



Historical fire regime and forest variability on two eastern Great Basin fire-sheds (USA)

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ABSTRACT

Proper management of naturally forested landscapes requires knowledge of key disturbance processes and their effects on species composition and structure. Spatially-intensive fire and forest histories provide valuable information about how fire and vegetation may vary and interact on heterogeneous landscapes. I constructed 800-year fire and tree recruitment chronologies for two eastern Great Basin fire-sheds using fire-scar and tree establishment evidence from 48 gridded plots (500 m spacing) and from fire-scarred trees between plots. Fire-sheds are located in the Snake Range of eastern Nevada (BMC) and Wah Wah Range of western Utah (LAW) and span a range in elevation and vegetation zones typical for the region. Estimates of point mean fire interval varied more than 10-fold at both BMC (7.8–125.6 years) and LAW (13.3–138.4 years). At BMC, a distinct within-fire-shed contrast in fire frequency was difficult to explain without invoking the possibility of spatially-variable human-caused ignitions. A majority of fires were small (<10 ha) but large fires (≥ 100 ha) accounted for 78% (BMC) to 89% (LAW) of cumulative area burned. Tree recruitment for mid-elevation, mixed-conifer stands was somewhat episodic and asynchronous among plots. Recruitment pulses were synchronous with multi-decade fire quiescent periods, and often followed large fires. I concluded that fire frequency was under strong topographic control and that fire severity was mixed and variable through time and space resulting in a dynamic mosaic of variable-aged, fire-initiated vegetation intermixed with long-lived, fire-resilient trees and open shrub–steppe communities (BMC). A major change in fire regime and forest composition began in the 1800s causing shifts in composition and structure at the stand scale and homogenization at the landscape scale. I recommend that management strategies prioritize the use of fire and surrogate treatments on mid-elevation forests that have deviated most from historic conditions and on associated shrub–steppe communities where conifer encroachment has occurred. Planned disturbances should be of mixed severity and sized to recreate vegetative mosaics at historic spatial scales.

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1. Introduction

Successful forest management and restoration strategies require a thorough understanding of natural disturbance regimes and their effects on vegetation. Fire histories provide a means to quantify past variation in fire regimes at various scales of time and space (Morgan et al., 2001; Keane et al., 2002). To effectively assess fire regime variability, fire regime reconstructions must have spatial and temporal resolution at the same or finer scales in which variation occurs (Wiens, 1989; Levin, 1992). Fire histories derived from tree-ring evidence provide a means for assessing the effects of broad- (e.g. climatic) to fine-scale (e.g. topographic) drivers of fire regime variability over long periods (Swetnam and Betancourt, 1998; Brown et al., 2001; Heyerdahl et al., 2001; Taylor

and Skinner, 2003; Grissino-Mayer et al., 2004). For example, investigations of the role of climate as a driver of historic fire occurrence are possible because tree-ring evidence of past fires can be fixed with annual precision. Consequently, considerable progress has been achieved in assessing the role of climate in synchronizing fire regionally as the number and spatial representation of fire chronologies increased in recent decades (Swetnam and Betancourt, 1990, 1998; Grissino-Mayer and Swetnam, 2000; Westerling and Swetnam, 2003; Kitzberger et al., 2007; Brown et al., 2008; Heyerdahl et al., 2008a,b).

Fire histories constructed from intensive, spatially-precise sampling strategies are useful for evaluating fine-scale controls of fire regime variation. Investigations suggest that topographic variables, interacting with vegetation, affect fire regime characteristics differently, depending on the biophysical context. For example, historic fire frequency varied with aspect in the Blue Mountains (Oregon and Washington) but only when terrain was steep, and

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when contrasting topographic facets were large and separated by barriers to fire spread (Heyerdahl et al., 2001). In addition, fire frequency did not differ with elevation when fuels matrices were continuous. Similarly, studies in the Klamath Mountains of California (Taylor and Skinner, 1998) failed to detect differences in fire frequency related to elevation (slope position) even though fire severity increased as species composition and age structure changed on intermediate and upper slopes. In contrast, fire frequency differed significantly in relation to differences in elevation and corresponding forest types in the southern Cascade Range (California; Bekker and Taylor, 2001) and was inversely related to fire size. In the Lake Tahoe Basin (California), fire frequency, fire severity, and cohort patch size varied in mixed-conifer forests with aspect and slope position (Beatty and Taylor, 2008). In the Sacramento Mountains (New Mexico) fire was more frequent at lower than at higher elevations but did not differ between ponderosa pine (*Pinus ponderosa*) and mixed conifer forest types (Brown et al., 2001). Fires were also more common on the west side of the range than on the more topographically heterogeneous east side. A similar pattern was reported for the Santa Catalina Mountains (Arizona) in which a larger mean fire size was inferred as the reason for the higher fire frequency associated with a more homogeneous landscape (Iniguez et al., 2008). These results inferred that fire frequency was controlled at the landscape rather than stand level, a result similar to what has been observed elsewhere (Heyerdahl et al., 2001; Margolis and Balmat, 2009).

When tree-ring-based forest histories are constructed in concert with fire histories they allow examination of linkages between fire regime and vegetation dynamics. Synchronous mortality or recruitment may be used to infer mixed- (Fulé et al., 2003; Taylor and Skinner, 2003; Brown and Wu, 2005) or high-severity (Bekker and Taylor, 2001; Beatty and Taylor, 2008; Bauer and Weisberg, 2009; Margolis and Balmat, 2009) fire regimes depending on spatial scale, whereas multi-aged stands are typically associated with low-severity fire (Taylor and Skinner, 2003; Brown and Wu, 2005). Demographic data are also used to delineate fire perimeters for fire-size calculation (Everett, 2008; Margolis and Balmat, 2009; Bekker and Taylor, 2010). Linked analyses facilitate assessment of the relative importance of fire regime, versus alternative drivers such as climate, in driving vegetation dynamics, and of how stable that relationship might be over time (Fulé et al., 2003; Brown and Wu, 2005; Iniguez et al., 2009).

Published studies are valuable as reference points for developing ecologically sound management strategies, however, it remains unclear how broadly results can be extrapolated. Additional work is needed particularly in regions and biophysical settings that are currently understudied (Swetnam, 2005). For example, most studies completed to date were conducted on landscapes of more or less continuous forest. Thus, new studies on topographically variable landscapes with spatially-complex vegetation patterns are needed. The mountains of the Great Basin provide such an opportunity.

The Great Basin includes 100+ mountain ranges in the northern, elevated section of the Basin and Range Province of western North America. The climate is dry due to rain shadow effects of the Sierra Nevada and Cascade Ranges to the west and Rocky Mountains to the east (Peterson, 1994). Montane vegetation types including alpine herblands, subalpine and mixed-conifer forests, treeless shrub-steppe and pinyon-juniper and mountain mahogany woodlands occur in more or less distinct zones across steep elevational gradients reflecting parallel gradients in temperature and precipitation (Harper et al., 1978). Zonation is further modified by slope, aspect, and substrate. Woodlands occupy the tops of many ranges of more modest elevation and conifer diversity decreases in the Great Basin from east to west reflecting bottlenecks in post-Pleistocene dispersal (Wells, 1983). Because of the steepness of

terrain, multiple abrupt changes in vegetation and consequently fuels matrices are often juxtaposed over short distances.

To date, there are few fire or forest histories published for the Great Basin. In a central Great Basin pinyon-juniper woodland study using both fire-scar and demographic tree data, Bauer and Weisberg (2009) concluded that historically fires were infrequent, small and of high severity resulting in long fire-cycle estimates. Spatial analysis indicated that the more mesic conditions associated with valley bottoms favored more frequent and larger fires before Euro-American settlement than more xeric upslope topography. Biondi et al. (2011) constructed a fire history for mixed-conifer woodland on Mt. Irish in the southeastern Great Basin using fire scares from predominantly ponderosa pine, but also white fir (*Abies concolor*). Across this study site, surface fire activity was high for multiple centuries until about 1860, concurrent with the time of Euro-American settlement, however, a lack of synchrony among scar dates supported an interpretation of mostly small fire size. Fire and forest history studies from outside the Great Basin also report a predominance of infrequent, patchy crown fire for pinyon-juniper woodlands (Floyd et al., 2000, 2008; Huffman et al., 2008) and that more frequent surface fires did not spread into woodlands from adjacent ponderosa pine communities (Huffman et al., 2008).

My objective was to produce spatially explicit, multi-century fire and tree recruitment histories for two fire-sheds that together are broadly representative of montane landscapes of the eastern Great Basin and to use these to test predictions of historic fire regime and tree recruitment variability. I selected geographically proximate fire-sheds to insure similarity in climatic pattern while allowing for variability in topography and anthropogenic use history. As used here, the term “fire-shed” designates a topographic unit somewhat sympatric to one or more small watersheds and corresponding to an area within which natural barriers are sufficiently permeable to allow fire to spread easily among all landscape components. I predicted that historical fire frequency would vary with topography and vegetation class and that fire intervals associated with mid-elevation, mixed-conifer forest stands would be shorter than those for sub-alpine forest or pinyon-juniper woodland stands found at adjacent higher and lower elevations. I predicted that most fires would be small but that the less frequent large fires would account for the majority of area burned and that fire frequency and fire extent would be spatially related. I assumed that evidence of tree recruitment synchrony (or lack thereof) would provide indirect evidence of variability in fire severity and I expected that fire severity would be lowest at mid-elevation, mixed-conifer forest stands in association with high fire frequency, and highest for subalpine forest and pinyon-juniper woodland stands. Therefore, I predicted that, recruitment for tree species in subalpine forest and pinyon-juniper woodland stands, and for fire-sensitive species in mixed-conifer stands, would be episodic as a result of the combined effects of higher fire severity and fire sensitivity; and mostly asynchronous for fire-tolerant species in mid-elevation, mixed-conifer stands. I also expected to find evidence for higher levels of tree recruitment, particularly for fire-sensitive species, after fire regimes changed concurrent with Euro-American settlement (~1865).

