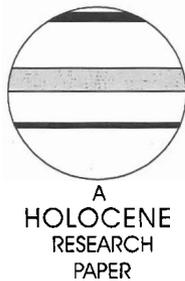


Holocene vegetation and fire history of the Coast Range, western Oregon, USA

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Abstract: Pollen and high-resolution charcoal records from three lakes were examined to reconstruct the vegetation and fire history of the Oregon Coast Range for the last 9000 years. The sites are located along a north-to-south effective precipitation gradient and changes in vegetation and fire activity provided information on the nature of this gradient in the past. The relation of vegetation to climate change was examined at millennial timescales and the relation between fire and climate was examined on centennial timescales by comparing fire-interval distribution and fire synchrony between sites. The pollen data indicate more fire-adapted vegetation during the early-Holocene period (c. 9000 to 6700 cal. yr BP), followed by a shift to forests with more fire-sensitive taxa in the mid Holocene (c. 6700 cal. yr BP to 2700 cal. yr BP) and modern forest assemblages developing over the last c. 2700 years. Comparisons of fire-interval distributions showed that the time between fires was similar between two of the three combinations of sites, suggesting that the moisture gradient has played an important role in determining long-term fire frequency. However, century-scale synchrony of fire occurrence between the two sites with the largest difference in effective precipitation suggests that centennial-scale shifts in climate may have overcome the environmental differences between these locations. Asynchrony in fire occurrence between the sites with more similar effective precipitation implies that local conditions may have played an important role in determining fire synchrony between sites with similar long-term climate histories.

Key words: Fire history, vegetation history, climate history, temperate rain forest, charcoal analysis, Oregon Coast Range, Holocene.

Introduction

Variations in Holocene climate have been a major cause of vegetation change in the Pacific Northwest (PNW) (Whitlock, 1992; Hebda and Whitlock, 1997). Fire is an important disturbance in PNW forests and acts as a catalyst in shaping vegetation patterns on all timescales (Agee, 1993). Thus, forests can respond not only to climate change directly, but also indirectly to climate-induced changes in disturbance regimes (Cwynar, 1987). While strong linkages exist between vegetation, fire and climate on short timescales (Westerling *et al.*, 2006), our understanding of these linkages in stand-replacement fire regimes is limited by the length of dendrochronologically based fire-history records. To gain an understanding of these types of regimes on longer timescales requires examination of plant remains preserved in lake sediments in the region.

Recent research has focused on two aspects of fire–climate–vegetation relations: the impact that century-scale climate variations have had on fire frequencies and the relative importance of local conditions such as fuel load and topography, and regional climate in determining

how synchronous fire regimes are within forests. Periods of dry environmental conditions in the western USA, as measured by lake levels and changes in vegetation, have been linked to increased fire frequencies over the last several thousand years (Hallet *et al.*, 2003a, b; Briles *et al.*, 2005; Power *et al.*, 2006). An examination of the spatial distribution of fires between and within watersheds has been used to assess the importance of local controls over fire (Heyerdahl *et al.*, 2001; Gavin *et al.*, 2003a), and the comparison of several local fire histories over time has provided evidence that climate forcing may not result in a uniform response among sites (Gavin *et al.*, 2006). We examined these aspects of fire–climate–vegetation relations in the seasonal rain forests of the Oregon Coast Range.

The seasonal rain forest ecoregion occupies a 60 to 200 km strip along the Pacific slope from Vancouver Island to northern California and encompasses the Oregon Coast Range and the western slopes of the more expansive Cascade Range to the east (Alaback and Pojar, 1997). A north-to-south precipitation gradient results from seasonal shifts in location and intensity of the northeastern Pacific subtropical high-pressure system (STH) and polar jet stream. In summer, the STH expands and the jet stream retreats northward, which results in increased large-scale subsidence and the suppression of precipitation

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in Oregon. In winter, the STH weakens and shifts southward, and the westerlies increase in strength and deliver the bulk of annual precipitation through storm systems that originate in the Gulf of Alaska.

The fire regime in the Oregon Coast Range has been characterized as consisting of widespread, infrequent, stand-replacing fires (Impara, 1997; Teensma *et al.*, 1991). For example, the Nestucca Fire of AD 1848 burned *c.* 120 000 ha, and the Tillamook fire of AD 1933 burned *c.* 106 000 ha of forests in the Oregon Coast Range (Munger, 1944). Recent fires have been associated with high fuel loads and low fuel moistures brought on by dry, hot summer conditions and strong, easterly winds produced by interior high-pressure cells centred east of the Cascade Range (Gedalof *et al.*, 2005; Trouet *et al.*, 2006). Logging activities have provided an ignition source since the early AD 1900s (Agee, 1993), but lightning is sufficiently frequent to also be an important ignition source (Roring and Ferguson, 1999).

In most seasonal rain forest areas, high wood-decay rates and fire severity have limited fire reconstructions based on tree-ring and stand-age records to the last *c.* 500 years (Agee, 1993). This short time span does not reveal the long-term importance of fire in the seasonal rain forest, nor the role of climate and vegetation (fuels) in controlling fire activity. In order to understand fire-climate-vegetation linkages on longer timescales, the palaeoecological records at three sites were examined. Our specific objectives were: (1) to examine the relationship between fire and forest communities in different environmental settings to better understand the ecological response to large-scale changes in the climate system; and (2) to determine if sites in different environmental settings showed similar and synchronous fire activity in the past, suggestive of a widespread response to short-term variations in climate, such as drought.

Study sites

Little Lake (44°09'56''N, 123°34'14''W, 210 m elevation), is a landslide-dammed lake in the central Coast Range of Oregon, 45 km east of the Pacific Ocean (Figure 1). It has a surface area of 1.5 ha, maximum water depth of 5 m, simple bathymetry, and perennial inflowing and outflowing streams that drain an area of 600 ha. Forests in the watershed are composed of *Pseudotsuga menziesii* (Douglas-fir) and *Tsuga heterophylla* (western hemlock), with some *Thuja plicata* (western red cedar) and *Pinus monticola* (western white pine). *Alnus rubra* (red alder) is common in recently disturbed and riparian areas, *Picea sitchensis* (Sitka spruce) is restricted to moist northern slopes and *Quercus garryana* (Oregon white oak) grows in nearby valleys and in the Willamette Valley to the east. Understorey species include *Polystichum munitum* (sword fern), *Sambucus racemosa* (elderberry), *Vaccinium L. spp.* (huckleberry), *Dryopteris spinulosa* (wood-fern) in moist locations and *Pteridium aquilinum* (bracken) a heliophytic plant that is abundant on disturbed sites. The Little Lake watershed experiences January and July mean monthly temperatures averaging 4.9°C and 18.0°C, respectively, and mean annual precipitation of *c.* 1690 mm (Gommes *et al.*, 2004).

