mount Pickett site (P11) misclassified as a Mount Constitution site due to a high *Pinus* percentage (66%). The cross-validation test also classifies 95% of the hollows correctly (Table 2). The DA scores of Mount Pickett and Mount Constitution sites are >1 and less than –1.5, respectively

Table 3. Discriminant analysis loadings for each taxon.

Pollen type	Discriminant analysis loading
Alnus	0.345
Pseudotsuga	0.324
Thuja	0.072
Abies	0.026
Picea	0.015
Tsuga heterophylla	–0.090
Pinus	–0.457

Note: Taxa with a DA loading greater than –0.44 are associated with Mount Pickett, and taxa with a loading less than –0.44 are associated with Mount Constitution.

(Fig. 3). Taxa associated with Mount Pickett (DA loadings greater than –0.44) include *Alnus*, *Pseudotsuga*, *Thuja*, *Abies*, and *Picea* (Table 3). *Pinus* is the only pollen type strongly associated with Mount Constitution (DA loading less than –0.44). *Tsuga heterophylla* (DA loading –0.09) lacks strong associations because pollen of this species is well represented in both areas.

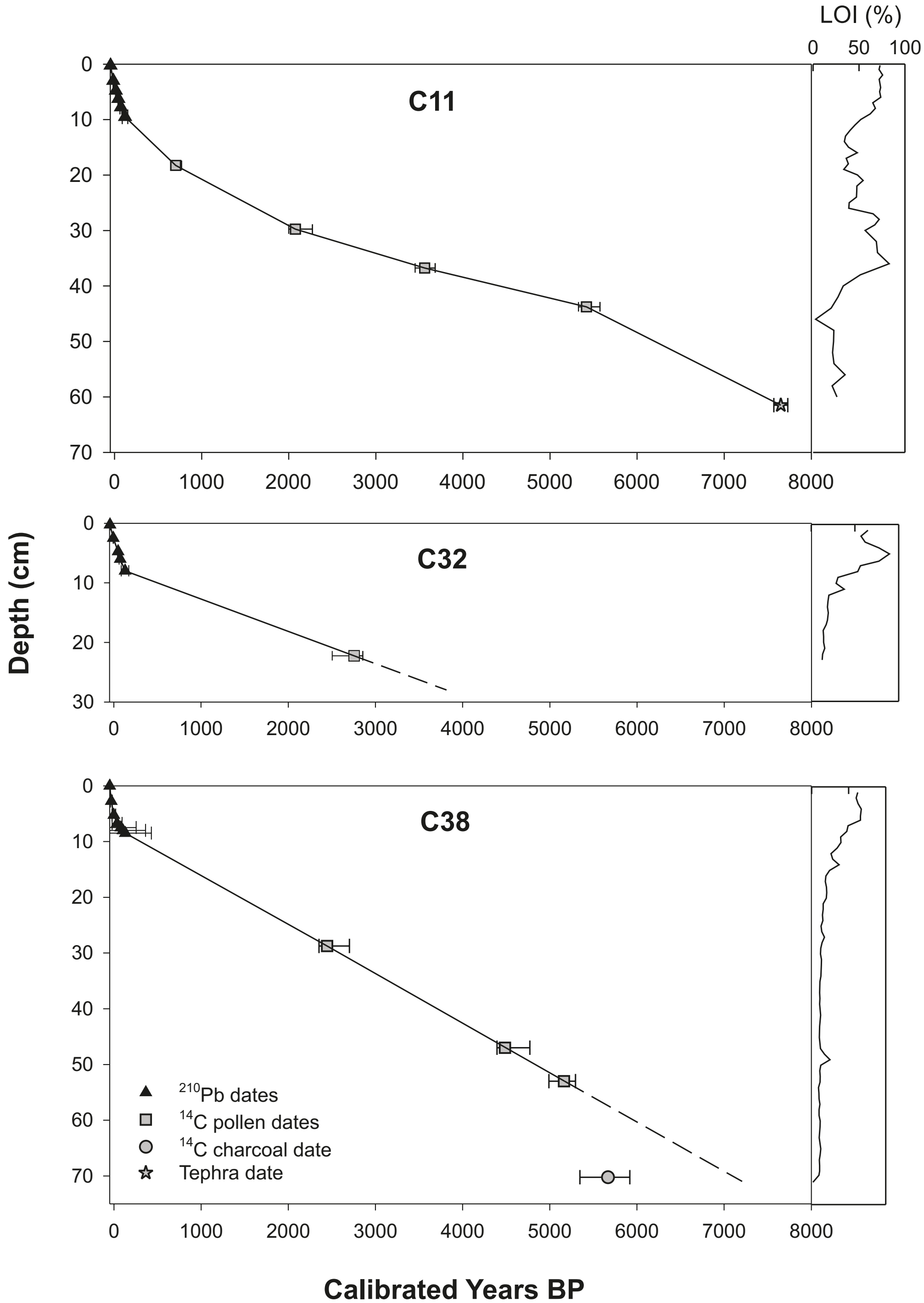
Sediment chronologies

Basal core ages and sedimentation rates varied among sites (Fig. 4; Tables 1 and 4). Core C11 is the oldest (7650 cal BP at 61.5 cm) (Table 1), followed by C38 (extrapolated to ca. 7200 cal BP at 70.25 cm) and C32 (ca. 2800 cal BP at 22.25 cm: extrapolated to ca. 3800 cal BP at 28 cm). Sedimentation rates were high (0.02–0.14 cm·year^{-1}) for the upper approximately 9 cm of each core (Table 4; Higuera 2002; P.E. Higuera, unpublished data) and then decreased greatly at lower sediment depths. The fastest sedimentation occurred at C11 between 43.5 and 61.5 cm (ca. 5400–7650 cal BP; 0.013 cm·year^{-1}) (Table 4) and the slowest at C11 between 36.75–43.25 cm (ca. 5300–3600 cal BP; 0.004 cm·year^{-1}).

