Research Article

Does Fuels Management Accomplish Restoration in Southwest Oregon, USA, Chaparral? Insights from Age Structure

Olivia C. Duren* and Patricia S. Muir

Department of Botany and Plant Pathology, Oregon State University,
2082 Cordley Hall, Corvallis, Oregon 97331, USA

*Corresponding author: Tel.: 001-541-223-1470; e-mail: oliviaduren@gmail.com

ABSTRACT

Fuels management is often intended to both reduce fire hazard and restore ecosystems thought to be impacted by fire suppression. Objectives to reduce fire hazard, however, are not compatible with restoration in many vegetation types. Application of ecologically incompatible treatments to poorly understood ecosystems can drain management resources and contribute to ecosystem degradation. Extensive areas of chaparral on Bureau of Land Management lands in southwest Oregon, USA, are annually targeted for fuels treatment. However, the fire ecology of this ecosystem is not well understood and the assumptions guiding treatment need and design are based on extrapolations from other ecosystems. We studied patterns in age structure of two obligate-seeding chaparral shrubs, sticky whiteleaf manzanita (*Arctostaphylos viscida* Parry) and buckbrush (*Ceanothus cuneatus* [Hook.] Nutt.) and assessed relationships with environment, fire, and potential livestock disturbance. Results indicate that chaparral of obligate seeding species encompasses a wide range of structures and responses to environment and fire throughout its range. While Mediterranean climate obligate-seeding shrub populations are typically even-aged, most stands unburned >30 yr were uneven-aged due to both recruitment in the absence of fire and to persistence of shrubs that predated the last fire. Fire suppression does not seem to have altered chaparral structure or fire severity, and current fuels treatments appear unlikely to reproduce stand structures observed in mature chaparral or in post-wildfire stands. Results underscore that effective fuels management should be both sensitive to regional variability and founded on ecosystem-specific data.

Keywords: age structure, *Arctostaphylos viscida*, *Ceanothus cuneatus*, chaparral, fuels management, grazing, Klamath region, obligate-seeder, southwest Oregon

Citation: Duren, O.C., and P.S. Muir. 2010. Does fuels management accomplish restoration in southwest Oregon, USA, chaparral? Insights from age structure. Fire Ecology 6(2): 76-96. doi: 10.4996/fireecology.0602076

INTRODUCTION

A century of fire suppression has altered the role of fire in maintaining historic structure, composition, and ecological processes in many semi-arid ecosystems (e.g., western dry coniferous forests; Agee 1991, Taylor and Skinner 1998). Fire suppression may also con-

tribute to fuels buildup and uncharacteristically intense wildfires that damage property and natural resources (Hessburg *et al*. 2005). Mitigating fire hazard to property and restoring ecosystems degraded by lack of fire have become central objectives of national fire policy in the US (Healthy Forest Restoration Act 2003). Fuels management can achieve both objectives in some ecosystem and fire regime types, but goals to reduce fire hazard are not compatible with restoration in many ecosystems. Where historic structures and fire regimes of ecosystems targeted for fuels management are poorly understood, the need for and design of fuels treatment are often extrapolated from better studied ecosystems (Keeley and Fotheringham 2001). Misguided application of ecologically incompatible treatments, however, can contribute to ecosystem degradation and failure to achieve management objectives (Hosten *et al*. 2006, Keeley 2007).

In an effort to reduce fire hazard and restore ecosystems assumed to have been degraded by a decline in fire, the Bureau of Land Management (BLM) has implemented landscape-scale fuels treatment programs in southwest Oregon wildlands (USDI 1998, USDI 2004*b*), treating over 5000 ha per year since the mid-1990s (USDI 2004*a*). However, managers lack information on the structures and fire regimes that likely prevailed prior to fire suppression in many ecosystem types. Chaparral shrubland, a Mediterranean climate community of dense, evergreen, drought-tolerant shrubs, is characteristic of southwest Oregon's low- to mid-elevation interior valleys, and extensive areas within this system are targeted annually for fuels treatments. Yet interior valley chaparral is one of the least understood ecosystems in the region (Hosten *et al*. 2006), and the structures and dynamics that characterize this chaparral and its response to fire suppression are little known. In southwest Oregon chaparral and elsewhere, the ability to satisfactorily evaluate the efficacy of fuels treatments is important due to their substantial impact on the landscape, potential conflict with other management objectives, and high expense.

The basic ecology of southwest Oregon interior valley chaparral is also poorly understood relative to other Mediterranean climate shrublands. Most precepts of chaparral ecology are based on studies from southern California (Keeley 2007), while northern ecosystems have received relatively little attention. Chaparral in southwest Oregon is near the northernmost limit of this vegetation type, and has been segregated from California chaparral by the Siskiyou Mountains for at least 4000 years (Detling 1961). The species that dominate southwest Oregon low- to mid-elevation interior valley chaparral, sticky whiteleaf manzanita (*Arctostaphylos viscida* Parry) and buckbrush (*Ceanothus cuneatus* [Hook.] Nutt.), range from Oregon to the southern Sierra Nevada, California, and Baja California, Mexico, respectively (Howard 1992, League 2005). Sticky whiteleaf manzanita and buckbrush are both easily fire-killed, non-sprouting obligate-seeder species that, in California chaparral, require fire-related cues for germination and lack the ability to recruit new individuals without fire (Keeley 1991, Keeley *et al*. 2005*b*). Fires in California chaparral are high severity and leave few, if any, aboveground survivors (Sugihara *et al*. 2006). Where age structures of obligate-seeder shrub species have been studied in California, shrubs form even-aged stands that date back to the last fire (Schlesinger and Gill 1978; Montygierd-Loyba and Keeley 1987; Keeley 1992, 1993). Differences in climate, fire history, and burning conditions over the geographic range of chaparral are, however, substantial (Keeley 2002, Moritz *et al*. 2004). Does variability within this ecosystem necessitate geographically adapted understanding of chaparral fire ecology and management? To address this question, we compared age structures of sticky whiteleaf manzanita and buckbrush in Oregon chaparral to age structures reported for these and other obligate-seeder species in California chaparral and elsewhere.