1.1. Study fire-sheds

Study fire-sheds are located 65 km apart in White Pine County, Nevada and Millard County, Utah, USA (Fig. 1). The first (BMC) includes forested and non-forested portions of Mill Creek and Burnt Mill Canyons, adjacent drainages within Great Basin National Park on the Snake Range. Elevation ranges from 2300 to 3344 m. The study area is approximately 4 km long and 1.5 km wide, with a total area of ~600 ha (Fig. 1). Conifers dominate on all aspects at

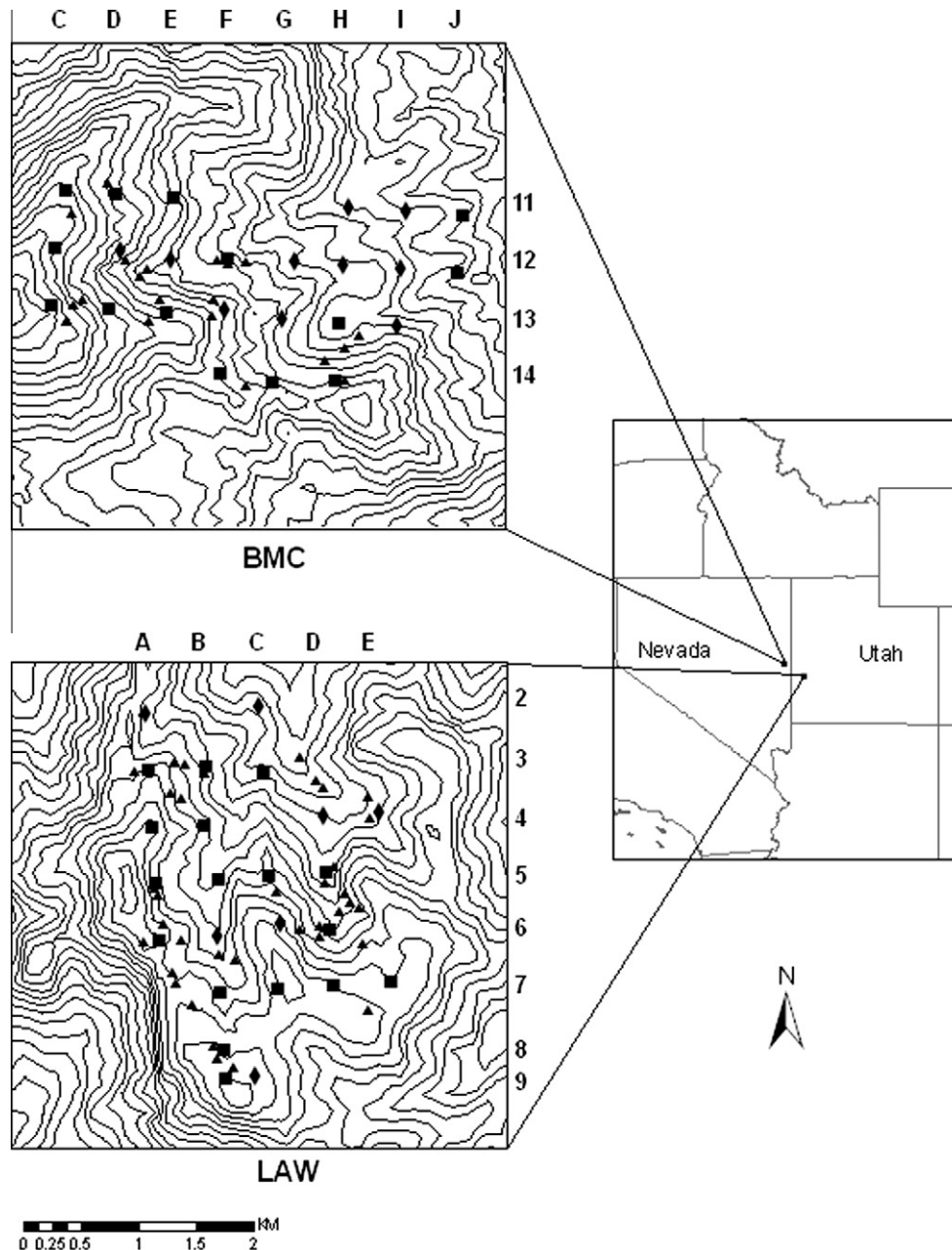


Fig. 1. Grids of plots (~500 m spacing) for fire-sheds located on the South Snake (BMC) and Wah Wah (LAW) Mountain Ranges. Plots are distinguished as squares (fire scars present) or diamonds (fire scars absent). Triangles designate locations for non-plot, fire-scarred sample trees or tree clusters (max area = 0.5 ha). Approximate area for each fire-shed is BMC 600 ha and LAW 525 ha.

upper and lower elevations and on north and east aspects at middle elevations with gradual transitions between subalpine and mixed-conifer forests, and pinyon–juniper woodlands. Sample numbers, fire tolerance ratings and life-history traits for tree species are summarized in Table 1. Quaking aspen (*Populus tremuloides*) is scattered throughout the dry mixed-conifer and subalpine forest types. Curlleaf mountain mahogany (*Cercocarpus ledifolius*) is a long-lived, tall shrub that becomes tree-like with age and is subdominant in mixed-conifer and pinyon–juniper stands and occurs in solid stands on south-facing slopes. Shrub–steppe communities dominated by mountain sagebrush (*Artemisia* spp.), mountain snowberry (*Symphoricarpos oreophilus*), Saskatoon serviceberry (*Amelanchier alnifolia*) and associated herbs occupy dry, mid-elevation slopes and are in various stages of encroachment

by single-needle pinyon pine (*Pinus monophylla*), white fir, and curlleaf mountain mahogany.

The second fire-shed (LAW) is located in the Lawson Cove drainage of the Wah Wah Mountains. Elevation ranges from 2200 to 2718 m. The study area is approximately 3.5 km long and varies in width from 0.5 to 2 km with a total area of ~525 ha (Fig. 1). Considerable rock is exposed on ridge tops, as cliff faces 1–30 m in height, and on talus slopes. Single needle pinyon pine and Utah juniper (*Juniperus osteosperma*) dominate lower elevations and are found throughout the study area. Other conifers are more or less restricted to upper elevations, drainage bottoms and/or north- and east-facing slopes. As with BMC, conifers species at LAW possess a mixture of fire-tolerance and life-history attributes (Table 1). Numerous small forest and woodland openings are dominated by

Table 1
Total number of trees sampled at BMC and LAW fire-sheds by species. Conifers are arranged in descending order based upon common elevational occurrence. Fire tolerance and life-history values are based upon Wright and Bailey (1982) and (Brown and Smith, 2000).

Common name	Scientific binomial	Fire-shed		Fire tolerance	Regeneration rate	Shade tolerance
		BMC	LAW			
		No. sampled				
<i>Conifers</i>						
Engelmann spruce	<i>Picea engelmannii</i>	61		Low	Rapid	High
Bristlecone pine	<i>Pinus longaeva</i>		50	Low	Slow	Low
Limber pine	<i>Pinus flexilis</i>	170		Mod	Mod	Low
Douglas fir	<i>Pseudotsuga menziesii</i>	74	25	Mod	Mod	Mod
White fir	<i>Abies concolor</i>	212	334	Low	Rapid	High
Ponderosa pine	<i>Pinus ponderosa</i>	43	145	High	Slow	Low
Rocky mountain juniper	<i>Juniperus scopulorum</i>		29	Mod	Slow	Low
Single-needle pinyon pine	<i>Pinus monophylla</i>	120	163	Low	Mod	Low
Utah juniper	<i>Juniperus osteosperma</i>	2	58	Low	Slow	Low
<i>Angiosperms</i>						
Quaking aspen	<i>Populus tremuloides</i>	5		Low	Rapid	Low
Curleaf mountain mahogany	<i>Cercocarpus ledifolius</i>	75		Mod	Mod	Low
Unknown		6	2			

low and medium-statured shrubs including black sagebrush (*Artemisia nova*), green ephedra (*Ephedra viridis*), and littleleaf mountain mahogany (*Cercocarpus intricatus*).

The Great Basin has been inhabited by humans for at least 13,000 years. These study fire-sheds were located near the convergence of influence for Western Shoshone, Ute, and Southern Paiute cultures immediately prior to Euro-American settlement (Simms, 2008). These inhabitants practiced mobile, hunter-gatherer economies in contrast to the more sedentary, semi-agricultural Fremont that occupied the area during the 13th century, and possibly some time before. Undoubtedly, fire was used to manipulate natural environments by these and earlier groups (Williams, 2004) however knowledge regarding specific practices and their impacts on vegetation is lacking (Griffin, 2002).