Pollen and charcoal records

Three informal vegetation and fire zones are identified in the sediment records based on visual inspection of trends in pollen and charcoal data (Figs. 5–7) and DA scores (Fig. 8): zone I (7650–5300 years BP); zone II (5300–2000 years BP), and zone III (2000 years BP to present). The C11 and

Fig. 4. Age–depth curves established from ^{210}Pb, ^{14}C, and tephra dates. Error bars are 95% CIs. Broken lines are the extrapolated portions of the curves.



C32 records are described together, because both are from mesic sites and show similar patterns in pollen and charcoal. The C38 record, which is close to the very xeric northern end of the plateau, differs from C11 and C32 and is described separately.

Cores C11 and C32 *(Figs. 5 and 6)*

In zone I (7650–5300 years BP; represented in C11), pollen or spore percentages for *Pinus* (mean 59%), *Alnus* (mean 22%), Cyperaceae (mean 53%), and *Pteridium* (mean 11%) are relatively high. *Tsuga heterophylla* percentages are low (mean 3%), and *Pseudotsuga* percentages fluctuate widely (0%–22%). Most samples are classified by DA as Mount Constitution (i.e., similar to modern samples from the same area), although several are classified as Mount Pickett (Fig. 8). The samples classified as Mount Pickett generally have low *Pinus* percentages (<50%) and relatively high *Alnus* (>20%) and *Pseudotsuga* (>10%) percentages. The main difference between zone I and modern Mount Constitution assemblages is that *Pteridium* and Cyperaceae are

Table 4. Sediment accumulation rates and sampling rates for each small hollow core.

Core identification No.	Core depth (cm)	Sedimentation accumulation rate (cm·year^{-1})	Sampling rate (years·0.25 cm^{-1})
C11	0.0–9.5	0.100*	5*
	9.75–18.0	0.017	15
	18.25–29.5	0.008	30
	29.75–36.5	0.005	55
	36.75–43.25	0.004	64
	43.50–61.5	0.013	19
C32	0.0–8.0	0.045*	6*
	8.25–22.25–(28.0)	0.006	45
C38	0.0–8.0	0.047*	5*
	8.25–53.0–(70.25)	0.009	28

Note: Sedimentation rates below 22.25 cm in C32 and below 53 cm in C38 are extrapolated.
*Rates for the topmost sediments are from Higuera (2002) and are presented as mean values for the given depth ranges.

much higher (means 11% and 53%, respectively, in zone I vs. 1% each in modern samples), whereas *Tsuga heterophylla* percentages are lower (mean 3% in zone I vs. 18% in modern samples). Zone I CHARs at C11 are consistently high (mean 1.3 pieces·cm^{-2}·year^{-1}) with multiple sharp peaks.

In zone II (5300–2000 years BP), the C11 and C32 assemblages are characterized by low *Pinus* (means 35% and 32%, respectively) and high *Alnus* percentages (means 45% and 63%, respectively). *Pseudotsuga* percentages are 2%–13% in C11 and 0%–4% in C32. *Tsuga heterophylla* percentages increase from 2%–5% to 8%–12% during zone II in C11 but are very low throughout in C32 (mean 0.9%). *Pteridium* percentages are very high (mean 56%) in C32 and moderately high (mean 10%) in C11. *Pinus* PARs decreased from about 3700 to 1900 grains·cm^{-2}·year^{-1}, whereas *Alnus* PARs increased from about 1200 to 2200 grains·cm^{-2}·year^{-1} across the zone I–II transition (Fig. 9). Nearly all pollen samples at both sites are classified by DA as modern Mount Pickett, although they have higher *Pinus* percentages than modern Mount Pickett samples (35% and 32% vs. 19%) and lower *Tsuga heterophylla* percentages (5% and 1% vs. 13%). *Pteridium* percentages are also much higher (11% and 56% vs. 1%).

Both cores show lower CHAR in zone II (mean 0.63 pieces·cm^{-2}·year^{-1} for C11 and 0.20 pieces·cm^{-2}·year^{-1} for C32), without the multiple sharp CHAR peaks seen in zone I at C11. The conspicuous exception is a single broad CHAR peak in C11 that spans >2 cm (>500 years). This peak is much broader than those of known fires in small-hollow records of the study area (Higuera et al. 2005), suggesting that it may be an artifact. It may have resulted from a single large piece of charcoal that fell into the hollow and then slowly disintegrated or perhaps from a fire that burned over the hollow itself and charred the surface organic material.

