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Fine-scale variation of historical fire regimes in sagebrush-steppe and juniper woodland: an example from California, USA

Richard F. Miller[A,B,D] *and Emily K. Heyerdahl*[C]

[A]Eastern Oregon Agricultural Research Center, Oregon State University, 67826-A Highway 205, Burns, OR 97720, USA.
[B]Current address: Rangeland Ecology and Management, Oregon State University, 202 Strand Ag Hall, Corvallis, OR 97331-2218, USA.
[C]USDA Forest Service, Rocky Mountain Research Station, 5775 US West Highway 10, Missoula, MT 59808, USA.
[D]Corresponding author. Email: richard.miller@oregonstate.edu

Abstract. Coarse-scale estimates of fire intervals across the mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana* (Rydb.) Beetle) alliance range from decades to centuries. However, soil depth and texture can affect the abundance and continuity of fine fuels and vary at fine spatial scales, suggesting fire regimes may vary at similar scales. We explored variation in fire frequency across 4000 ha in four plant associations with differing soils in which mountain big sagebrush and western juniper (*Juniperus occidentalis* subsp. *occidentalis* Hook.) were diagnostic or a transitory component. We reconstructed fire frequency from fire-scarred ponderosa pine (*Pinus ponderosa* P. & C. Lawson) in one association. The other three associations lacked fire-scarred trees so we inferred fire frequency from establishment or death dates of western juniper and a model of the rate of post-fire succession we developed from current vegetation along a chronosequence of time-since-fire. Historical fire frequency varied at fine spatial scales in response to soil-driven variation in fuel abundance and continuity and spanned the range of frequencies currently debated. Fire intervals ranged from decades in areas of deep, productive soils where fine fuels were likely abundant and continuous, to centuries in areas of shallow, coarse soils where fine fuel was likely limited.

Additional keywords: fire history, grassland, Lava Beds National Monument, mountain big sagebrush, ponderosa pine, succession, tree rings, western juniper.

Introduction

The Intermountain West, USA is largely composed of sagebrush-steppe (*Artemisia* spp.), and juniper (*Juniperus* spp.) and piñon pine (*Pinus* sp.) woodlands (West 1983) that form plant associations (community types of definite floristic composition, uniform habitat and physiognomy) and alliances (uniform group of associations sharing one or more dominant or diagnostic species, generally in the upper stratum) across the region (Grossman *et al*. 1998). These diagnostic species can also occur in other alliances and associations during various stages of succession. Different alliances and plant associations typically intermingle in mosaics across the landscape (Urban *et al*. 1987). These mosaics primarily result from spatial heterogeneity in soils, microtopography and disturbance regimes (Passey *et al*. 1982; Jensen 1989; Miller *et al*. 2005; Davies *et al*. 2007).

In the past, fire played an integral role in determining the dynamics, composition, structure and persistence of vegetation across the sagebrush-steppe and piñon and juniper woodlands (Wright and Bailey 1982; Miller and Tausch 2001). Prior to the late 1800s, fire was largely responsible for maintaining sagebrush-steppe communities by limiting conifer encroachment (Burkhardt and Tisdale 1976; Miller and Tausch 2001). However, fire regimes have changed since the late 1800s, resulting in an increase in the encroachment of conifers into areas they did not previously inhabit and the expansion of annual weeds (e.g. Whisenant 1990; Pellant and Hall 1994; West 2000; Miller and Tausch 2001; Heyerdahl *et al*. 2006; Johnson and Miller 2008; Miller *et al*. 2008). Land managers would like to use fire to restore presettlement vegetation composition and structure but have little quantitative information about historical regimes, especially spatial variation in those regimes, resulting in intense debate over the historical role of fire in maintaining these landscapes. Coarse-scale estimates of fire intervals across the big sagebrush alliance range from decades to centuries (e.g. Wright and Bailey 1982; Frost 1998; Brown and Smith 2000; Baker 2006). These coarse-scale estimates may not account for the fine-scale variation that is relevant for resource management and environmental dialogue, and has led to opposing coarse-scale views of the use of fire in big sagebrush alliances, from applying frequent fire to increase landscape-scale structural diversity to largely excluding fire.

We propose that the role of fire was spatially complex across a range of scales in this semiarid region, and included a wide range of fire intervals. The drivers of spatial variation in fire regimes

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here include topography and soils, which influenced vegetation composition and structure and thus fuels (Pyne *et al*. 1996) and can determine the successional stage that is most persistent through time. In sagebrush and juniper plant associations, soil characteristics (i.e. texture, depth to clay layers and total depth), microtopography (i.e. concave, convex) and incident radiation (a function of slope and aspect) vary across space and influence the spatial heterogeneity of vegetation (West *et al*. 1978; Passey *et al*. 1982; Barker and McKell 1983; Jensen *et al*. 1990; Johnson and Miller 2006; Davies *et al*. 2007). These drivers can vary at fine spatial scales (tens to thousands of hectares), and so fire regimes likely varied at similarly fine scales across sagebrush-steppe and juniper woodlands in the Intermountain West, as they have in other more mesic forested plant communities (e.g. Heyerdahl *et al*. 2001; Taylor and Skinner 2003). Variation in elevation and aspect influences the spatial patterns of fire frequency by influencing the kind of vegetation, and the abundance, moisture content and structure of fuels (e.g. Skinner 1978; Heyerdahl *et al*. 2001).

