Fire regimes, pre- and post-settlement vegetation, and the modern expansion of western juniper at Lava Beds National Monument, California

2003 Final Report

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Abstract

Fire has maintained vegetation in a dynamic state across Lava Beds National Monument (LABE), and limited the establishment of western juniper and curl-leaf mountain mahogany over time. The historical range of variation of pre-settlement vegetation across LABE constantly changed between grassland, shrub steppe, and western juniper woodland. The broad spatial and temporal range in structure and composition of historical vegetation resulted from interactions between climate, the heterogeneous landscape, and the wide range of fire regimes, which existed across LABE. Specifically, differences in site potential (determined by soils, slope, aspect, and elevation) strongly influenced the abundance and structure of fuels, and hence fire behavior. Consequently, fire regimes varied from high frequency/low severity to low frequency/high severity. Historically, mean fire-return intervals ranged from 8-9 years (1750-1904) in some plant association types to over 150 years in others. Historical mean fire-return intervals were more frequent in productive sites than in sites where production is limited by moisture availability. Western juniper establishment and the presence or absence of pre-settlement trees of this species appeared to be closely associated with fire regimes. Historically, fire created a heterogeneous mosaic of plant communities.

Introduction

Western juniper (*Juniperus occidentalis*[1]) has occupied its historical range since 4800-6600 BP, based on macrofossils (leaves, twigs, and seeds) from pack rat middens in caves and pollen cores (Bedwell 1973, Mehringer and Wigand 1984, Wigand 1987). During this time, the range of western juniper has expanded and contracted in response to variation in climate and fire regimes (Mehringer 1985, Mehringer and Wigand 1990). However, it is currently expanding its range at a rate exceeding that of any expansions during the previous 5,000 years (Miller and Wigand 1994). Specifically, over ninety percent of modern western juniper woodlands have developed in the last 100 years (USDI-BLM 1990). Today, this species occupies 1.4 million ha in northeastern California (Wieslander and Jensen 1946) and 2 million ha in eastern Oregon (Gedney et al. 1999). Western juniper trees generally do not survive fire, and so the cause of this rapid post-settlement expansion of western juniper in part is likely to be fire exclusion (Burkhardt and Tisdale 1976, Miller and Rose 1999). Fires were excluded from this region by livestock grazing, which removed the fine fuels that carry fire, in the late nineteenth century, followed by active fire suppression in the twentieth century. The modern expansion of western juniper has changed the functioning of the ecosystems into which it has encroached. As this species gains dominance, it alters water, nutrient and energy cycles, and plant composition and structure and hence wildlife habitat. As tree density increases and shrubs and herbs decline, plant communities move outside their range of historical variation (Miller et al. 2000). Furthermore, the reduction in understory fuel, through the loss of shrubs and herbs, further limits the spread of fire and contributes to the shift from fire-maintained grassland, or shrub/grassland communities, to western juniper woodlands.

[1] Scientific nomenclature from: Cronquist, A. A.H. Holmgren, N.H. Holmgren, and J.L. Reveal. 1972-1996. Intermountain-flora: vascular plants of the Intermountain West, USA.

Similar to its history elsewhere (Bedwell 1973, Wigand 1987), western juniper arrived at Lava Beds National Monument (LABE) ca. 5300 BP (Mehringer and Wigand 1984), where it has undergone a rapid modern expansion. Historically, fires were probably an important ecosystem process at LABE, based on the presence of charred wood, fire-scarred pre-settlement trees, and abundant post settlement trees. However, modern fires are rare. Historically, the distribution of western juniper and other species, at LABE varied across a gradient of moisture availability that is driven by variation in topography and soils. This variation in moisture availability resulted in differences in the abundance and continuity of fuels, and hence to spatial variation in fire regimes. For example, old western juniper trees, some in excess of 300 years, occur at LABE, typically occupying rocky lava flows and relatively dry, coarse-textured pumice soils in plant communities characterized by western needlegrass (*Stipa occidentalis*). These low-productivity sites supported little understory vegetation and hence fire spread was limited, allowing western juniper trees to reach maturity. In contrast, many other sites did not historically support mature western juniper trees, based on our observations of tree size, growth form, and lack of large dead trees (>30 cm in diameter), and old photographs (Johnson and Smathers 1976). These sites are in the relatively more productive plant associations[2] occupied by bluebunch wheatgrass (*Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*). Like western juniper, mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) occurs throughout LABE, but varies across plant associations with varying moisture availability. Specifically, the dominant diagnostic perennial grass in these plant associations (in order of decreasing moisture availability) is (i) Idaho fescue, (ii) bluebunch wheatgrass, (iii) Thurber's needlegrass (*Stipa thurberiana*), or (iv) western needlegrass (Franklin and Dyrness 1973, Shiflet 1994). Although past work suggests pre-settlement fire-return intervals within several plant associations in the mountain big sagebrush alliance[3] were less than 25 years (Miller and Tausch 2001), pre-settlement fire regimes likely varied among plant associations within this alliance at LABE.

LABE has instituted a prescribed fire program in response to its concerns over the recent expansion of western juniper, the loss of pre-settlement plant communities, and an increase in fuel loads. However, the lack of information on historical fire regimes and pre-settlement vegetation structure and composition has limited the Park Service's ability to design a prescribed fire program that simulates historical conditions.

Goals and Objectives

Primary goals of LABE include restoring plant communities to within their range of historical variation (Johnson and Smathers 1976). Part of achieving this goal will be restoring the fire regimes that were important in maintaining such communities in the past, but no longer operate. Consequently, LABE is developing a long-term fire management plan. To effectively use prescribed fire as a restoration tool, managers at LABE must know the structure, composition,

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[2] **Plant association** is a subgroup within an alliance characterized by an additional diagnostic species from any strata (Grossman et al. 1998; e.g. mountain big sagebrush/Idaho fescue).

[3] **Alliance** is a physiognomically uniform group of plant associations sharing one or more dominant or diagnostic species (e.g., mountain big sagebrush), which, as a rule, are found in the uppermost stratum of the vegetation (Grossman et al. 1998).

and dynamics of pre-settlement vegetation and the role that fire historically played in maintaining it. This information would allow LABE to evaluate the degree to which existing vegetation[4] differs from that of the past, predict potential future changes in the presence or absence of fire, and attempt to restore pre-settlement plant communities.

Our objectives were to answer the following questions for plant associations currently occupied by western juniper in the southern half of LABE:

1. What was the composition and structure of pre- and post-settlement vegetation (i.e., before and after Eurasian settlement, ca. 1870) in the different plant associations?
2. How frequent and severe were pre-settlement fires (before ca. 1870), and did fire regimes vary among the plant associations?
3. After fire exclusion, were western juniper woodlands more likely to develop rapidly in some plant associations than in others?

To achieve our objectives, we first identified six plant associations. To characterize the vegetation that currently exists in these plant associations (i.e., post-settlement vegetation), we measured plant characteristics at 18 sites[5], which are stratified by plant association and time-since-last-fire. We inferred pre-settlement vegetation in these plant associations from post-settlement vegetation, historical fire regimes, and a model of the rate of post-fire succession that we developed from chronosequences of existing vegetation. We reconstructed historical fire regimes from fire scars, the establishment dates of post-fire cohorts of trees, and the death dates of trees killed by fire.

Study area

Lava Beds National Monument, 77 kilometers southwest of Klamath Falls, Oregon in Siskiyou and Modoc Counties in northeastern California, lies in the Basin and Range province (Franklin and Dryness 1973). Elevation ranges from 1,228 m along the shore of Tule Lake in the northeast, to 1,725 m in the southwest. The climate is cool and semi-arid, and is characteristic of the northern Intermountain region. Average annual precipitation at the monument's headquarters is 39 cm with the majority (90%) falling between October and June (average for 1946-2001; Fig. 1). Fire weather occurs during July, August and early September, and dry lightning storms are common during this period. Scattered cinder cones and basalt flows characterize the geology. Soils in the southern portion of LABE are primarily Vitrandepts, which are gravelly to cobbly sandy loams formed from pumice. Soils on which western juniper is a diagnostic species are typically coarser with gravely sand to stony cobbly loams, strongly influenced by pumice (Erhard 1980).

The Park Service's archival records of fire indicate that only 3500 acres burned at LABE between 1910 and 1931, increasing to 18,600 acres during the 1930s. The fires of 1941 and

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[4] **Existing vegetation** is the current expression of floristic composition and variation in structure (Grossman et al. 1998). Existing vegetation is a function of plant association and time since the last fire.

[5] **Site** is an area representing a plant association x time-since-fire combination, which is floristically and structurally similar.

1949 were the most extensive during the 20th century covering approximately 60,000 acres. During the decades of 1950 and 1960 only a few small fires burned across LABE. In 1973 a 950-acre fire threatened the headquarters and visitor center. This threat prompted the beginning of a prescribed fire program at LABE to reduce fuel loads and decrease the expansion of western juniper. Since the 1973 wildfire, all fires greater than one hectare have been prescribed.

At the southern end of LABE, we identified six plant associations that are currently occupied by old and/or young western juniper trees (Table 1; corresponding Habitat Types defined by Erhard are listed in Appendix 1). The distribution of these plant associations across LABE is a function of temperature and available moisture, which are in turn functions of slope, aspect, soil, and elevation. The plant associations we identified at LABE are common throughout the range of western juniper (Eddleman et al. 1994, Miller et al. 2000).

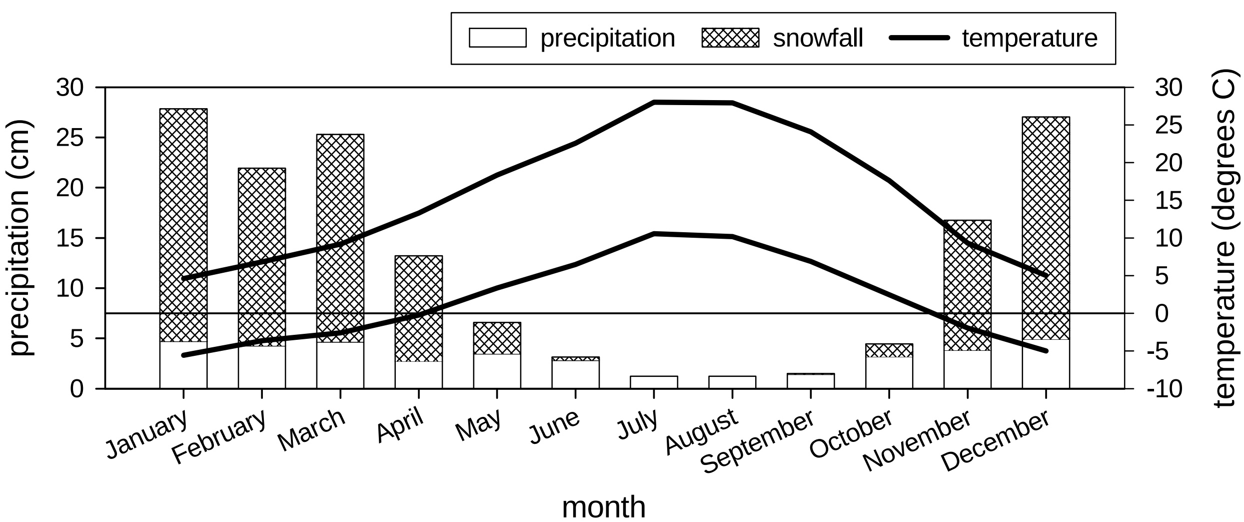

Figure 1. Climate of Lava Beds National Monument, recorded at headquarters (1976-2001).

Figure 2. Map of plant associations and macroplot locations at Lava Beds National Monument.

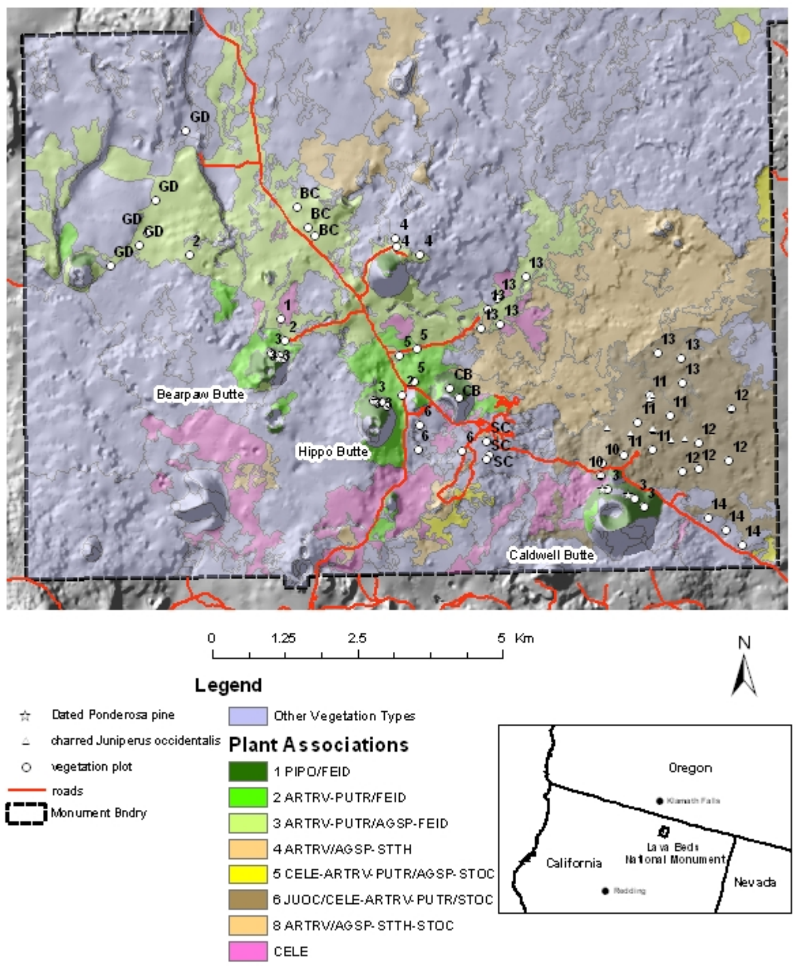

Table 1. Diagnostic species used to define plant associations at the south end of LABE, and the existing vegetation sampled in each plant association. Plant associations are numbered in order of decreasing moisture availability, and are consistently numbered throughout this document.