Zone III (2000 BP to present) samples are characterized by a return to high *Pinus* pollen percentages (mean 69% in C11 and 79% in C32) and lower percentages of *Alnus* (14% and 8% in C11 and C32, respectively) and *Pteridium* (5% in C11 and 8% in C32). *Pinus* and *Alnus* PARs return to zone III values. Zone III pollen assemblages are classified as similar to modern Mount Constitution (Fig. 8). As in zone I, the zone III samples have somewhat lower *Tsuga heterophylla* (mean 8% in C11 and 5% in C32) and higher *Pteridium* percentages than modern Mount Constitution samples. After the last charcoal peak in C32, *Tsuga heterophylla* pollen increases sharply (to 42% at the surface), *Pseudotsuga* pollen increases slightly (to 8%), and *Pinus* pollen decreases sharply (to 23%). This recent change is not seen in C11.

Zone III CHARs are higher on average than in zone II (means 0.70 and 0.98 pieces·cm^{-2}·year^{-1} in C11 and C32, respectively) with several distinct peaks in both cores. At C11, CHARs begin to increase ca. 2500 years BP, whereas they remain low until ca. 700 years BP at C32.

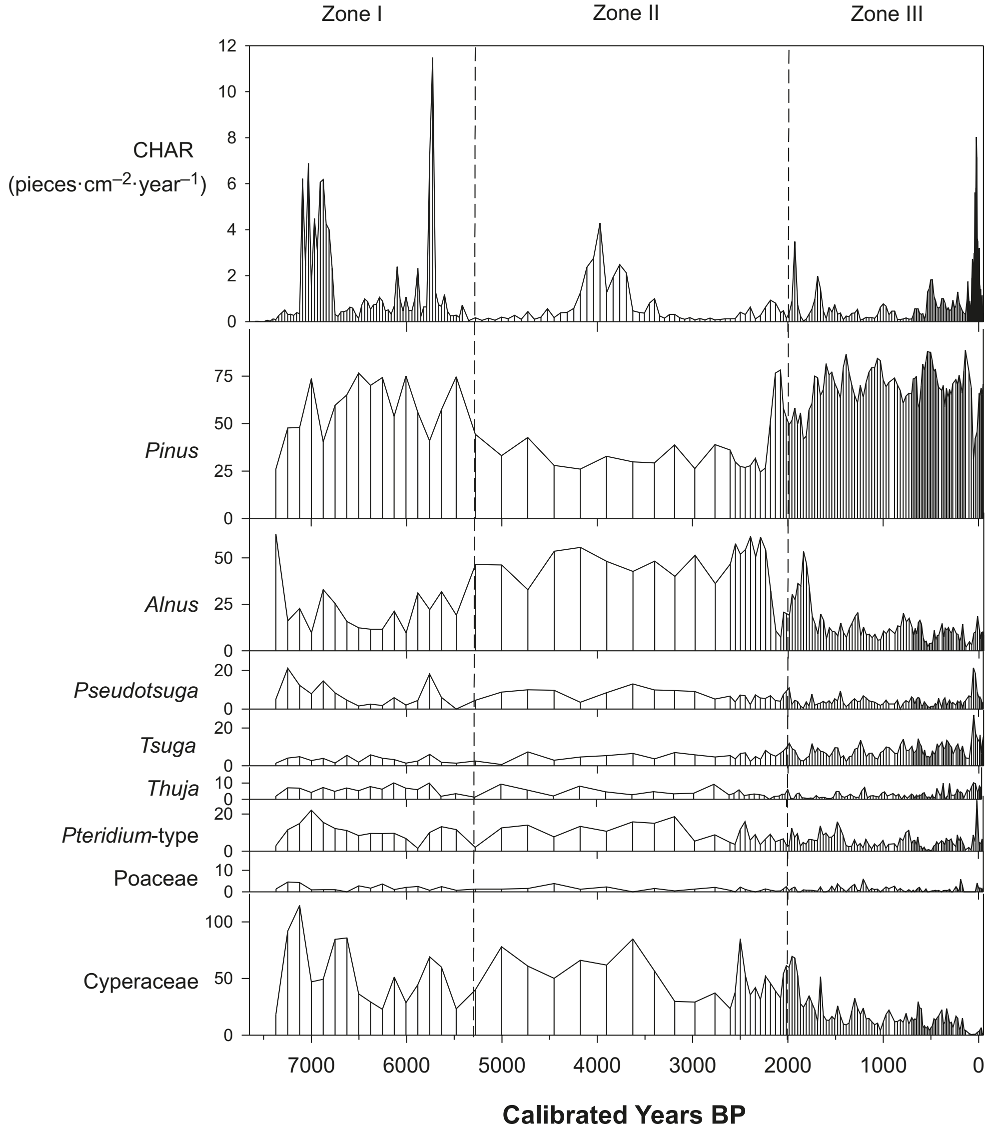
Core C38 *(Fig. 7)*

Zone I at C38 is characterized by very high *Pinus* and Cyperaceae percentages (means 72% and 38%, respectively) and relatively low percentages of *Pseudotsuga*, *Tsuga heterophylla*, and *Alnus* (means 3.0%, 4.3%, 18%, respectively). Most samples are classified as modern Mount Constitution (Fig. 8), although they have higher *Pinus*, Cyperaceae, and *Pteridium* percentages and lower *Tsuga heterophylla* percentages than modern Mount Constitution assemblages. CHARs are moderately high (mean 0.74 pieces·cm^{-2}·year^{-1}), with multiple sharp peaks.