Lava Beds National Monument, in north-eastern California, is an ideal place to explore fine-scale variation in historical fire regimes in sagebrush-steppe and woodlands. Vegetation at the monument is similar to much of the mountain big sagebrush and western juniper alliances in the Intermountain West (Shiflet 1994; Miller *et al*. 2000). In response to variation in the texture and depth of the soil, these two species occur in a fine-scale mosaic and are the diagnostic species or transitory component of four major plant associations in the monument (Erhard 1980). Furthermore, there is abundant evidence of presettlement fire regimes at the monument in the form of fire-scarred and fire-killed trees, and live trees that established after fire.

Our objective was to determine if historical fire regimes varied at fine spatial scales across a 4000-ha area in Lava Beds National Monument. To do this, we inferred historical fire regimes from tree rings (fire scars on ponderosa pine trees and establishment or death dates of western juniper trees) and a model of the rate of post-fire succession that we developed by measuring current vegetation along a chronosequence of time-since-fire plots in the study area.

Study area

Our study area, the southern half of Lava Beds National Monument in north-eastern California, is 77 km south-east of Klamath Falls, Oregon (Fig. 1). Livestock were introduced into the area in the late 1860s shortly after the Modoc Indian War. Due to limited water, the study area was primarily grazed by sheep with steady use continuing through the early 1950s and than declining until domestic livestock grazing ended in 1972 (Erhard 1980). Records maintained by the monument indicate that the climate is cool and semiarid, with average temperature extremes at monument headquarters of 28°C in July and −6°C in January (1946–2001). Average annual precipitation is 39 cm with the majority (90%) falling between October and June (1946–2001). The monument has extensive basaltic lava flows and scattered cinder cones. The elevation of the study area ranges from 1340 to 1585 m along a gentle north-easterly aspect (0–10% slope, ranging to 40% on the cinder cones). Fire weather occurs in July, August and early September, and dry lightning storms are common during these months. Modern fire records maintained by the monument include 20 wildfires that burned ~33 000 ha between 1911 and 1973, with the largest (>16 000 ha) occurring in 1941. Since 1973 the monument has implemented an active fire-suppression program with fire personnel located on site.

Most of the southern half of the monument is covered by four plant associations (Erhard 1980): (1) pine–fescue (*Pinus ponderosa–Festuca idahoensis*); (2) sage–fescue (*Artemisia tridentata* subsp. *vaseyana–Festuca idahoensis–Pseudoroegnaria spicata*); (3) sage–bluebunch (*A. tridentata* subsp. *vaseyana–Pseudoroegnaria spicata–Achnatherum thurberianum*); and (4) juniper–needlegrass (*Juniperus occidentalis–A. tridentata* subsp. *vaseyana–Achnatherum occidentale*). Mountain big sagebrush occurs in all four associations, being a transitory component in pine–fescue when fire intervals are relatively long. Other shrubs common to the four associations are bitterbrush (*Purshia tridentata* (Pursh.) DC) and grey and green rabbitbrush (*Ericameria nauseosa* var. *nauseosa* (Pallas ex Pursh.) Nesom & Baird and *Chrysothamnus viscidiflorus* (Hook.) Nutt., respectively). Western juniper can establish and mature in the absence of fire in all four associations (Miller *et al*. 2005). The four associations are contiguous with no major physical barriers to fire spread between them (e.g. recent lava flows, Fig. 1) and grow in areas that differ in soil depth and texture (USDA Forest Service and Soil Conservation Service 1986). Soils are primarily derived from eolian deposits of pumice and ash, which are underlain by basalt. Underlying the pine–fescue association are inceptisols that are medial–skeletal, frigid, andic xerocherpts with depths of greater than 100 cm and textures from gravelly sandy loam to extremely cobbly loam. Underlying the sage–fescue association are mollisols that are cobbly and gravelly sandy loamy, mixed, mesic, aridic argixerolls. Soil depth in this plant association is moderately deep (60–150 cm) and the texture ranges from gravelly sandy loam to cobbly loam to extremely cobbly heavy loam. Soils that underlie the sage–bluebunch association are stoney and very cobbly loam-skeletal, mixed, mesic, lithic argixerolls with thin, weakly developed mollic horizons. Soils are shallow to moderately deep (35–60 cm), half that of the pine–fescue or sage–fescue soils. Under the juniper–needlegrass association are entisols that are cindery, mesic, typic, xerothents. Soil depth is shallow (30–60 cm) and texture is gravelly loamy coarse sand pumice to extremely gravelly coarse sand. The diagnostic grasses of the four associations reflect a tolerance for this variation in soil depth and texture, from cool–wet to warm–dry (Idaho fescue > bluebunch wheatgrass > Thurber needlegrass > western needlegrass; Shiflet 1994).