Lost Lake (45°49'30''N, 123°34'40''W, 460 m elevation), lies on a fault block 30 km east of the Pacific Ocean (Figure 1). It has a surface area of 6 ha, maximum water depth of 6 m, simple bathymetry with no discernable outflow channel and a catchment of *c.* 33 ha. *Pseudotsuga menziesii* is less common than at Little Lake with forest mainly composed of *Tsuga heterophylla*, *Thuja plicata* and *Alnus rubra*, with some *Picea sitchensis* and *Abies grandis*. Understorey species include *Salix spp.*, *Rubus spectabilis* (salmonberry), *Acer circinatum* (vine maple), with *Dryopteris spinulosa* on more mesic settings and *Pteridium aquilinum* in drier or disturbed areas. The watershed experiences January and July

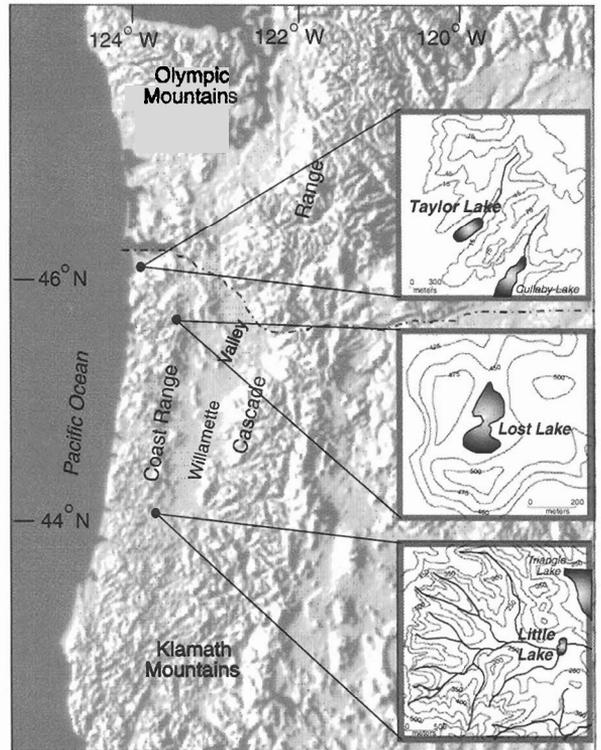


Figure 1 Location of study sites in the Oregon Coast Range. Insets show watershed topography

mean monthly temperatures of 4.7°C and 16.6°C, and a mean annual precipitation of *c.* 1705 mm (Gommes *et al.*, 2004).

Taylor Lake (46°06'02''N, 123°54'24''W, elevation 4 m) is located on the northern Oregon coast approximately 1 km from the Pacific Ocean (Figure 1). The lake is 4 ha in size with a maximum water depth of 4.5 m, a simple bathymetry and a seasonally active outflow channel that drains a watershed of *c.* 63 ha. The lake was formed when sand accumulation dammed the stream draining the watershed (Rankin, 1983). The forests around Taylor Lake are dominated by *Tsuga heterophylla*, *Picea sitchensis*, *Thuja plicata* and *Alnus rubra*. Understorey species are similar to those at Lost Lake. The Taylor Lake watershed experiences temperatures averaging 5.3°C in January and 15.6°C in July, and *c.* 1920 mm of precipitation (Gommes *et al.*, 2004).

The moisture gradient between sites can be illustrated by comparing January and July amounts of effective precipitation (precipitation minus potential evapotranspiration) for each watershed based on 1961–1990 interpolated climate-station data (Gommes *et al.*, 2004) where positive values indicate a surface moisture surplus and negative values indicate a surface moisture deficit. Effective precipitation values for Little Lake (January 225 mm, July –162 mm), Lost Lake (January 224 mm, July –133 mm) and Taylor Lake (January 270 mm, July –118 mm) indicate that the severity of summer drought conditions among the three watersheds is greatest at Little Lake and least at Taylor Lake.

Methods

The field and laboratory methods for each record were similar. Sediment cores were collected from the deepest part of each lake using a 5 cm diameter modified piston sampler (Wright *et al.*, 1983). Cores were extruded in the field, wrapped in cellophane and