	Trees		**Shrubs**			**Grasses (cool/moist------------------------->warm/dry)**			
Plant Association Existing Vegetation	ponderosa pine	western juniper	mountain big sagebrush	bitterbrush	mountain mahogany	Idaho fescue	bluebunch wheatgrass	Thurber's needlegrass	western needlegrass
(1) PIPO/FEID	**X**					**X**			
JUOC/CELE/FEID		X			X	X			
JUOC/CELE-ARTRV/FEID		X	X		X				
FEID-AGSP						X	X		
(2) ARTRV-PUTR/FEID			**X**	**X**		**X**			
JUOC/ARTRV-PUTR/FEID-AGSP		X	X	X		X	X		
FEID-AGSP						X	X		
FEID-AGSP						X	X		
(3) ARTRV-PUTR/AGSP-FEID			**X**	**X**		**X**	**X**		
ARTRV-PUTR/AGSP-FEID (FEID-AGSP)			X	X		X	X		
ARTRV-PUTR/AGSP			X	X			X		
ARTRV/AGSP			X				X		
AGSP-FEID						X	X		
AGSP-FEID						X	X		
(4) ARTRV/AGSP-STTH			**X**				**X**	**X**	
ARTRV/AGSP-STTH			X				X	X	
(5) CELE-PUTR-ARTRV/AGSP-STOC			**X**	**X**	**X**		**X**		**X**
CELE-PUTR-ARTRV/AGSP-STOC			X	X	X		X		X
(6) JUOC/CELE-ARTRV-PUTR/STOC		**X**	**X**	**X**	**X**				**X**
JUOC/CELE-ARTRV-PUTR/STOC		X	X	X	X				X
JUOC/CELE-ARTRV-PUTR/STOC		X	X	X	X				X
JUOC/CELE-ARTRV-PUTR/STOC		X	X	X	X				X
ARTRV-PUTR/STOC-STTH			X	X				X	X
ARTRV-PUTR/STOC			X	X					X

Methods

Fire history

Ponderosa pine/Idaho fescue plant association (1. PIPO/FEID)

We reconstructed historical fire regimes in the ponderosa pine/Idaho fescue plant association from fire scars on ponderosa pine trees. Fire-scarred trees were restricted to the north face of cinder cones at LABE (particularly Caldwell, Hippo, and Bearpaw Buttes). Most of the pre-settlement ponderosa pine trees in this plant association were probably killed by an outbreak of western pine beetles (*Dendroctonus brevicomis* Leconte) in the dry 1920s (Park Service archival records). From a census of these dead trees on Caldwell, Hippo, and Bearpaw Buttes, we identified those trees with the greatest number of well-preserved scars (19-31 trees per cinder cone; Appendix 2), and removed one to three partial cross sections per tree. The partial cross sections were sanded until the cell structure was visible under 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, using a master chronology that we developed from ca. 20 live ponderosa pine trees growing on the southern border of LABE (Holmes 1983, Swetnam et al. 1985). Samples from four of the fire-scarred trees could not be crossdated and were excluded from further analyses. To determine the calendar year of fire occurrence, we noted the year in which each scar formed. We also noted the position of each scar within the ring (earlywood, latewood, ring boundary or unknown) as an indication of the season during which the fire burned. The season of cambial dormancy (i.e., the period represented by the ring boundary) spans two calendar years: from the time the cambium stops growing in the summer of one year until it resumes in the spring of the following year. For this study, we generally assigned ring-boundary scars to the *preceding* calendar year because most modern fires at LABE occur in the summer. However, scars from a given fire can have a range of intra-ring positions because the timing of radial growth varies across the landscape (Fritts 1976) and because fires may burn for several months (Parsons and van Wagtendonk 1996). For one fire on Bearpaw Butte (1817) scars occurred in the earlywood of most trees (7) but on the preceding ring boundary of some (3; also, 3 trees with scars of unknown season for this fire). We inferred that the scars in all intra-ring positions were created by a single fire burning early in the growing season of 1817 and therefore assigned the 3 ring-boundary scars to the *following* calendar year (1817), i.e., the same year as the earlywood scars. Scar position could not always be determined where rings were narrow, especially in the vicinity of scars, or because rot or insect galleries obscured scars.

The dates of fire scars from all samples on a cinder cone were combined into a single record of fire occurrence for that cone (Dieterich 1980). General features of fire frequency were assessed using fire charts in which time lines for each tree sampled have crossbars identifying years with evidence of fire (Dieterich 1980, Grissino-Mayer 1995).

Mountain big sagebrush-bitterbrush/Idaho fescue (2. ARTRV-PUTR/FEID)
Mountain big sagebrush-bitterbrush/bluebunch wheatgrass-Idaho (3. ARTRV-PUTR/AGSP-FEID)
Mountain big sagebrush/bluebunch wheatgrass-Thurber's needlegrass (4. ARTRV/AGSP-STTH)
Curl-leaf mountain mahogany-bitterbrush-mountain big sagebrush/bluebunch wheatgrass-western needlegrass (5. CELE-PUTR-ARTRV/AGSP-STOC) plant associations

The year of the last known fire was determined from Park Service archival records for the majority of sites sampled in these plant associations (Table 2). However, for site 2, we had no archival fire date. Consequently, we used the establishment dates of the oldest western juniper trees at a macroplot as a minimum estimate of the date of the last fire, because western juniper trees generally do not survive fire.

Western juniper/curl-leaf mountain mahogany-mountain big sagebrush-bitterbrush/western needlegrass plant association (6. JUOC/CELE-ARTRV-PUTR/STOC)

At some sites in this plant association, we found dead, charred western juniper trees (sites 10, 11 and 12). To obtain the date of the fire that killed them, we used a chain saw to remove partial cross sections from portions of the bole of 19 of these trees that did not appear to have been eroded or consumed by fire. In addition, we removed a partial cross section from one live, scarred western juniper tree. We sanded and crossdated these sections as described above, and determined the date of the last annual ring formed as an indication of the year the fire burned. One of the samples did not crossdate and was excluded from further analyses.

Existing vegetation

Sampling design

To characterize existing vegetation across the southern half of LABE, we sampled 63 plots (51 rectangular and 12 circular), distributed among our six plant associations (Tables 1 and 2, Fig. 2, Appendix 3). To estimate the rate of post-fire succession, we further stratified macroplots within plant associations by the date of the last known fire. We determined the last fire date from archival records (1920-present; Table 2). Although the archival record did not include any recent fires in the western juniper/curl-leaf mountain mahogany-mountain big sagebrush-bitterbrush/western needlegrass plant association (6. JUOC/CELE-ARTRV-PUTR/STOC), there were obvious differences in western juniper density and age structure within this plant association, which we inferred was due to a difference in fire history. Therefore, we placed macroplots in both sections.

The rectangular macroplots were 40 x 60 m (Appendix 4), each with three 60 m transects, located 0, 20, and 40 m along the short axis of the rectangle. One to 5 macroplots were placed within each site (plant association and time-since-fire combination), depending on the area occupied by each plant association (Table 2). Dense stands of curl-leaf mountain mahogany on the north side of Bearpaw, Hippo, Caldwell, and Crescent Buttes (sites 3, CB) made it difficult to mark macroplot boundaries and lay out 60 m lines. Consequently, in place of a single 40 x 60 m macroplot, we sampled existing vegetation in 3 circular plots (15 m in radius) on each cinder cone. The area sampled in three of these plots is similar to that sampled in one rectangular plot (2121 m^2 versus 2400 m^2, respectively).

Table 2. Existing vegetation at LABE, by plant association. Date of last known fire was either (i) determined from LABE archival records, or (ii) reconstructed from tree rings for this study. Stage of western juniper woodland succession was determined from branch leader growth (Miller et al. 2000; Table 3). Plant associations are numbered in order of decreasing moisture availability.

Plant Association	(1) PIPO/FEID[1]			(2) ARTRV-PUTR/ FEID			(3) ARTRV-PUTR/AGSP-FEID					(4) ARTRV/ AGSP-STTH	(5) CELE-PUTR-ARTRV/AGSP-STOC	(6) JUOC/CELE-ARTRV-PUTR/ STOC				
Site	3	CB	CB’	2	5	1	GD	SC	BC	6	4	13b	8	10	11	12	13a	14
Trees																		
Cover%	5	13.2	0	2	t[2]	0	7.5	0.3	0	0	0	6.1	0.8	20.6	20.4	7.7	1.4	1
#/Ha	252	291	0	53	2	0	104	14	0	0	0	53	25	100	127	53	34	26
Dead/Ha	16[4]	20[4]	230[4]	1[4]	5[4]	8[4]	0	22[4]	3[4]	4[4]	0	2.6[4]	18[4]	27[5]	20[5]	54[5]	5.1[5]	18[5]
Total/Ha	268	311	230	54	7	8	104	36	3	4	0	57	43	127	146	107	38	44
Stage of woodland succession	mid	mid	0	early	0	0	early-mid	early	0	0	0	early	early	late OG	late OG	early	early	early
Mt mahogany cover %	80	80	0	5	0	0	1	0	0	0	0	0	1	3	4	1	0	1
Shrub cover %	5	0.5	1	45	15	10	30	11.6	5.9	5	3.2	24	37	14	8.5	26	18	34
Herb Cover%																		
P. Grass	6	3.6	40	25	30	22	19	7	29	26	35	8	4	1	t	t	4	t
A. Grass	2.8	t	1	t	t	t	t	t	1.5	1	t	t	t	t	t	t	t	1.5
P. Herb	t	t	5	t	t	t	0.8	t	t	t	t	t	t	t	t	t	t	t
A. Herb	t	t	1	t	t	t	t	t	t	6	t	t	t	t	t	t	t	1.2
Total herb cover	8.8	3.6	47	26	30	22	20	7	30.5	32	35	8	4	<2	<1	<1	4	<3
Bare ground %	10	4	30	25	35	40	23	39	34	30	42	60	55	54	67	49	65	33
Fine fuel (Kg/ha)	483	-	2005	550	1174	-	-	-	-	2359	1929	255	203	-	105	-	-	-
Macroplots #	9[3]	3[3]	1	3	3	1	5	3	3	3	3	5	3	2	5	5	3	3
Last fire	1893/ 1904	Late 1800s	1990s	Late 1800	1986	1989	1941	1973	1986	1996	1994	1941	1924	1856	1856	1856	1941	1941

[1] AGSP= Agropyron spicatum, ARTRV=Artemisia tridentata ssp vaseyana, CELE=Cercocarpus ledifolius, FEID=Festuca idahoensis, JUOC=Juniperus occidentalis, PIPO=Pinus ponderosa, STOC= Stipa occidentalis, STTH=Stipa thurberiana.
[2]t = trace (<0.5%)
[3]circular plots with 15m radius
[4] Majority of dead western juniper trunks or stumps < 30 cm diameter versus [5] >30cm

Tree size and establishment dates

In each macroplot, we recorded the number of live and dead trees, and the stage of woodland succession (Table 2). Stage of woodland succession was subjectively determined for each macroplot using characteristics developed by Miller et al. (2000; Table 3). For each live tree, we recorded its species, canopy diameter (two perpendicular measurements per tree), height, and basal diameter (at 30 cm height). Canopy area was calculated from the measured canopy diameters $((D1+D2/4)^2 * \pi)$ and summed into a total live-tree canopy cover for each macroplot. We included one shrub species, curl-leaf mountain mahogany in the overstory functional group, rather than the shrub functional group because it formed an overstory canopy (3-4 m in height) above the shrub layer, which was composed of mountain big sagebrush and bitterbrush. Mountain mahogany was only abundant in the ponderosa pine/Idaho fescue plant association (1. PIPO/FEID). We measured canopy cover of curl-leaf mountain mahogany the same way we measured shrub canopy (described below). For each dead tree, we noted indications of it age, specifically size (small (<15 cm), medium (15-30 cm) or large (>30 cm)) and the presence of basal fluting, which is usually well developed in trees over 200 years old.

For most macroplots with trees, we estimated the establishment dates of those 20 live trees that were nearest to the plot center. However, the remaining macroplots contained fewer than 20 live trees, either because trees were not abundant (< 53 trees/ha; sites 2, 8, 12, 13a & b, 14), or not present because the macroplot had burned since 1973 (sites CB', 1, 5, SC, BC, 6, 4)). Consequently, in the low-density macroplots that burned prior to 1973, we estimated the establishment dates of all live trees within the macroplot but also included enough live trees outside, but near, the macroplot, to total 20 trees. We did not estimate tree establishment dates in macroplots that had burned since 1973 because of live trees were absent. To estimate the establishment dates of large trees (>8 cm basal diameter), we removed an increment core ca. 30 cm above ground. To account for the number of years for these trees to reach coring height, we estimated the rate of height growth in each plant association by cutting 12, 30 cm tall trees that had minimal overstory competition. The rate of height growth did not differ significantly among plant associations (ANOVA, p value = 0.90), so we pooled the data from all cut trees (n=107), and applied the same correction factor to all the trees we cored in the study area (9 years to reach 30 cm). To estimate the establishment dates of small trees (<8 cm basal diameter), we removed a disk at ground level. Cores and disks were brought back to the laboratory at the Eastern Oregon Agricultural Research Center, mounted, sanded until the cell structure was visible with a binocular microscope, and ring counted. Most cores (98%) intersected or were within 10 rings of the pith. For samples that did not include the pith, we used transparent overlays of concentric circles to estimate the number of rings to pith.