Euro-American settlers arrived in the region in the 1860s, however the nature of settler use differs considerably for the two fire-sheds. Specifically, the BMC fire-shed was grazed in summer by domestic cattle from the 1860s to 1999 (NPS, 2009). In contrast, livestock did not have access to the LAW fire-shed until domestic sheep were introduced to the area for winter-spring grazing in the 1880s (Murdock and Welsh, 1971). Sheep have not used this fire-shed for several decades.

2. Methods

2.1. Field sampling and sample preparation and analysis

Evidence for fire and tree recruitment history reconstructions was collected from 24 plots in each fire-shed and opportunistically from fire-scarred trees between plots (Fig. 1). Plot grids were located across each study area with spacing at 500-m intervals along cardinal directions. Plots were arranged to span a broad range in elevation and forest type (see Brown et al., 2008; Heyerdahl et al., 2011). Across both sites, plots were located primarily on upper (40%) and middle (33%) slope positions with lower slope (17%) and ridge top (10%) positions represented to a lesser degree. Within-plot slope estimates varied from 12% to 58%. Across plots, aspect was largely representative of the study area for both fire-sheds. Plot identity within the resulting grid was specified by alphanumeric couplets designating row (east–west) and column (north–south) location.

I used an n-tree density-adapted sampling method to select study trees for each plot (Jonsson et al., 1992; Lessard et al., 2002) with a maximum plot size of 0.5 ha (40 m radius). Sample trees generally included the 30 nearest to plot center (mean

29.3; range 7–36) with at least 20-cm diameter breast height (DBH = 1.4 m). I sampled a total of 1404 plot trees, 76% of which were alive while the rest were snags (10%), logs (12%), and stumps (2%). Increment cores were removed from live trees without fire scars at 10–20 cm above ground level. Surface fire evidence was collected from 83 fire-scarred plot trees as one or more partial cross-sections cut to pass through injured portions of the bole and pith (Arno and Sneek, 1977). Cross-sections were also cut from sound remnants. Remnants judged as un-datable were counted and classified by the presence or absence of surface char. I sampled 170 additional fire-scarred trees (44% live) within a search radius of ~80 m from each plot center and between plots using a targeted approach (Van Horne and Fulé, 2006).

All cores and cross-sections were sanded until cell structure was visible using a binocular microscope. Samples from 81% (1270) of all trees sampled were successfully cross-dated using a combination of locally-developed ring-width chronologies (skeleton plots) and lists of marker years (Stokes and Smiley, 1968). Samples that could not be dated were excluded from further analysis. I treated pith dates as recruitment dates, employing no correction factors because of unknown time lapses between germination year and the year each tree reached sample height. I estimated years-to-pith for samples in which pith was missing by matching ring curvature and spacing to that of concentric rings in a transparent overlay (Applequist, 1958). Using this method, estimates of pith year were determined for 94% (1193) of all cross-dated trees.

2.2. Fire frequency analysis

Fire-scarred trees were associated with 14 and 19 plots at BMC and LAW, respectively. I assigned a calendar year to each fire scar. Fire scars that could not be dated to annual accuracy were excluded. Abrupt, multi-year changes in ring width were treated as evidence of fire if at least one tree at the site had a fire scar corresponding to the same year. Scars associated with ring boundaries result from fires that occur either late in the year after ring growth is complete or early in the following year before ring growth is initiated. Typically, these scars are assigned to a calendar year based upon the predominant pattern of fire seasonality in modern or historic records. I assigned ring-boundary scars to pre-boundary years when one or more trees at the site had evidence of late season fire in the same year and to the post-boundary year when fire-scar evidence suggested a fire occurred early in the following year. Based upon a pilot study (Kitchen and McArthur, 2003), fire-scars were assigned to the post-boundary year when these criteria proved inconclusive.

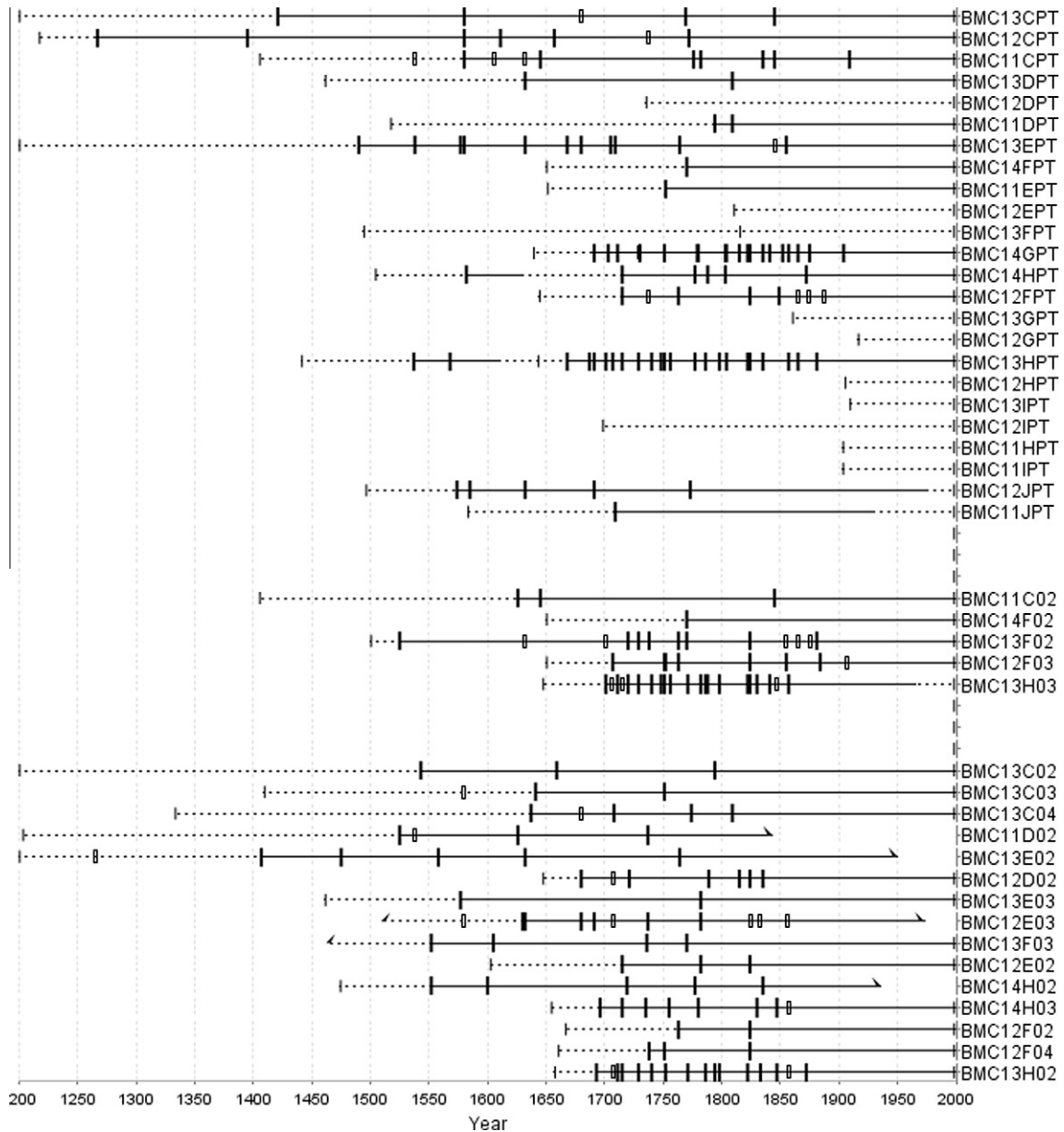


Fig. 2. Fire history chronologies for the Burnt Mill Canyon (BMC) fire-shed located on the Snake Mountain Range. Lower axis designates calendar years (1200–2000). Horizontal lines represent plot composite chronologies (top group), composite chronologies for clusters with ≥ 3 trees (middle group), and chronologies for single trees or tree pairs (bottom group). Within groups, chronologies are arranged by elevation with highest elevation plots or trees at the top of each group. Alphanumeric codes on the right indicate plot identity. Solid horizontal lines indicate chronologies are in recording status. Solid vertical lines indicate years with fire scars and open vertical lines designate injuries or abrupt changes in ring widths for individual chronologies.

I constructed composite fire chronologies (Dieterich, 1980) using all fire-scarred trees located within 40 m (0.5 ha) of plot centers (mean 2.6; range 0–16 trees) and for tree clusters outside of plots (mean 2.9; range 2–5 trees) with a maximum inter-tree distance of 80 m. This limit on composite-area size represents an appropriate compromise when estimating point fire frequency from composite chronologies by addressing the competing risks of underestimation due to incomplete fire-record preservation on individual trees and overestimation due to indiscriminate inclusion of fires recorded from widely scattered trees (Kitchen, 2010). I calculated mean fire interval (MFI) from composite and single-tree chronologies that included a minimum of three fire years using program FH2 (Grissino-Mayer, 2001). I treated composite MFI values as estimates of point mean fire interval (PMFI) when based upon the combined records of three or more trees. PMFI estimates were derived from one- and two-tree chronologies by

multiplying MFI values by 0.8 to correct for a higher probability of unrecorded fires. Kitchen (2010) recommended single-tree correction factors of 0.5–0.72. Though arbitrary, the use of a correction factor of 0.8 here reflects the inclusion of potentially more complete two-tree composites and an inclination to be conservative in estimating fire frequency. Topographic position and elevation values for PMFI estimates for two or more trees were derived from either plot centers or averaged single-tree values. Non-plot chronologies were assigned alphanumeric labels based upon nearest plots (Figs. 2 and 4).