In zone II, the C38 pollen record remains relatively constant. *Pinus* percentages remain high (mean 67%). *Alnus* (19%), *Pseudotsuga* (5%), and *Tsuga heterophylla* (6.5%) increase but only slightly. *Pinus* and *Alnus* PARs are essentially the same as in zone I. Nearly all samples are classified by DA as similar to modern Mount Constitution (Fig. 8); however, as before, they have higher *Pinus* and lower *Tsuga heterophylla* percentages than modern samples. Although the pollen record remains relatively constant, the charcoal record changes sharply: CHARs are consistently low (mean 0.23 pieces·cm^{-2}·year^{-1}) with few peaks.

Zone III shows high *Pinus* percentages (73%), and low *Alnus* and *Pteridium* percentages (12% and 5.5%, respectively). *Tsuga heterophylla* and *Alnus* pollen percentages increase slightly after the last fire. Fossil samples are classified as similar to modern Mount Constitution, although *Pinus* percentages remain higher and *Alnus* and *Tsuga heterophylla* percentages lower. CHARs are higher (mean 1.3 pieces·cm^{-2}·year^{-1}) than in zone II, with several distinct peaks.

Fig. 5. Pollen diagrams and charcoal accumulation rate (CHAR) for site C11. All pollen data are shown as percentages or ratios relative to the sum of all terrestrial pollen types except sedge (Cyperaceae) and grass (Poaceae). Spore percentages are shown as a ratio of spores to the same pollen sum. See the text for a description of the charcoal and pollen zones.



Discussion

Vegetation and fire history of Mount Constitution

Zone I (7650–5300 years BP)

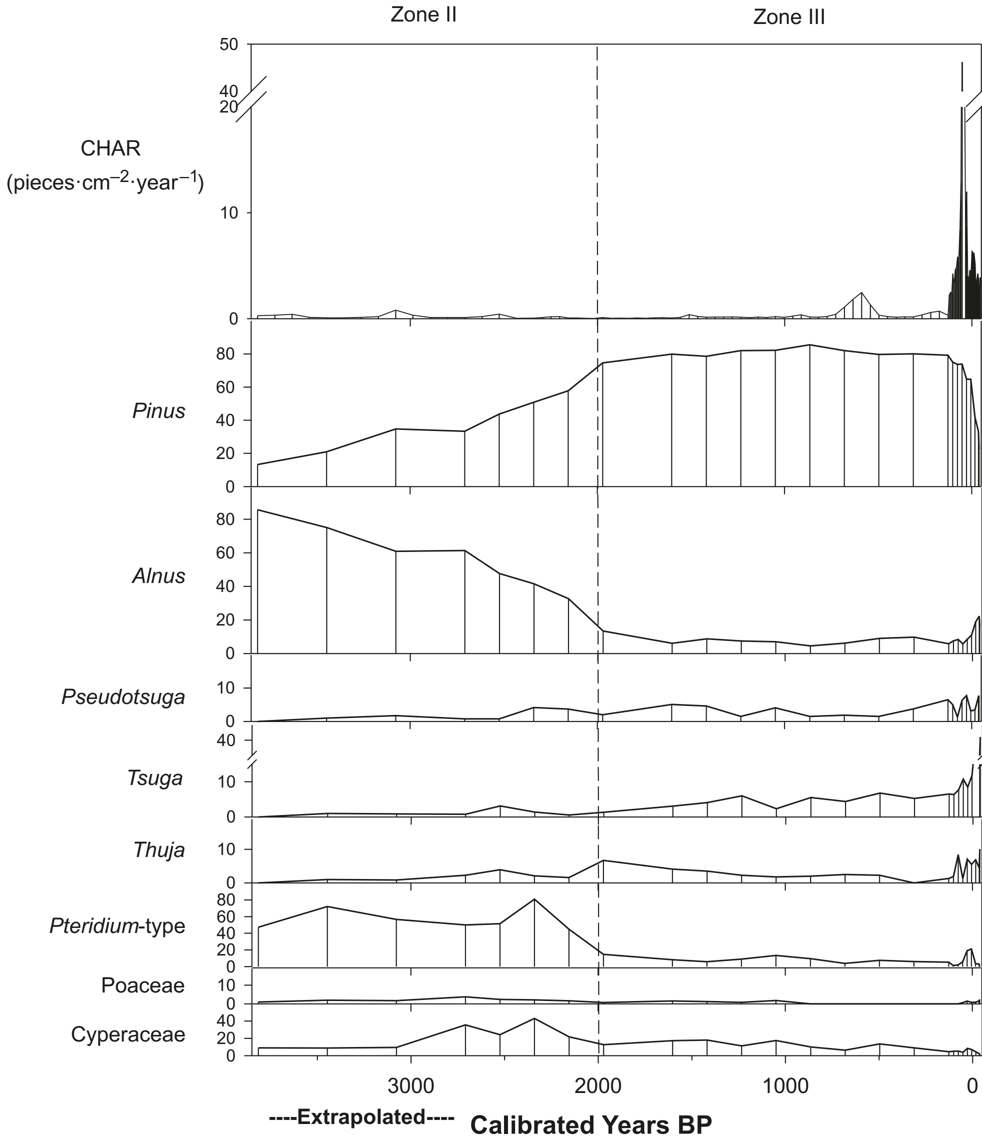
The similarity of C11 and C38 pollen assemblages to those from modern Mount Constitution forests (Fig. 8) suggests that Zone I forests across the Mount Constitution plateau resembled xeric forest types within the modern *Tsuga heterophylla* Zone. High CHARs indicate that fire was common, and the occasional sharp peaks suggest that at least some of the fires were severe. Thus, the fire regime was probably also similar to that of dry *Tsuga heterophylla* Zone forests, with episodic and variable burns creating a landscape mosaic of diverse stand ages and structures (Means 1982; Morrison and Swanson 1990; Agee 1993).