Our primary objective was to describe patterns in southwest Oregon chaparral age structures and assess their relationships to environment, fire, and disturbance history. We asked:

1) Do obligate-seeder shrub species exhibit even-age structure, which characterizes other Mediterranean climate populations; or is there significant inter-fire recruitment or fire survivorship, exhibited as uneven-aged structure?
2) If significant inter-fire recruitment or fire survivorship occurs, what mechanism(s) might enable them?
3) If multiple age structures occur, what environmental, fire, or potential livestock disturbance variables are most strongly associated with different age structures?
4) What do age structures suggest about the nature of fire effects in chaparral?
5) Do the results have implications for the utility of fuels management in chaparral restoration?

Our results advance understanding of the basic ecology of these northern chaparral ecosystems and indicate that chaparral comprised of purportedly obligate-seeder shrub species demonstrates a wide range of structures and responses to environment, fire, and livestock disturbance. Our increased understanding of variability within Mediterranean climate shrublands enhances the ability of managers to design fire and fuels prescriptions appropriate to the diverse structures and functions within these ecosystems. Our data also underscore the need for ecosystem-specific data on which to design effective management of vegetation in complex landscapes.

METHODS

Study Area

Study sites fall within the steep, rugged Klamath ecoregion of southwest Oregon (Figure 1), a landscape of complex topography,

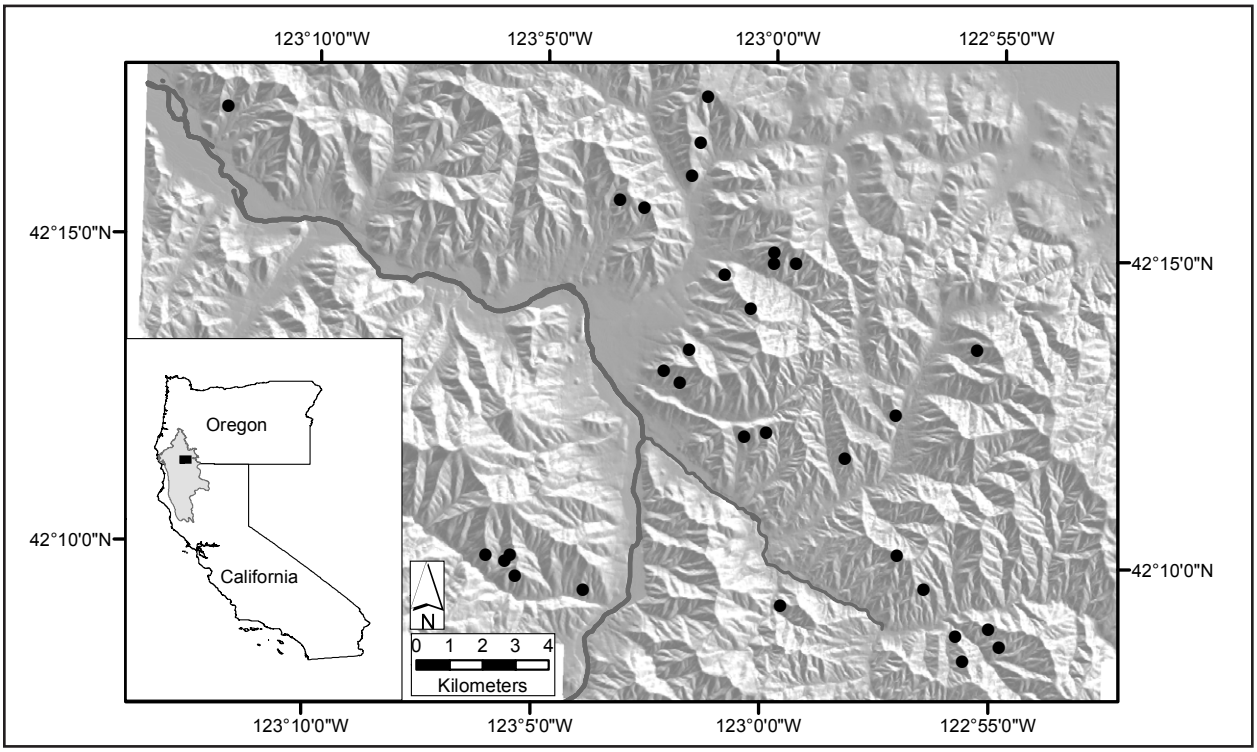

Figure 1. Location of study area within the Klamath ecoregion (inset, shaded, study area marked with ■), and distribution of sites (●) within the study area, southwest Oregon, USA, in 2007. Seventh and eighth order streams are shown.

microclimate, and vegetation. Our focus was on the low- to mid-elevation (500 m to 1200 m) interior valley foothills of the Applegate watershed, within the BLM managed Applegate Adaptive Management Area (approximately 42°8' to 42°20' N and 122°53' to 123°12' W). This area has a Mediterranean climate of cool, wet winters and hot, dry summers, and is in the driest climatic zone of the Klamath ecoregion (Atzet and Wheeler 1982). Mean annual precipitation is about 654 mm, 12 % of which falls June through September; July mean maximum temperature is 32.0 °C and January mean minimum temperature is −1.3 °C (Western Regional Climate Center [WRCC]; <http://www.wrcc.dri.edu/Climsum.html>). A complex geological history has given rise to highly diverse, relatively undeveloped, well-drained soils with upper horizon depths of 36 cm to 85 cm (Natural Resources Conservation Service 2008).