2.3. Fire size analysis

Fires recorded at these sites certainly burned in irregular patterns both inside and outside of grids making estimation of historic burn area difficult. Within fire-sheds, estimation of surface

fire extent was hampered by uneven temporal and spatial distribution of fire-recording trees. Evidence based upon recruitment synchrony could not be used to estimate fire size because pulses generally lacked sufficient temporal precision to link to specific fires. I calculated two-dimensional proxies for burn area, or fire size, using UTM coordinates from trees with fire scars assigned to the same calendar year. Fire size area was calculated as the area equal to that of the smallest rectangle that could include all coordinates of recording-trees with sides oriented along cardinal directions (minimum fire size = 1 ha). Although imperfect, this approach minimizes bias caused by an unequal record through time and uneven distribution of fire-scarred trees through space. The latter was particularly important at BMC where significant portions of the fire-shed were not historically forested. Given the obvious lack of precision, the proxy values presented here are best viewed in relative terms rather than as precise estimates of actual fire extent. Thus I used calculated proxy values to group fires into small (<10 ha), medium (≥ 10 and <100 ha), and large (≥ 100 ha) classifications.

I used a χ^2 goodness-of-fit test ($\alpha = 0.05$) for each fire-shed in order to assess whether fire size varied spatially with fire frequency. Fire frequency groupings were based upon PMFI estimates of: ≤ 25 years; > 25 and ≤ 50 years; and > 50 years. Observed values were the proportions of fires in each size class assigned to chronologies from each of the fire frequency groupings. Expected values were the overall proportions of fires in each size class regardless of fire frequency group.

2.4. Tree recruitment analysis

I created species-specific recruitment chronologies for all plots by grouping pith dates into 10-year bins. Pith dates for non-plot fire-scarred trees were included with those of the closest plot. These trees were typically older than many plot trees therefore their inclusion provided greater temporal depth for the recruitment record.

I visually compared temporal variability in tree-recruitment to variability in the occurrence of large fires and to an independent, tree-ring-based index of the Palmer Drought Severity Index (PDSI), a high frequency (annual) measure of June through August drought. I averaged values for four grid points closely associated with the fire-sheds (grid points 71, 72, 86, and 87; Cook et al., 2004).

Fire dates from BMC and LAW were composited into site-level chronologies for a regional analysis of climate-fire interactions across 18 sites in Utah and eastern Nevada (Brown et al., 2008). Basic fire regime and forest demographic data for the same set of sites are presented in Heyerdahl et al. (2011) without interpretation.

3. Results

3.1. Fire frequency

Point mean fire interval (PMFI) estimates ranged from 11.2 to 106.0 years for nine plots at BMC (Fig. 2). PMFI estimates varied from 7.8 to 109.5 years for four non-plot tree clusters and from 9.5 to 100.4 years for six pairs and eight individual trees, for a total of 27 PMFI estimates at BMC. Fire frequency was correlated with elevation ($r^2 = 0.570$; $p < 0.001$; Fig. 3) and as predicted, fire intervals were shortest (low PMFI estimates) for mid-elevation (2500–2800 m) mixed-conifer stands and became gradually longer with increasing elevation. Most lower elevation, pinyon-juniper woodland plots lacked sufficient fire scar evidence to support a PMFI estimate, however, plot 12J was an exception with an intermediate estimated PMFI of 50 years. Although I was not able to cross-date

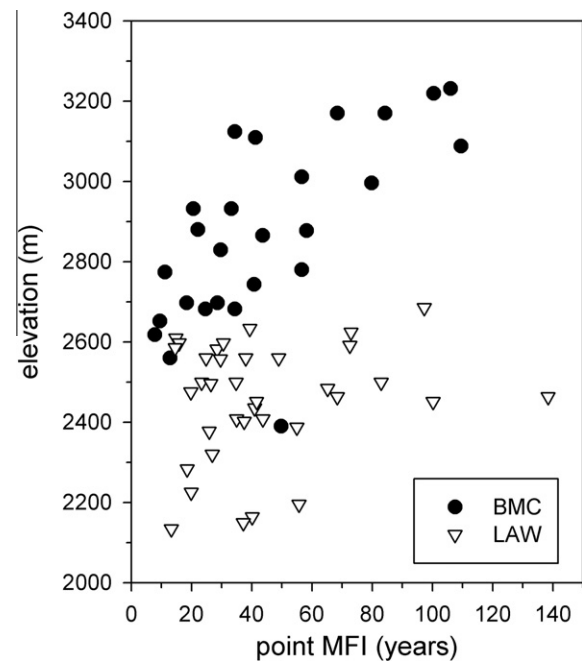


Fig. 3. Correlation between elevation and point mean fire interval estimates for BMC ($r^2 = 0.570$; $p < 0.001$) and LAW ($r^2 = 0.030$; $p = 0.314$) fire-sheds.

fire-scars samples taken from five mature mountain mahogany trees located in woodland and shrub-steppe communities, their presence provided direct evidence that periodic surface fire shaped at least portions of these communities. PMFI estimates were generally shorter for chronologies sampled from lower- and mid-slope positions (mean 22.9, range 7.8–43.6 years) than for those taken from upper and ridge positions (mean 84.2, range 11.2–109.5 years).

PMFI estimates for 10 plots at LAW ranged from 24.8 to 100.2 years (Fig. 4). Estimated PMFI varied from 14.8 to 68.4 years for 10 non-plot tree clusters and from 13.3 to 138.4 years for four pairs and 12 individual trees, for a total of 36 PMFI estimates at LAW. Variation in PMFI was not correlated with elevation ($r^2 = 0.030$; $p = 0.314$; Fig. 3) or slope position with mean PMFI estimates for lower, middle and upper (including ridge-top) slope positions of 44.9, 46.5 and 39.0 years, respectively. Although the fire-shed lacked true subalpine forests, multiple Great Basin bristlecone pine (*Pinus longaeva*) trees were sampled in three, upper elevation plots, thus these plots might be thought of as transitional. Average estimated PMFI for two of these plots (8B, 9B) was 85.0 years (Fig. 4). Fire-scars were absent or insufficient for estimating PMFI for five pinyon-juniper dominated plots. Estimated PMFI for a sixth (7C) was 73 years. Extreme ages of fire sensitive trees and the lack of fire evidence (neither fire scars nor char) at two pinyon-juniper plots (2C and 4D; Fig. 4) suggest that some portions of this landscape were largely unaffected by fire over long (> 800 years) time periods.

3.2. Fire size

Fires were assigned to 99 years at BMC and 124 years at LAW. Recorded fires spanned 640+ years at both sites (Figs. 2 and 4). As predicted, most fires at both fire-sheds were classified as small (BMC 64%, LAW 60%) with medium- and large-sized fires approximately equal for both fire-sheds (BMC medium 20%, large 16%; LAW medium 16%, large 24%; see examples Fig. 5). First and last dates for large fires were 1538 and 1865 at BMC and 1423 and 1825 at LAW. Mean, minimum, and maximum intervals for large