Pteridium and especially Cyperaceae were much more common in zone I than in modern Mount Constitution forests, and *Tsuga heterophylla* was substantially less common. In modern Mount Constitution forests, Cyperaceae species grow mainly in wet areas (including small hollows), so the lower modern Cyperaceae percentages may mean that the hollows have filled in since zone I, reducing canopy openings. *Pteridium* currently grows both in hollows and on the forest floor but produces abundant spores only in the sun (Conway 1957). Thus, the high representation of *Pteridium* in zone I is also consistent with larger hollow size. Alternatively, the zone I forest floor may have been a better habitat for *Pteridium* and Cyperaceae because *Tsuga* was less common than at present. Because *Tsuga heterophylla* is the most shade tolerant and casts the deepest shade of any tree species on Mount Constitution (Minore 1979; Barnes et al. 1998), its rarity in zone I may have allowed more light to reach the forest floor, favoring *Pteridium* growth and spore production.

Zone II (5300–2000 years BP)

Beginning about 5300 BP, the vegetation near C11 began

Fig. 6. Pollen diagrams and charcoal accumulation rate (CHAR) for site C32. All pollen data are shown as percentages or ratios relative to the sum of all terrestrial pollen types except sedge (Cyperaceae) and grass (Poaceae). Spore percentages are shown as a ratio of spores to the same pollen sum. See the text for a description of the charcoal and pollen zones. Dates before ca. 2800 BP are extrapolated.