Methods

Modern vegetation and post-fire succession

To calibrate our model of the rate of post-fire succession (e.g. Yanish 2002; Miller *et al*. 2005; Johnson and Miller 2006), we measured the modern herb cover (grass–forbs), shrubs and trees at 53 plots sampled over 4000 ha. We sampled plots across a chronosequence of time since fire (5–145 years, Table 1). For most plots, we obtained the date of the last fire from written records. However, the last fire in some plots occurred before such records were kept, beginning in 1911. For these plots, we obtained the date of the last fire from fire scars (described below)

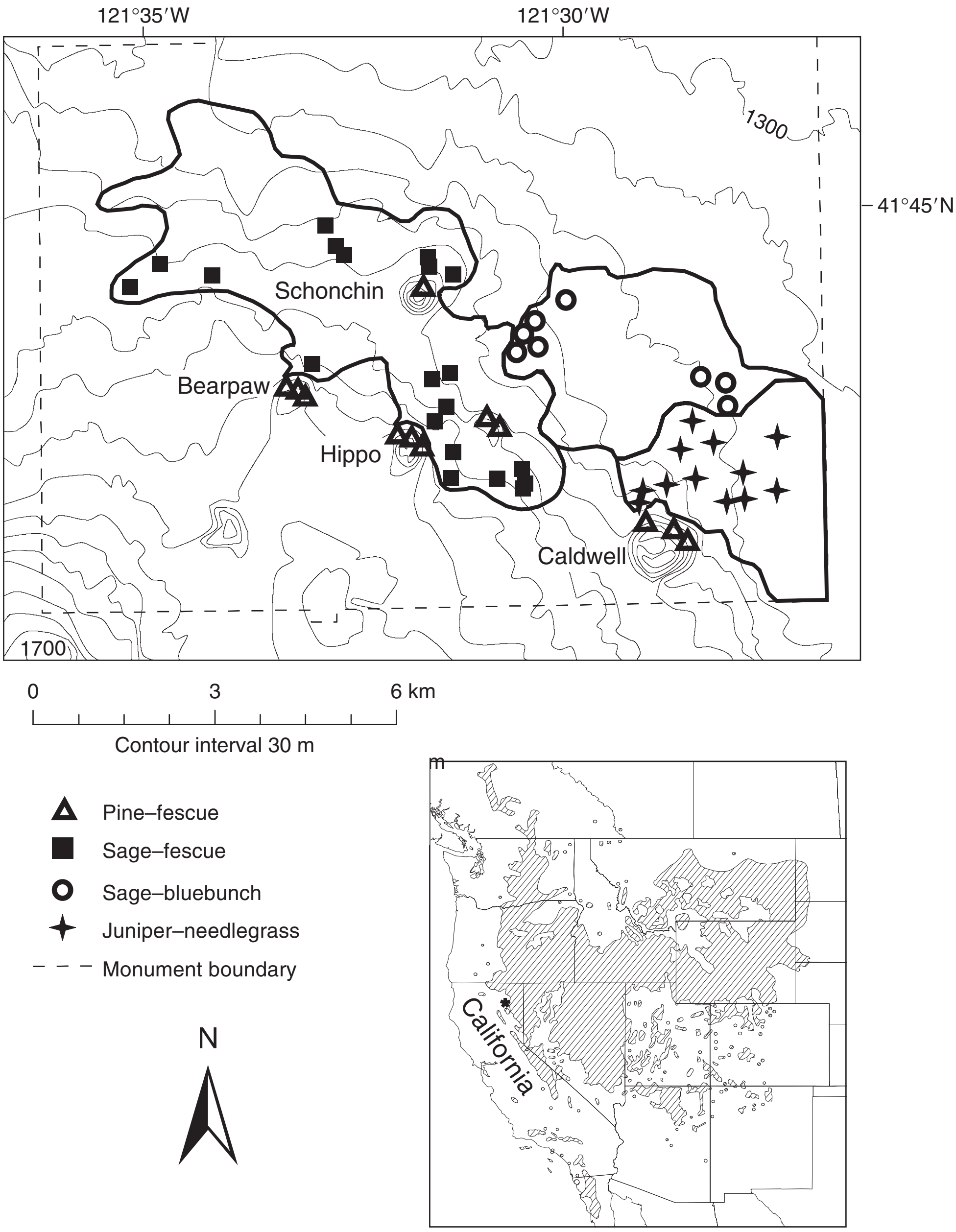

Fig. 1. The study area (4000 ha) in the southern half of Lava Beds National Monument, California, showing locations of plots sampled for vegetation in the four plant association types. The extent of the sage–fescue (2000 ha), sage–bluebunch (1000 ha) and juniper–needlegrass (800 ha) plant associations are shown by heavy lines. The pine–fescue association (200 ha) occurred only on the north sides of the cinder cones, but fire-scarred trees occurred on only three of these (Bearpaw, Hippo and Caldwell Buttes). The shaded area in the lower map shows the combined range of all the subspecies of big sagebrush (USGS Earth Surface Process 1999).

or from charred western juniper trees we found in the juniper–needlegrass association and that we assumed were killed by a fire. To obtain the date of this fire, we used a chainsaw to remove partial cross-sections from 19 western juniper trees that had charred bark, sampling only portions of the bole that were not eroded or consumed by fire. In addition, we removed a partial cross-section from one live, scarred western juniper tree in the same area that also had charred bark. We sanded and crossdated these sections as described below, and determined the date of the last annual ring formed as an indication of the year the fire burned. We could not crossdate one of the samples and so excluded it from further analyses.