Interior valley chaparral in the Klamath ecoregion is a regionally uncommon vegetation type that supports a unique assemblage of flora and fauna, including several species of concern (Hosten *et al*. 2006, USFWS 2009). Chaparral of buckbrush and sticky whiteleaf manzanita dominates relatively hot, dry slopes, interspersed with grasslands (Figure 2); other shrub associates include birchleaf mountain

Figure 2. Distribution of vegetation communities in the Applegate Valley of southwest Oregon, USA, in 2007. Chaparral (here, buckbrush) and grasslands dominate relatively hot, dry slopes, while more mesic areas support hardwoods and conifers. The red vegetation (center) indicates a recent fire. Compare shrub cover in undisturbed chaparral (black box and generally above road running horizontally in center) and in chaparral treated in hand cut pile-and-burn fuels reduction (white box and generally below road).

mahogany (*Cercocarpus betuloides* Nutt.), bearbrush (*Garrya fremontii* Torr.), Klamath plum (*Prunus subcordata* Benth.), and Pacific poison oak (*Toxicodendron diversilobum* [Torr. and A. Gray] Greene) (Pfaff 2007*b*). More mesic chaparral sites also support scattered trees, including Oregon white oak (*Quercus garryana* Dougl.), California black oak (*Quercus kelloggii* Newberry), Pacific madrone (*Arbutus menziesii* Pursh.), ponderosa pine (*Pinus ponderosa* C. Lawson), and Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirbel) Franco.). In the Applegate Valley, sticky whiteleaf manzanita and buckbrush form closed canopy chaparral (canopy cover 91 % to 99 %; Perchemlides *et al*. 2008), but also form open understories in oak and conifer-dominated communities (Pfaff 2007*b*). This study focused on the first structural type.

Native Americans managed parts of the watershed with fire for at least 4000 yr, but their practices were replaced by Euro-American mining, ranching, and high-frequency burning in the early 1850s (LaLande 1995). Fire suppression was probably not effective in the Applegate Valley until the late 1920s to early 1930s (LaLande 1995). Unlike southern California chaparral, where fire frequency has increased since Euro-American settlement (Keeley and Fotheringham 2001), fire suppression appears to have reduced fire occurrence and fire size several fold in southwest Oregon interior valley chaparral (Duren 2009). Fuels reduction treatments have been implemented since the mid-1990s (USDI 2004*a*), with stated objectives for chaparral including both fire hazard reduction and restoration (USDI 1998, USDI 2004*b*); treatment size has ranged from 0.09 ha to 381 ha (average 21 ha) (USDI 2006). Logging and ranching continue today in parts of the watershed.

Field Methods

We located 31 study sites in chaparral that represented a range of times since fire (22 yr to ≥111 yr), as recorded on BLM fire maps (USDI 2006), and four chaparral community types, as defined by species relative cover (buckbrush chaparral, manzanita chaparral, manzanita-oak chaparral, and open-oak chaparral; Pfaff 2007*b*). Sites were located in areas previously treated with hand-cut pile and burn fuels reduction (16 sites; treated 1 yr to 8 yr prior to sampling) and in undisturbed chaparral (15 sites). Site centers in fuels-treated areas were designated in a geographic information system (GIS) either as the centroid of an area defined by the coincidence of a fuels treatment unit with a chaparral type and time since fire, or as the centroid of an area defined by a chaparral type and time since fire. Site slopes were 13 % to 34 % and aspects ranged from SE to NW.

In fall 2007, we sampled 15 to 25 sticky whiteleaf manzanita and buckbrush individuals at each site from a 50 m × 4 m transect that ran in a random direction from the site center. We sampled the closest shrub stump or living individual to the transect center at 3 m intervals; stumps that were too rotten or damaged to age, which were rare, and shrubs that may have germinated after treatment (<1.6 cm diameter at ground height), were excluded. When necessary, additional transects parallel to the first were sampled until at least 15 shrubs were included. Shrubs were excavated to the stem-root junction to obtain the most accurate age; samples were taken at this point by cutting a thin cross-section and recording shrub diameter at sampling height. All stems were sampled in cases where there were multiple stems. We estimated densities of sticky whiteleaf manzanita and buckbrush (individuals ≥1.6 cm diameter at ground height), and trees (individuals ≥5 cm diameter at breast height) prior to treatment (or current density, for untreated sites) by counting shrub and tree genets in a 4 m wide strip along the first 50 m transect.

Lab Methods and Data Analysis

Shrub ages and quantifying stand age structure. Shrub cross-sections were sanded (120 to 240 grit) and growth rings counted un-

der a dissecting microscope at 7× to 15× power (Figure 3). If rings were partially obscured by internal decay or insect activity, or if a single shrub was represented by multiple stems at the root crown, multiple counts were made and the oldest count was used for that individual. Sample age count was adjusted for year since treatment when applicable and only samples older than the treatment were retained.

Shrub cross-sections yielded either high quality age counts (clear ring count from bark to pith); satisfactory age counts (nearly complete count with ≤10 rings estimated to be missing); or poor quality age counts (count compromised by center rot or insect damage, >10 rings missing). Ages of some samples with poor quality counts were estimated with non-parametric multiplicative regression (NPMR; McCune 2006). These regression models were built in HYPERNICHE version 1.34 (© MjM Software, Gleneden Beach, Oregon, USA) using high quality samples; models were then used to estimate ages for poor quality samples of each species separately. Model building was implemented using local mean, Gaussian weights, and minimum average N* = 1; minimum N* = 1 was required to produce an age estimate. Predictor variables available for each model were sample diameter; height at which the sample was taken; time since last recorded fire (as an indicator of expected age of shrubs with fire-stimulated germination); mean outer ring width, calculated from the combined width of rings across the last 20 yr, or the last 10 yr of growth for shrubs <20 yr old, measured to the nearest mm; and chaparral community type. The response variable, sample age, as well as the predictor variables

Figure 3. Cross-section of sticky whiteleaf manzanita (left) and buckbrush (right) collected in 2007 from interior valley chaparral in southwest Oregon, USA. Rings were clearly defined with sharp boundaries between latewood and earlywood (insets).

sample diameter and height at cut, were log-transformed prior to analysis.