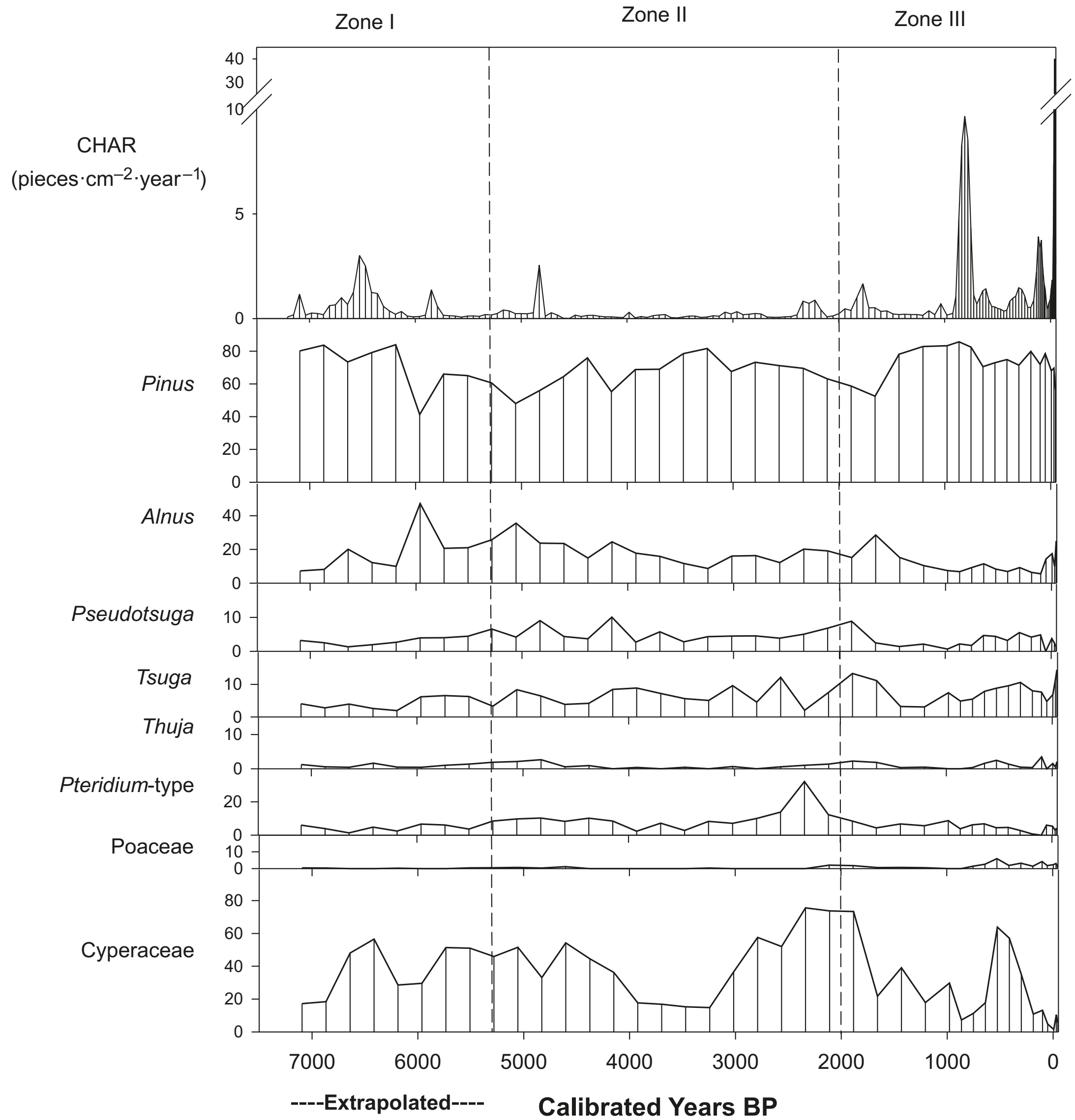


to resemble modern Mount Pickett forests, probably dominated by *Pseudotsuga menziesii* and *Tsuga heterophylla*, with only a minor component of *Pinus contorta*. Although the C32 record only goes back to ca. 3800 years BP, its forest history probably followed a similar trajectory. Despite higher *Alnus* pollen percentages and PARs in zone II, *Alnus rubra* was probably still uncommon, as it is in present-day Mount Pickett forests. *Alnus* is an extremely prolific pollen producer and is typically overrepresented in pollen samples. For example, *Alnus* currently contributes about 50% of the arboreal pollen to the sampled Mount Pickett hollows but accounts for only 3% of the basal area of trees within 100 m of these hollows (L.B. Brubaker, unpublished data).

Although the species composition of forests near C11 and C32 was apparently similar to modern Mount Pickett forests during this period, the fire regime apparently was not. Modern Mount Pickett forests are characterized by fires every 100–200 years, which result in high CHARs (Higuera et al. 2005), contrasting sharply with the low CHARs during zone II at C11 and C32. These differences suggest that fire frequency and (or) intensity were much lower in zone II than in the modern Mount Pickett (and Mount Constitution) forests, despite the similarity in vegetation.

In contrast to C11 and C32, stand composition near C38 shows little evidence of change during zone II. Although CHAR decreased sharply, indicating a fire regime different from present, *Pinus* continued to dominate the pollen rain. There are two possible explanations for this pattern. The first is the most obvious: fire frequency and (or) intensity decreased, but *Pinus* remained important in the local vicinity of the hollow, even though it decreased elsewhere on the plateau. However, because site conditions (e.g., soil depth and topography) in the immediate vicinity of hollow C38 are similar to those near the other two hollows, there is no clear reason why *Pinus* should not have also decreased near C38. An alternative possibility, which we consider more likely, is that

Fig. 7. Pollen diagrams and charcoal accumulation rate (CHAR) for site C38. All pollen data are shown as percentages or ratios relative to the sum of all terrestrial pollen types except sedge (Cyperaceae) and grass (Poaceae). Spore percentages are shown as a ratio of spores to the same pollen sum. See the text for a description of the charcoal and pollen zones. Dates before ca. 5200 BP are extrapolated.



Pinus remained dominant on rocky outcrops and scoured ridgelines ~500 m to the north of C38 and that these populations strongly influenced the C38 hollow pollen record. *Pinus contorta* var. *murrayana* is favored by poor soils and can maintain itself on xeric sites even in the absence of fire (Lotan and Critchfield 1990). Because *Pinus* pollen is prolifically produced and well dispersed (Prentice 1985; Dunwiddie 1987; Hebda and Allen 1993), *Pinus contorta* on these nearby areas would be well represented in past C38 pollen assemblages, as it is today. Thus, the lack of an apparent change in the pollen rain at C38 may mean that poor sites nearby continued to be dominated by *Pinus* and that these populations dominated the pollen rain.

Zone III (2000 years BP to present)

Beginning at 2000 years BP, increased *Pinus* percentages and PARs at C11 and C32 indicate that nearby forests regained a significant component of *Pinus*. The pollen changes at these sites, plus the unchanging assemblages at C38, suggest that forests across the Mount Constitution plateau again became similar to modern Mount Constitution forests, except that *Tsuga* remained substantially less common than today. Increased CHARs suggest that fire frequency, severity, and (or) extent increased at all sites, leading to the modern regime of one fire every 100–200 years. *Tsuga* apparently achieved its current abundance in Mount Constitution forests only within the last 100–200 years.