Shrubs

We measured live and dead shrub canopy cover and density, by species. Shrub canopy cover was measured in each macroplot along 3, 30 m transects placed in the center of the 60 m lines (Appendix 4). Canopy gaps < 15 cm wide within a single shrub were not recorded. Shrub density (excluding mountain mahogany) was recorded in 3, 2 x 30 m plots placed along each 30 m transect. In the circular plots, shrub cover was measured along two 30 m transects placed perpendicular and parallel to the slope contour.

Table 3. Characteristics of successional stages during woodland encroachment into the mountain big sagebrush alliance (modified from Miller et al. 2000).

Characteristic	Early	Mid	Late	Closed
Juniper Dominance	Subdominant	Codominant	Dominant	Dominant
Tree Canopy	Open, actively expanding, cover ≤ 5%	Actively expanding, cover 6 to 20%	Canopy expansion greatly reduced, cover 21-30%	Canopy expansion stabilized, over > 30%
Leader Growth (Dominant Trees)	Good terminal & lateral growth	Good terminal & lateral growth	Good terminal growth, reduced lateral growth	Reduced terminal growth, lateral growth absent
Crown Lift* (Dominant Trees)	Absent	Absent	Lower limbs beginning to die where tree canopy > 40%	Present where tree canopy > 40%
Potential Berry production	Low	Moderate to High	Low to Moderate	Rare to Low
Tree Recruitment	Active	Active	Reduced, limited primarily to beneath trees	Absent
Leader Growth (Understory Trees)	Good terminal & lateral growth	Good terminal & lateral growth	Reduced terminal & lateral growth; reduced ring growth	Absent, some mortality; reduced ring growth
Shrub Layer	Dominant	Codominant	Subdominant ≥ 40% dead	Near absent ≥ 85% dead

*Crown lift is the mortality of lower limbs usually due to shading from neighboring trees.

Herbs
We estimated herbaceous and ground cover by functional groups (perennial grasses, perennial forbs, annual grasses, annual forbs, litter, bare ground, rocks, biological crusts and mosses) in 20, 0.2 m^2 microplots at 3 m increments along each 60 m transect (n = 60 per macroplot). Nested frequency was recorded for all herbaceous plant species in 0.02, 0.2, and 0.4 m^2 plots every 3 m along each 60 m line (n = 60 per macroplot; Appendix 4). In the circular plots, we measured frequency and functional group ground cover in microplots placed at 3 m increments along two 30 m transects placed perpendicular and parallel to the slope contour (n = 60 per macroplot).

Fine fuels
We measured existing fine fuel loads in three macroplots each at least one site for each of the six plant associations (Table 2). To estimate the rate of accumulation of fine fuel for some plant associations (1. PIPO/FEID; 2. ARTRV-PUTR/FEID; and 3. ARTRV-PUTR/AGSP-FEID), we measured existing fine fuel loads in two time-since-fire sites per plant association. Herbaceous vegetation was clipped to ground level in 30, 1 m^2 plots placed at 6 m intervals along 3, 60 m transects within each macroplot. Samples were dried for 48 hours at 60ºC and weighed.

Inferring pre-settlement vegetation
We inferred pre-settlement vegetation composition and structure for each of the six plant associations we sampled at LABE, from (i) the chronology of western juniper establishment that we reconstructed in each plant association, (ii) the mean fire-return interval for each plant association (from archival records or reconstructed from tree rings) and (iii) a model of the rate

of post-fire succession that includes all plant associations. This model estimates the rate of change from grassland to shrub steppe to woodland, following fire. We derived this model from the existing relative cover of three plant functional groups: (i) grasses, (ii) shrubs (excluding curl-leaf mountain mahogany), and (iii) overstory (i.e., trees, western juniper plus curl-leaf mountain mahogany), measured in a chronosequence of time-since-last fire macroplots.

Results and Discussion

Western juniper cover has greatly increased across the south end of LABE (Fig. 3.). However, fire regimes varied among these plant associations, and influenced vegetation dynamics both temporally and spatially. Below, we summarize historical fire regimes, and pre- and post-settlement vegetation, by plant association, in decreasing order of moisture availability.

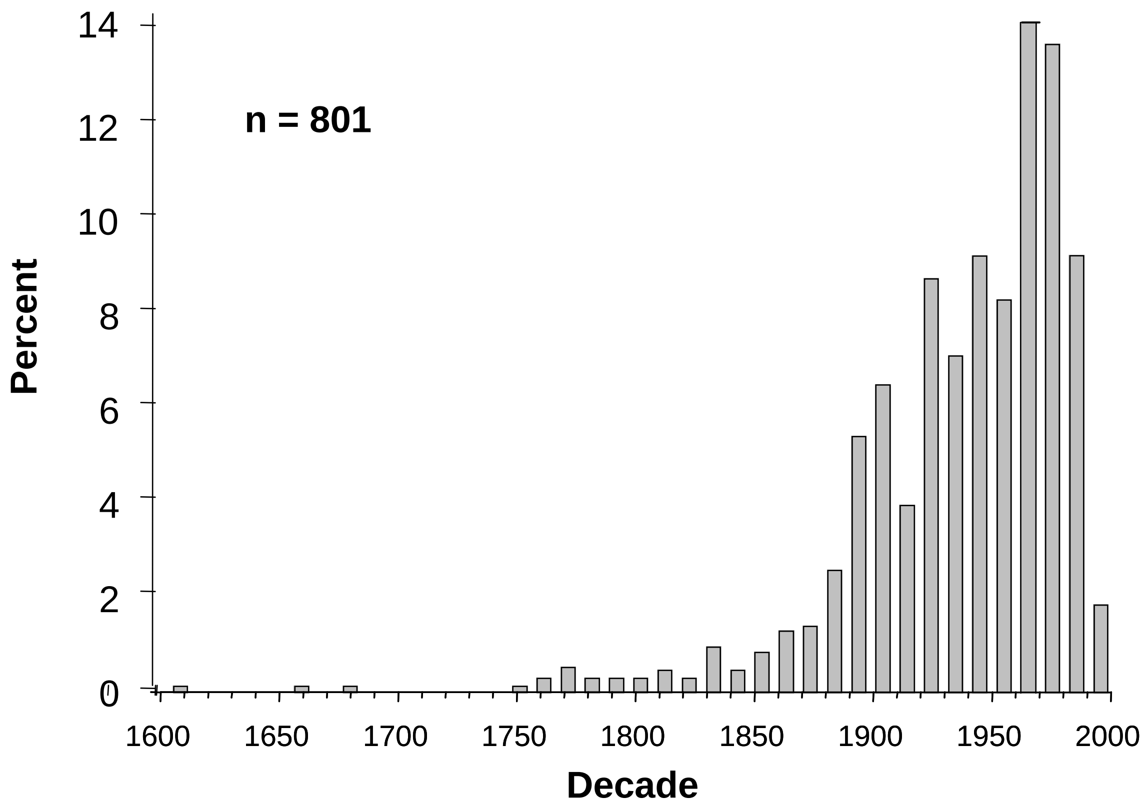

Figure 3. Establishment of western juniper, by decade, measured in macroplots across all plant associations in the south half of Lava Beds National Monument.

Model of the rate of post-fire succession

Our model of the rate of post-fire succession predicts that perennial grasses will dominate for ca. 20 years following fire (Fig. 4). Like western juniper, the dominant shrubs that occur in the plant associations we identified at LABE generally do not survive fire. Tree establishment in the early years following fire is probably limited by low shrub density, both because seed-disseminating birds need shrubs for perching and because western juniper seeds require protected microsites to establish (Burkhardt and Tisdale 1976, Eddleman 1987, Miller and Rose 1995, Soulé and Knapp 2000). American robins (*Turdus migratorius*) and Townsend solitaries (*Myadestes townsendi*), primary vectors of western juniper seed dissemination (Lederer 1977, Poddar and Lederer 1982), typically fly a short distance from the seed source (average of 44 m) to a post-foraging perch, which is usually another tree or shrub, or the ground beneath a woody canopy (Chavez-Rameriz and Slack 1994, Schupp 1993, Chambers et al. 1999).

Following dominance by perennial grasses, our model of the rate of post-fire succession predicts that mountain big sagebrush and bitterbrush will co-dominate with grasses within 20 to 30 years, increasing to dominant status in 40 to 60 years, then decline in relative abundance 80 years following fire. Western juniper canopies develop slowly for the first 45-50 years following establishment (Fig. 5), and so this species remains sub-dominant during that time. After this time, the canopies of western juniper expand rapidly and can co-dominate with shrubs within 70 to 80 years following fire (Fig. 4). Successional patterns are similar for Utah junipers (*Juniperus osteosperma*) and single needle pinyon pine (*Pinus monophylla;* Barney and Frischknecht 1974, Miller and Tausch 2001, Tausch and West 1995). Predicting the rate of succession from shrub steppe to woodland after 80 years is tenuous. The timing of this shift depends on the density of western juniper establishment over time. At LABE, this shift has been fastest in the ponderosa pine/Idaho fescue plant association (1. PIPO/FEID). Based on the current ages and density of western juniper on these cinder cones, trees will dominate within the next 20-30 years (i.e., ca. 120 years following fire). In contrast, the most moisture-limited plant association studied at LABE (6. JUOC/CELE-ARTRV-PUTR/STOC; site 12), is still in the mid-transitional state from shrub steppe to woodland 150 years following fire.

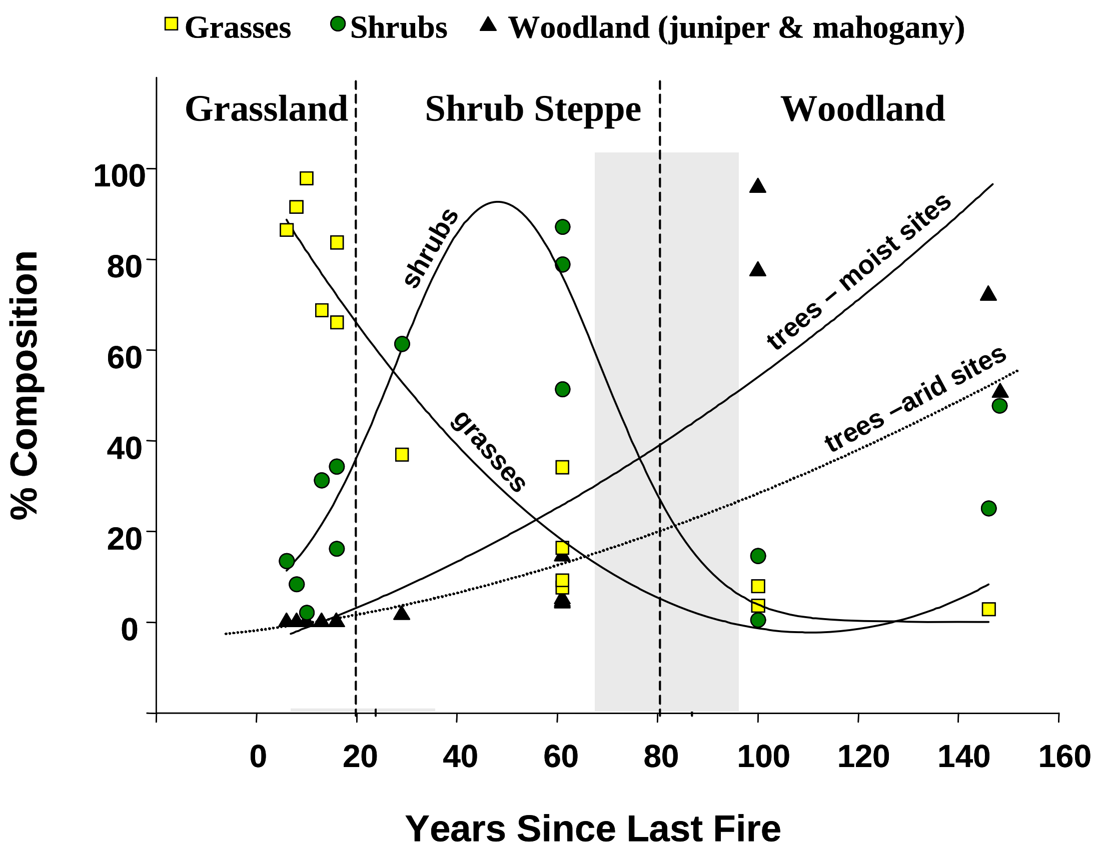

Figure 4. Model of the rate of post-fire succession from grassland to shrub steppe to western juniper woodland. Shrubs and trees co-dominate during the period shown in gray. Percent composition is derived from measured cover of existing herb (i.e., grass), shrub (excluding curl-leaf mountain mahogany), and overstory layer (i.e., trees, western juniper plus curl-leaf mountain mahogany) at Lava Beds National Monument. Moist sites are those plant associations that contain Idaho fescue while arid sites are those that contain western needlegrass.