Obligate-seeding shrubs in the genera *Arctostaphylos* and *Ceanothus* produce easily recognizable annual rings in southern California (Keeley 1993). We tested whether sticky whiteleaf manzanita and buckbrush in our study area can be reliably aged by assessing, for a subset of high quality samples (n = 20 of each species), the correspondence between a 'marker ring' (an unusually narrow ring) and a known calendar year of unusually low precipitation, using methods similar to Yamaguchi (1991) and Keeley (1993). This yielded an integrated estimate of error in age counts, which included error in ring counting; error introduced by false or missing rings; and error introduced by asynchronous response among shrubs, such as when an individual's narrowest ring was a response to injury rather than drought. Basing error assessment on the narrowest ring(s) relative to nearby rings, rather than on cross-dating using measured ring widths, is useful for shrubs in the genera *Arctostaphylos* and *Ceanothus* because absolute ring widths vary around the bole due to fluting. The year 1949 was used as the drought year for sticky whiteleaf manzanita, and 1976 was used as the drought year for buckbrush; precipitation in these years was 50.8% and 37.7% lower than the 65 yr average, respectively (WRCC). (The earlier year was not used for buckbrush because few high quality samples were old enough.) The general region (20 ring span) in which the ring corresponding to the drought year should have been laid down was identified; establishing a broad target region allowed for the possibility of missing and false rings and counting error. The ring count from the bark to the narrowest ring in this region was compared to the number of years between the year that the shrub was cut and the drought year. The difference between the ring count and the year count was the estimated integrated error. In the case of multiple small rings, the ring that gave the largest error was used, such that our error estimates were generous.

Quantification of the distribution of sampled shrub ages in each stand (its age structure), allowed us to describe patterns in age structure, compare them among stands, and assess relationships among age structures, environment, and disturbance history. Age structures were characterized by six attributes: median age, skew, kurtosis, variance, coefficient of variation (CV), and range in ages divided by median age. In fuels-treated stands, we could not determine whether a shrub was alive when it was cut during treatment; such knowledge would improve resolution of age structures. However, a comparison of age structure characteristics between similarly aged treated and untreated stands (in which only live shrubs were sampled), indicated that possible sampling of some dead shrubs in treated stands was unlikely to affect inferences about age structure and, in particular, unlikely to falsely make age distributions differ from the expected even-aged structure (Duren 2009).

We mapped each stand in the space defined by its age structure attributes using nonmetric multidimensional scaling (NMS) ordination, implemented in PC-ORD version 5.15 (© MjM Software, Gleneden Beach, Oregon, USA). Ordination allows age structures to be considered on continuous gradients rather than breaking them into artificial types. Age distribution characteristics were first relativized by their standard deviates so that each contributed equally to stand placement in the ordination (McCune and Grace 2002). Nonmetric multidimensional scaling was run using Euclidean distance with a random starting configuration and 250 runs with real data; the final solution was produced by rerunning NMS with the best ordination as the starting configuration. Two outlier stands were detected ($SD \geq 2.0$), but both were retained because no aspect of the ordination substantially changed when they were removed.

Age structure and environment, wildfire, and potential livestock disturbance. We evaluated the relationships of age structure patterns

to site environmental characteristics including climate, terrain, geology and soils, and stand structure (Table 1) (climate, terrain, soils datasets from Pfaff [2007*a*]). Many of these factors may influence site soil temperature and moisture, which in turn are related to shrub germination and recruitment and stand development dynamics (Christensen and Muller 1975, Schlesinger and Gill 1980, Zammit and Zedler 1993, Keeley *et al*. 2005*a*). Age structure patterns were also assessed in relation to wildfire history (maximum fire-free interval, minimum fire-free interval, and point fire frequency) for fires >40 ha, 1895 to 2005 (Pfaff 2007*a*, USDI 2006); year of last fire was not included because this variable was used to estimate some cross-section ages. The site value for each variable was calculated as the average of the values sampled in a GIS at site center and 50 m from center in each cardinal direction. We used Pearson's correlation coefficients to evaluate relationships between age structure patterns (ordination axes) and environmental and fire history variables. Quantitative variables with skew >1 were log-transformed to improve homogeneity of variance.

Disturbances by domestic livestock can influence age structure by damaging mature shrubs and seedlings (Deveny and Fox 2006) and altering shrub germination and recruitment microenvironments (Jones 2000, Deveny and Fox 2006). The absence of reliable historic grazing records within the study area (apart from those kept since *circa* 1970; K. Hackett, BLM, personal communication) prevented a direct analysis of grazing influences on age structures. We therefore modeled potential livestock utilization of sites based on factors known to influence the distribution of cattle across complex terrain, including slope (e.g., Pinchak *et al*. 1991), proximity to water or roads (e.g., Hosten *et al*. 2007), and the interaction of these factors. (While sheep were important early in the Euro-American settlement period, cattle have been the primary grazers in the study area for the last century; LaLande 1995). We described potential livestock utilization of each site in terms of site distance to the nearest road, trail, or water source, and average slope from road or water source to site. Distances were found in a GIS using a tool that calculates true overland distance accounting for topography. Because livestock access to a site is influenced by the interaction of distance and slope from access point to the site, we also described potential livestock site utilization in terms of a road access index and a water access index (distance to nearest road or water multiplied by the absolute value of the slope between the site and the nearest road or water, respectively).

Records for recent grazing history (since *circa* 1971) at each site (USDI 2008) allowed us to assess the number of years that the site had been ungrazed and the seasonality of grazing (spring to early summer, spring to midsummer, and summer to late summer), and allowed us to compute a grazing intensity index by

Table 1. Measures of environmental site characteristics and stand structure patterns.