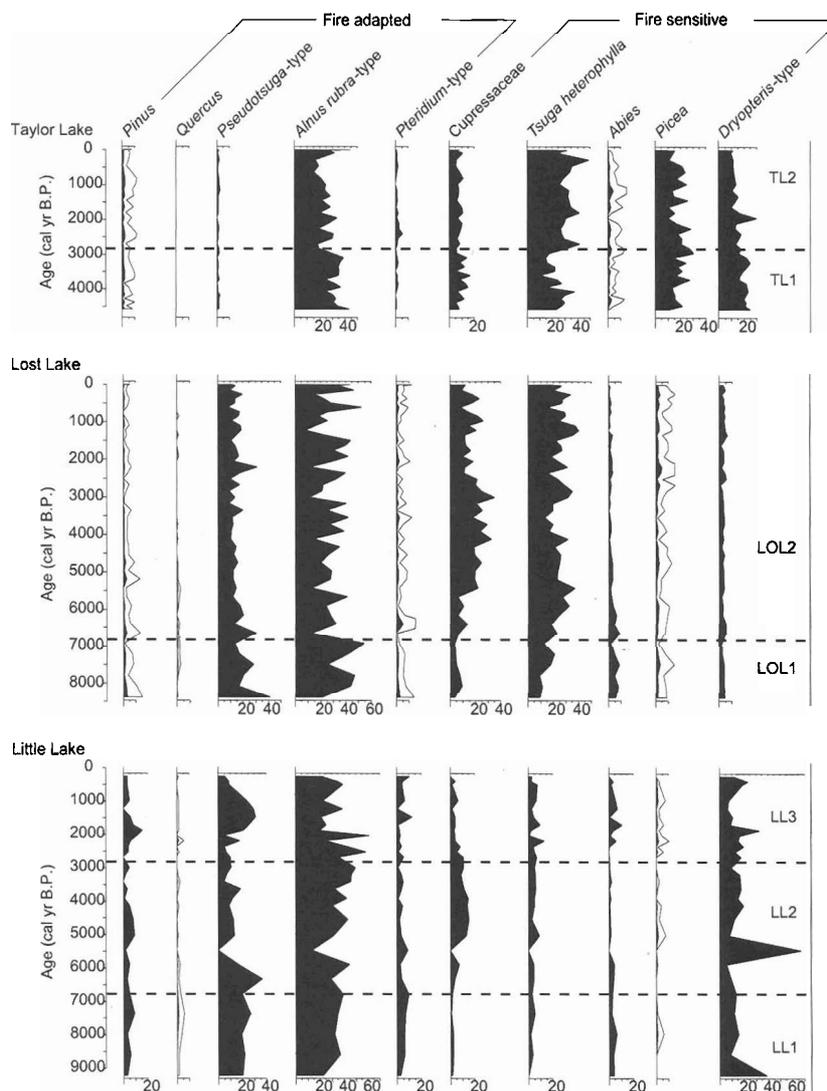


Figure 2 Pollen percentage rates for selected taxa from Taylor Lake, Lost Lake and Little Lake plotted against the age for each core. Pollen percentages for Little Lake are from Worona and Whitlock (1995). Taxa are designated as fire-adapted or fire-sensitive (Agee, 1993). Horizontal lines mark pollen-zone boundaries based on a constrained cluster analysis (CONISS; Grimm, 1987)

aluminum foil, and transported back to the laboratory where they were refrigerated. In the laboratory, the cores were sliced longitudinally, described and subsampled for pollen and charcoal analysis.

Pollen analysis

At Lost and Taylor lakes, 1 cm³ samples were taken every 10 cm for pollen extraction following the procedures of Faegri *et al.* (1989). A known amount of *Lycopodium* pollen was added to each sample prior to processing in order to calculate pollen accumulation rates. The pollen samples were mounted in silicon oil and examined at magnifications of 400 to 1000 \times . Pollen was identified to the lowest taxonomic level possible based on modern pollen collections at the University of Oregon and published atlases. A minimum of 400 terrestrial grains were identified. Haploxylyon-type and Diploxylyon-type *Pinus* grains were assigned to *P. monticola* (western white pine) and *P. contorta* (lodgepole pine), respectively, based on their present coastal distribution. *Pseudotsuga*-type pollen was attributed to *P. menziesii* (Douglas-fir), and *Picea* pollen was assumed to represent *P. sitchensis*. *Abies* pollen was attributed to *A. grandis* (grand fir) and *A. amabilis* (Pacific silver fir), both of which grow above

1000 m elevation in the northern Oregon Coast Range as well as in the Cascade Range. Cupressaceae pollen was attributed to *Thuja plicata* (western red cedar), and *Chamaecyparis nootkatensis* (yellow cedar), which occurs rarely in the Oregon Coast Range, is also a possible contributor. Pollen grains that could not be identified were labelled 'Unknown'. Terrestrial pollen percentages were calculated using the sum of terrestrial pollen and spores, excluding *Polystichum*-type spores which were very abundant. Percentages of aquatic taxa were calculated based on total terrestrial and aquatic pollen and spores. The pollen percentage diagrams were divided into zones based on constrained cluster analysis (CONISS; Grimm, 1987). Assemblages were then compared with modern pollen rain from different vegetation types to infer past vegetation and climate (Pellatt *et al.*, 1997; Minckley and Whitlock, 2000) (Figure 2). The pollen record from Worona and Whitlock (1995) was used to describe the vegetation history at Little Lake (Figure 3).

Charcoal analysis

In the laboratory, subsamples of 3–5 cc were taken at contiguous 1 cm intervals and soaked in 5% solution of sodium hexametaphosphate