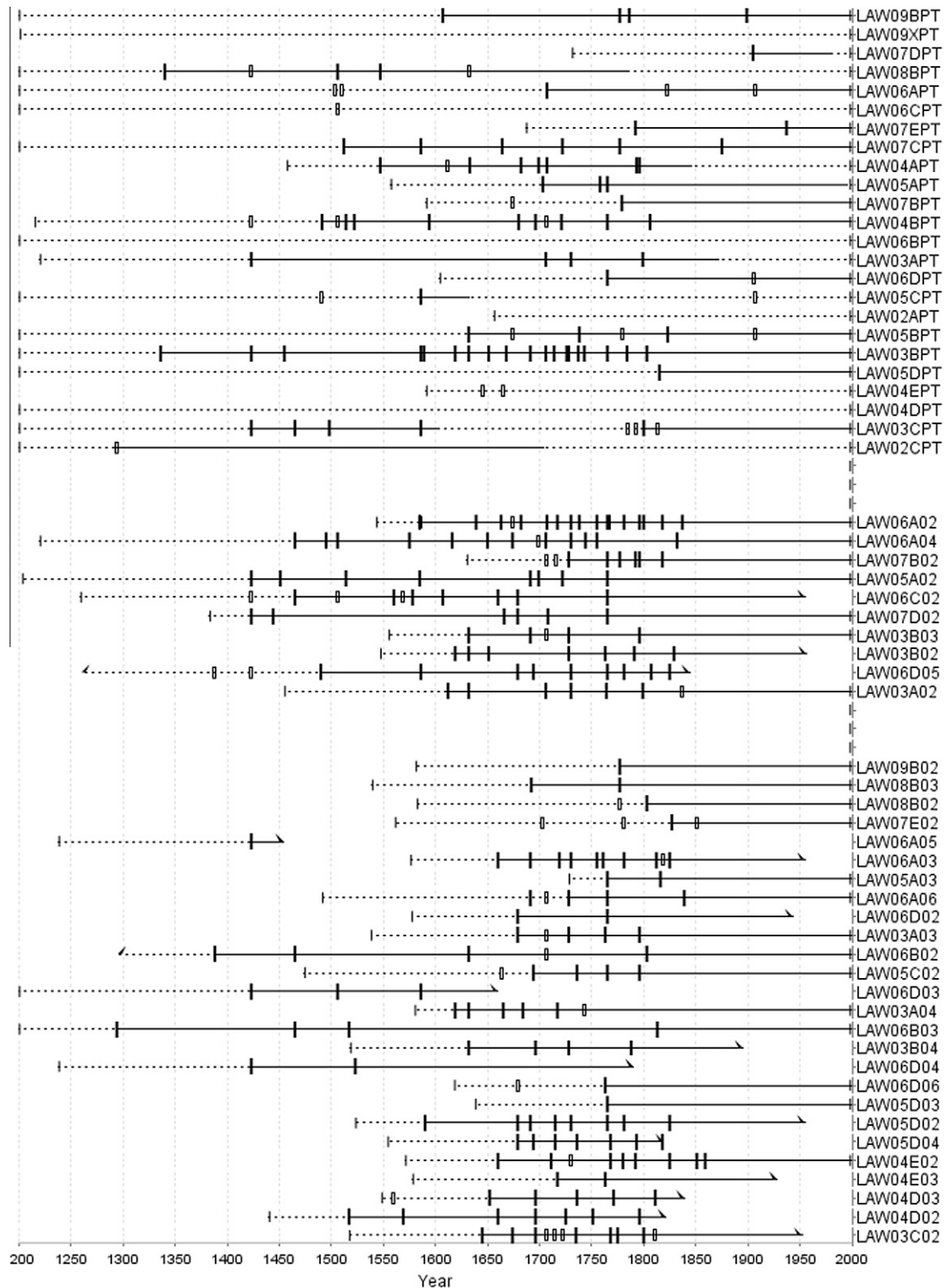


Fig. 4. Fire history chronologies for the Lawson Cove (LAW) fire-shed located on the Wah Wah Mountain Range. Lower axis designates calendar years (1200–2000). Horizontal lines represent plot composite chronologies (top group), composite chronologies for clusters with ≥ 3 trees (middle group), and chronologies for single trees or tree pairs (bottom group). Within groups, chronologies are arranged by elevation with highest elevation plots or trees at the top of each group. Alphanumeric codes on the right indicate plot identity. Solid horizontal lines indicate chronologies are in recording status. Solid vertical lines indicate years with fire scars and open vertical lines designate injuries or abrupt changes in ring widths for individual chronologies.

fires were 22, 1 and 67 years at BMC and 14, 1, and 42 years at LAW.

Based upon a running sum of calculated area for all fires, estimated cumulative burn area at the BMC fire-shed was 4507 ha, a

total equal to ~ 7.5 times the area of the fire-shed. Of this total, 3%, 19%, and 78% was attributed to small, medium, and large fires. Estimated cumulative burn area at the LAW fire-shed was 7892 ha, a total equal to ~ 15 times the area of the fire-shed. Of this total, 1%,

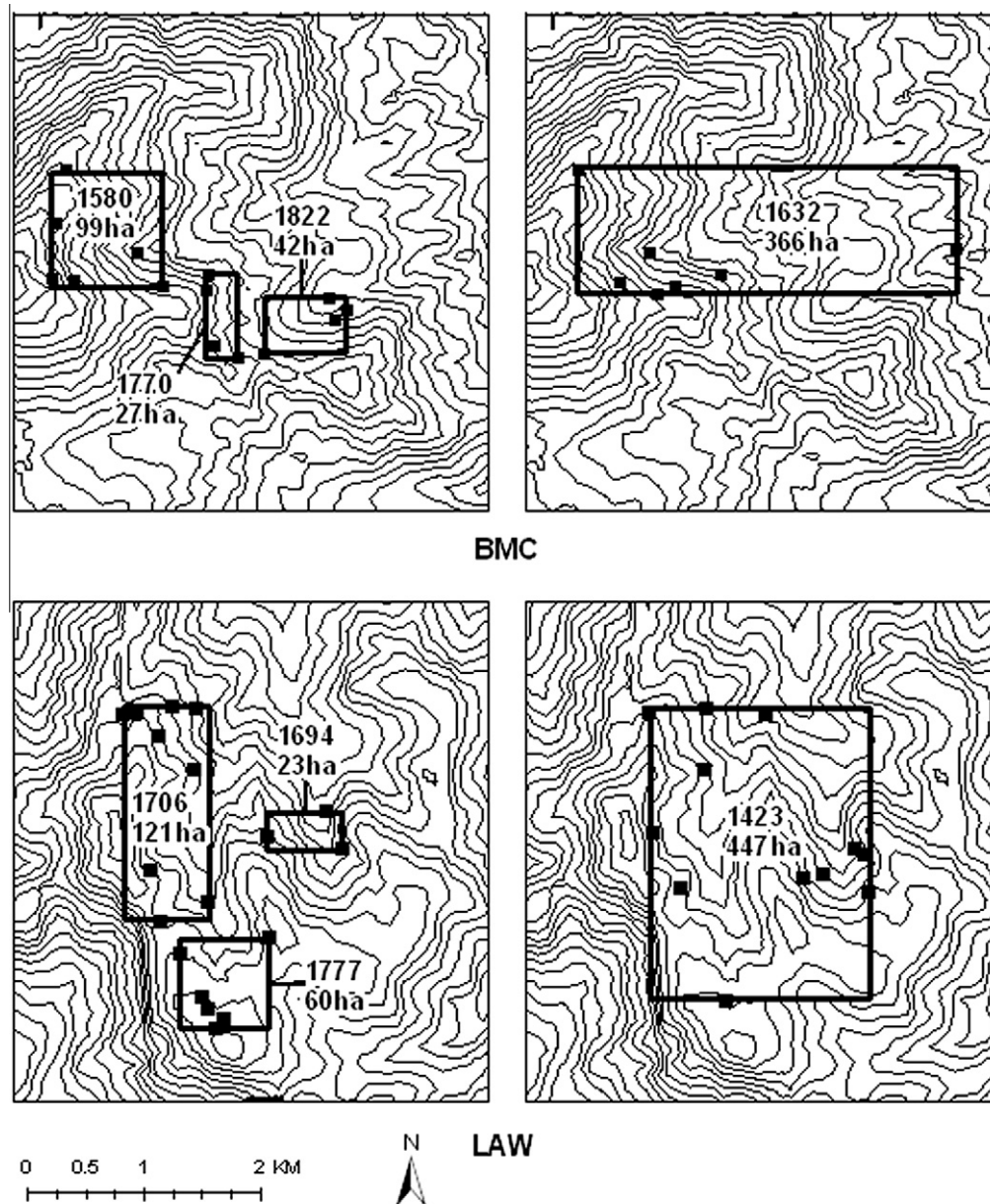


Fig. 5. Examples of how fire size (burn area) estimates were calculated for BMC and LAW fire-sheds where size is equal to the area of the smallest rectangle that is able to include all coordinates of trees recording fire for the year with sides oriented in cardinal directions. Fire-shed, year, and estimated burn area (ha) are given for each example.

10%, and 89% was attributed to small, medium, and large fires. Consequently, even though small fires accounted for more than 60% of the total number of fires, they were responsible for only a small fraction of the area burned. Conversely, approximately one in five fires were classified as large fires which were in turn responsible for more than 80% of the area burned. Thus while years with relatively small fires were common in both fire-sheds, the majority of the area that burned did so during less frequent, large-fire years.

Fires of all size classes burned across the range of elevations at both fire-sheds (see examples Fig. 5). Averaged across all BMC sample points, the proportions of fires experienced by size classification were 41% small, 27% medium, and 32% large. Results of the χ^2 goodness-of-fit tests revealed that size-class proportions did not differ significantly from expected values for high and medium fire-frequency groupings but did for the low fire-frequency (longer intervals) grouping ($\alpha = 0.05$). In the latter case, fire-size proportions were 54% small, 26% medium, and 20% large, indicating that

small fires had greater importance and large fires had lesser importance in forest stands with long fire intervals relative to those with shorter intervals. Relative fire-size proportions for the LAW sample points were 30% small, 17% medium, and 53% large and were not significantly different for any fire-frequency grouping.