Most vegetation plots (41) were rectangular (40 × 60 m, with three 60-m transects located at 0, 20 and 40 m along the short axis of the rectangle). However, extremely dense stands of western juniper and curl-leaf mountain mahogany (*Cercocarpus* *ledifolius* Nutt.) in the pine–fescue association limited visibility and mobility and made accurately setting up and measuring rectangular plots very difficult. Therefore, for each of the 12 plots in this association we combined the data from three circular plots of roughly the same combined area as a single rectangular plot (15-m radius; 2121 m^2 *v.* 2400 m^2, respectively). In each rectangular plot, we estimated the total cover of grasses plus forbs and bare ground, in 0.2-m^2 quadrats, placed at 3-m increments along each of the three 60-m lines ($n = 60$ per rectangular plot). In each circular plot, we placed the quadrats at 3-m increments along two 30-m transects through plot centre, perpendicular and parallel to the slope ($n = 20$ per circular plot). In each rectangular plot, we measured live shrub canopy cover by species, along three 30-m transects placed in the centre of each of the three 60-m transects (Boyd *et al.* 2007). Shrub cover was measured from the beginning to end of each segment of contiguous live canopy including open gaps <15 cm. In each circular plot, we measured live shrub canopy cover using the same method but along two 30-m transects placed perpendicular and parallel to the slope. To determine the density and cover of western juniper trees, we recorded the number of live and dead trees of this species in each plot. For each live tree, we recorded species and canopy diameter (two perpendicular measurements per tree). We calculated canopy area from the measured canopy diameters $\left(\left(\frac{D1+D2}{4}\right)^2 \times \pi\right)$ and summed it into a total live-tree canopy cover for each plot.

We estimated the establishment dates of live western juniper trees, summarised by decade, to provide a coarse description of post-fire woodland succession across the four plant associations. We estimated the establishment dates of the 20 live western juniper trees that were closest to the centre of each plot. There were no live trees in or near seven of the 53 plots because they were killed by recent fires (Table 1). To estimate the establishment dates of sapling size or larger trees (>8-cm basal diameter), we removed an increment core ~30 cm above ground. To account for the number of years for these trees to reach coring height, we averaged the ages of 107 open-grown trees that were ~30 cm tall and added it to the age of all cored trees (9 years). To estimate the establishment dates of small trees (<8-cm basal diameter), we removed a disk at ground level. Cores and disks were sanded until the cell structure was visible with a binocular microscope, and the rings counted. Unlike other species of juniper, tree-ring series in western juniper reliably form annual rings (Holmes *et al.* 1986). Most cores (98%) intersected the pith or were within 10 rings of it. For samples that did not intersect the pith, we used transparent overlays of concentric circles to estimate the number of rings to pith. We also estimated the establishment dates of 11 old western juniper trees that occurred on rocky inclusions outside our plots in the juniper–needlegrass association. We summarised all estimated establishment dates by decade.

We tallied dead trees to estimate their abundance before the last fire. The majority of the dead western juniper trees were snags with only an outer shell of sapwood remaining. Therefore we could not estimate their establishment dates. However, we assumed that dead trees with well-developed basal fluting established before 1860, because such fluting is commonly found on trees >150 years old (Waichler *et al.* 2001).

We measured modern fine-fuel loads of standing herbaceous dead in early September 2002 for eight combinations of plant association and time-since-fire (Table 1). We clipped herbaceous vegetation to ground level in thirty 1-m^2 plots placed at 6-m intervals along three 60-m transects. The vegetation was dried for 48 h at 60°C and weighed.

We assumed that soils with a mollic epipedon formed under areas historically dominated by grass or grass and shrub (Buol *et al.* 1997). We identified mollic epipedons from field descriptions of the soils, primarily the colour and thickness of any A horizon. At each plot we used a Munsell colour chart (Munsell Color 1994) to determine if a mollic A horizon was present (chroma <3.5 moist; colour values of ≤3 moist and ≤5 dry).