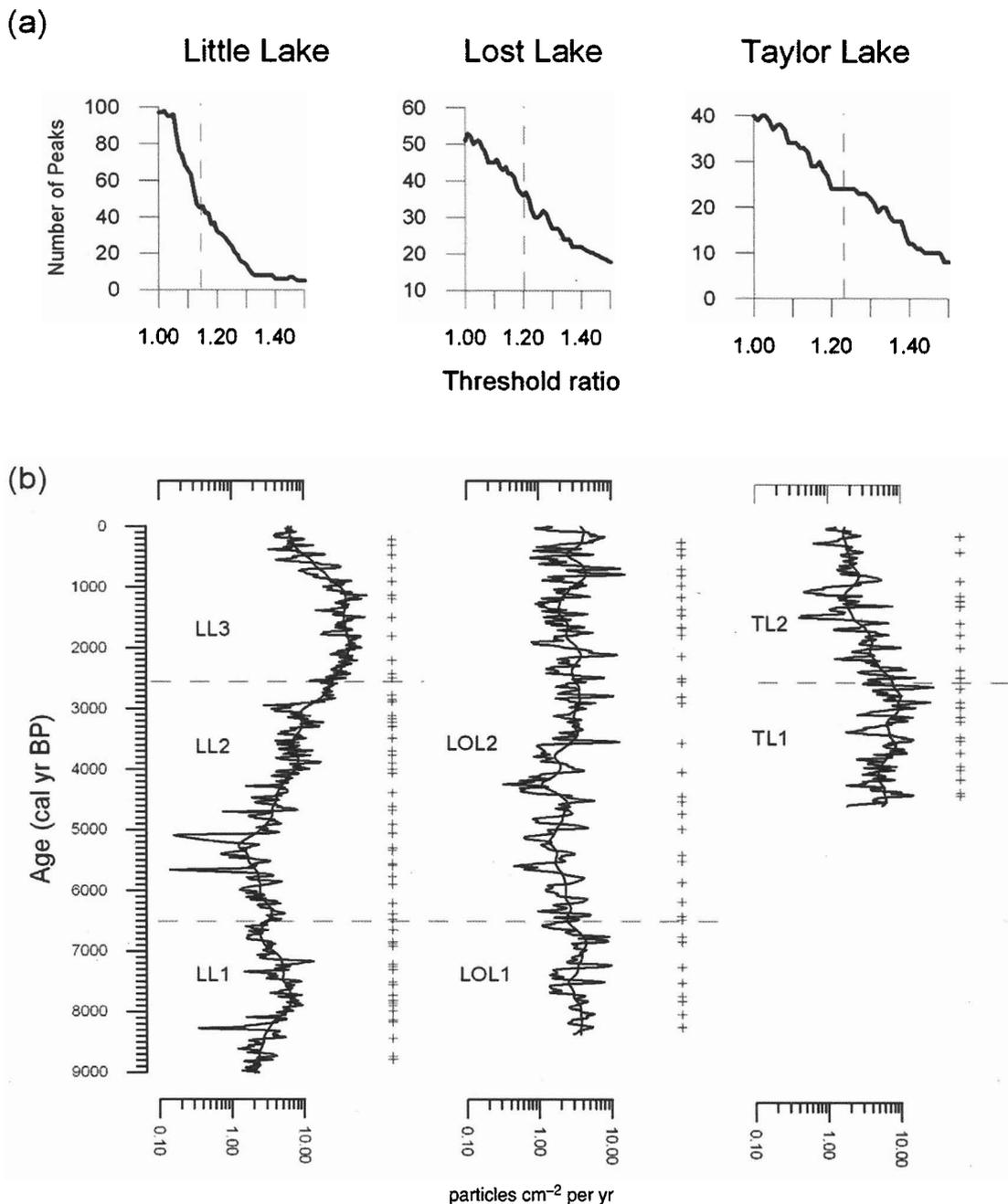


Figure 3 (a) Distribution of CHAR peaks using a range of threshold ratios from 1.00 to 1.50. Dashed line indicates value chosen for peak detection from each record, 1.12 for Little Lake (Long *et al.*, 1998), 1.20 for Lost Lake (Long, 2003) and 1.25 for Taylor Lake (Long and Whitlock, 2002). (b) Decadal CHAR values from Little, Lost and Taylor Lakes. Peaks are designated as (+). Horizontal lines, at *c.* 6700 cal. yr BP and *c.* 2700 cal. yr BP are the pollen zone boundaries at each site, and indicate shifts in forest vegetation. The mean fire intervals \pm standard error in years, within each pollen zone are: LL1 110 ± 20 (range 30–300, $n = 17$), LL2 150 ± 20 (range 30–320, $n = 18$), LL3 210 ± 30 (range 60–400, $n = 12$); LOL1 220 ± 40 (range 80–420, $n = 8$), LOL2 220 ± 30 (range 50–660, $n = 29$); TL1 140 ± 40 (range 20–460, $n = 10$), TL2 220 ± 30 (range 80–430, $n = 13$)

for 24 h. The samples were then gently washed through a series of nested screens with mesh sizes of 250 and 125 μm . The sieved samples were examined at 50 \times magnification, and all charcoal particles greater than 125 μm were tallied (Long *et al.*, 1998).

Variations in charcoal accumulation rates (CHAR) provided the fire history reconstruction, and we used the decomposition approach of Long *et al.* (1998). Charcoal counts for each sample were converted to concentration data (particles/cm) and then interpolated to

pseudo-annual values. These values were then averaged over ten year intervals. Charcoal accumulation rates (CHAR) (particles/cm² per yr) were calculated as averaged concentration divided by average span, where average span, in this case, was a decade. This approach preserves the total mass of charcoal better than if raw influx was simply interpolated to CHAR values. Conversion to average decadal CHAR was done to standardize the record to equal-time intervals and minimize the influence of variations in the time represented by

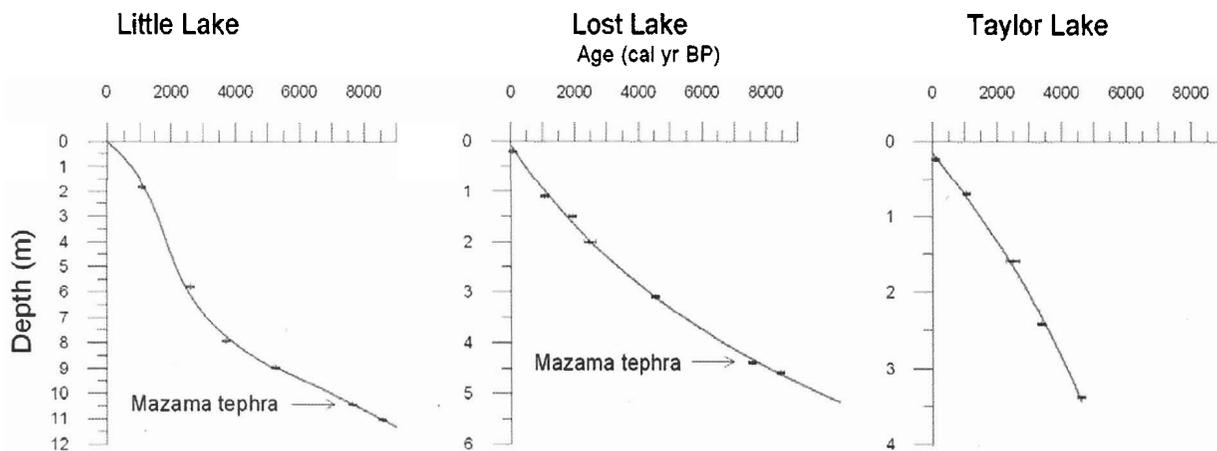


Figure 4 Age versus depth curves for Little, Lost and Taylor lake sediment cores. Bars represent two standard deviations from calibrated radiocarbon date

each 1 cm sample that arise from variations in sedimentation rate over the length of the record.

The charcoal record was decomposed into two components: background CHAR (BCHAR) and peaks. BCHAR is the slowly varying trend in charcoal accumulation which likely varies as a result of changes in fuel composition, inputs of charcoal introduced from the watershed or littoral zone of the lake or charcoal introduced from fires outside the watershed (Marlon *et al.*, 2006). Peaks, which are positive deviations from BCHAR, represent input of charcoal as a result of a fire event. The CHAR time series were logarithmically transformed for variance stabilization ($\text{Log}(\text{CHAR}+1)$) (CHAPS software P. Bartlein, unpublished data, 2003) before being decomposed into BCHAR and peak components (Marlon *et al.*, 2006). The background component was determined using a moving locally weighted mean with the weights determined by the tricube weight function (Cleveland, 1979). The peak component was determined by comparing the CHAR to the background value assigned to that time step. If the CHAR exceeded the BCHAR at that time by a prescribed threshold ratio, it was designated a peak. CHAR peaks are hereafter referred to as 'fire episodes', because a charcoal peak may represent one or more fire events. The number of CHAR peaks per unit of time is designated as the 'fire-episode frequency'.