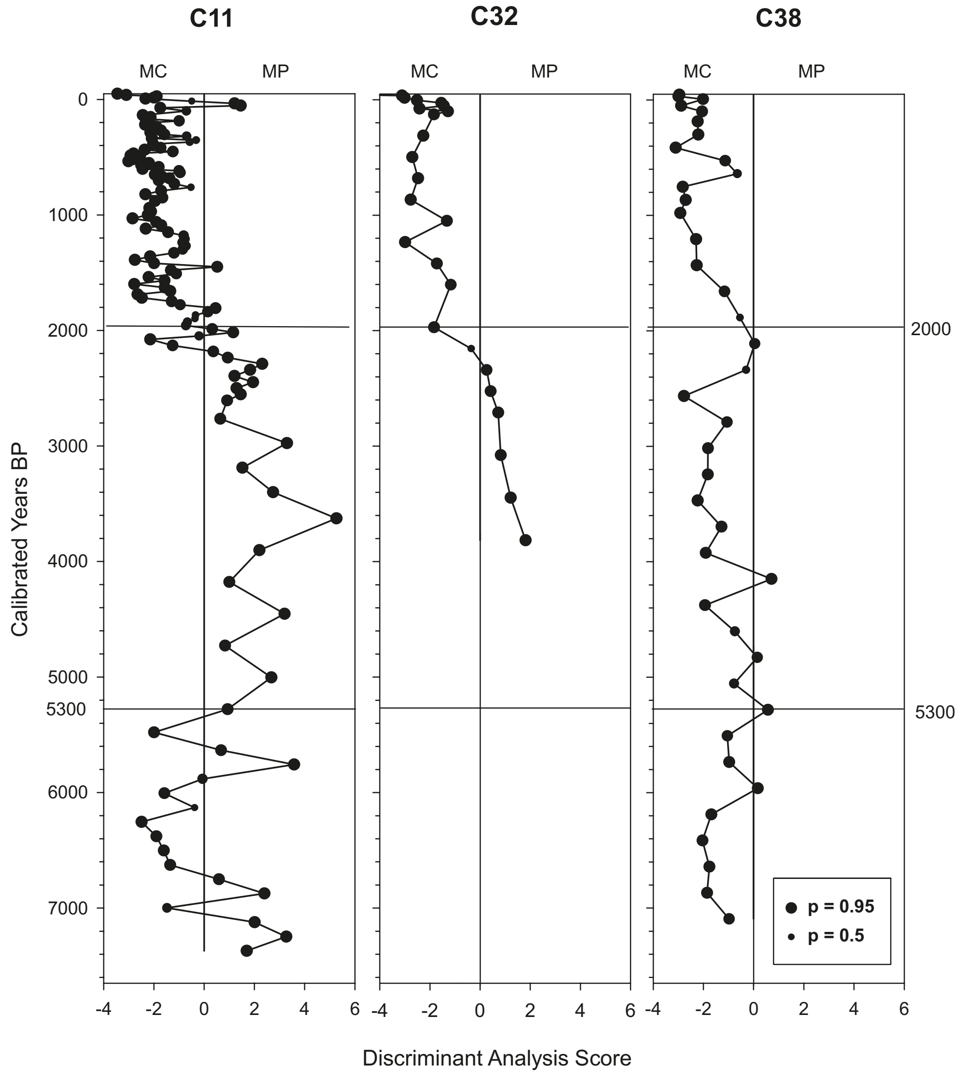
Controls of long-term forest dynamics of individual stands on Mount Constitution

The data presented here suggest several broad questions about controls of long-term forest dynamics on Mount Constitution:

What happened 5300 years ago?

The vegetation and fire regimes on Mount Constitution

Fig. 8. Discriminant analysis scores of fossil samples. The size of the solid circles indicates the probability of membership in either Mount Constitution (MC) or Mount Pickett (MP) modern assemblages; 82% of the samples have a ≥95% probability of membership in one of the two assemblages.



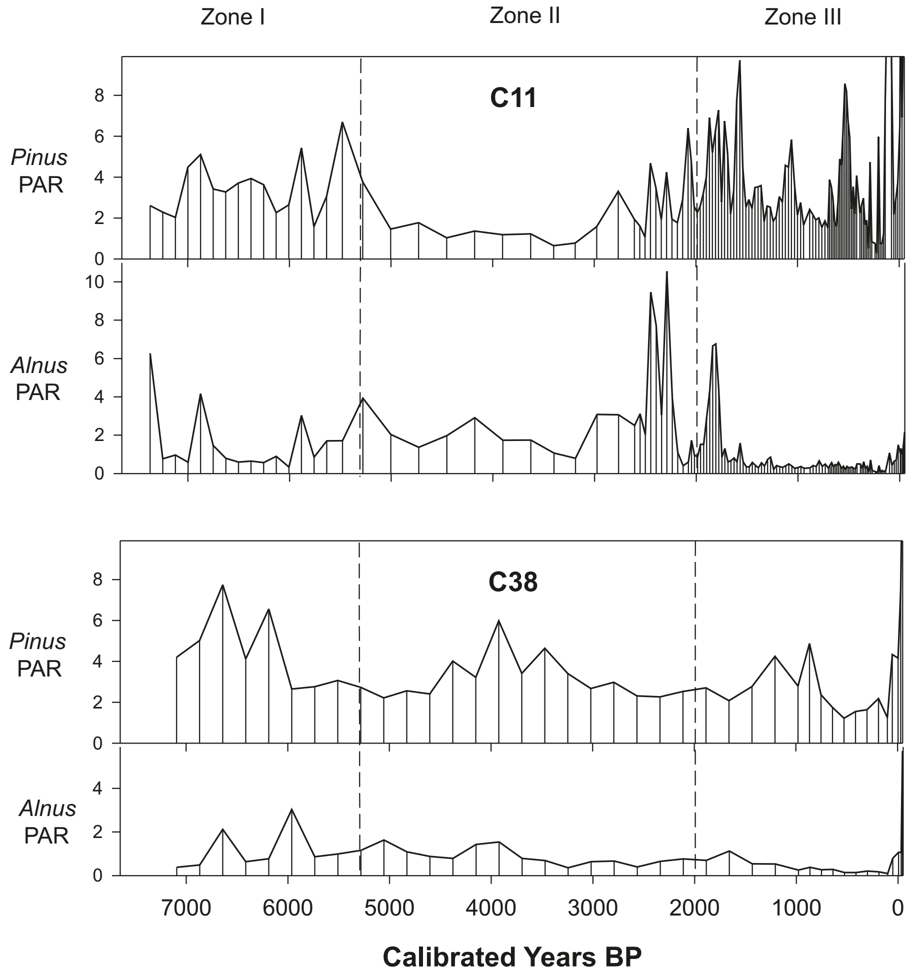
5300–7000 years ago were similar to those at present, suggesting that the climate was also similar. However, something clearly changed about 5300 years BP, because *Pinus* decreased and *Alnus* and *Pseudotsuga* increased on the central and south-central plateau, and charcoal production decreased across the entire plateau.