	Measures
Climate	Annual precipitation, actual annual evaporation, summer evaporation
Terrain	Aspect folded to reflect potential moisture status (= |180 − |aspect – 225||; McCune 2007), elevation, slope shape, slope aspect, percent slope, potential direct incident radiation and heat load (both indices of solar interception), sixth field watershed membership
Geology and soils	Parent material, surface soil horizon depth, percent clay, percent silt, percent sand, cation exchange capacity, pH
Stand structure	Tree basal area, shrub density

multiplying the BLM-allotted Animal Unit Months (AUMs, where one AUM is an allotment for one cow and calf for one month) by the number of allotted grazing months, and dividing by the area in each allotment.

We assessed the relationship between stand age structure and inferred livestock disturbance by calculating correlations between livestock variables and ordination axes. Quantitative variables with skew >1 were log-transformed. We also developed regression models in which age structure, as described by ordination axis scores for each site, was assessed against potential livestock disturbance and recent grazing history variables (NPMR, local mean, Gaussian weights, and minimum average N*=1).

Grazing could facilitate shrub recruitment in the absence of fire by creating gaps in the shrub canopy that enabled soil heating, or by mechanically scarifying seed, or impede recruitment by damaging seedlings. We evaluated the relationship between shrub density and livestock variables, and between fire-free recruitment and livestock variables, using NPMR regression models with specifications described previously.

RESULTS

Shrub Ages and Age Structures

A total of 485 shrubs were aged, with cross-sections nearly evenly distributed between sticky whiteleaf manzanita and buckbrush. The oldest sticky whiteleaf manzanita sampled was >146 yr old and 44 samples of this species were ≥100 yr (diameters 10 cm to 50 cm). The oldest buckbrush sampled was >114 yr old and three buckbrush were ≥100 yr (diameters 16 cm to 43 cm). Rot in cross-sections of both species, and the stem axis-splitting growth pattern of old buckbrush, which obliterates the pith, makes it likely that these sections and sections from many more individuals were older than their counted or estimated ages.

Sixty-four percent of cross-sections had complete or nearly complete age counts from bark to pith, and their ages were not estimated. The NPMR satisfactorily modeled ages for poor quality cross-sections of both species (sticky whiteleaf manzanita: $xR^2 = 88\%$, $P = 0.047$; selected predictors included section diameter and mean ring width of last 20 yr; buckbrush: $xR^2 = 69\%$, $P = 0.047$; selected predictors included section diameter, chaparral community type, and expected stand age from fire history maps). Ages were estimated for 13% of cross-sections (12% sticky whiteleaf manzanita, 1% buckbrush) using NPMR. Estimated ages averaged 13 yr older than counted ages for these sections. For cross-sections that yielded poor quality counts but when the regression-estimated age was less than actual age count, ages were not adjusted (23% of sections).

The calendar years corresponding with narrow marker rings were fairly synchronous across sites within species, suggesting a common response to an annual environmental cue. Annual rings were also implied by consistency of ring counts with the year of the last stand-replacing fire and ring count agreement across samples and across species in young stands. In sticky whiteleaf manzanita, counts to narrow rings missed the 1949 drought year by a mean of ±2.1 yr (maximum ±8 yr; based on the absolute value of years missed). In buckbrush samples, counts to narrow rings missed the 1976 drought year by a mean of ±2.6 yr (maximum ±5 yr). With this method, the integrated error depends on the number of years over which it is estimated. Assuming that error rate is constant over time and scaling according to the number of years of growth of each sample, all samples had an estimated mean integrated error of ±10 yr or less. Ring count overestimation and underestimation were equally likely, suggesting that false or missing rings, if present, were equally common. We incorporated estimated integrated error in our definition of age structure types:

even-aged stands were those in which all shrub age counts were within ±20 yr of each other, and uneven-aged stands were those with range in shrub ages greater than ±20 yr. Shrubs that recruited in the absence of fire were defined as those with age counts >20 yr younger than the last known fire, and fire survivors were shrubs with age counts >20 yr older than the last known fire.

Most stands had uneven-aged structures, showing either prolonged recruitment in the absence of fire, substantial fire survivorship, or both (Figure 4, Table 2). Only 10 of 31 stands (32 %) were even-aged, and 8 of these were burned <30 yr prior to field study. Nearly all sites unburned for >30 yr were uneven-aged due to shrubs that recruited in the absence of fire (>20 yr younger than last known fire), fire survivors (>20 yr older than last known fire), or both. Comparison of age structures with recorded fire history suggests omissions in the fire record.