Recent CHAR peaks at each site were compared with the age of known fires in order to select an appropriate window-width for BCHAR and threshold ratio for identifying peaks. A background window width of 600 yr provided the best smoothing of CHAR values to characterize centennial-scale trends without being influenced by individually large CHAR values (Long *et al.*, 1998; Long and Whitlock, 2002) (Figure 3). A range of threshold ratios (1.00 to 1.50) were examined to identify values that correctly identified the age of known fires and other distinct peaks, assumed to be local fire events, that occurred prior to the historical or dendrochronological record. The threshold values that satisfied these criteria were 1.12 at Little Lake (Long *et al.*, 1998), 1.20 at Lost Lake (Long, 2003) and 1.25 at Taylor Lake (Long and Whitlock, 2002) (Figure 3). We acknowledge that different decomposition methodologies, such as identifying peaks by calculating residuals (peak-background) (Gavin *et al.*, 2006) or transformation of the data, may affect the CHAR analysis. However, we feel that the methodology used in this study is appropriate and provides accurate reconstructions of fire history for these seasonal rain forest sites.

We performed a non-parametric two-sample Kolmogorov-Smirnov test between each record in order to test the null hypothesis that the distributions of time-between-fire episodes (TBF) (ie,

fire interval) from each site were identical (Clark, 1989). Identical TBF distributions would suggest that the factors that affect fire episode occurrence, such as fuel loads, fuel moisture and climate conditions, were similar between sites, while different TBF distributions would suggest the opposite. Also, following Gavin *et al.* (2006), we examined the synchrony of fire-episode occurrence between sites at centennial to millennial scales using a modification of the bivariate Ripley's K-function (Ripley, 1977). The bivariate K-function tests for attraction or repulsion between two classes of points in a two-dimensional space. Here we used the bivariate K-function modified for one dimension (ie, time) (Doğs, 1989). The K-function was transformed into the L-function $L_{AB}(t)$, where values >0 indicate synchrony and values <0 indicate asynchrony in fire episodes within a time window of t years. We calculated 95% confidence intervals based on 1000 simulations in which one record was shifted a random number of years relative to the other, wrapping the fire-episodes series from the end to the start of the record (Gavin *et al.*, 2006). Because the Taylor Lake record spanned the last 4600 years, we tested for synchrony between Little and Taylor, Lost and Taylor and among all three sites over the last 4600 years. We also tested the Little and Lost fire-episode records for synchrony over the last 8400 cal. yr BP.

Results

The lake-sediment cores from Little (11.33 m in length), Lost (4.60 m in length) and Taylor (3.43 m in length) lakes can be characterized as containing upper sediments fine-detritus gyttja grading to basal sediments of inorganic silty clay. Little Lake and Lost Lake cores contained 2 cm thick (10.44–10.46 m depth) and 1 cm thick (4.38–4.39 m depth) tephra layers, respectively, that were attributed to the eruption of Mt Mazama in southwestern Oregon.

Chronology

The chronology for each record was based on ^{14}C dates from sedimentary charcoal, sedimentary ^{210}Pb dates and the age of Mazama 'O' tephra (Zdanowicz *et al.*, 1999) recovered at Little and Lost lakes. Eleven of 16 ^{14}C dates came from charcoal particles. A bulk sediment date was obtained near the base of each lake record and ^{210}Pb dates were used near the top of the cores from each lake to compare the time of high CHAR values with known watershed fires. All ages were converted to calibrated years before present (cal. yr BP) based on CALIB 4.2 (Stuiver *et al.*, 1998). The chronology at Little Lake was based on a third-order polynomial

regression curve from 0 to c. 5250 cal. yr BP and second-order polynomial from c. 5250 to 9000 cal. yr BP. At Lost and Taylor lakes, the chronologies were based on third- and second-order polynomial regression curves, respectively (Figure 4).

Gavin *et al.* (2003b) working on Vancouver Island, have shown that the 'in-built' age of charcoal from long-lived rainforest species can be as high as 670 years with a mean error of c. 270 years. While acknowledging the potential error in chronologies associated with the 'in-built' age of charcoal, we assume the chronologies established at Little, Lost and Taylor lakes are reliable enough to compare the records on century timescales for three reasons. First, the simple bathymetry of each lake minimizes the chance that re-deposition of charcoal, a possible source of old charcoal, occurred within the lake and that the charcoal picked for dating from each sample was produced from the same fire episode (Whitlock and Larson, 2001). Thus, it is unlikely then that a single tree is distorting the age determinations. Second, the age–depth curves are relatively linear and do not demonstrate sudden shifts, which would be indicative of significant 'in-built' age effects (Figure 4). Finally, using the mud–water interface age and Mazama tephra (7630 cal. yr BP, Zdanowicz *et al.*, 1999) alone at Little and Lost lakes gave similar average sedimentation rates as those obtained from age models based on radiometric dates (eg, Little: radiometric age model 8.01 yr/cm; mud–water interface–Mazama model 7.29 yr/cm; Lost: radiometric age model 20.1 yr/cm; mud–water interface–Mazama model 17.5 yr/cm). At Taylor Lake, ^{14}C -dated wood established the age of dune formation, and thus lake initiation, at c. 4600 cal. yr BP (Rankin, 1983), which is the same basal date extrapolated by the radiometric age model.

Pollen records

The last 9000 years of the Little Lake pollen record (Worona and Whitlock, 1995) were divided into three pollen zones (Long *et al.*, 1998) (Figure 2). Zone LL1 (c. 9000 to 6700 cal. yr BP) consisted of high percentages of *Pseudotsuga menziesii* and *Alnus rubra* with some presence of *Quercus* and *Pteridium*. This pollen assemblage suggests that the watershed was dominated by *Pseudotsuga menziesii* with *Alnus rubra* growing in recently disturbed and riparian areas and *Quercus* growing on the driest sites. The high amounts of *Pteridium* suggest forest was more open than today. This pollen assemblage is similar to those found in present-day forests of the central Cascades of Oregon (Sea and Whitlock, 1995). Zone LL2 (c. 6700 to 2700 cal. yr BP) had increases in shade-tolerant, fire-sensitive species, including *Tsuga heterophylla*, *Thuja plicata* and *Picea sitchensis*, along with the continued presence of *Pseudotsuga menziesii* and *Alnus rubra*. The increase in fire-sensitive species suggests a shift toward the more closed, mesic forest of the present day (Minckley and Whitlock, 2000). Zone LL3 (c. 2700 cal. yr BP to present) had abundant *Pseudotsuga menziesii* and *Alnus rubra* pollen, but increases in fire-sensitive *Picea sitchensis* and *Abies* were also present. This period suggests the development of the present-day forest of *Pseudotsuga menziesii* and *Alnus rubra* and areas of mesic forest conifers. The mixture of conifers suggests a complex of early and late seral stands in the watershed (Long *et al.*, 1998).