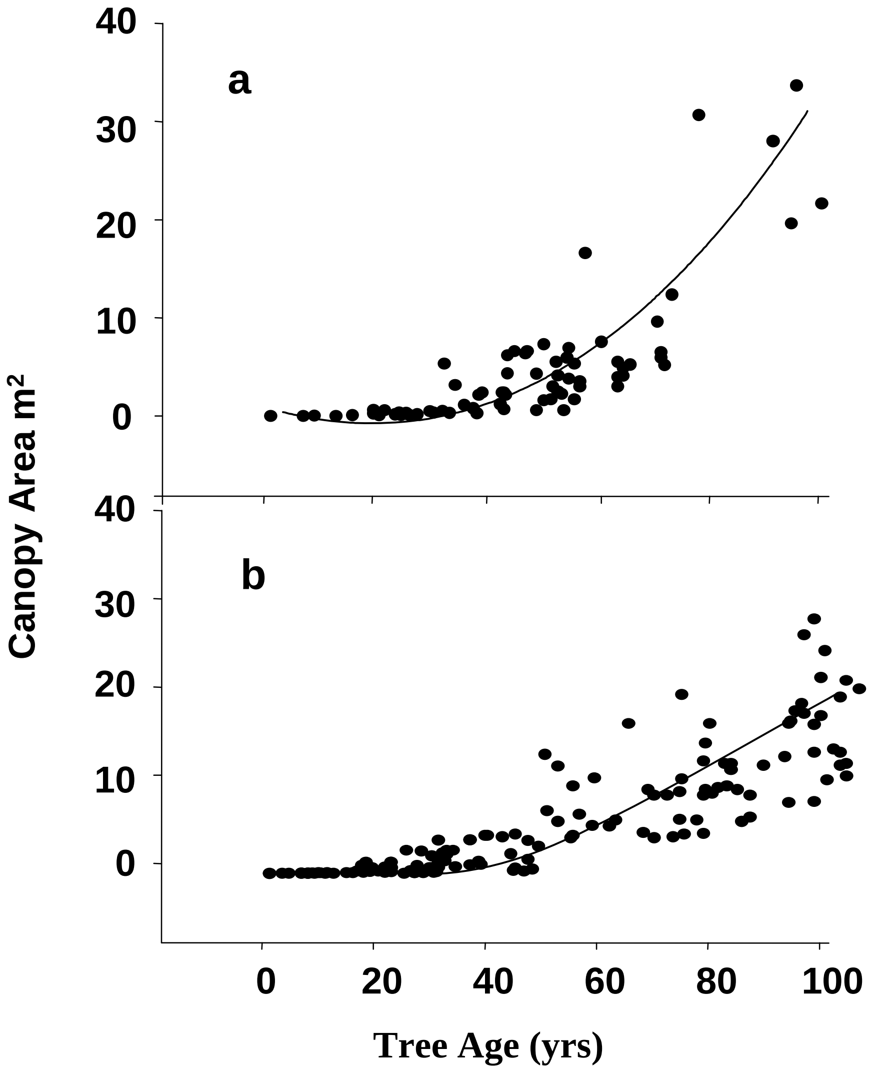

Figure 5. Rate of canopy development in young western juniper trees (≤ 100 years old) at Lava Beds National Monument, in (a) mesic plant associations (site 3; 1. PIPO/FEID) and (b) dry plant associations (sites 10, 11, 12, and 13a; 6. JUOC/CELE-ARTRV-PUTR/STOC).

(1) Ponderosa pine/Idaho fescue plant association
(PIPO/FIED; sites 3, CB and CB')

Historical fire regime

We reconstructed a history of surface fires in this plant association on the north aspects of Bearpaw, Hippo, and Caldwell Buttes (site 3), from 578 fire scars on 63 ponderosa pine logs, stumps and snags (Table 4). Composite surface fires were frequent, and were similar among the three cinder cones (Fig. 6). Median fire-return intervals during the period 1750 to 1904 were 8 to 9 years per cinder cone but ranged from 1 to 37 (Fig. 7). We were able to assign an intra-ring position to half (49%) of the 372 scars that were formed during the analysis period (1750-1904). The distribution of scars by intra-ring position was similar among the three sampling areas (Fig. 8). Of the scars to which we could assign an intra-ring position, about half were created by fires burning when the cambium was dormant (48% ring-boundary scars). The rest of the scars were created during the growing season, about equally divided between the early- and latewood (28% and 23%, respectively).

Pre-settlement fires in this plant association were generally frequent and low in severity, based on the low density of large, old ponderosa pine trees, short fire-return intervals reconstructed from fire scars, and the lack of large, dead western juniper.

Table 4. Amount of evidence used to reconstruct surface fire history in the ponderosa pine/Idaho fescue plant association (1. PIPO/FEID) on the cinder cones. Number of scars includes the entire period of record and also includes duplicate scars (e.g., scars from both sides of a catface).

Cinder cone	Size of sampled area (ha)	Number of trees crossdated	Number of fire scars
Bearpaw	2	18	218
Hippo	4	15	112
Caldwell	10	30	248
TOTAL	16	63	578

Western juniper succession

Curl-leaf mountain mahogany currently dominates the existing vegetation, occupying 80% of the overstory canopy. However, western juniper densities are sufficient to fully occupy the site (160-309 trees/ha; Miller et al. 2000). Western juniper began establishing across the three cinder cones after the last fire events on these sites (Fig. 9a). There was no evidence that western juniper was part of the pre-settlement vegetation.

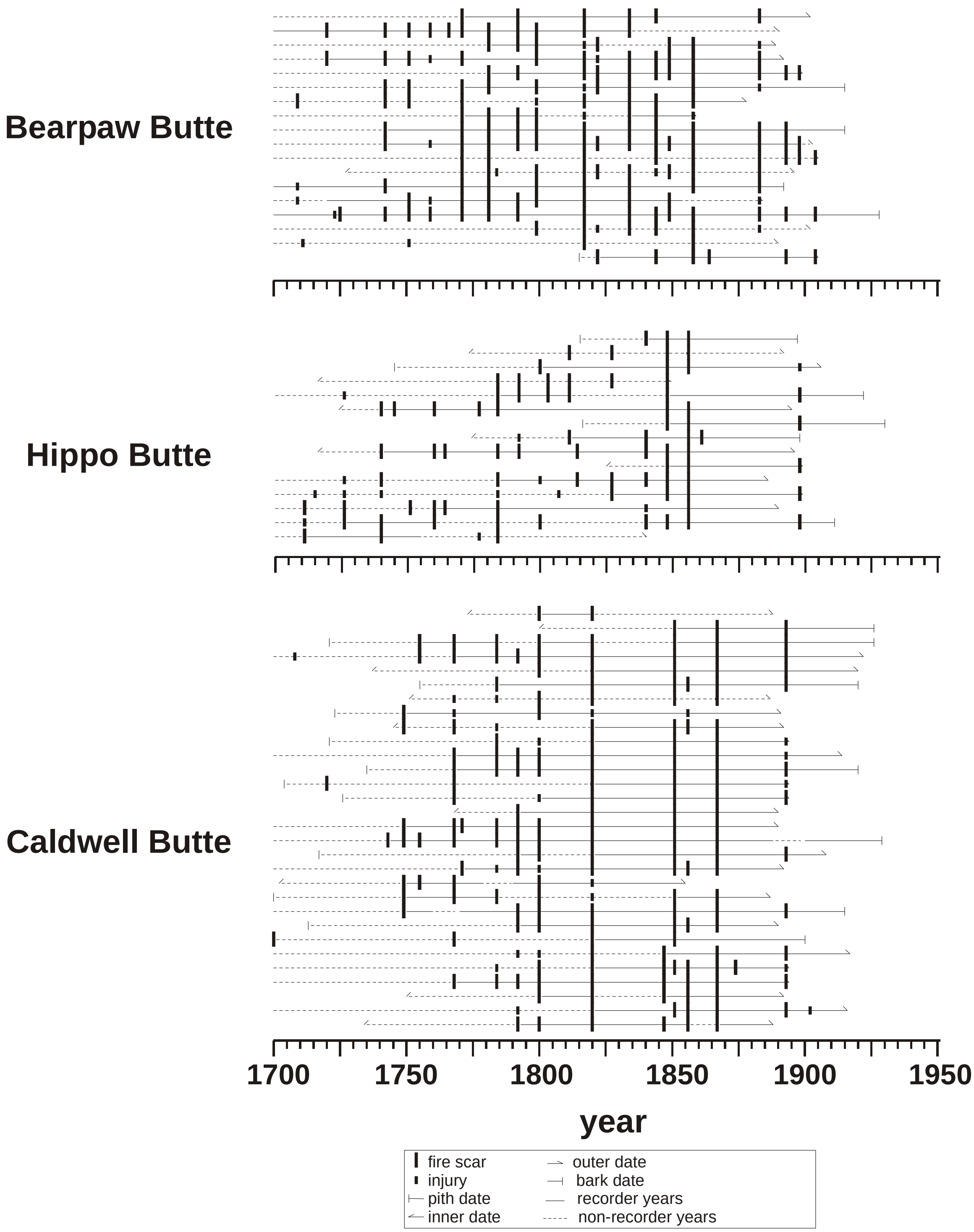

Figure 6. Chronology of surface fire occurrence on sampled cinder cones. Each horizontal line shows the fire-scar record for a single tree through time.

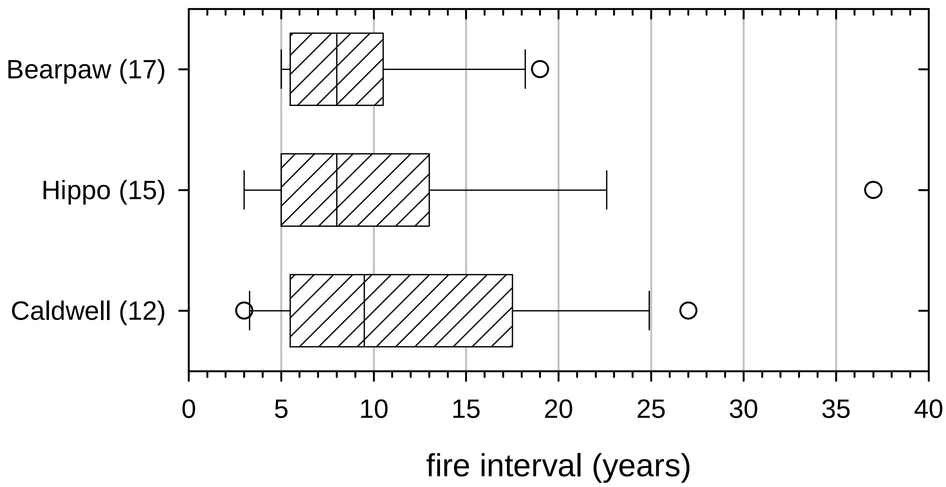

Figure 7. Fire frequency on sampled cinder cones (1750-1904). The boxes enclose the 25th to 75th percentiles of the distribution of composite fire intervals on each cinder cone. The whiskers enclose the 10th to 90th percentiles. The vertical line across each box indicates the median and all values falling outside the 10th to 90th percentiles are shown as circles.

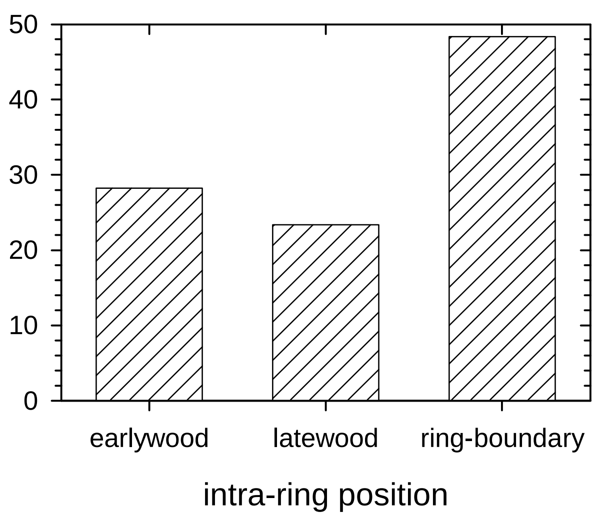

Figure 8. Seasonality of surface fires (1750-1904), composited across all three sampled cinder cones (Hippo, Bearpaw and Caldwell Buttes). Intra-ring position of fire scars is shown as a percentage of total scars for which intra-ring position could be determined (i.e., 49% of 372 scars).

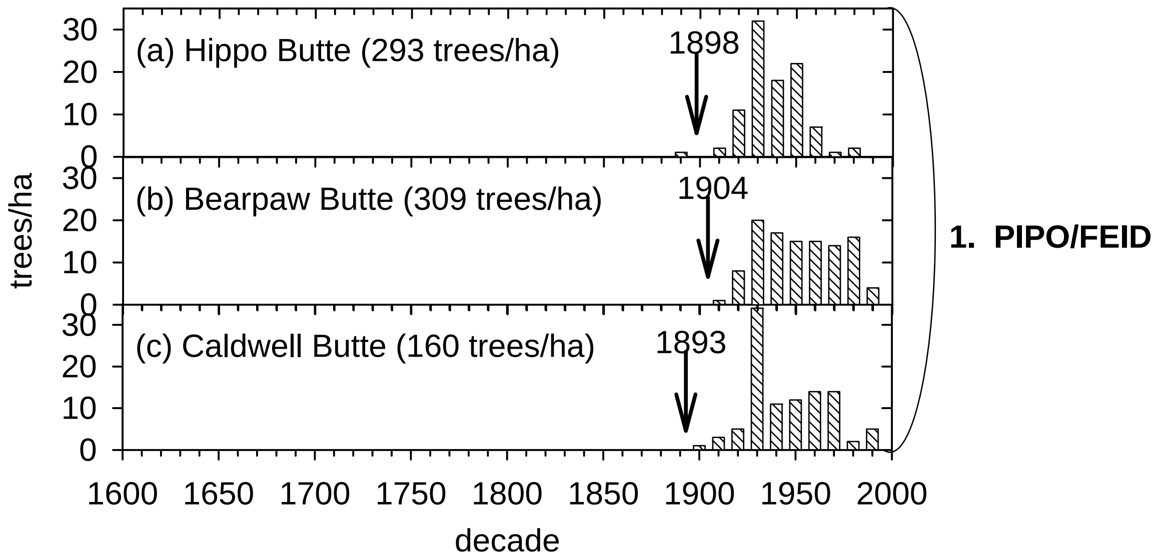

Figure 9a. Establishment dates of western juniper trees on the sampled cinder cones (Hippo, Bearpaw and Caldwell Buttes). Tree density is given in parentheses and the date of the last fire is indicated by an arrow. The macroplots sampled on these cinder cones all lie within site 3, in the ponderosa pine/Idaho fescue plant association (1. PIPO/FEID).