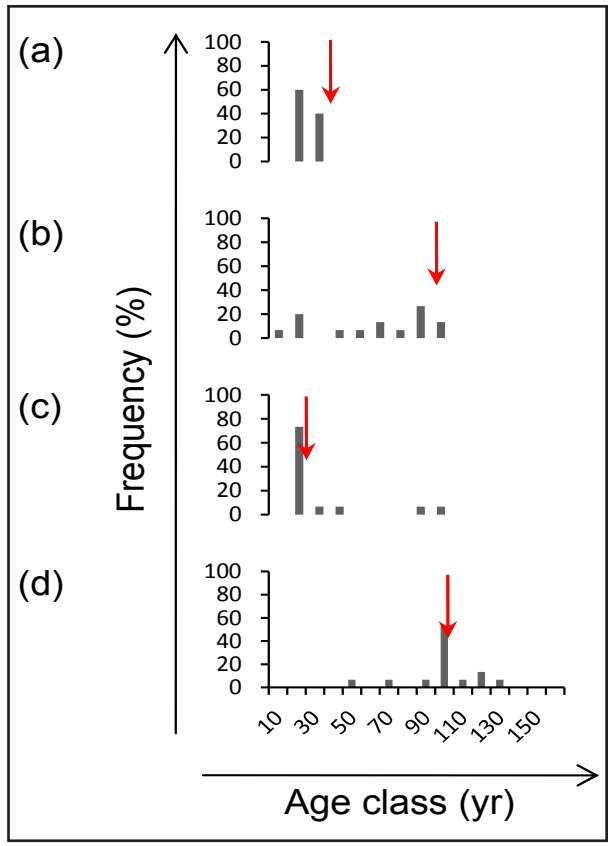

Figure 4. Age distributions for representative chaparral study sites in southwest Oregon, USA, in 2007, showing even-aged stands (all sample ages within 40 yr of each other; a). Nearly all sites unburned for >30 yr were uneven-aged due to (b) shrubs that recruited in the absence of fire (>20 yr younger than last known fire), (c) shrubs that survived the last known fire (>20 yr older than last known fire), or (d) both. Arrows indicate year of last known fire.

Shrub Recruitment in the Absence of Fire and Fire Survivorship

Fire-free recruitment of shrub seedlings appeared to be prolonged, often lasting several decades; most (64 %) fire-free recruits were buckbrush. We also occasionally observed asexual recruitment by layering, particularly in older individuals of whiteleaf manzanita when the main stem was in poor health. Because each sampled shrub was dug out to the roots, we could easily differentiate between seedlings and layered recruits, and layered recruits were few. Although 4 % to 100 % of shrubs in stands unburned 30 yr recruited in the apparent absence of fire, with the proportion of recruits increasing as stands aged, such recruitment contributed on average only 46 new shrubs per hectare per decade (range 6 to 100 shrubs).

Shrubs that apparently survived fire contributed a mean basal area of 8.0 m² ha^{-1} to sampled stands (range 0.0 m² ha^{-1} to 79.4 m² ha^{-1}); most (93 %) survivors were sticky whiteleaf manzanita. Fires in all sites appeared to have been high severity since the early 1900s. Given that canopy cover of interior valley chaparral within the study area is typically almost complete (Peterson 1916, Perchemlides *et al*. 2008), fires appeared to have burned ≥93 % canopy cover in sampled stands (estimated mean surviving canopy cover 60 m² ha^{-1}, range 0.0 m² ha^{-1} to 565 m² ha^{-1}, based on the number of survivors in each stand and a mean canopy cover of 1.5 m² per individual sticky whiteleaf manzanita [Howard 1992]). One third of the shrubs designated as either re-

Table 2. Percent of shrubs sampled in each stand by age class and chaparral vegetation type in southwest Oregon in 2007. Bolded values in red indicate age class corresponding to recorded year of last fire; where no shrub ages corresponded to a fire, fire occurrence is represented by a red X. Stands without bolded values have not had a recorded fire in at least 111 yr.

		Age class (yr)														
	Chaparral vegetation type	**1 - 9**	**10 - 19**	**20 - 29**	**30 - 39**	**40 - 49**	**50 - 59**	**60 - 69**	**70 - 79**	**80 - 89**	**90 - 99**	**100 - 109**	**110 - 119**	**120 - 129**	**130 - 139**	**140 - 149**
Even-aged stands	Buckbrush		7	**93**												
	Buckbrush			**100**												
	Sticky whiteleaf manzanita/ Oregon white oak		53	**47**												
	Sticky whiteleaf manzanita/ Oregon white oak		47	**40**	13											
	Open Oregon white oak/ chaparral	7	64	**29**												
	Buckbrush		73	27					**X**							
	Buckbrush		53	47					**X**							
	Sticky whiteleaf manzanita			80	20				**X**							
	Sticky whiteleaf manzanita							7	27	67			**X**			
	Open Oregon white oak/ chaparral							29	14	57			**X**			
Stands with fire-free recruits	Sticky whiteleaf manzanita/ Oregon white oak				4	4	21	**25**	25	21						
	Open Oregon white oak/ chaparral				7	27	13	**33**	13	7						
	Open Oregon white oak/ chaparral		40	13	13	20			**7**	7						
	Buckbrush			13	7	27	33	20			**X**					
	Open Oregon white oak/ chaparral		20	7	7		20	7	27	13	**X**					
	Sticky whiteleaf manzanita/ Oregon white oak			7	7				7	47	13	7	**13**			
	Open Oregon white oak/ chaparral		13	4	22	35	13	13					**X**			
	Buckbrush				13	40	27	13	7				**X**			
Stands with fire survivors	Open Oregon white oak/ chaparral		73	**7**		7				13						
Stands with fire-free recruits and fire survivors	Open Oregon white oak/ chaparral			7	7	27	27	**20**		7			7			
	Sticky whiteleaf manzanita/ Oregon white oak					8	31		**23**	23		8		8		
	Buckbrush			13		7	13	47	**13**			7				
	Sticky whiteleaf manzanita		13	27		13	13	7	**X**	20		7				
	Sticky whiteleaf manzanita		7	40					**13**	7	27	7				
	Sticky whiteleaf manzanita/ Oregon white oak						7			13		20	20	27	13	
	Sticky whiteleaf manzanita/ Oregon white oak				29				14	14	**X**	14	14			14
	Sticky whiteleaf manzanita/ Oregon white oak					7		7		7	47	**7**	20	7		
	Sticky whiteleaf manzanita			7		29	7	29	7	14	7	**X**				
	Sticky whiteleaf manzanita		7							53	33		**7**			
	Sticky whiteleaf manzanita/ Oregon white oak		25		4				4	13	4	29	**17**		4	
	Buckbrush		7	13	13	7	27	13	7			13	**X**			

cruits or survivors were uncertain due to poor or estimated ages. Fire-free recruits and fire survivors were, however, clearly apparent within age structures even when samples with poor or estimated ages were excluded.