The Lost Lake pollen record was divided into two zones and spanned c. 8400 years (Long, 2003) (Figure 2). Zone LOL1 (c. 8400 to 6750 cal. yr BP) featured high percentages of *Alnus rubra*, *Pseudotsuga menziesii*, *Tsuga heterophylla* with some *Abies* and *Quercus*. Zone LOL2 (c. 6700 to present) indicates a decrease in *Pseudotsuga menziesii* and *Quercus* pollen and an increase in *Tsuga heterophylla* and Cupressaceae pollen percentages. The pollen record suggests that during Zone LOL1 time, the forest was composed of stands of *Alnus rubra* on disturbed or riparian settings, with mixed stands of *Pseudotsuga menziesii* and *Abies grandis* occupying the remainder of the watershed. The closest modern pollen analogues come from mid-elevation forests of the western

Cascades (Barnosky, 1985; Minckley and Whitlock, 2000). Over the last 6700 years, the forest became dominated by *Tsuga heterophylla*, Cupressaceae (likely *Thuja plicata*), and *Alnus rubra* and *Pseudotsuga menziesii* were less common. The abundance of shade-tolerant *Tsuga heterophylla* and *Thuja plicata* in this zone suggests a more-closed forest than before (Long, 2003).

The pollen record at Taylor Lake spanned the last c. 4600 years and was divided into two zones (Long and Whitlock, 2002) (Figure 2). Zone TL1 (c. 4600 to 2700 cal. yr BP) showed high percentages of *Alnus rubra*, *Tsuga heterophylla* and *Picea sitchensis* pollen along with abundant *Dryopteris* spores. The vegetation is inferred to be similar to southern Coast Range forests of today (Minckley and Whitlock, 2000). Zone TL2 (c. 2700 cal. yr BP to present) shows an overall increase in *Tsuga heterophylla* and a decrease in *Alnus rubra* pollen. *Picea* and Cupressaceae percentages remained similar to those of Zone TL1. This zone marks the establishment of the present-day closed *Picea sitchensis* and *Tsuga heterophylla* forests (Minckley and Whitlock, 2000).

Charcoal data

The BCHAR values from Little Lake between c. 9000 and 4000 cal. yr BP were > 2 particles/cm² per yr and between 4 and 6 particles/cm² per yr from c. 8000 to 7000 cal. yr BP (Figure 3). Between c. 4000 and 1200 cal. yr BP, BCHAR values increased to a maximum of 38 particles/cm² per yr before declining to present-day values of 9 particles/cm² per yr. At Lost Lake BCHAR levels showed little variability throughout the record. Values were initially 3 to 4 particles/cm² per yr, then decreased to 1 to 2 particles/cm² per yr by c. 6200 cal. yr BP. From c. 6200 to 3600 cal. yr BP, values remained low before increasing to 3 to 4 particles/cm² per yr over the last 3600 cal. yr BP except for the period from c. 1600 to 1100 cal. yr BP when background levels were 2 particles/cm² per yr. By comparison, Taylor Lake BCHAR values were between 4 and 6 particles/cm² per yr from c. 4600 to 3700 cal. yr BP and then increased to 9 particles/cm² per yr by c. 2700 cal. yr BP. From c. 2700 cal. yr BP to present, BCHAR values steadily declined to present-day values of 1–2 particles/cm² per yr (Figure 3).

The CHAR peak record from Little Lake shows distinct trends in the peak frequency. From c. 9000 to 6700 cal. yr BP the mean fire interval (MFI) was 110 ± 20 yr (range 30–300, $n = 17$) (Figure 3). From c. 6700 to 2700 cal. yr BP, MFI increased to 150 ± 20 (range 30–320, $n = 28$), and over the last c. 2700 years it lengthened to 210 ± 30 yr (range 60–400, $n = 12$), which is similar to present-day estimates of 150–300 years for *Tsuga heterophylla* forests of the Coast Range (Agee, 1993; Impara 1997). The Lost Lake CHAR peak record shows modest shifts in peak frequency over the last c. 8400 years (Figure 3). From c. 8400 to 6700 cal. yr BP MFI was 220 ± 40 years (range 80–420, $n = 8$). Over the last c. 6700 years the MFI remained 220 ± 30 (range 50–660, $n = 29$), but with a mixture of both long and short fire intervals. The charcoal MFI of 220 years is also within present-day estimates of *Tsuga heterophylla* forests of the Coast Range (Teensma *et al.*, 1991). At Taylor Lake, peak frequency decreased over the last 4600 years. From c. 4600 to 2700 cal. yr BP, MFI was 140 ± 40 years (range 20–460, $n = 10$) (Figure 3), and in the last c. 2700 years, it increased to 220 ± 30 years (range 80–430, $n = 13$), which is similar to the present-day MFI estimates of 300 years or greater in *Picea sitchensis* forests (Agee, 1993).

The results of the non-parametric two-sample K-S tests showed that the null hypothesis of identical TBF (ie, fire intervals) distributions between Little and Taylor lakes and between Lost and Taylor lakes cannot be rejected (Table 1). Little and Lost lakes K-S results showed that the TBF populations were not identical. The K-S test results for Little and Taylor, and Lost and Taylor lakes suggests that there has been a common frequency at which fuel and climate conditions combined to create fire episodes

Table 1 Two-sample Kolmogorov-Smirnov comparisons of time between fires

Sites	(D) ^a	P (95%)
Little–Lost	0.2918	0.033
Little–Taylor	0.2062	0.418
Lost–Taylor	0.1633	0.796

^a(D), maximum difference between cumulative distributions.

in these watersheds. The difference in Little and Lost lakes TBF populations implies that either fuel and/or climate conditions necessary for fire episodes were not occurring at the same rates between these watersheds.

The bivariate K-function results indicated shared high fire activity at all three sites at a time scale of 100 years over the last 4600 years (Figure 5). The comparison between sites gave mixed results. Little and Taylor lake records showed multiple time periods of 100, 300, 800, 1000 and 1300 years, in which fire episodes were occurring in a synchronous pattern over the last 4600 years. The Lost and Taylor lake comparisons indicate that fire episode occurrence has been asynchronous over the last 4600 years, and the Little and Lost lake records showed synchrony when records were examined at 100-yr time steps but fire episodes occurred independent of each other when examined at increasingly longer time periods.