The most likely explanation for the prominence of mesic species at central and south-central sites and the low charcoal production across the whole plateau is that the climate became wetter or possibly cooler, allowing mesic species to displace xeric species on intermediate sites and decreasing fire frequency and (or) severity everywhere. Changes in vegetation and (or) disturbance regime have been noted in other Pacific Northwest records around 5000 BP, though the changes elsewhere were not as distinct as those seen in the Mount Constitution plateau small hollows. Cupressaceae pollen or macrofossils increased around 5000–6000 years BP at several sites on southern Vancouver Island and the adjacent mainland mountains, sometimes accompanied by increases in other mesic species (Brown and Hebda 2002*a*, 2003; Hallett et al. 2003; Prichard 2003). Charcoal deposition simultaneously decreased at some sites (Brown and Hebda 2002*a*, 2003) but remained constant at others (Brown and Hebda 2003; Prichard 2003) and increased at one (Hallett et al. 2003). Although the overall pattern is not totally consistent, the occurrence of synchronous vegetation and fire-regime changes throughout the Pacific Northwest suggests a change in regional climate, and the majority of the evidence suggests that conditions became wetter or cooler.

What happened 2000 years ago?

The increase in charcoal and decrease in *Alnus* pollen on Mount Constitution around 2000 years BP suggest a return to drier and (or) warmer conditions. As with the previous change, shifts in vegetation or disturbance regime have been noted at several other Pacific Northwest sites around 2000 years BP. Charcoal deposition or fire frequency increased at most sites (Brown and Hebda 2002*a*, 2003; Hallett et al. 2003), and Cupressaceae decreased at one (Brown and Hebda 2002*a*). Temperature reconstructions from fossil

Fig. 9. Pollen accumulation rate (PAR; 1000 grains·cm^{-2}·year^{-1}) for *Pinus* and *Alnus* at sites C11 and C38.



midge communities in southern British Columbia lakes suggest that lake water also became warmer at this time (Palmer et al. 2002).

Brown and Hebda (2002*b*) suggested that the increase in fire around 2000 years BP in southern Vancouver Island was due to increased ignitions by Native Americans rather than to a change in climate. Burning by Native Americans could have influenced the recent fire regime on Mount Constitution, because Native Americans routinely burned open meadows, such as those on the south side of Mount Constitution, to stimulate regrowth of *Camassia* and *Pteridium* (White 1980; Peterson and Hammer 2001), and even an occasional escaped fire could have significantly influenced the fire regime. However, because pollen deposition also changed in the Mount Constitution hollows around 2000 years BP, lake temperatures increased at the same time, and charcoal accumulation at some sites decreased rather than increasing (Brown and Hebda 2003), it seems unlikely that anthropogenic ignitions were the only cause of the observed vegetation and charcoal changes. Although Native burning cannot be ruled out as a local contributing factor in the Mount Constitution forests, climate change was probably the main driver of the changes around 2000 years BP.

Why did vegetation respond differently at different sites?

Our small-hollow records combined with records from other sites in the coastal Pacific Northwest show that vegetation on different sites responded differently to the apparently wetter and (or) cooler climatic conditions between 5300 and 2000 years BP. For example, forest composition apparently remained stable on the scoured ridgetops at the north end of the Mount Constitution plateau, but *Pinus* decreased and *Alnus rubra* increased markedly in the central and south-central plateau. Lake records on southern Vancouver Island suggest similar but less dramatic vegetation changes (Brown and Hebda 2002*a*, 2003), whereas Puget Lowland lake records show no change over this period (Barnosky 1981; Tsukada and Sugita 1982; McLachlan and Brubaker 1995).

The variability in these pollen records probably reflects the combined effects of differences in local environmental conditions, ecological tolerances of the species present, and pollen source areas of sites. Soils on the scoured ridgetops near C38 may be so thin and nutrient-poor that only xeric-adapted *Pinus contorta* can grow there, even under conditions more mesic than the present. However, the less extreme sites of the central Mount Constitution plateau and Vancouver Island support a mix of species, some of which are mesic-adapted (*Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Alnus rubra*) and some of which are xeric-adapted (*Pinus contorta*), so even small climatic changes may tip the balance toward one group over the other. The changes may be more sharply defined in the Mount Constitution records than on Vancouver Island because we sampled small hollows instead of lakes, thus reducing the noise resulting from sampling multiple vegetation types (Sugita 1993, 1994; Parshall and Calcote 2001). In contrast, Puget Lowland forests probably did not change, because they are dominated by a suite of long-lived mesic species (*Pseudotsuga*, *Tsuga heterophylla*, and *Thuja plicata*) that are so well adapted to the regional climate that minor climate changes do not affect species composition.

Changes in the vegetation and fire regime of individual forest stands are thus determined by both regional scale (climate) and site-specific (soil and topography) factors, as well as the ecological characteristics of the dominant species. The fine spatial scale of small-hollow records provides a sharp focus on these changes that may be very useful for understanding the spatial complexity of vegetation and fire changes over a broader climatic region. Such information about landscape influences on vegetation responses to regional climate is essential to planning for potential future climatic scenarios, particularly in complex terrain of western North America (McKenzie et al. 2003; Diaz and Millar 2004; Bunn et al. 2005).

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