Existing vs. pre-settlement vegetation

The existing vegetation in this plant association lies outside the range of variation in pre-settlement vegetation. A nearly contiguous layer of fine fuels (ca. 2000 kg/ha ca. 10 years following fire; Table 2) and slopes generally > 30% were sufficient to support the frequent surface fires that we reconstructed from tree rings for this plant association prior to ca. 1900 (Fig. 7). These fires likely maintained an open ponderosa pine community, with Idaho fescue dominating the understory. Any western juniper trees that established would have been killed by fire before they reached maturity, preventing succession to western juniper woodland. We predict that in the absence of fire, the north aspects of the cinder cones will be dominated by western juniper, as this plant association is elsewhere (Miller et al. 2000). Under this scenario fine fuel loads will decline to < 500 kg/ha and the fire regime will shift to infrequent, high-severity fires.

(2) Mountain big sagebrush-Bitterbrush/Idaho fescue plant association (ARTRV-PUTR/FEID; sites 2, 5 and 1)

Historical fire regime

The historical fire regime in this plant association was likely similar to that in the ponderosa pine/Idaho fescue plant association (1. PIPO/FEID). The sites in this plant association did not retain a tree-ring record of historical fires, nor is there an archival record of fire. However, they lie near sites in the ponderosa pine/Idaho fescue plant association (1. PIPO/FEID) on Bearpaw and Hippo Buttes, and have a similar western juniper age structure, suggesting they burned at the same time as the cinder cones, in the late 1800s (Figs. 9a & b). We have no fine fuel data for this plant association for the first 10 years following fire. However, since moisture availability in this plant association is between that in the 1. PIPO/FEID and 3. ARTRV-PUTR/AGSP-FEID plant associations, fine fuel abundance a decade after fire is probably similar to that measured tat sites 4, 6, and CB' (ca. 2000 kg/ha).

We hypothesize that the historical mean fire-return interval in this plant association was between 10 and 20 years, based on the following:

1. It is likely that most fires on the adjacent cinder cones spread beyond the base of the cones because there are no major barriers to fire spread at the base of the cinder cones;
2. It is unlikely that fires always ignited on the cinder cones;
3. It is likely that fine fuel loads during the first 10 years following fire were comparable to those in the ponderosa pine/Idaho fescue (1. PIPO/FEID) plant association;
4. Fire-return intervals would have to be short enough to limit the development of mature western juniper trees;
5. Fire-return intervals elsewhere in this plant association ranged from 10 to 20 years (Houston 1973, Burkhart and Tisdale 1976, Miller and Rose 1999, Miller et al. 2001).

Fire severity probably ranged from low to moderate, varying with climate, the length of the fire-return interval, and the amount of shrub canopy that had developed since the last fire. Tree age structure, the absence of live pre-settlement or large dead western juniper, fine fuel loads, and the juxtaposition with the ponderosa pine/Idaho fescue plant association (1. PIPO/FEID), suggest a fire regime of frequent, low- to moderate-severity fires.

Western juniper succession

Mature western juniper trees were not part of the pre-settlement vegetation in this plant association, based on the current lack of live or dead mature western juniper trees. Sites where fire has been absent for 100 years (site 2) are rapidly approaching the transition from shrub steppe to woodland (Figs. 4 and 9b, Table 2). Establishment of western juniper has occurred following the last fire events occurring on Hippo and Bearpaw Buttes (1898 and 1904, respectively). Our data suggest few western juniper trees establish within the first 15 years following fire (sites 5 & 1). The low densities of dead trees killed by recent fires in this plant association were small (diameter <15 cm), suggesting these sites were in the very early stages of western juniper woodland development.

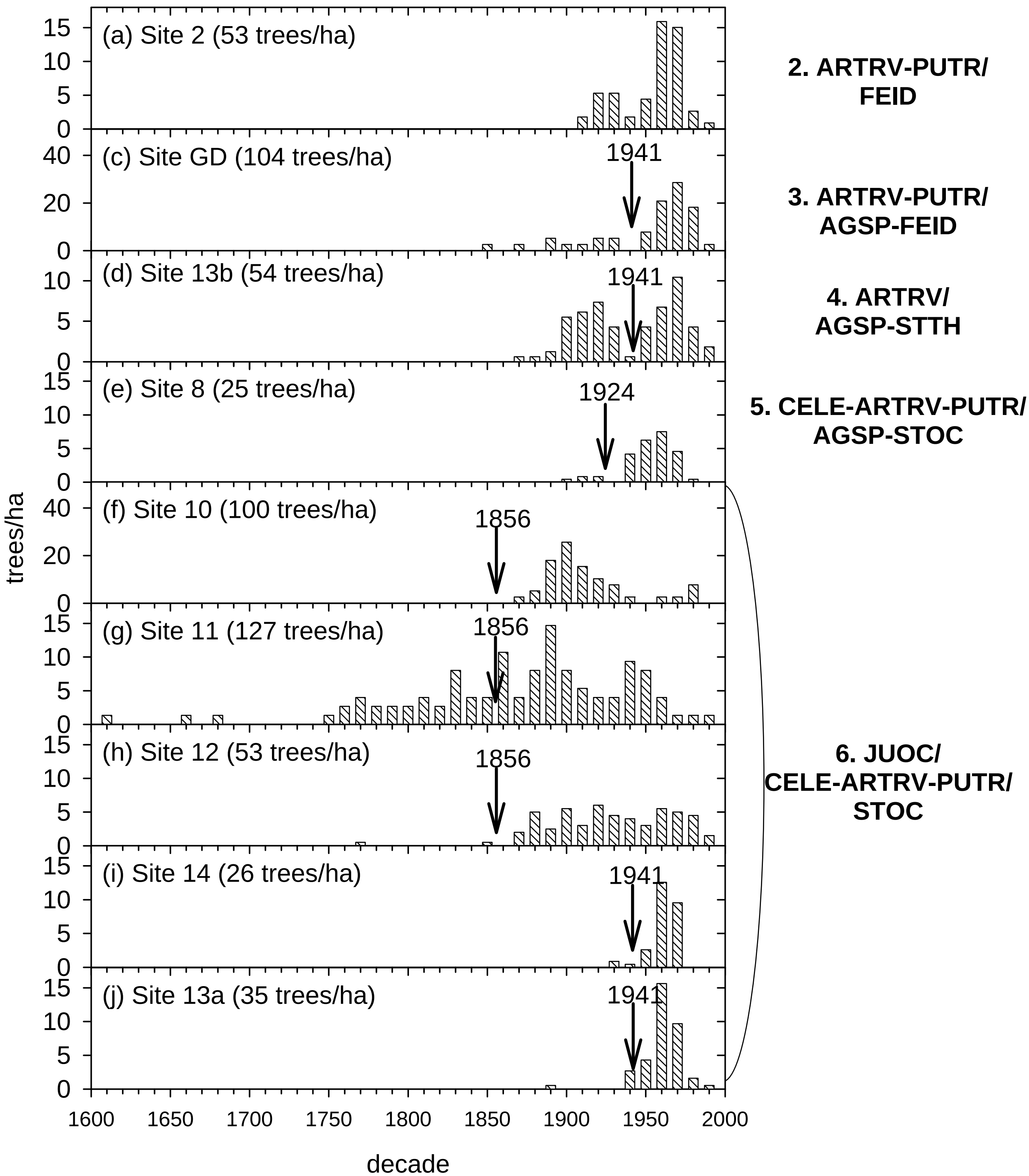

Figure 9b. Establishment dates of live western juniper trees at all the sites that contained such trees. Total live western juniper density for the site is given in parentheses, and the date of the last fire is indicated by an arrow. Plant associations are indicated on the right side of the figure.

Existing vs. pre-settlement vegetation

The existing vegetation on site 2 in this plant association lies outside the range of historical variation for pre-settlement vegetation. This plant association is currently in the mid succession stage of woodland development (Table 3). Vegetation is characterized by a dominant overstory of mountain big sagebrush and bitterbrush (45% canopy cover) and young western juniper trees (Fig. 9b). In contrast, perennial grasses likely dominated this plant association in the first 10 years after fire, followed by shrubs 10 to 20 years after fire (sites 5 & 1). The cover and density of these shrubs (mountain big sagebrush and bitterbrush) probably did not exceed 20% historically, based on our model of the rate of post-fire succession and our estimates of the historical mean fire-return interval. Mature western juniper likely did not occupy this plant association prior to 1900.

(3) Mountain big sagebrush-Bitterbrush/Bluebunch wheatgrass-Idaho fescue plant association (ARTRV-PUTR/AGSP-FEID; sites GD, SC, BC, 6 and 4)

Historical fire regime

The sites in this plant association did not retain a tree-ring record of historical fires. However, archival records indicated several sites (GD, SC, and BC) burned in 1941. In addition, all sites with the exception of GD have been prescribed burned since the 1990s. We hypothesize that mean fire-return intervals were less than 30, and possibly less than 20 years, and fire severity was low to moderate. There were no live or dead pre-settlement western juniper trees in this plant association, suggesting that pre-settlement fire-return intervals were frequent enough to prohibit the development of mature western juniper. Elsewhere, the maximum fire interval limiting the development of mature western juniper is 50 years (Burkhardt and Tisdale 1976, Bunting 1984, Miller and Tausch 2001). However, in this plant association at LABE, the vegetation structure, percent bare ground, fine fuel loads (near 2000 kg/ha during the first 10 years following fire), and juxtaposition to the ponderosa pine/Idaho fescue (1. PIPO/FEID) and mountain big sagebrush – bitterbrush/Idaho fescue (2. ARTRV-PUTR/FEID) plant associations, which have fire-return intervals of 10-20 years, would suggest mean fire-return intervals considerably less than 50 years.

Western juniper succession

Mature western juniper trees were not part of the pre-settlement vegetation in this plant association, based on the current lack of live or dead mature western juniper trees (Fig. 9b). The low density of small dead western juniper trees (diameter = <15cm) in the recently burned sites (SC, BC, 6, 4) suggest western juniper was in the early stage of succession prior to the last fire. The majority of trees currently growing at the GD site established after the 1941 fire. Trees that established between 1850 and 1941 were located in the two macroplots at the south end of this site, which appeared to have been burned by a mixed severity fire in 1941. Western juniper trees in these two macroplots are approaching the mid phase of woodland development (Table 3).

Existing vs. pre-settlement vegetation

The existing vegetation on sites that burned since 1973 is probably within the range of historical variation for pre-settlement vegetation. However, vegetation at the GD site, which burned in 1941, probably lies outside this range. If mean fire-return intervals were historically less than 20 to 30 years, this plant association was likely dominated by perennial grasses during the first 10 years after fire, followed by shrubs during the second 10 to 20 years (Fig. 4). So at site GD, 60 years after fire, existing shrub canopy cover likely exceeds historical levels for this plant association (30 vs. 20%, respectively) as does western juniper cover and density.

(4) Mountain big sagebrush/Bluebunch wheatgrass-Thurber's needlegrass plant association (ARTRV/AGSP-STTH; site 13b)

Historical fire regime

The sites in this plant association did not retain a tree-ring record of historical fires. However, archival records indicate that the one site we sampled burned in 1941, in a mixed-severity fire. The absence of trees establishing prior to 1860 suggest that another fire occurred in the early to mid 1800s, possibly the 1856 fire that we reconstructed in an adjacent plant association (6. JUOC/CELE-ARTRV-PUTR/STOC; Fig. 9b). The existing vegetation suggests that the pre-settlement fire regime was sufficient to limit the establishment of large mature western juniper trees. The maximum fire-free interval that limits western juniper encroachment is estimated to be 50 years (Burkhardt and Tisdale 1976, Bunting 1984, Miller and Tausch 2001). Increased bare ground and lower fine fuel abundance (Table 2) and continuity would suggest mean fire-return intervals were probably longer than the more mesic plant associations at LABE, i.e., those that include Idaho fescue. Therefore, we hypothesize that pre-settlement mean fire-return intervals were 50 years, ± 20 years, and of moderate to high severity, as they are elsewhere in relatively dry communities characterized by the big sagebrush group (Wright and Bailey 1982).

Western juniper succession

Mature western juniper trees were not part of the pre-settlement vegetation in this plant association, based on the current lack of live or dead mature western juniper trees (Fig. 9b). However, this plant association is currently occupied by early to mid successional western juniper woodland (Tables 2 and 3). The oldest trees on the site we sampled established in the late 1800s with a second pulse following the 1941 fire (Fig. 9b).