Historical fire regimes of the four plant associations

In the pine–fescue association, we reconstructed a multicentury history of surface fires on three cinder cones from dead fire-scarred ponderosa pine trees that likely died during an outbreak of western pine beetle (*Dendroctonus brevicomis* LeConte, 1876) in the dry 1920s. We removed one to three partial cross-sections from those trees with the greatest number of well-preserved scars (19–31 trees sampled over 2–10 ha per cinder cone). We sanded these sections until the cell structure was visible with a binocular microscope. We assigned calendar years to tree rings using a combination of visual crossdating of ring widths and cross-correlation of measured ring-width series (Holmes 1983; Swetnam *et al.* 1985) using a ring-width chronology that we developed from live ponderosa pine trees growing on the southern edge of the monument. We could not crossdate samples from four of the fire-scarred trees and so excluded them from further analyses. We identified the calendar year in which each scar formed to determine the year of fire occurrence. In addition to fire scars, we obtained a small amount of supporting evidence of fire (10% of all fire dates, 1750–1904) from injuries that were likely caused by fire, i.e. eroded fire scars (ones for which much or all of the overlapping, curled woundwood rings were destroyed by subsequent fires or rot) and abrupt changes in the width of annual rings (Landsberg *et al.* 1984; Sutherland *et al.* 1991). However, because factors other than fires can cause abrupt changes in cambial growth, we used such a change in a given sample as evidence of a fire only when it was synchronous with a fire scar on another tree at the same cinder cone. For each cinder cone, we combined the chronology of fire scars and fire-caused injuries from all trees into a composite record (Dieterich 1980) and computed fire intervals from those years during which at least two trees had a fire scar or fire-caused injury.

To infer historical fire regimes in the remaining three plant associations (sage–fescue, sage–bluebunch and juniper–needlegrass), we used our model of the rate of post-fire succession, which we developed under 20th-century climatic conditions, and the presence of old western juniper trees, and mollic soil horizons. We defined old trees as those more than 140 years old (i.e. those that established before Eurasian settlement in the late 1860s) and recognised them from their estimated establishment dates or the presence of basal fluting if their establishment dates could not be estimated due to missing or rotten centres. The presence of old western juniper trees indicates a long period without fire because this species is readily killed

Table 1. Evidence of past fire regimes in four mountain big sagebrush plant associations in the southern half of Lava Beds National Monument
Fine fuel loads were measured in 2003. Settlement occurred in the late 1860s. The presence of mollic soil horizons indicates that a grassy understorey likely dominated the plots in the past

	Mesic ———									——— Dry	
Variable	Pine–fescue		Sage–fescue						Sage–bluebunch	Juniper–needlegrass	
Time since last fire (years)	11	97–108[A]	5	7	15	28	60	97	60	145a[B]	145b
Number of plots sampled	1	11	3	3	3	3	5	3	8	5	7
Soil depth (cm)	100+		60–150						35–60	30–60	
Soil texture	Gravelly, sandy to extremely cobbly loam		Gravelly sandy loam to cobbly loam to extremely cobbly heavy loam						Stoney and very cobbly loam	Gravelly loamy coarse sand pumice to extremely gravelly coarse sand	
Date of last fire from											
Fire-scarred ponderosa		X									
Park Service records	X	X	X	X	X	X	X		X		
Post-fire succession								X			
Fire-killed juniper										X	X
Mollic horizons dominant?	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No	No	No
Juniper density (trees ha^{-1})	0	268	4	0	7	36	104	54	57	146	38
$>$140 years – dead	No	No	No	No	No	No	No	No	Yes	Yes	Yes
$>$140 years – live	No	No	No	No	No	No	No	No	No	Yes	Yes
$<$140 years – live	No	Yes	No	No	No	Yes	Yes	Yes	Yes	Yes	Yes
Juniper (% cover)	0	5	0	0	0	0	8	2	6	20	2
Mountain mahogany (% cover)	0	80	0	0	0	0	1	5	0	0	0
Shrubs (% cover)	1	5	5	3	15	12	30	45	24	9	18
Herbaceous (% cover)	47	9	32	35	30	7	20	26	8	0	4
Bare ground (% cover)	30	10	30	42	35	39	23	25	63	67	51
Fine-fuel load (kg ha^{-1})	2005	483	2359	1929	1174	–	–	550	255	105	–

[A]Range of composite fire intervals from fire scars for Bearpaw, Hippo and Caldwell Buttes.
[B]145a was a mixed-severity fire, whereas 145b was a stand replacement fire.

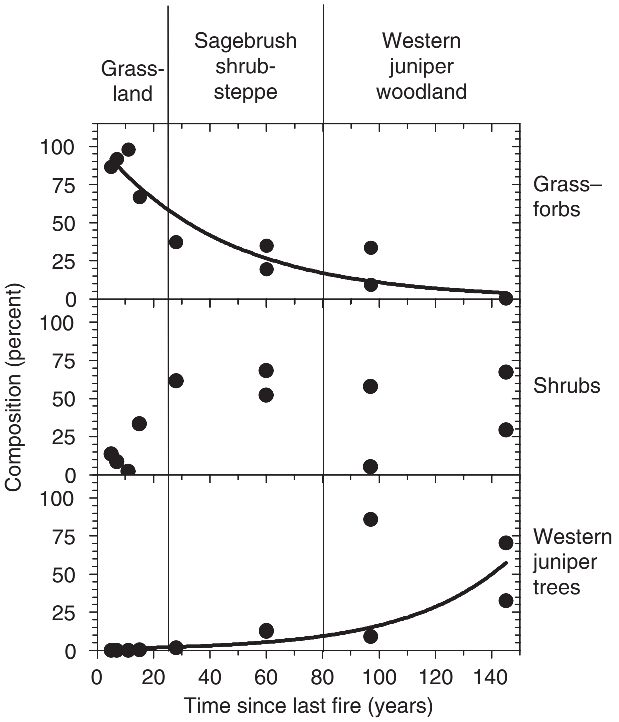

Fig. 2. Post-fire succession in the southern half of Lava Beds National Monument. Percentage composition was computed from the modern herb cover of grass–forbs, shrubs and western juniper trees in plots sampled along a chronosequence of time since fire in the four major plant associations in the study area. The transition at 80 years between shrub-steppe and woodland is for the relatively mesic sites whereas 120 years is more representative of relatively dry sites.