Age Structures in Relation to Environment, Wildfire, and Potential Livestock Disturbance

Variation in age structure characteristics among stands was well represented by the NMS ordination (99.4% cumulative R^2 over three axes, all $P \leq 0.01$ from a Monte Carlo test with 250 randomized runs; stress = 2.54, 54 iterations; instability <0.00001). Two of the axes primarily separated even-aged stands from uneven-aged stands (even-aged stands had low relative range, variance, or coefficient of variation in shrub ages, and relatively low median ages). The third axis separated stands in terms of age distribution kurtosis and skew.

Study sites represented a considerable range in climate, terrain, geology, stand structure, and fire history. Sites were particularly varied in elevation (520 m to 1140 m), aspect (117° to 301°), annual precipitation (655 mm to 841 mm), surface soil horizon depth (36 cm to 85 cm), and tree basal area (0 m^2 ha^{-1} to 36 m^2 ha^{-1}) (Duren 2009). Despite the range in environmental and fire history variables across sites, only two inter-related variables of the 34 considered were substantially related ($r \geq |0.500|$) to patterns in age structure: density (genets m^{-2}) of buckbrush alone and density of sticky whiteleaf manzanita and buckbrush together tended to be higher in stands that had even-aged structure. Correlations of other variables with any axis were weak ($r < |0.405|$). (Some caution is warranted in the interpretation of ordination results and assessment of correlations with environment and disturbance, as both known and estimated shrub ages were included in derivation of the stand age structure parameters on which ordinations were based.)

Study sites were also quite variable in potential livestock utilization, with some on level ground close to roads, trails, or water, and others likely accessible only with difficulty (site distance to nearest road or trail 16 m to 578 m, mean 211 m; slope from road to site 68% downhill to 38% uphill, mean |25%|; site distance to nearest seasonal or perennial water 118 m to 2052 m, mean 411 m; slope from water to site 7% to 57% uphill, mean 28%). Sites also differed in seasonality and estimated intensity of recent (*circa* 1970s) grazing. Most sites had not been grazed for ≥23 yr (n = 26), three sites were ungrazed for 11 yr, and two sites were actively grazed. Potential livestock disturbance and recent grazing history, however, were not related to patterns in age structure ($r < |0.350|$ for correlations between livestock variables and ordination axes, $xR^2 < 0.16$ for the best NPMR models of age structure ordination scores). Differences in fire-free recruitment or shrub density between sites were also not related to livestock variables ($xR^2 < 0.35$ and $xR^2 < 0.19$ for the best NPMR recruitment and density models, respectively; $P > 0.5$ for both models).

DISCUSSION

Chaparral and other Mediterranean climate species are often organized into life history groups based on capabilities for fire-related population expansion (Keeley 1991). The shrub species that dominate low- and mid-elevation southwest Oregon chaparral, sticky whiteleaf manzanita and buckbrush, are both reported to be obligate-seeders in southern California that are fire-killed, require fire-related cues for germination, and lack the ability to recruit new individuals in the absence of fire (e.g., Keeley 1991, Keeley *et al*. 2005*b*). In California chaparral and in other Mediterranean climate systems, obligate-seeders are thought to form stands in which shrub ages generally date to the most recent fire (e.g., Keeley 1992, Zammit and Zedler 1993, Ooi *et al*. 2006). In contrast, all but two of our southwest Oregon stands unburned >30 yr were uneven-aged due to appreciable fire survivorship

and widespread recruitment during fire-free periods. The prevalence of obligate-seeder shrubs that appear to have recruited in the absence of fire suggests that this life history group is capable of a more plastic response to environment, fire, and livestock disturbance, and supports more structural variation, than has generally been accepted.

Variable Ability of Obligate-Seeder Shrubs to Recruit in the Absence of Fire

Recruitment of species with mostly refractory seeds in the absence of fire can be facilitated by solar heating of the soil surface (Christensen and Muller 1975). This is a plausible mechanism for stimulating buckbrush seed germination in our study sites, as maximum surface soil temperatures in gaps between shrubs (68.5 °C; Duren 2009) were comparable to temperatures known to significantly increase seed germination of this species (Keeley 1987). Germination stimulants of sticky whiteleaf manzanita are less well understood (e.g., Kauffman and Martin 1991, Keeley 1991), and mechanisms for recruitment of this species in the absence of fire are uncertain. Recruitment did not appear to be related to factors likely to influence soil heating or seedling water stress (Duren 2009), or to potential livestock disturbance. Young stands (<30 yr since fire) with relatively high shrub density lacked fire-free recruits, but two older stands with relatively low shrub density and, presumably, more opportunities for soil heating, also lacked such recruits. We found no relationship between even-agedness and other site characteristics, which, along with the predominance of older uneven-aged stands, suggests that most unburned chaparral stands eventually develop uneven-aged structure across the range of environments represented in the study area. Even though a small proportion of seeds from obligate-seeders are non-refractory and can produce seedlings in the absence of fire (Keeley 1987), successful inter-fire recruitment of obligate-seeders in Mediterranean type ecosystems is rare because seedlings are generally thought to not establish successfully in intact, robust shrublands (Biswell and Gilman 1961, Christensen and Muller 1975, Enright and Goldblum 1999, Ooi *et al*. 2006). In contrast, we found that, although fire-free recruits showed evidence of suppressed growth rates (Duren 2009), they persisted to at least 46 yr of age.