Existing vs. pre-settlement vegetation

With the exception of western juniper size and density, the existing vegetation probably lies near the historical range of variation for this plant association. Historically, the successional stage likely varied from grassland to shrub steppe, depending on the time since fire (Fig. 4). Historically, some western juniper trees would have established in the shrub steppe but would not have reached the degree of maturity some of them have now reached. Continued fire exclusion will eventually result in western juniper woodland, which lies outside the range of historical variation in this plant association.

(5) Curl-leaf mountain mahogany-Bitterbrush-Mountain big sagebrush / Bluebunch wheatgrass-Western needlegrass plant association (CELE-PUTR-ARTRV/AGSP-STOC; site 8)

Historical fire regime

The sites we sampled in this plant association did not retain a tree-ring record of historical fires. However, archival records report that this site burned in 1924. The high percentage of bare ground and low herbaceous cover would limit the spread of fires across this plant association. Periodic fires were probably supported by several years of wetter than average conditions preceding the fire event to allow the build up of fine fuels (Baisan and Swetnam 1990, 1997, Miller and Rose 1999). The current lack of large, live or dead western juniper trees suggests that historically, this plant association sustained a mean fire-return interval of <50 years.

Western juniper succession
Tree density was very low for this site. Most trees established between 1940 and 1980 (Fig. 9b) supporting the occurrence of a fire in 1924.

Existing vs. pre-settlement vegetation
Existing vegetation may fall within the historical range of variation for this plant association. Plant cover was highly variable across the site we sampled. In the absence of fire we would expect the continued increase in western juniper to result in a western juniper woodland.

(6) Western juniper/curl-leaf mountain mahogany-mountain big sagebrush-bitterbrush/western needlegrass plant association (JUOC/CELE-ARTRV-PUTR/STOC; sites 10, 11, 12 and 13a)

Historical fire regime
Tree-ring evidence suggests that two fires burned in this plant association at LABE. First, the death dates of charred western juniper trees indicate that this plant association last burned in 1856. Second, the scarcity of trees establishing prior to 1750 (site 11, Fig. 9b) suggests a severe fire may have burned in the early 1700s. In addition, the large size of the trees killed by the 1856 fire suggests a relatively long fire-free interval prior to this fire, consistent with our estimate of a fire in the early 1700s. One site in this plant association (13a) did not have evidence of a fire in 1856. However, the stand replacement fire that burned this site in 1941 likely removed any evidence of previous fires.

Tree structure, age distribution, and charred wood across this plant association suggest that the pre-settlement fire regime varied from moderate to high severity with relatively long fire-return intervals. These long intervals likely resulted from the limited continuity and abundance of fine fuels (Table 2). The two major fires, in the mid 1800s and early 1700s, suggest an interval of 150+ years. In 1856, the difference in fire severity across this plant association can probably be attributed to weather conditions at the time of fire and/or a difference in fuel abundance and structure (e.g., relative abundance in trees and shrubs). Periodic fires were probably supported by several years of wetter than average conditions preceding the fire event to allow the build up of fine fuels (Basian and Swetnam 1990, Miller and Rose 1999).

Western juniper succession
Historically, this plant association was occupied by open to fully developed stands of young and old western juniper trees (Table 2, Fig. 9b). Currently, the most extensive and dense stands of western juniper are located in the vicinity of Valentine Cave (site 11), which supports 127 live trees/ha. Limited lateral leader growth and recruitment of western juniper suggests the woodland overstory is fully developed at this site (Table 3), and nearly half the trees here established prior to settlement. The presence of old western juniper trees, extensive post-settlement establishment of this species, and the presence of charred wood throughout site 11 suggest the 1856 fire was mixed severity here. In contrast, sites 10 and 12 are adjacent to site 11, but are occupied by a

young stand of western juniper trees. The current lack of live pre-settlement trees and presence of abundant large, fluted, charred stumps (>30 cm) on these two sites, suggest that the 1856 fire was high severity (Table 2, Fig. 9b). The density of dead pre-settlement trees (27-54 trees/ha) suggests these two sites were occupied by open to well developed woodlands prior to the 1856 fire. Our observation of widely scattered large stumps across site 13a suggests that western juniper also occupied this site prior to settlement but at low densities.

Existing vs. pre-settlement vegetation
The composition and structure of existing vegetation in this plant association probably lies within its range of historical variation. The current lack of very old trees (>500 years) except on rock inclusions, the mixed tree-age structure, and an abundance of charred wood across these sites suggest that although infrequent fire played an important role in past vegetation dynamics, intervals were long enough to allow the establishment of western juniper shrub steppe and woodlands composed of trees exceeding 100 years old. Plant composition suggests that shrubs and trees will co-dominate (Table 3) after 150 years following a fire, trees becoming dominant in less than 250 years of initial establishment.

Conclusions

Our vegetation composition, tree age distribution, and fire history data suggest that, across the southern half of LABE:

- Historically, fire regimes were heterogeneous, varying across plant associations and ranging from frequent, low-severity to infrequent, high-severity regimes.
- These fires historically prevented the development of western juniper woodlands across most, but not all, of the 6 plant associations that we studied.
- The physiognomy of pre-settlement vegetation varied both across plant associations and through time, so that sites were in a range of successional stages varying from grassland to shrub steppe to woodlands, depending on the plant association and time-since-last fire.
- As a consequence of recent fire exclusion, western juniper has greatly expanded since the late 1800s.
- In the continued absence of fire, most plant associations will eventually be dominated by western juniper and hence will be outside their range of historical variation in vegetation composition and structure.

Historically, fire regimes varied among plant associations. As a consequence, restoring plant associations to their historical range of variation will require restoring fire differently among the plant associations. Our data suggest that infrequent fire in the fuel-limited western juniper/curl-leaf mountain mahogany-mountain big sagebrush-bitterbrush/western needlegrass plant association (6. JUOC/CELE-ARTRV-PUTR/STOC) was probably in a continual state of change between shrub steppe and western juniper woodland, and that western juniper trees were part of the pre-settlement vegetation. Therefore, this plant association probably does not require restoration of fire. In contrast, on the more productive sites, especially those with Idaho fescue (1. PIPO/FEID, 2. ARTRV-PUTR/FEID and 3. ARTRV-PUTR/AGSP-FEID), western juniper is a newcomer, encroaching into these communities since the late 1800s. Sites within these plant associations that have not recently burned probably differ in both structure and composition from pre-settlement vegetation and so fire should be restored to these communities.

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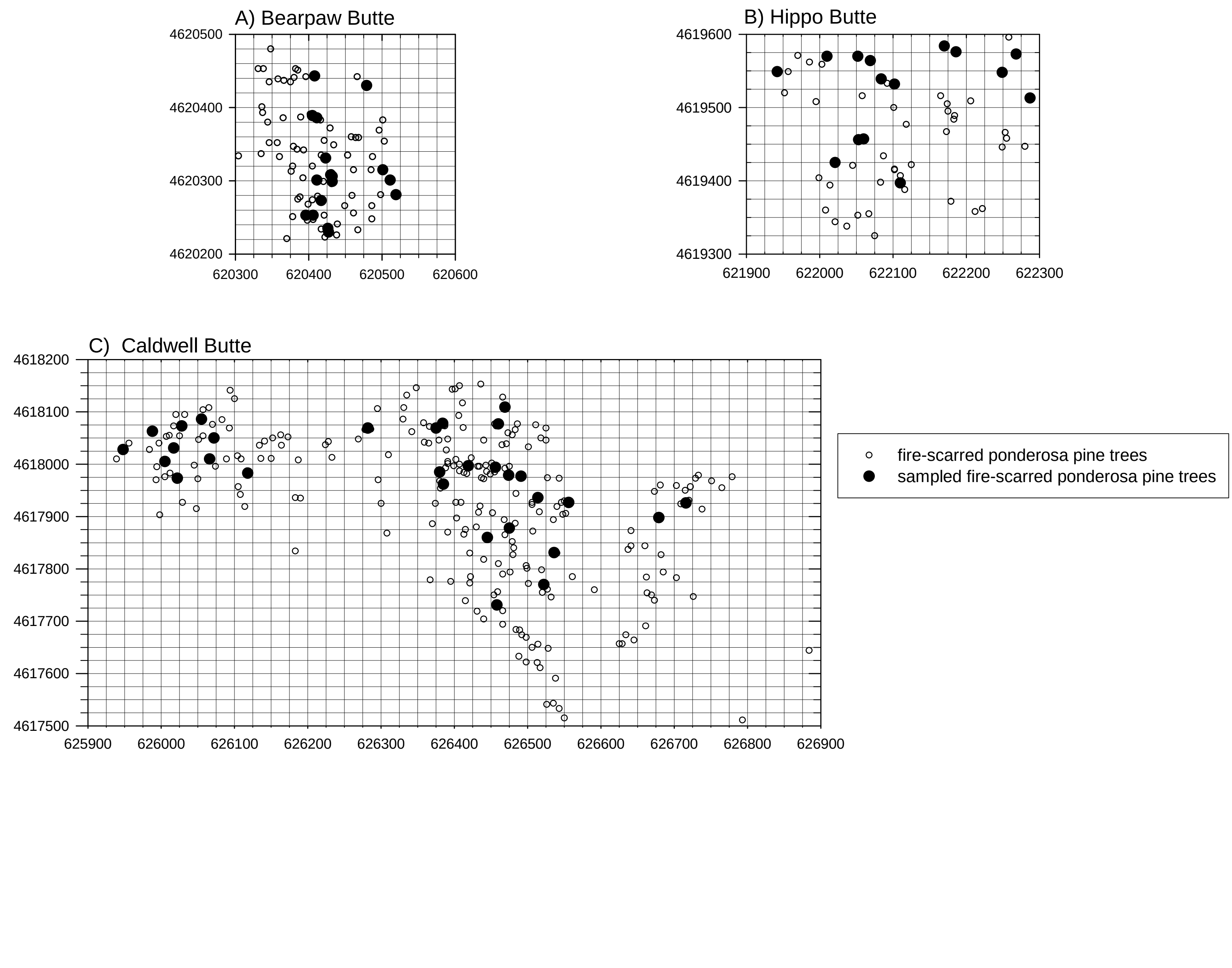
Appendices

Appendix 1. Habitat types defined by Erhard (1980) that correspond with the plant associations sampled at LABE. Dates of last known fires are from LABE archival records and dates reconstructed from tree rings for this study. Western juniper status is the woodland successional stage determined from Miller et al. (2000; Table 3)

Plot ID	**Habitat Types** (from Erhard 1980)	**Last Fire**	**Plant Association** Existing Vegetation	**Juniper Status**
			PIPO/FEID	
3	FEID[1]/CELE/JUOC (4100)	1893, 1898	JUOC/CELE/FEID	mid
	FEID/PUTR/PIPO (4000)	& 1904		
			ARTRV-PUTR/FEID	
2	FEID-AGSP/ CELE-ARTRV (3900)	apprx 1898	JUOC/ARTRV-PUTR/FEID-AGSP	early
	FEID-AGSP/ CELE-ARTRV (3900)	1989	FEID-AGSP	0
1	FEID-AGSP/CELE-ARTRV (3900)	1986	FEID-AGSP	0
5				
			ARTRV-PUTR/AGSP-FEID	
CB	FEID/CELE/JUOC (4100)	late 1800s	JUOC/CELE-ARTR	late
WB	FEID/CELE/JUOC (4100)	unknown	CELE-ARTRV/AGSP-FEID	mid
GD	AGSP/STTH/ARTRV (5200)	1941(49)	ARTRV-PUTR/AGSP-FEID (FEID-AGSP)	early-mid
SC	BRTE-AGSP-STTH-STOC (1600)	1973	ARTRV-PUTR/AGSP	early
BC	AGSP-STTH/ARTRV (5200)	1986	ARTRV/AGSP	0
CB	FEID/CELE/JUOC (4100)	apprx 1990	AGSP-FEID	0
6	BRTE-AGSP-STTH-STOC (1600)	1996	AGSP-FEID	0
4	AGSP-STTH/ARTRV (5200)	1996	AGSP-FEID	0
			ARTRV/AGSP-STTH	early
13b	AGSP-STTH-ARTRV (5200)	1941(49)	ARTRV/AGSP-STTH	
			CELE-PUTR-ARTR/AGSP-STOC	early
8	AGSP-STTH-STOC/ARTRV (4800)	1941	CELE-PUTR-ARTR/AGSP-STOC	
			JUOC/CELE-ARTR-PUTR/STOC	
10	STOC/ARTRV/JUOC (6100)	1856	JUOC/CELE-ARTRV-PUTR/STOC	late
11	STOC/ARTRV/JUOC (6100)	1856	JUOC/CELE-ARTRV-PUTR/STOC	mix-age late
12	STOC/ARTRV/JUOC (6100)	1856	JUOC/CELE-ARTRV-PUTR/STOC	early
14	STOC/ARTRV/PIPO (5700)	1941	ARTRV-PUTR/STOC-STTH	early
13a	AGSP-STTH-STOC/ARTRV(4900)	1941	ARTRV-PUTR/STOC	early

[1] AGSP= *Agropyron spicatum*, ARTRV=*Artemisia tridentata* ssp *vaseyana*, CELE=*Cercocarpus ledifolius*, FEID=*Festuca idahoensis*, JUOC=*Juniperus occidentalis*, PIPO=*Pinus ponderosa*, STOC= *Stipa occidentalis*, STTH=*Stipa thurberiana.*

Appendix 2. Locations of all fire-scarred trees (hollow symbols). Those sampled for this study are indicated by filled symbols.