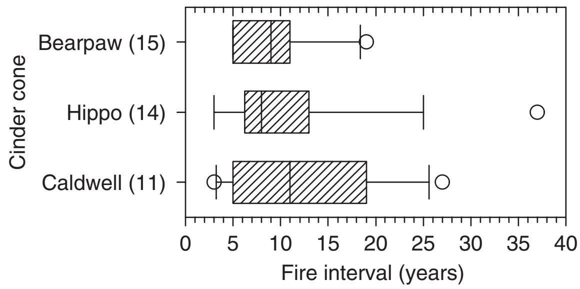

Fig. 3. Composite fire intervals in the pine–fescue plant association, reconstructed from fire-scarred ponderosa pine trees sampled on the north sides of three cinder cones (1750–1904, Fig. 1), with the number of intervals in parentheses. Fire-scarred ponderosa pine did not occur on Schonchin Butte. The boxes enclose the 25th to 75th percentiles of the distribution of fire intervals composited for each cinder cone. The whiskers enclose the 10th to 90th percentiles. The vertical line across each box indicates the median and all values falling outside the 10th to 90th percentiles are shown as circles. The trees were sampled over 2, 4 and 10 ha at Bearpaw, Hippo and Caldwell Buttes, respectively.

when young (less than ~50 years) due to its low crown base (Burkhardt and Tisdale 1976; Miller *et al*. 2005).

Results

Modern vegetation and post-fire succession

Mountain big sagebrush was a dominant species in at least one successional state in all four plant associations; its relative abundance was dependent on time since fire (Fig. 2). The grass–forbs component varied from subordinate to dominant across plant associations, with relative abundance varying with time since fire (Fig. 2). Western juniper trees occurred in every association, but the presence of live trees >140 years old or large dead trees with well-developed basal fluting, suggesting the presence of trees before the 1860s, occurred in only two of the plant associations (Table 1). We found 685 live western juniper trees in our plots. We estimated the establishment dates of 445 of these trees (65%) and found that most of them established after 1860 (408 or 92%). Old live ponderosa pine trees were rare (only seven trees) and old dead ponderosa pine trees were common only in the pine–fescue association.

Our model of the rate of post-fire succession in the relative cover of grass and forbs, shrubs and western juniper trees for the first 140 years following fire suggests that grass and forbs likely dominate for about the first 25 years (Fig. 2). After this time, the relative cover of grass–forbs declines as the relative cover of shrubs increases followed by the increase and eventual dominance of western juniper. From this, we inferred that plots with fire intervals of less than 25 years were historically dominated by grasses and therefore would have soils with mollic horizons. We also inferred that plots not historically dominated by grasses (and so lacking mollic horizons) that had old western juniper trees (i.e. live trees that established before 1860 or dead trees with well-developed basal fluting) likely had fire intervals >80 years, i.e. long enough to allow these fire-sensitive trees to persist.

Historical fire regimes of the four plant associations

Pine–fescue plant association

Fire was historically frequent in this association. We cross-dated fire-scarred sections from 63 ponderosa pine logs and snags, which yielded 372 fire scars and 42 fire-caused injuries during the analysis period (1750–1904). The composite median interval was 8 years (range 3–37 years; Fig. 3). During most fire years for each cinder cone, fires were recorded across much of the sampled area for that cone but generally did not spread between cones. Scars were created on an average of 73% of the recording trees per cinder cone per fire year (range 17–100%). Of the 12–16 fire years per cinder cone, only two to four were synchronous between pairs of cones, and of these only one was synchronous among all three cones (1792). The fire-scar dates and associated metadata are available through the International Multiproxy Paleofire Database (ftp://ftp.ncdc.noaa.gov/pub/data/paleo/firehistory/firescar/northamerica/uslbb001.fhx and also uslbb001.txt, uslbc001.fhx, uslbc001.txt, uslbh001.fhx, uslbh001.txt, accessed 29 February 2008). We found mollic soil horizons in this plant association, indicating that it likely had a persistent grassy understorey in the past, consistent with its deep, loamy soils and our model of the rate of post-fire succession. This association lacked live or dead western juniper trees >140 years old, indicating that such trees likely did not occupy this plant association before 1860 (Table 1, Fig. 4*a*–*c*). Rather, the overstorey likely contained only scattered ponderosa pine.