Discussion

Throughout the PNW, palaeoecological records show changes in forest composition that have been attributed to regional climate changes during the Holocene (Cwynar, 1987; Thompson *et al.*, 1993; Mohr *et al.*, 2000; Briles *et al.*, 2005). Among the large-scale controls of climate were the changes in the latitudinal and seasonal distribution of insolation and ocean–atmospheric interactions, which in turn controlled the strength and location of circulation features, such as the SHT. Greater-than-present summer insolation between c. 14 000 and 6000 cal. yr BP strengthened the influence of the STH in summer, decreased precipitation, increased net radiation and consequently temperature and potential evapotranspiration, and likely decreased effective moisture (Bartlein *et al.*, 1998). The result was a warmer and drier climate in the PNW during the early Holocene than today (Thompson *et al.*, 1993). Decreasing summer insolation since c. 6000 cal. yr BP has weakened the STH and allowed more storm systems to penetrate the region and thus created cooler and wetter conditions than before.

The vegetation history from Little, Lost and Taylor lakes features shifts in forest composition that are consistent with warm dry conditions in the early Holocene (c. 9000 to 6700 cal. yr BP), cooling in the mid Holocene (c. 6700 to 2700 cal. yr BP), and the establishment of present-day climate in the last c. 2700 years. However, the north-to-south effective precipitation gradient between Little, Lost and Taylor lakes accounts for differences in forest composition among sites (Figure 2). For example, the overall pollen percentages of fire-sensitive taxa, such as *Picea* and *Tsuga heterophylla*, are lowest at the driest site, Little Lake, and highest at the wettest site, Taylor Lake. In contrast, fire-adapted taxa, such as *Pinus*, *Quercus* and *Pseudotsuga menziesii*, show the opposite trend with higher percentages at Little Lake and low percentages or an absence at Taylor Lake. The vegetation changes at Lost Lake represent an intermediate position response on this gradient with significant *Abies*, *Pinus* and *Quercus* in the early Holocene, and then a shift to fire-sensitive *Tsuga*, *Picea* and *Thuja* as the climate became wetter in the mid Holocene.

The overall record of fire-episode frequency also tracks climate conditions that affect long-term forest composition. High fire-episode frequency occurs in conjunction with forests comprised primarily of fire-adapted taxa and lower fire-episode frequency is associated with forest dominated by fire-sensitive taxa. The individual site comparisons of fire-interval populations (K-S test) and fire episode synchrony (bivariate K-function tests) indicate that Little and Taylor lakes have had the same distributions of fire intervals and synchrony of fire episodes. These results suggest that when conditions that precipitated fire episodes occurred at Taylor Lake they also occurred at Little Lake. The Lost and Little lake comparison indicates that the fire interval populations are not similar between sites but that synchrony for fire episodes is at centennial timescales, also suggesting that when conditions that precipitated fire episodes occurred at Lost Lake they also occurred at Little Lake. However, they did not occur at Lost Lake with the same regularity as at Little Lake. This may be the result of higher effective precipitation at Lost Lake or it may be related to the differences in watershed size between the two locations. A larger Little Lake watershed may have provided more opportunities for fires to be recorded as a result of a larger source area for charcoal (Whitlock and Larson, 2001). The Taylor and Lost lake comparisons indicate that fire-interval populations are similar, but that fire-episode occurrence is not synchronous. This implies that although the length of time between fire episodes is similar, the actual timing of fire episodes is not. This could be the result of specific site differences, such as local topography and fire weather, between the two watersheds having more control at a local scale than long-term regional climate. Lost Lake is located at a higher elevation and likely experiences different daily weather conditions than Taylor Lake. There is also a difference in forest composition between the sites that may have had an effect on fuel conditions also enhancing the spatial heterogeneity of fires across the landscape, a characteristic that is often observed in dendrochronological fire history reconstructions (Heyerdahl *et al.*, 2001). Similar site to site differences in fire histories were found by Gavin *et al.* (2006) working in southern British Columbia, suggesting that local conditions at times can exert more control over local fire histories than regional climate conditions.

The synchrony of fire occurrence among all three sites at a 100-yr time period implies that the controls of fire episodes (eg, fuel loads, fuel moisture and climate conditions) occurring on century timescales led to widespread fire activity despite the persistent environmental gradient. It is likely that this synchrony is related more to changes in climate conditions than fuel loads as the 100-yr synchrony window spans several vegetation zones. Tree-ring studies of the last c. 800 years from Oregon and Washington identified two such periods of extensive fires, AD 1400 to 1650 and AD 1801 to 1925 (Weisberg and Swanson, 2003). Drought is independently inferred from negative values of the Palmer Drought Severity Index (PDSI) (Cook *et al.*, 2004) for western Oregon during both periods. Fire episodes are also registered in all three charcoal records from c. 600 to 450 cal. yr BP and 200 to 75 cal. yr BP (Figure 5).

Examining the fire episodes at 100-yr time steps for the last 4600 years at all three sites reveals an increase in fire-episode frequency between c. 4200 and 3000 cal. yr BP, and 2000 to 1200 cal. yr BP (Figure 6). Mohr *et al.* (2000) showed high fire activity centred around c. 4000 cal. yr BP from several sites in the Klamath Mountains of northern California while Hallet and Hills (2006), working in southeastern British Columbia, indicate that fire activity was declining during this period, implying that the controls of fire activity, such as seasonal drought intensity were not uniform across the larger PNW region. Alternatively, Mohr *et al.* (2000) Hallet and Hills (2006) and fire history studies from southern