3.3. Tree recruitment

I assigned a mean of 21.9 post-1200 pith dates to plot recruitment chronologies at BMC. Recruitment values for recent decades were truncated because of the minimum sample DBH restriction. A small pulse of recruitment for limber pine (*Pinus flexilis*; moderate fire tolerance) and Engelmann spruce (*Picea engelmannii*; low fire tolerance) from subalpine plots (13C and 11C) spanned the late 1400s to early 1500s (Figs. 6 and 7), however there is insufficient evidence for making inferences about the role of fire in regulating tree recruitment during this early period. With one exception, tree

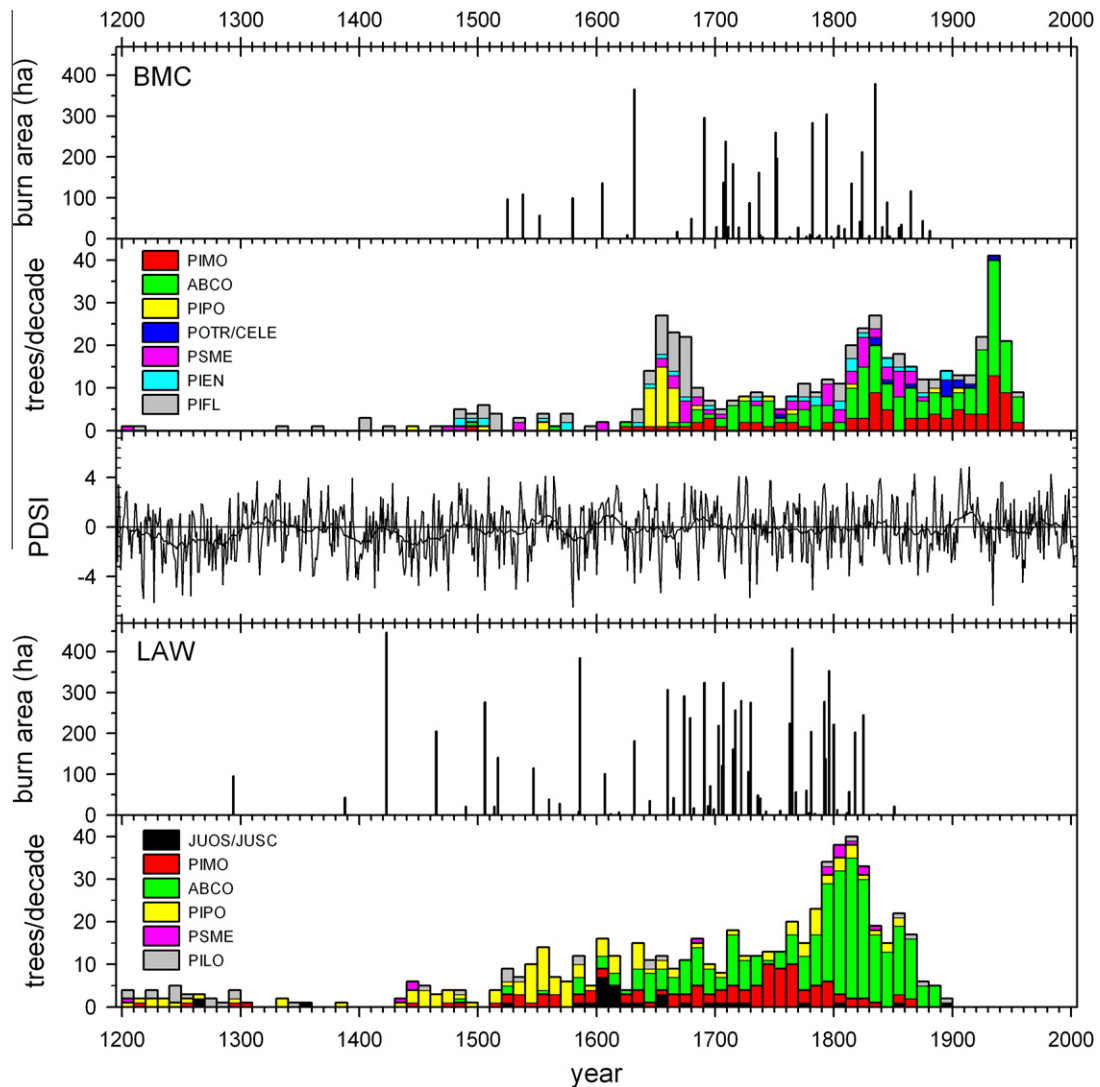


Fig. 6. Fire size (burn area) estimates and tree recruitment (all plots combined) for BMC (top two panels) and LAW (bottom two panels) fire-sheds across 800 years (1200–2000). Tree recruitment dates are in 10-years bins by species. For BMC, red = pinyon pine, green = white fir, yellow = ponderosa pine, dark blue = quaking aspen and curleaf mountain mahogany, rose = Douglas fir, light blue = Engelmann spruce, and grey = limber pine. Colors for LAW are the same except for these changes: black = Utah and Rocky Mountain juniper and grey = Great Basin bristlecone pine. Annual variation in Palmer Drought Severity Index (PDSI) is plotted in center panel for comparison. Negative PDSI values are indicative of drought where the degree of departure from the mean (center line) is indicative of drought intensity. Positive departures indicate wetter conditions in the same manner. Decadal-scale variation in PDSI indices is shown by line smoothed with a cubic spline that retains 50% of variation over segments of 25 years. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

recruitment for plots in the sub-alpine association (11C, 12C, 12D, 13C, 13D and 13E) was asynchronous during the study period. In contrast, a recruitment pulse dominated by fire-tolerant ponderosa and limber pines in the mid-1600s was characterized by an extended period of low fire activity that followed a large fire dated to 1632 (Figs. 5 and 6). This pulse was manifest at one subalpine plot (11D) and multiple mixed-conifer plots (Fig. 7), and was unique for ponderosa pine in the BMC record. The frequency and intensity of annual drought during this period, as measured by annual PDSI fluctuations, was about average with the long-term record. Evidence is lacking for a landscape-level recruitment response to a large fire hiatus that occurred between fires dated to 1752 and 1782, however, a surge in white fir recruitment for plot 14G suggests that fire and fire-free intervals could at times be important for synchronizing tree establishment at the stand scale. A multi-species, multi-plot recruitment pulse is centered on the early 1800s, a period of few large fires and little drought (Fig. 6). Recruitment at BMC of the fire-sensitive species, white fir was essentially continuous at the landscape scale (Fig. 6) with

temporally distinct pulses occurring in different plots (Fig. 7). A lack of trees before the late 1800s for six plots (11H, 11I, 12G, 12H, 13G and 13I; Fig. 7) is strong evidence of a more extensive, mostly treeless shrub-steppe than exists today at BMC. Starting in the late 1800s, expansion of the fire-sensitive species, white fir and pinyon pine into these areas coincided with the loss of fire in the fire-shed and a period of favorable climatic conditions (Figs. 2, 6 and 7), and provides evidence that fire was necessary to maintain this vegetation type. Contrary to what was expected, there was no parallel recruitment increase in previously-forested plots during this same period. Pinyon pine recruitment in persistent woodland plots (12I, 12J and 11J) was continuous to sporadic suggesting a lesser role than predicted for fire in structuring this vegetation type.

I assigned a mean of 25.8 (range 5–39) post-1200 pith dates to plot recruitment chronologies at LAW. The lack of recruitment evidence after about 1900 is largely due to the 20-cm sample DBH restriction. I sampled ponderosa, pinyon, and bristlecone pines and Douglas fir (*Pseudotsuga menziesii*; moderate fire tolerance)

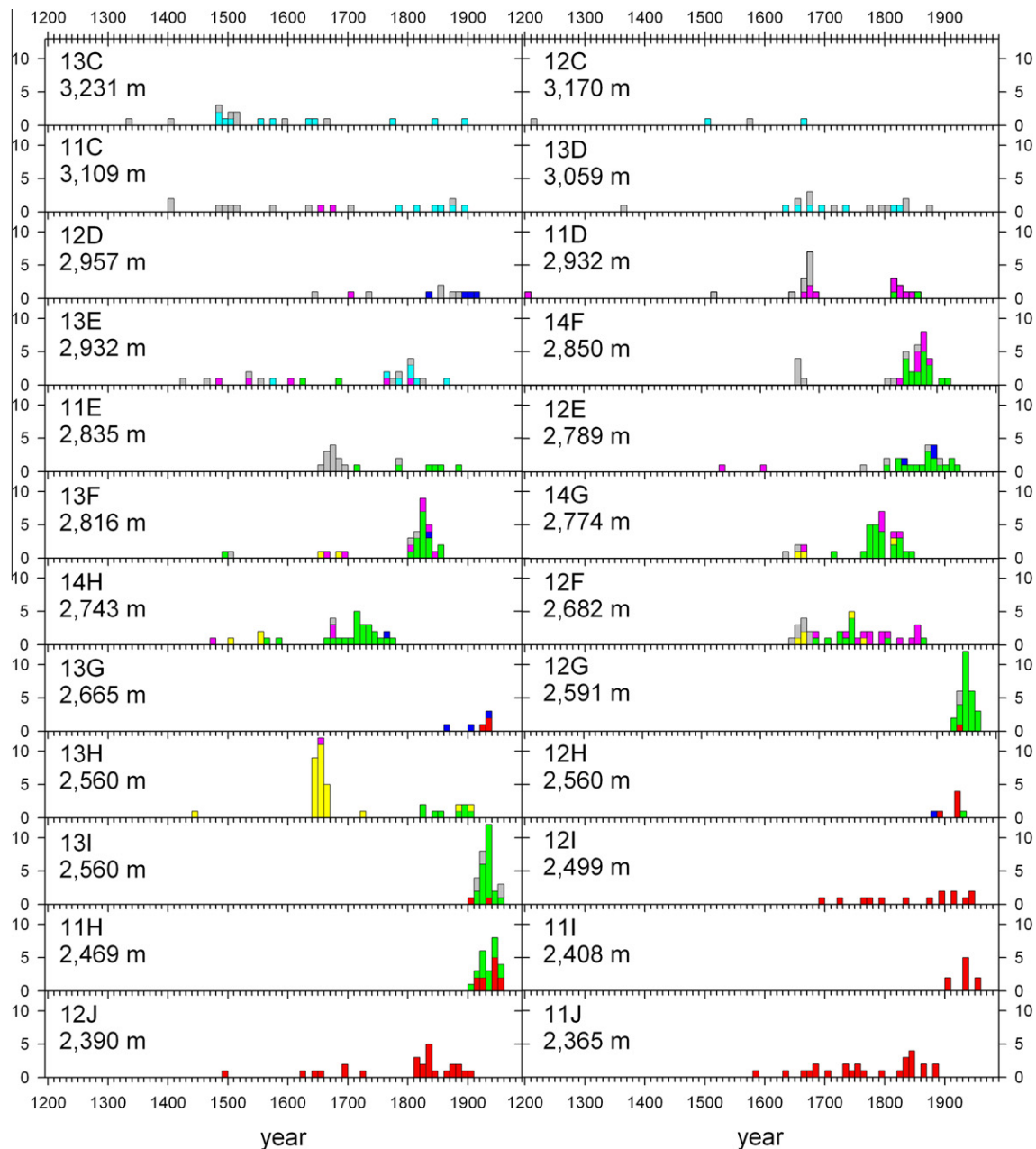


Fig. 7. Individual panels show tree recruitment by plot (1200–2000) at the BMC fire-shed with plots arranged from top to bottom in order of decreasing elevation. Alphanumeric codes indicate plot locations. Recruitment dates are based on pith dates placed in 10-year bins. Tree species are; red = pinyon pine, green = white fir, yellow = ponderosa pine, dark blue = quaking aspen and curlleaf mountain mahogany, rose = Douglas fir, light blue = Engelmann spruce, and grey = limber pine. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