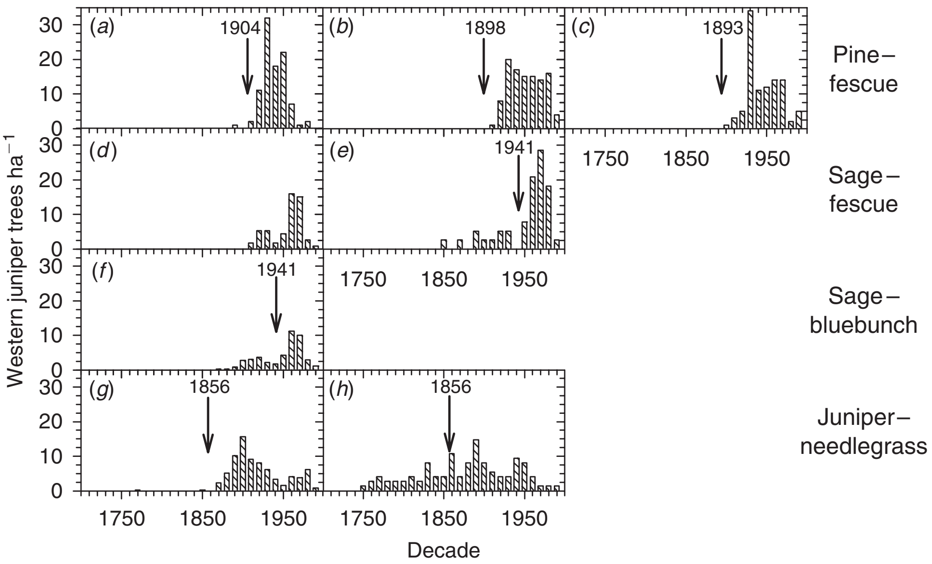

Fig. 4. Establishment dates of live western juniper trees for plots within each plant association in which such trees occurred: pine–fescue (*a–c*), sage–fescue (*d*, *e*), sage–bluebunch (*f*), juniper–needlegrass (*g*, *h*) associations. The date of the last fire is indicated by an arrow for each plot for which it is known. Trees were cored or sectioned 30 cm above ground level. Dead western juniper trees (not shown) occurred only in the juniper–needlegrass association.

Sage–fescue plant association

The lack of live or dead western juniper trees with basal fluting in this association suggests that historical fire intervals were short enough to limit the development of large western juniper trees or woodlands (Fig. 4*d*, *e*). Tree age structure and the presence of mollic soil horizons suggest that the plant composition was historically dominated by grasses or codominated by grasses and shrubs. Consistent with its deep, loamy soils, the modern abundance and continuity of fine fuels we measured in this association were similar to those of the pine–fescue association during the first 10 years following fire (~2000 kg ha^{-1} and grass–forbs cover over 30%; Table 1). Frequent ignition during the dry season, adjacency to the pine–fescue association, and sufficient fuel loads suggest the potential for relatively short fire intervals (<25 years), which would support the historical persistence of grass and forbs communities and limited sagebrush.

Sage–bluebunch plant association

We inferred that historical fire intervals in this association were many decades long, intermediate to those of the pine–fescue or sage–fescue associations and the juniper–needlegrass association. Although a few plots had weak mollic soil horizons, most plots lacked them, indicating that grasses did not persist as a dominant component of this plant association in the past. Rather, fire intervals were possibly much longer than 25 years resulting in persistent shrub cover, and low grass cover in the past. Although there were no live old western juniper trees in this plant association (Table 1, Fig. 4*f*), scattered large western juniper snags with well-developed basal fluting (18 ha^{-1}, likely killed by the 1941 fire) indicate that some fire intervals were long enough in the past to allow the establishment of large individual trees (>80 years between fires) but not long enough for closed woodland to develop.

Juniper–needlegrass plant association

The age structure and death dates of western juniper trees suggest that fire intervals were substantially longer in this association than in the others. The presence of both live and dead old western juniper trees indicates that fire intervals were long enough to allow the development of closed woodland (127 trees ha^{-1}). Live trees in our plots were up to 250 years old and those on nearby rock inclusions were even older (300 to over 500 years). All plots lacked mollic soil horizons, indicating limited persistent grass cover in the past.

Discussion

Historical fire regimes varied within our small study area

Historically, fire regimes varied among the four intermingled plant associations that dominate our relatively small 4000-ha study area, likely due to soil-driven variation in the amount and continuity of fine fuel, and in fact cover the range of coarse-scale estimates of fire intervals (decades to centuries). In our study area, fine-fuel biomass ranged from 100 to 2000 kg ha^{-1}, varying across plant associations and time since fire, similar to the annual production of fine fuels reported for the mountain big sagebrush alliance (700–2700 kg ha^{-1}; Shiflet 1994). Bare ground cover varied from 10 to nearly 70% (Table 1). The fine-scale spatial variation we found in fire regimes was more likely due to spatial variation in fine fuel than to spatial variation in fire ignition or climate across our small study area. Based on Park Service archival records and the fire frequency we reconstructed in the pine–fescue association, ignition was likely sufficient to result in relatively short fire intervals across the monument but not all of the landscape burned at these short intervals. For example, the low-frequency juniper–needlegrass association is juxtaposed with the high-frequency pine–fescue association at the base of Caldwell Butte (Fig. 1) but it appears that fire rarely spread between these two associations in the past even though they are not separated by a barrier to fire spread such as a recent lava flow. We suggest that this was because the fine fuels that carry fire were sparse on the shallow, coarse soils of the juniper–needlegrass association but abundant and contiguous on the deep, loamy soils of the pine–fescue association, resulting in poor fire spread (hence low frequency) in the former but enhanced fire spread (hence high frequency) in the latter. Others have reported changes in plant composition, structure and abundance in mountain and Wyoming big sagebrush communities across changes in soil texture, depth and depth to the clay accumulation layer (Bt horizon) (Passey *et al*. 1982; Jensen 1989; Davies *et al*. 2007).