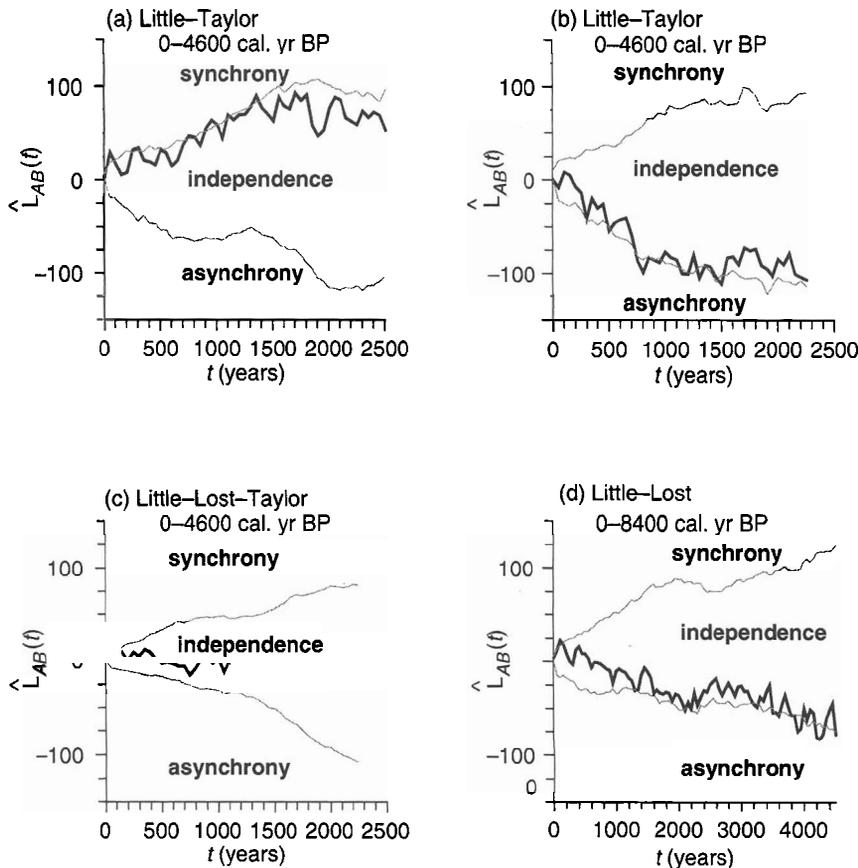


Figure 5 Bivariate L -functions plotted against time windows for fire-episode history comparisons. Plots (a) Little–Taylor, (b) Lost–Taylor, and (c) Little–Lost–Taylor Lake fire-episode records compared over the last 4600 years. Plot (d) Little–Lost Lake fire-episode records compared over the last 8400 years. Grey lines are 95% confidence ranges based on 1000 randomizations of shifting the records relative to each other (Gavin *et al.*, 2006). The dashed horizontal line identifies the 100-yr time window

British Columbia (Hallett and Walker, 2000; Hallett *et al.*, 2003b) show increases in fire frequency between *c.* 2400 and 1300 cal. yr BP. In addition, Gavin *et al.* (2003a), working on Vancouver Island, also show higher than present-day fire frequency from *c.* 1800 to 900 cal. yr BP. This region-wide increase in fires between *c.* 2400 and 900 cal. yr BP suggests a relatively consistent centennial-scale control on fire activity (ie, increased seasonal drought conditions) during this period. In contrast, a comparison of the Little and Lost lake records from 8400 to 4600 cal. yr BP revealed no coherent trends. It may be that differences in local environment during the mid and early Holocene were more important in determining fire activity than the large-scale controls of regional climate. The vegetation history between the sites also confirms differences in local environments during this period.

The only pollen change associated with periods of high fire activity was an increase in disturbance-adapted *Alnus rubra* from *c.* 4200 to 3000 cal. yr BP at Taylor Lake, when fire episode frequency rose to 6 fires per 1000 years (Figure 6). The other sites showed no discernible vegetation response to individual fire episodes or widespread fire periods. The pollen sampling interval may have been at too low a sampling resolution to match changes in the high-resolution charcoal data. Alternatively, these long-lived forests may not have been sensitive to climate changes on centennial and shorter timescales that governed fire activity.

Climate models that project future changes in precipitation (Leung and Ghan, 1999; Mote *et al.*, 2003) suggest that yearly precipitation in the PNW may increase over the next century, but

that snowpacks will likely decrease. The decrease in snowpack may lead to an earlier and more extensive summer drought (Westering *et al.*, 2006). Shafer *et al.* (2005), who examined future predictions of moisture index in the PNW, also suggest summer drought is likely to intensify over the next century. Increases in the number and extent of fires in interior PNW forest over the last several centuries have been connected with an increase in seasonal and decadal drought conditions (Heyerdahl *et al.*, 2001; Hessl *et al.*, 2004). The evidence presented here suggests that increases in drought conditions led to fires throughout the Coast Range despite the differences between sites. Given the prospect of longer drier summers in the future the possibility of widespread fires in the Coast Range seems likely. Understanding shifts in forest composition may be more difficult. Higher fire-episode frequency in the past was associated with forests dominated by Douglas-fir and alder; however an increase in fire-sensitive species, over the last 4600 years, has come despite the apparent synchrony in fire occurrence between sites. Therefore, it is important to use the past responses to drought conditions to inform both the current conceptual models of forest recovery after fire and the projections of forest response to future climate changes.

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C. Long designed the study, analysed the data and wrote the manuscript. C. Whitlock assisted with the study design, data interpretation

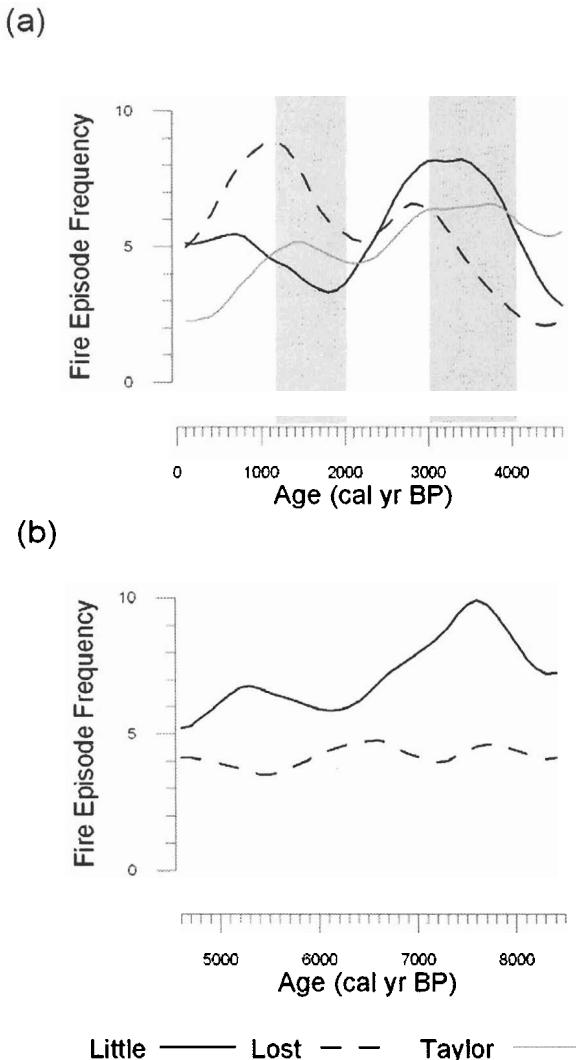


Figure 6 (a) Little, Lost and Taylor Lake fire-episode frequency per 100 years plotted as the number of events per 1000 years for the last 4600 years. Grey boxes highlight the periods c. 4000 to 3000 cal. yr BP and c. 2000 to 1200 cal. yr BP when fire-episode frequency is increasing at all three sites. (b) Little and Lost fire-episode frequency per 100 years plotted as number of events per 1000 years from c. 4600 to 8400 cal. yr BP

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