trees that established throughout the 1200s (Fig. 6). This contrasts with the almost complete void of recruitment for the 120 years that started at about the year 1300. This was contrary to what I expected based upon the PDSI proxy record which points to longer and deeper droughts in the 1200s than in the 1300s (Fig. 6), however the record for this early period is inadequate to make inferences about the effects of fire on tree recruitment. A recruitment pulse of primarily ponderosa pine (see plots 6A, 4B, and 5C; Fig. 8) occurred shortly after a large fire dated to 1423 (Fig. 5) that was in turn followed by a long, fire-quiet period (Fig. 6). The PDSI curve suggests that the first few decades of this period were largely drought-free. A second recruitment pulse dominated by ponderosa pine occurred in the 1500s. During this time an 80-year hiatus in large-scale fire was synchronized with what appears to

have been a long period of favorable climate as suggested by a lack of drought years in the PDSI record (Fig. 6). After this time, limited ponderosa pine recruitment at LAW lacked synchrony at both landscape and stand scales. Mixed-species recruitment pulses in plots 7B, 3A, 6D, and 4E followed a large fire dated to 1586. Two moderate-sized fires were exceptions to the otherwise long (74-year) fire-quiet period that followed (Fig. 6). In contrast, nine large fires were dated to the period between 1660 and 1730 (71 years). In spite of the clear difference in fire activity, total tree recruitment at the landscape scale was similar for these sequential periods. Recruitment during a mid-1700s fire quiet period included a mixed-species pulse in plot 4A and one of pinyon pine in plot 2A (Fig. 8). As with BMC, white fir recruitment at LAW was highly synchronous at the plot scale but mostly asynchronous at the

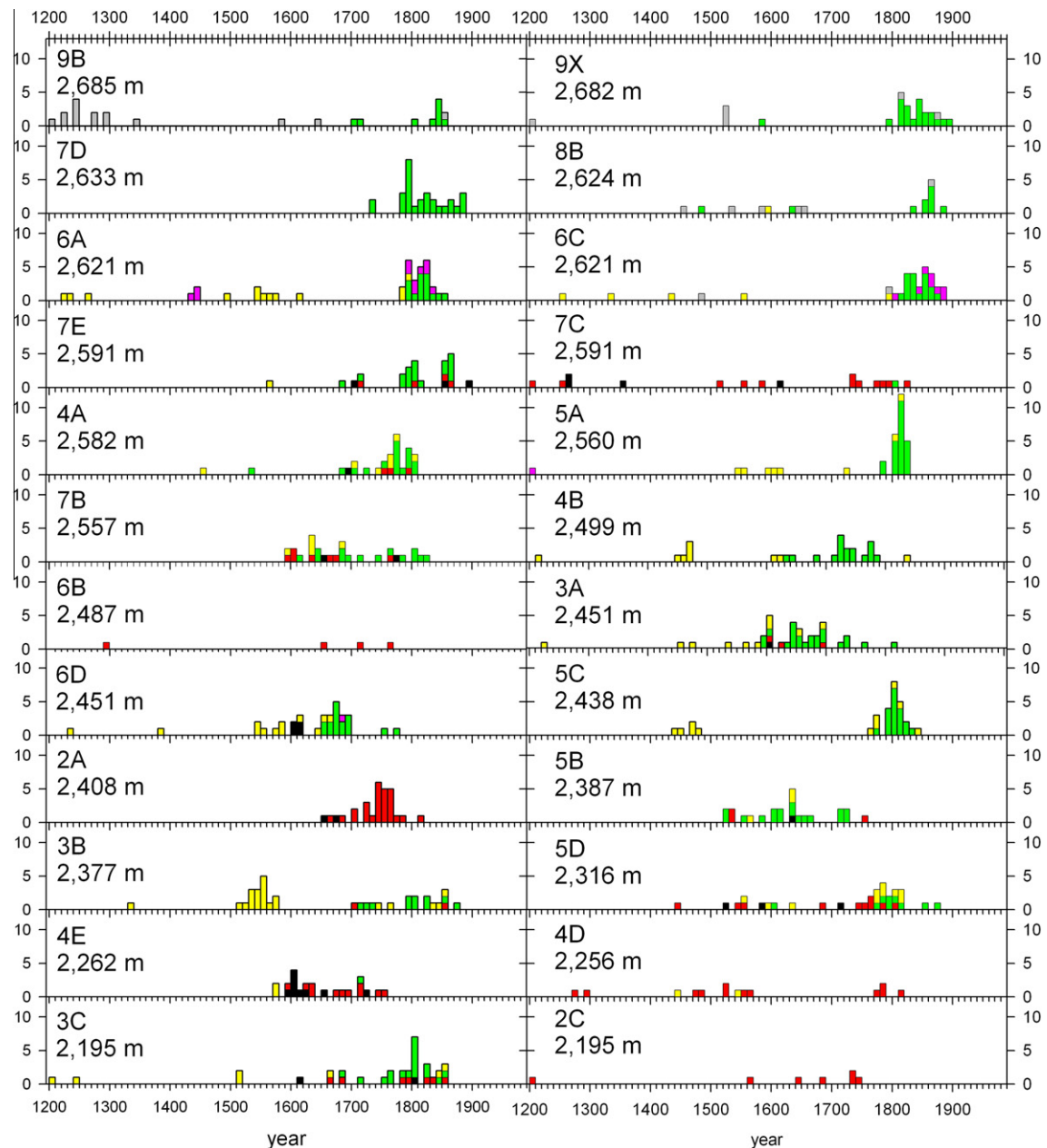


Fig. 8. Individual panels show tree recruitment by plot (1200–2000) at the LAW fire-shed with plots arranged from top to bottom in order of decreasing elevation. Alphanumeric codes indicate plot locations. Recruitment dates are based on pith dates placed in 10-year bins. Tree species are: black = Utah and Rocky Mountain juniper, red = pinyon pine, green = white fir, yellow = ponderosa pine, rose = Douglas fir, and grey = Great Basin bristlecone pine. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

landscape scale with temporally distinct pulses occurring in separate plots (Fig. 8). A widespread pulse of recruitment in the late 1700s to early 1800s (Figs. 7 and 8) provides a notable exception to the pattern of among-plot asynchrony and appears to be in response to broad-scale disturbance associated with large fires dated to 1763 and 1765, but not to have been affected by a series of large fires during the several decades that followed (Fig. 6).

With the exception of the pinyon pine pulse observed in plot 2A, recruitment in pinyon–juniper woodland plots (2C, 4D, 4E, 6B, 7C) was essentially asynchronous across spatial scales (Figs. 6 and 8). Most juniper trees that co-dominated on old growth pinyon–juniper plots (2C, 4D, 6B, 7C) could not be cross-dated, however as many as 1445 rings were counted per tree. Although exact ages could not be determined due to the unknown effects of false and missing rings, these trees were clearly very old. In

contrast to BMC, I found no evidence in support of an extensive, tree-less shrub–steppe at LAW prior to Euro-American settlement.

4. Discussion

At the landscape scale, fire recurred frequently at both fire-sheds for several centuries however the spatial distribution of surface fire was highly uneven, resulting in a more than 10-fold difference among PMFI estimates. Differences in PMFI were correlated with elevation and slope position at BMC, but not at LAW. The lack of an elevation effect at LAW was likely due to the relatively narrow range in elevation (~500 m versus ~1000 m at BMC) and to the lower maximum elevation (absence of a true subalpine vegetation zone) for this fire-shed (Fig. 3). Longer fire intervals have

been associated with higher fire severity due to buildup of fuels (Brown et al., 2001; Bekker and Taylor, 2001; Beaty and Taylor, 2008; Margolis and Balmat, 2009) however, evidence of that kind of relationship was lacking here. In fact the pulsed recruitment that is cited as evidence of higher fire severity (Brown and Wu, 2005; Bekker and Taylor, 2010; Heyerdahl et al., 2011), was most pronounced in mid-elevation plots where fire was also most frequent (Fig. 7), and was mostly absent in BMC subalpine stands where evidence of nonlethal surface fire (fire-scars) was common. This combination of relative high fire frequency based upon fire scars and localized recruitment pulses is indicative of a mixed-severity fire regime especially for middle-elevation, mixed-conifer stands.