Despite sparse fine fuels, fires may have spread between plant associations in the study area during windy conditions when fire brands could ignite fires across gaps in fine surface fuels. Although we did not quantify the threshold of fine fuel loadings for fires to move freely across the landscape under non-windy conditions, fine fuel loads of $<250\,\mathrm{kg\,ha^{-1}}$ and bare ground exceeding 50% appear to have supported only infrequent fires, as in our sage–bluebunch association (Table 1). This is similar to other sagebrush-steppe communities, where a minimum of $300\text{–}500\,\mathrm{kg\,ha^{-1}}$ of fine fuel was required to carry a fire under moderate weather conditions (Britton *et al*. 1981; Brown 1982).

The rates of plant succession during the late 19th and throughout the 20th centuries in plant associations at Lava Beds National Monument are similar to those elsewhere in the semiarid Intermountain Region. After fire, mountain big sagebrush canopy cover typically returns to preburn levels (20–30%) in 30–36 years, although recovery can range from 15 to >50 years (Harniss and Murray 1973; Barney and Frischknecht 1974; Watts and Wambolt 1996; Ziegenhagen 2004). The post-fire recovery time of sagebrush depends in part on temporal variation in climate and seed source, particularly during the first 2–3 post-fire years (Ziegenhagen 2004), which may have caused the variation in timing of shrub establishment that we saw at our plots (Fig. 2) and that others have reported. In south-eastern Oregon and south-western Idaho, following the reestablishment of mountain big sagebrush, western juniper can begin dominating relatively cool–wet or warm–dry sites after 80–120 years, respectively (Johnson and Miller 2006). We can only speculate on how the rate of 20th-century succession compares with the presettlement rate. Wetter, cooler conditions would have likely resulted in more rapid rates of woodland establishment (Fritts and Xiangdig 1986; Johnson and Miller 2006) but could have also increased the potential for fire resulting from an increase in fine fuels (Baisan and Swetnam 1990, 1997; Miller and Rose 1999).

Consequences of 20th-century fire exclusion on some plant associations

Throughout the 20th century, the heterogeneity of fire intervals across the four plant associations has declined probably because of the reduction of fine fuels directly by livestock grazing and indirectly by active fire suppression, leading to an increase in mountain big sagebrush in at least two associations and western juniper encroachment across all four associations and hence a decline in grass–forbs (Fig. 2). In the southern half of Lava Beds National Monument, 20th-century fire exclusion has changed the dominant persistent successional state in the pine–fescue and sage–fescue plant associations, leading to the loss of fine-scale variation in plant structure and composition. As time since fire increased, these associations approached a successional state similar to that of the associations that historically had a longer fire interval (sage–bluebunch and juniper–needlegrass). Initially, the relative cover of shrubs and western juniper trees increased, whereas grass–forbs cover decreased (Fig. 2). Because surface fires depend on fine fuels to spread, increasing time since fire in this ecosystem initially leads to a decrease in the potential for surface fires to spread, as grasses and forbs are out-competed by shrubs and trees. This initial decrease in the potential for surface fires is accompanied by an increase in the potential for crown fires due to an increase in the cover of ladder fuels (shrubs and small western juniper trees; Brown 1982). Eventually, however, western juniper trees increase in cover and the surface and ladder fuels provided by the shrubs and small trees decline (Fig. 2; Tausch *et al*. 1981; Miller *et al*. 2000), reducing the susceptibility of the study area to fire and leading to greater homogeneity in vegetation structure among plant associations. Despite the fact that soils played an important role in plant composition, structure and abundance, and hence fuel and fire frequency, western juniper can dominate all four plant associations in the absence of fire. Others have reported juniper species encroaching and dominating mountain and Wyoming big sagebrush plant associations (Miller *et al*. 2000; Johnson and Miller 2008) in addition to other plant associations with very different soils (i.e. riparian and aspen; Miller and Rose 1995; Wall *et al*. 2001) and where the lack of remnant large trees suggests juniper did not occupy these sites before settlement in the late 1860s.

Both resource management and environmental dialogue have focussed on coarse-scale estimates of fire intervals for the mountain big sagebrush alliance. However, soils, the drivers of spatial variation in historical fire regimes in sagebrush-steppe and juniper woodland communities, can vary at relatively fine scales and result in a similarly fine-scale mosaic of fire regimes. If the goal of management is to maintain or restore vegetation to its historical range of variation, managers should consider the potential fine-scale variation in fire regimes that was important in maintaining landscape heterogeneity in our study area in the past and is likely to have been important elsewhere in the Intermountain West.

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