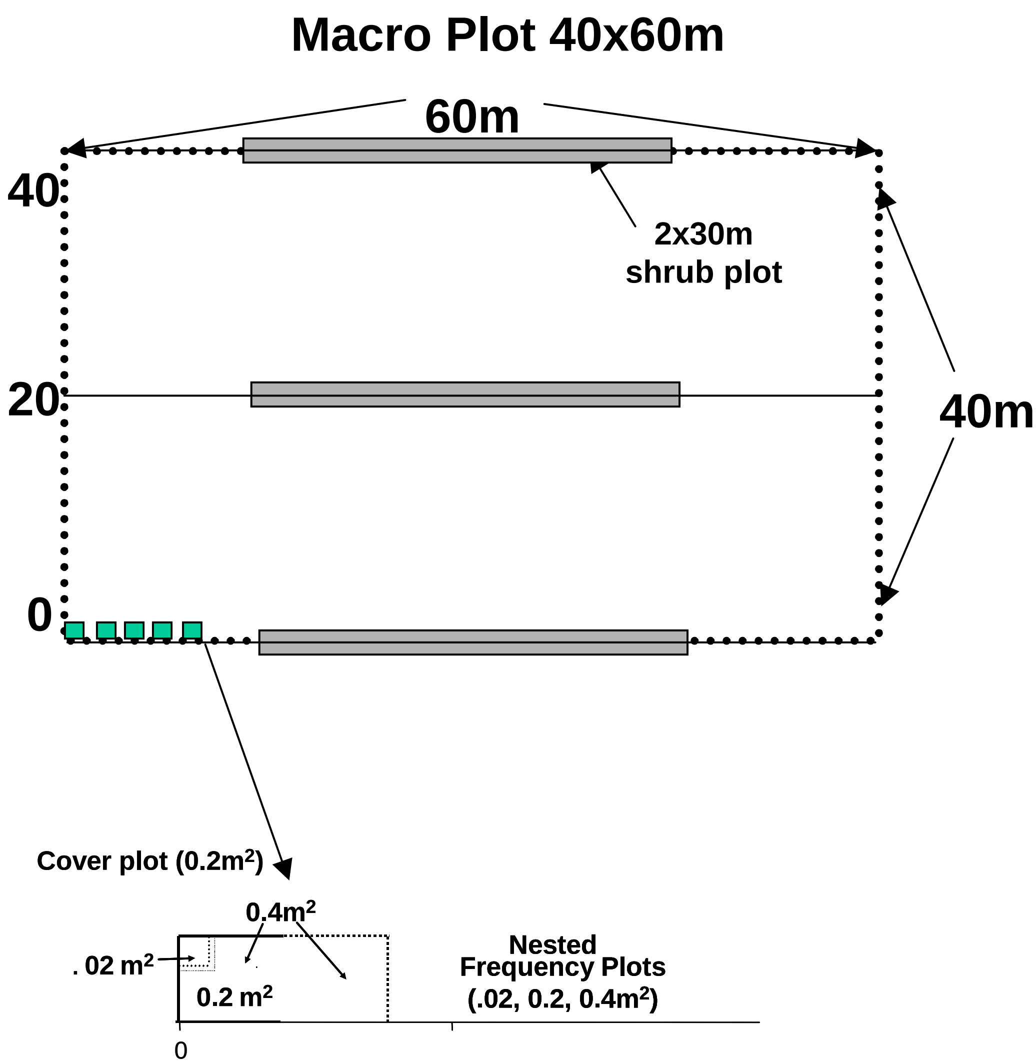


Appendix 3. Plot description and locations.

Site	Plot	Current Physiognomy	Plant Association	UTM	UTM
4	1	grassland	ARTRV-PUTR/AGSP-FEID	622854	4622075
4	2	grassland	ARTRV-PUTR/AGSP-FEID	622461	4622202
4	3	grassland	ARTRV-PUTR/AGSP-FEID	622436	4622354
BC	1	grassland	ARTRV-PUTR/AGSP-FEID	621050	4622398
BC	2	grassland	ARTRV-PUTR/AGSP-FEID	620920	4622542
BC	3	grassland	ARTRV-PUTR/AGSP-FEID	620742	4622885
13	1	shrub steppe	JUOC/CELE-ARTRV-PUTR/STOC	627374	4619862
13	2	shrub steppe	JUOC/CELE-ARTRV-PUTR/STOC	627359	4620288
13	3	shrub steppe	JUOC/CELE-ARTRV-PUTR/STOC	626950	4620382
13	4	shrub steppe	JUOC/CELE-ARTRV-PUTR/STOC	624242	4620876
13	5	shrub steppe	JUOC/CELE-ARTRV-PUTR/STOC	623896	4620793
13	7	shrub steppe	JUOC/CELE-ARTRV-PUTR/STOC	624197	4621313
13	8	shrub steppe	JUOC/CELE-ARTRV-PUTR/STOC	624674	4621695
13	9	shrub steppe	JUOC/CELE-ARTRV-PUTR/STOC	624011	4621137
SC	1	shrub steppe	ARTRV-PUTR/AGSP-FEID	624044	4618620
SC	2	shrub steppe	ARTRV-PUTR/AGSP-FEID	623992	4618861
SC	3	shrub steppe	ARTRV-PUTR/AGSP-FEID	624007	4618543
6	1	shrub steppe	ARTRV-PUTR/AGSP-FEID	623588	4618694
6	2	shrub steppe	ARTRV-PUTR/AGSP-FEID	622853	4619130
6	3	shrub steppe	ARTRV-PUTR/AGSP-FEID	622819	4618702
8	1	shrub steppe	CELE-ARTRV-PUTR/AGSP-STOC	623285	4617459
8	2	shrub steppe	CELE-ARTRV-PUTR/AGSP-STOC	623685	4617587
8	3	shrub steppe	CELE-ARTRV-PUTR/AGSP-STOC	623887	4617756
GD	1	shrub steppe	ARTRV-PUTR/AGSP-FEID	618288	4623005
GD	2	shrub steppe	ARTRV-PUTR/AGSP-FEID	618158	4622441
GD	3	shrub steppe	ARTRV-PUTR/AGSP-FEID	618816	4624207
GD	5	shrub steppe	ARTRV-PUTR/AGSP-FEID	617518	4621869
GD	6	shrub steppe	ARTRV-PUTR/AGSP-FEID	618016	4622239
14	1	shrub steppe	JUOC/CELE-ARTRV-PUTR/STOC	628414	4617069
14	2	shrub steppe	JUOC/CELE-ARTRV-PUTR/STOC	628132	4617316
14	3	shrub steppe	JUOC/CELE-ARTRV-PUTR/STOC	627824	4617532
1	1	shrub steppe	ARTRV-PUTR/FEID	620443	4620965
2	1	shrub steppe	ARTRV-PUTR/FEID	618877	4622060
2	2	shrub steppe	ARTRV-PUTR/FEID	620531	4620596
2	3	shrub steppe	ARTRV-PUTR/FEID	622548	4619644
5	1	shrub steppe	ARTRV-PUTR/FEID	622798	4620446
5	2	shrub steppe	ARTRV-PUTR/FEID	622747	4619890
5	3	shrub steppe	ARTRV-PUTR/FEID	622505	4620339
C.B.	1_1	mahogany	PIPO/FEID	623525	4619601
C.B.	1_2	mahogany	PIPO/FEID	623377	4619770
WB	1	shrub steppe	CELE-ARTRV-PUTR/FEID-AGSP	616979	4621945
WB	2	shrub steppe	CELE-ARTRV-PUTR/FEID-AGSP	617203	4621565
10	1	juniper/shrub	JUOC/CELE-ARTRV-PUTR/STOC	625963	4618256
10	2	juniper/shrub	JUOC/CELE-ARTRV-PUTR/STOC	625989	4618481
11	1	juniper/shrub	JUOC/CELE-ARTRV-PUTR/STOC	626867	4618709
11	2	juniper/shrub	JUOC/CELE-ARTRV-PUTR/STOC	626614	4619189
11	3	juniper/shrub	JUOC/CELE-ARTRV-PUTR/STOC	627162	4619304

Site	Plot	Current Physiognomy	Plant Association	UTM	UTM
11	4	juniper/shrub	JUOC/CELE-ARTRV-PUTR/STOC	626380	4618607
11	5	juniper/shrub	JUOC/CELE-ARTRV-PUTR/STOC	626812	4619652
12	1	juniper/shrub	JUOC/CELE-ARTRV-PUTR/STOC	628188	4618512
12	2	juniper/shrub	JUOC/CELE-ARTRV-PUTR/STOC	628220	4619405
12	3	juniper/shrub	JUOC/CELE-ARTRV-PUTR/STOC	627651	4618818
12	4	juniper/shrub	JUOC/CELE-ARTRV-PUTR/STOC	627376	4618328
12	5	juniper/shrub	JUOC/CELE-ARTRV-PUTR/STOC	627663	4618375
3	1_1	mahogany	PIPO/FIED	620498	4620285
3	1_2	mahogany	PIPO/FIED	620419	4620330
3	1_3	mahogany	PIPO/FIED	620280	4620373
3	2_1	mahogany	PIPO/FIED	626094	4618030
3	2_2	mahogany	PIPO/FIED	626712	4617713
3	2_3	mahogany	PIPO/FIED	626565	4617855
3	3_1	mahogany	PIPO/FIED	622293	4619461
3	3_2	mahogany	PIPO/FIED	622187	4619541
3	3_3	mahogany	PIPO/FIED	622058	4619545

Appendix 4. Macroplot layout which includes 60 m transects, 2x30 m shrub plots, and nested frequency plots for herbaceous vegetation.



Appendix 5: Plant species list; code, scientific and common names**.**

Code	Scientific Name	Common Name
ACMI2	*Achillea millefolium*	common yarrow
AGGL	*Agoseris glauca*	short-beaked or pale agoseris
AGSP	*Agropyron spicatum*	bluebunch wheatgrass
ANDI2	*Antennaria dimorpha*	low pussy-toes
ANGE3	*Antennaria geyeri*	pinewoods pussy-toes
ANMI3	*Antennaria microphylla*	littleleaf pussy-toes
ANRO2	*Antennaria rosea*	rosy pussy-toes
ANTEN	*Antennaria sp.*	everlasting; pussy-toes
ARABI	*Arabis sp.*	rockcress
ARDR	*Arabis drummondi*	Drummond's rockcress
ARHO2	*Arabis holboellii*	Holboell's rockcress
ARSP	*Arabis sparsiflora*	sicklepod rockcress
ASCU	*Astragalus cusikii*	
ASFI	*Astragalus filipes*	threadstalk or basalt milkvetch
ASPU9	*Astragalus purshii*	woolly-pod milkvetch
ASTRA	*Astragalus sp.*	Milkvetch; locoweed
BRTE	*Bromus tectorum*	cheatgrass
CAMA5	*Calochortus macrocarpus*	sagebrush mariposa
CAPI3	*Castilleja pilosa*	hairy or parrot-headed paintbrush
CARO5	*Carex rossii*	Ross' sedge
CASTI	*Castilleja sp.*	paintbrush
CHDO	*Chaenactis douglasi*	false-yarrow, Douglas' dustymaiden
COGR4	*Collomia grandiflora*	large-flowered collomia
CRAC2	*Crepis acuminata*	long-leaved hawksbeard
DELPH	*Delphinium sp.*	larkspur; delphinium
ERFI2	*Erigeron filifolius*	thread-leaf fleabane
ERIGE	*Erigeron sp.*	
ERLI	*Erigeron linearis*	desert yellow daisy
ERNU3	*Eriogonum nudum*	barestem buckwheat
ERST4	*Eriogonum strictum*	strict buckwheat
ERUM	*Eriogonum umbellatum*	sulfur buckwheat
FEID	*Festuca idahoensis*	Idaho fescue
CYFR	*Cystopteris fragilis*	brittle bladder-fern
FRAL2	*Frasera albicaulis*	white-stemmed frasera
GETR	*Geum triflorum*	old man's whiskers
HIAL	*Hieracium albertinum*	western hawkweed
LEPU	*Leptodactylon pungens*	prickly phlox
LIPE2	*Linum perenne*	blue flax
LIRU4	*Lithospermum ruderale*	Columbia puccoon;stoneseed
LOMAT	*Lomatium sp.*	biscuit-root
LYSP2	*Lygodesmia spinosa*	spiny skeletonweed
MACA2	*Machaeranthera canescens*	hoary aster
MICRO	*Microseris sp.*	

PEDE4	*Penstemon deustus*	hot-rock or scabland penstemon
PELA7	*Penstemon laetus*	mountain blue or gay penstemon
PENST	*Penstemon sp.*	
PHHE	*Phacelia heterophylla*	varileaf phacelia
PHHO	*Phlox hoodii*	Hood's phlox
PHLO2	*Phlox longifolia*	long-leaf phlox
PHLOX	*Phlox sp.*	
POA	*Poa sp.*	bluegrass
POAM	*Poa ampla*	alkalai bluegrass
POGL9	*Potentilla glandulosa*	sticky cinquefoil
PONE	*Poa nevadensis*	Nevada bluegrass
POSA	*Poa sandbergii*	Sandberg bluegrass
SECA2	*Senecio canus*	woolly groundsel
SIDO	*Silene douglasii*	Douglas' silene
SIHY	*Sitanion hystrix*	bottlebrush squirreltail
SILEN	*Silene sp.*	
STOC2	*Stipa occidentalis*	western needlegrass
STTH2	*Stipa thurberiana*	Thurber's needlegrass
TRDU	*Tragopon dubis*	yellow salsify
VUOC	*Vulpia octoflora*	six-weeks fescue
ZIPA2	*Zigadenus paniculatus*	panicled death-camas

Appendix 6. Herbaceous species frequency across sites.