For the most part, fire frequency in persistent pinyon-juniper woodlands could not be inferred directly but length of fire-free intervals clearly ranged from moderate to very long; the latter associated with old-growth stands at LAW on fire protected sites. These stands were unaffected by many proximal fires (low to moderate severity) over the course of several centuries suggesting that the effects of abrupt changes in topographic features (e.g. soil depth, rock cover and aspect (solar exposure)) on fuels parameters (e.g. tree and shrub density and fine fuel production and continuity) were sufficient to consistently exercise fine-scaled control of fire spread. Recruitment evidence also supported an interpretation of variability in fire severity for this vegetation type. Results are consistent with contemporary views that suggest that qualitatively distinct fire regime classes (e.g. frequent, mixed-severity to infrequent, high-severity) can be appropriately applied to the pinyon-juniper woodland vegetation type (Baker and Shinneman, 2004; Romme et al., 2003; Romme et al., 2008). It is also clear that a broad range in specific fire regime parameters (i.e. frequency and severity) may be observed for the same landscape as topographically-related changes in vegetation and fuels are manifest over short distances.

I observed a substantial difference in mid-elevation fire-frequency estimates for the two principal sub-drainages of the BMC fire-shed. The shortest PMFI values at BMC (mean = 10.4 years) were associated with plots 13H and 14G and two closely associated clusters located in the southern fork of the fire-shed (Figs. 1 and 2). Average PMFI for plot 12F and five non-plot clusters was 26.7 years and represent the highest fire frequency within the northern fork of the fire-shed. A lack of pre-1900 trees on plots from the mid-elevation ridgeline that separates these sub-drainages supports an interpretation that this part of the fire-shed was occupied by shrub-steppe vegetation, implying some degree of fuel discontinuity between the adjoining forested slopes (Huffman et al., 2008; Iniguez et al., 2008). However, I was unable to deduce a topographic explanation for the more than twofold difference in PMFI values associated with these matched sub-drainages in which elevation, slope, and forest composition are similar.

Alternatively, I suggest that the higher fire frequency observed for the south drainage may have been due to differential Native American ignition rates. A case can be made to support the hypothesis based upon an interest in active management of bighorn sheep (*Ovis canadensis*) habitat (Williams, 2004). Bighorn sheep are native to the Snake Range. Periodic burning would have maintained vegetation in the open, park-like or treeless state that this species requires (Risenhoover and Bailey, 1985; Singer et al., 2000). Burning would also initiate periodic freshening of grasses, providing desirable forage for these large herbivores. Fire might also have been used to drive game during the hunt (Williams, 2004). Bighorn sheep prefer proximal (<300 m) escape cover, usually in the form of rocky ledges (Singer et al., 2000; McKinney et al., 2003) such as those found adjacent to the south sub-drainage but only at greater distances from the north sub-drainage. It is likely that frequent fire was key to maintaining sufficient wild sheep habitat in the past, and the absence of substantial burning over the past

century has contributed to a shortage of suitable habitat on this and similar mountains today.

The abrupt loss of frequent fire at BMC was more or less synchronous with Euro-American settlement suggesting that the change was due to removal of fine fuels by livestock, disruption of Native American burning practices, or some combination of these factors (Covington and Moore, 1994; Kay, 1995). This change occurred several decades earlier at LAW and approximately 50 years before domestic sheep were introduced to the area (Murdock and Welsh, 1971). Multi-decade reductions in fire occurrence in the late 1700s and early 1800s have been reported for other ponderosa pine and mixed-conifer forests elsewhere in the region (Swetnam and Baisan, 1996; Heyerdahl et al., 2001; Brown and Wu, 2005; Skinner et al., 2008; Iniguez et al., 2009). This hiatus in fire activity corresponds to an extended cool period with reduced amplitude in inter-annual wet-dry oscillations, conditions favorable for reduced fire activity (Kitzberger et al., 2001). Thus climate might be invoked to explain the multi-decadal gap between fire regime change and the introduction of domestic sheep at LAW. However, no parallel early 1800s disruption in fire regime was observed for BMC or for a similar Great Basin location (Biondi et al., 2011), suggesting that climate alone may not provide a satisfactory explanation for the asynchrony in fire regime change. An alternative hypothesis assumes that ignitions were a limiting factor and that a differential disruption of human ignition patterns could have been linked to a major perturbation in the regional human population. Although a late-1700s arrival for Euro-American diseases to the region might be considered overdue (Reff, 1991; Butzer, 1992), a delayed, disease-induced depopulation event is plausible given low Great Basin population densities (Simms, 2008). Consequently, a spatially uneven reduction in anthropogenic burning might have been expected as survivors repeatedly adjusted occupation patterns across the landscape.

Inferences regarding the spatial distribution of fires by size class have important implications regarding spatial heterogeneity of fire frequency. Iniguez et al. (2008) observed in the Santa Catalina Mountain of southeastern Arizona that within-study-area differences in fire frequency were due primarily to the relative size and not frequency of widespread fires and implied a somewhat equal contribution from small fires to localized fire frequency. In that study, local fire frequency was subject to the continuity of landscape-level fuels matrices as controlled by surrounding topography. I observed a similar pattern at BMC where the importance of small fires increased and large fires decreased in stands where fire intervals were longest. I infer that this shift in the relative importance for small and large fires applies primarily to upper slopes at higher elevations because that was where longer fire intervals were concentrated. By extension, I also infer that the relatively higher fire frequency experienced on some parts of the landscape was not the product of a disproportionate number of small fires but instead resulted from increased fire numbers across fire-size groupings. No such pattern emerged at LAW in spite of a wide range in PMFI and an abundance of both large and small fires. Thus fire frequency at LAW varied independently of fire size, suggesting strong fine-scale control of fire occurrence and spread. This was likely due to the combined effects of the broken topography and the vegetative heterogeneity that characterized this fire-shed.

Tree recruitment predictions were not well supported by the data. A strong pattern of recruitment synchrony for subalpine and woodland species was expected but not observed. Instead, both continuous and pulsed recruitment was observed across multiple centuries for plots from these vegetation types suggesting stability across a range in fire regimes. A high degree of recruitment synchrony for mid-elevation, mixed-conifer stands was also not expected and suggests that fire severity was moderate and mixed with stand-level recruitment pulses common for fire sensitive

white fir and rare for more fire-tolerant ponderosa and limber pines and Douglas fir.

Recruitment pulses were often synchronized with fire-quiet periods manifest at stand to landscape scales, a pattern similar to that observed by Brown and Wu (2005). The asynchronous timing of these pulse events suggests that recruitment occurred during fire-free intervals that varied spatially. Recruitment was likely enhanced during these periods by favorable climatic conditions (Brown and Wu, 2005). The result was a landscape mosaic of different-aged cohorts and multi-aged patches intermixed with mostly treeless elements (BMC). An exception to this pattern was the widespread recruitment synchronization at LAW in the late 1700s and early 1800s. This white fir-dominated surge of tree establishment followed a large fire dated to 1765 suggesting that this fire may have caused a widespread disturbance of sufficient severity to promote new tree establishment across a large area. Conversely, a series of seven large fires over the next 60 years produced no observable impact on recruitment for this fire sensitive species suggesting that fire severity was sufficiently low that any change in tree recruitment caused by the fires was not detectable in this study. Thus, knowledge of widespread fire events was not sufficient alone to predict tree recruitment response without a better understanding of how fire severity varied across the landscape.

A decline in fire activity began in early-1800s at both fire-sheds and ended in an almost complete loss of fire by about 1825 at LAW and 1865 at BMC. Subsequently, stand densities and associated fuel loads have increased (Heyerdahl et al., 2011) and forest composition and structure have become more homogenized at the landscape scale. The impact is greatest for mid-elevation forests where fire-free intervals were shortest. In addition, historically non-forested shrub-steppe landscapes at BMC are becoming stocked with trees, increasing fuels continuity across vegetation types. Higher-elevation, sub-alpine forests and lower-elevation persistent woodlands where historic fire intervals were longest have been the least affected by the altered disturbance regime. Loss in heterogeneity at both fire-sheds will result in a shift from fine- to broader-scale control of fire, increasing risks for large catastrophic crown fire across all vegetation types (Bekker and Taylor, 2010).

Restoration of fire resilient vegetation to these and similar fire-sheds will require appropriate combinations of natural processes (e.g. lightning-ignited fire) and active management. Priority should be given to restoring structural heterogeneity at mid-elevations where fire regime and vegetation are furthest removed from historical conditions. Strategies for both mixed-conifer and tree-encroached shrub-steppe types should be developed. I recommend incorporation of appropriate combinations of, spatially-limited fire (i.e. during low risk conditions) and fire-surrogate (mechanical) treatments at 1- to 25-ha spatial scales that over time recreate a mosaic of vegetative conditions (Allen et al., 2002; Larson and Churchill, 2012). Treatment severity should be mixed with care taken to preserve individuals of fire-tolerant species (i.e. ponderosa pine) that have declined over the recent past (due to logging). A reduction in the risk for extreme fire events resulting from high fuel loads and landscape homogenization will require sustained efforts by those charged with stewardship of these lands.

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