Site and Plot Size (m2)

	1			2			3			4			5			6			8		
Species	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**
ACMI	8.3	26.7	33.3	0.6	6.7	11.1	0	0.8	1.9	1.7	11.7	17.8	0.6	11.7	18.3	0	10	14.4	0	0	0.6
AGGL				0	0.6	0.6	0	0	0.3				0	0.6	0.6						
AGSP	16.7	56.7	66.7	3.3	20.6	27.8	0.8	8.1	11.7	13.9	60	72.2	6.7	31.1	41.1	13.9	41.7	60.6	3.9	17.8	21.7
ANDI2	0	3.3	3.3	2.2	8.3	10				0.6	1.7	1.7	0.6	3.9	6.7						
ANDO										0	1.1	1.1									
ANDR										0	1.7	1.7									
ANGE3				0.6	2.8	3.3	0	0.3	0.6										1.7	13.3	25.6
ANGR				0	0	1.1															
ANMI3																					
ANRO2				0.6	0.6	0.6	0.8	2.8	4.7				1.1	4.4	6.7	1.1	8.3	8.9			
ANTEN										1.1	2.2	2.2									
ARABIS	0	1.7	1.7	0	1.7	3.9	0	1.7	2.5	0	0.6	0.6	0	0	0				0.6	3.3	5
ARDR																					
ARHO2							0	0	0												
ARSP							0	0	0												
ASCU				0	0.6	0.6															
ASFI													0	0	0.6						
ASPU9				0	2.8	2.8				0	0	0	1.1	5	7.2	0	0.6	1.1			
ASTRA				0	0.6	0.6							0	0.6	1.1						
BRTE	3.3	20	30	0.6	5.6	9.4	0.3	2.5	3.9	13.9	35.6	40	3.9	18.3	22.2	31.7	74.4	82.2	12.8	53.9	64.4
CAMA5				0	0	0.6				0	1.1	1.1				0	1.1	2.2			
CAPI3	0	1.7	8.3																		
CARO5	0	1.7	3.3	2.2	12.2	17.2	0	1.4	2.2	0	0.6	0.6	0.6	1.1	1.7	0.6	4.4	8.9	3.3	25.6	37.2
CASTI	1.7	3.3	3.3				0.8	2.8	2.8										2.2	12.2	16.7
CHDO				0	0	0.6				0	0	0	0	0	0	0	0	0	0	0.6	2.8
COGR4																					

	10			11			12			13			14			BC			CB			GD			SC		
Species	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**
ACMI										0.2	0.4	0.4	0	0	0	0	1.7	3.3				0.8	7.5	8.3	0.6	3.9	5
AGGL																											
AGSP	1.7	7.5	9.2	0	0	0	0	0.3	0.3	4.4	14.3	21.9	0.6	1.1	1.1	13.9	46.1	61.7	0	2.5	6.3	5.8	31.7	45.8	11.1	38.3	56.7
ANDI2										0	0	0.2				0.6	1.7	1.7				2.5	9.2	10.8			
ANDO																											
ANDR																											
ANGE3													0	2.2	4.4				0	1.3	1.3	0	0	0			
ANGR																											
ANMI3				0	0.3	0.3																					
ANRO2										0	0.2	0.6	0	3.3	7.2	0	0	0.6				0	0	0.8	0.6	7.2	8.9
ANTEN																											
ARABIS	0	0.8	5.8	0	5.3	6.7	0.7	6.7	9.3	0.2	1.9	3.1	0	2.8	2.8	0	0.6	1.1	0	0	2.5	0	1.7	4.2	0	0.6	1.7
ARDR				0	0	0																					
ARHO2																											
ARSP				0.3	0.3	0.3				0	0	0.2															
ASCU																											
ASFI																											
ASPU9													0	0	0.6							0	0	0.8			
ASTRA																											
BRTE	7.5	24.2	33.3	7.7	30.7	39.3	6	27	34.3	10.4	49.6	59.3	27.8	77.2	82.8	30.6	76.7	81.7				1.7	10	14.2	20	71.1	79.4
CAMA5										0	0	0.4										0	0	0.8	0	1.1	2.2
CAPI3																											
CARO5	0	0.8	3.3	0.3	1.7	2.3	0	0	0	0.9	3.1	4.8	3.3	12.2	19.4	0	0	0.6	1.3	3.8	6.3				1.1	9.4	11.1
CASTI																0	0	0							1.1	3.3	6.1
CHDO	0	2.5	2.5	0.3	0.7	1	0	1	2.7	0.2	0.4	0.6	0	1.7	2.2	0	0	0				0	0.8	0.8	0	2.2	2.2
COGR4													0	0.6	0.6												

Appendix 6 (cont.). Herbaceous species frequency across sites.

	Site and Plot Size (m2)																																																		
	1			2			3			4			5			6			8			10			11			12			13			14			BC			CB			GD			SC		
Species	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**	**0.02**	**0.2**	**0.4**
CRAC2	0	13.3	21.7	0	3.3	5.6	0	0.6	0.8	1.7	11.1	22.2	1.1	6.7	10.6	0.6	3.9	5.6	0	1.1	1.1	0	0.8	0.8				0	0	0	0.2	1.1	1.5	0	0	0.6	0.6	12.2	16.1				0	8.3	10.8	1.1	5	7.8
DELPH																																		0	0	1.7												
ERFI2	0	1.7	10	0	1.7	2.8				0	0.6	2.8	0.6	1.7	3.3	0.6	1.1	1.7													0	0.2	0.4				0.6	10	15				0	3.3	4.2	0	0.6	0.6
ERIGE																																											0	0	0.8			
ERLI																																					0	1.1	1.7				0	0	0.8			
ERNE																															0	0	0.2															
ERNU3							0	0.6	0.6							0	0	1.1	0	2.8	3.3	0	5	7.5	0.3	2.3	2.3	0	2.3	3	0	0.4	0.7	0	1.7	1.7												
ERST4				0.6	1.7	3.3				0	0.6	1.1	0.6	3.9	5.6				0.6	1.1	1.1																			0	1.3	1.3						
ERUM				0	3.9	3.9	0.8	3.6	6.7	0	0.6	0.6	0.6	2.2	3.3	0	0	0	6.1	13.9	16.1	1.7	5	12.5	6.3	23.3	36.7	0	4.3	5.3	0.2	1.1	1.5	0	0	0.6				0	3.8	5						
FEID	13.3	65	81.7	16.7	57.2	67.2	10.8	32.5	34.4	11.1	50.6	61.7	20	71.1	77.2	3.3	12.8	17.8	0	0.6	0.6	0	0	0							0.2	0.4	0.4				0	2.8	4.4	15	42.5	46.3	23.3	67.5	75	0	0	0.6
FERN SP.																																														0	0.6	0.6
FRAL				0	1.1	1.1				0.6	2.2	4.4	0.6	3.3	6.7	0	0	0																			0	0	0.6				0	1.7	2.5			
FRAL2													0	0	0.6																																	
GETR							0	0	0.3				0	0.6	0.6																									0	1.3	1.3						
HECY							0.6	2.5	3.6																																							
HIAL							0	0	0																																							
KOMA	8.3	23.3	30	2.2	16.7	21.7	0	0.3	0.3	1.7	5.6	7.2	2.8	27.2	36.7	0	1.7	4.4													0.6	1.9	2.6				1.1	7.8	8.9				2.5	19.2	29.2			
LEPU	0	3.3	3.3	0	1.7	2.2				1.7	4.4	7.2	0	0	1.1				0	0.6	0.6	0.8	2.5	2.5	0.7	3.7	5.7	0	0	0	1.7	6.7	9.1	0	5	6.1	0	0	0				0	2.5	4.2			
LIPE2				0	5.6	6.7	0	0.6	1.1	0	0	0	0	1.7	3.9	0.6	1.1	1.1	1.7	8.9	11.7	0	0.8	0.8				0	0	0				0	0.6	2.2	0	0.6	0.6							0	0	0.6
LIRU4							0	0.8	1.7																						0	0.2	0.2	0	0.6	0.6												
LOMAT	0	1.7	1.7	0	3.3	4.4																															0	0.6	1.1				0	0.8	1.7			
LYGOD							0	0.6	0.6	0	0	0							0	0.6	0.6																0	0	0									
LYSP2																															0	0.2	0.4															
MACA2				0	0.6	0.6													0	3.9	6.1	0	0	0.8				0.3	0.3	0.7	0	0.7	1.5	1.1	14.4	18.3	0.6	1.7	3.9									

Appendix 6 (cont.). Herbaceous species frequency across sites.

	Site and Plot Size (m2)																																																		
	1			2			3			4			5			6			8			10			11			12			13			14			BC			CB			GD			SC		
Species	0.02	0.2	0.4	0.02	0.2	0.4	0.02	0.2	0.4	0.02	0.2	0.4	0.02	0.2	0.4	0.02	0.2	0.4	0.02	0.2	0.4	0.02	0.2	0.4	0.02	0.2	0.4	0.02	0.2	0.4	0.02	0.2	0.4	0.02	0.2	0.4	0.02	0.2	0.4	0.02	0.2	0.4	0.02	0.2	0.4	0.02	0.2	0.4
MACH																												0	0.3	1																		
MICRO																0	0	0																														
MINT																			0.6	0.6	0.6																											
PEDE4																						0	1.7	2.5	0	1.3	2.7				0	0.1	0.1															
PEDU																												0	0	0.3	0	0.3	0.3															
PELA7																0	0.6	0.6																												0	0.6	0.6
PENST				0	3.3	4.4	0	3.6	5.3	0	0.6	0.6	0	1.7	1.7	0	0.6	0.6	0	0	0	0	2.5	2.5	0	0	0	0	1.7	2.3	0.6	2.4	3.5	0	1.1	1.1	0	5.6	10	0	1.3	2.5	0	3.3	5	0	1.7	2.2
PHHE							0	0	0.3	0	0	0	0	0	0.6	0	1.1	2.2	0.6	6.7	9.4				0	1	1.3	0.7	1.7	3.3	0	1.3	1.5	0.6	12.2	16.7										1.1	11.1	18.3
PHHO							4.4	21.4	26.1				3.9	6.7	7.8	2.2	9.4	12.8													0.7	2.8	4.6	0	1.1	1.1	1.1	3.9	6.7	5	12.5	18.8	3.3	20.8	24.2	0	1.1	1.1
PHLO2													0.6	0.6	0.6																																	
PHLOX	0	3.3	3.3	1.1	6.7	8.3																																										
PHRA																						0	0.8	0.8	0	0	0.7																					
POA																												0	0	0.3																		
POAM	0	1.7	1.7	0	1.1	2.2	0	0.3	0.3	1.1	6.7	7.2										1.7	3.3	4.2	0.3	0.3	0.3							0.6	0.6	1.1	0.6	0.6	0.6									
POGL9							0.6	3.3	4.7																															0	1.3	2.5						
PONE	0	1.7	8.3	1.1	5	5.6	0	1.4	2.8	7.8	38.3	52.2	2.8	12.2	16.7	0.6	12.2	20	0	6.1	8.3	3.3	14.2	19.2	1.7	6.7	11	0.7	1.7	2.7	2.2	15.9	21.7	0	2.8	3.3	1.7	16.7	21.7							2.2	12.8	20
POSE	13.3	55	65	3.3	20.6	30	0.6	5	7.5	8.9	37.8	45	1.1	23.3	25.6	2.8	23.9	30.6	1.7	18.3	29.4	0	4.2	5	0.3	1.7	2.3	0	0	0	4.4	24.1	29.4	0	2.2	2.2	12.2	65	73.9	1.3	2.5	2.5	1.7	30	36.7	2.8	22.2	30
SECA2				0	0.6	0.6	0	0	0.3				0	0	0.6				0.6	3.3	4.4	0	3.3	3.3	0.3	1.7	2	0.7	4	8.3	0	0.7	2.2	0	1.1	1.1	0	0.6	1.1							0	1.1	1.1
SIDO																																														0	0.6	0.6
SIHY	0	10	16.7	1.7	18.3	26.7	0.3	3.1	3.9	1.1	5.6	9.4	0.6	2.8	4.4	0.6	2.2	4.4	2.8	14.4	23.9	0	16.7	22.5	1	6	13	2	14	18.7	1.3	10.4	17.8	0	7.8	12.2	3.9	12.2	20				0	0	1.7	1.1	3.3	6.7
SILEN							0	0.3	0.3				0.6	1.7	1.7																																	
STOC2				0.6	1.7	1.7				2.2	11.7	15	0.6	0.6	2.2	0.6	5.6	10.6	1.1	8.3	12.2	3.3	22.5	35.8	1.7	13.3	22	2	15.3	23.7	1.5	8.1	12	2.2	12.2	17.8	0	1.1	2.2							0	11.7	21.1
STTH2	0	16.7	35	3.9	27.2	38.3	0	0	0	5.6	25.6	38.9	3.9	24.4	38.9	1.1	22.2	32.2	1.7	2.8	3.3	0	0	1.7	0	0.3	0.3	0	0	0	3.9	23	31.5	0	3.3	5	10.6	57.2	67.2				6.7	40	53.3	2.2	21.7	32.2
TRDU										0	0	0				0	1.1	1.1																			0	0	0.6							0	1.1	2.8
VUOC	0	0	1.7	0.6	0.6	0.6				0	3.3	3.3	0	2.2	2.2																0.2	0.7	0.7				1.1	4.4	5.6				0	0.8	0.8			
ZIPA2																															0.2	0.2	0.6															