Frequent recruitment and persistence of obligate-seeder species in some unburned chaparral ecosystems, but not others, raises the question of why the propensity for recruitment in the absence of fire differs between parts of the chaparral range, despite similar species composition. Sticky whiteleaf manzanita and buckbrush clearly have strongly fire-stimulated germination in southwest Oregon, as they do elsewhere; seedling numbers after fire are at least an order of magnitude higher than after disturbance by fuel reduction thinning (Perchemlides 2006). Nonetheless, non-fire recruits of buckbrush have occasionally been noted in the northern regions of this vegetation type (Biswell and Gilman 1961, Duncan *et al*. 1987, Safford and Harrison 2004, Deveny and Fox 2006), although age structures of obligate-seeding chaparral have not been studied north of Lake County, California (latitude 39°). It is possible that these obligate-seeders, buckbrush in particular, are less dependent on fire for recruitment than has been previously thought. Instead, successful recruitment in the absence of fire may be partly controlled by environment. We suggest that regions conducive to fire-free germination and persistence of recruits may have greater summer soil moisture compared to areas that lack recruitment. The coincidence of heat and moisture lowers germination temperatures and increases germination rates for *Ceanothus* species (Kauffman and Martin 1991). Mean summer precipitation (June to August) generally increases over the range of chaparral from the south to the north (PRISM Climate Group 2006). Higher summer moisture may also allow for seedling per-

sistence by alleviating some of the acute competition that drives shrub thinning in southern California chaparral (Schlesinger and Gill 1980, Zammit and Zedler 1993). For instance, we did not find that shrub growth rates or shrub density were lower on more xeric aspects, as they are in southern California (Zammit and Zedler 1993, Keeley *et al*. 2005*a*). It is unclear whether gaps and opportunities for soil heating are more common in northern chaparral than in the south; southwest Oregon sites seem to be somewhat less dense than reported elsewhere for similarly aged chaparral (e.g., Keeley 1992), but stand-level shrub cover is high (91% to 99%; Perchemlides *et al*. 2008), suggesting that shading may be similar between regions.

Differences in seed pools among populations may also contribute to regional differences in chaparral demographic dynamics. Obligate-seeder species often have polymorphic seed pools comprised of both refractory and non-refractory seeds (Keeley 1991), and relatively isolated populations may have a greater proportion of non-refractory propagules (e.g., Gauthier *et al*. 1996). Some Mediterranean climate shrubs produce both light seeds, which account for most recruitment between fires, and heavier, heat-resistant seeds that produce most seedlings after fires (Delgado *et al*. 2001). Polymorphisms that track geographic or environmental trends occur in some species cued to post-fire recruitment. For example, the degree to which germination was smoke-stimulated was related to latitude for an Australian species (Tieu *et al*. 2001), and some serotinous trees may be able to partially track changing fire regimes by increasing the ability to recruit without fire during long fire-free intervals (Gauthier *et al*. 1996).

Inferences on Fire Regimes and Fire Effects in Southwestern Oregon Interior Valley Chaparral

Age structures indicate that high severity fires have been characteristic of chaparral in our study area at least since the first decade of the 1900s, which is consistent with historic records (e.g., Peterson 1916). This may indicate that fire suppression has had little effect on fire behavior in interior valley chaparral. Shrub communities and the xeric aspects on which they are often found tend to burn with higher severity than other areas within the Klamath ecoregion (Taylor and Skinner 1998, Odion *et al*. 2004, Alexander *et al*. 2006). High severity fires are also characteristic of chaparral in many other parts of its range (e.g., Sugihara *et al*. 2006) and favor chaparral persistence by clearing encroaching trees (Taylor and Skinner 1998, Nagel and Taylor 2005) and stimulating germination of obligate-seeding species (Moreno and Oechel 1991, Odion and Davis 2000).

Although high severity fire appears to be a shared attribute across much of the range of chaparral, the presence of obligate-seeding shrubs in southwest Oregon that survived fire or recruited in the absence of fire may suggest regional differences in other fire regime characteristics. For example, the appreciable number of shrub survivors in many of our stands, in contrast with zero survivorship reported for southern California stands (Schlesinger and Gill 1978, Montygierd-Loyba and Keeley 1987, Keeley 1992) implies that fires may burn with comparatively greater stand-level spatial complexity. High fire patchiness was associated with survival of fire-sensitive shrubs in another Mediterranean type ecosystem as well (Ooi *et al*. 2006). While shrub fire survivors were noted in chaparral of California's northern Sierra Nevada (Nagel and Taylor 2005), to our knowledge, no quantification of survivorship exists with which we can compare our results.

Obligate-seeding shrub communities have been suggested to be resilient to fire return intervals from 25 yr to 150 yr (Keeley *et al*. 2005*c*). Shrubs in southwest Oregon interior valleys that recruited in fire-free periods or survived fire may indicate that chaparral in our study area is tolerant of fire regimes with even higher temporal variability. The ability of

shrubs to recruit in the absence of fire can allow population persistence during fire-free intervals that exceed shrub longevity. Such bet-hedging strategies are advantageous when fire frequency is unpredictable (Enright and Goldblum 1999). Shrub fire survivors, on the other hand, may enable population persistence in the face of fire intervals shorter than the time needed to mature and accumulate a sufficient seed bank, which usually cause local extirpation of obligate-seeding shrubs (Duncan *et al*. 1987, Haidinger and Keeley 1993, Enright and Goldblum 1999, Jacobsen *et al*. 2004). Species with life history traits similar to sticky whiteleaf manzanita and buckbrush are estimated to require minimum fire-free intervals of 20 yr to 30 yr for population persistence (Keeley and Fotheringham 2006, Syphard *et al*. 2006). If spatially complex fires leave shrub survivors that produce seed, however, very short fire intervals may not eradicate sticky whiteleaf manzanita and buckbrush populations as long as most fire intervals allow many of shrubs in a stand to reach reproductive age and replenish propagule stores. Differences between southwest Oregon interior valley chaparral and other studied chaparral communities in the degree of dependence on fire-related cues for recruitment, and possibly in some fire regime characteristics, imply that many precepts of chaparral ecology and management should be tailored on a geographic basis.

The fire regime that characterized southwest Oregon interior valley chaparral prior to Euro-American settlement is uncertain, and regimes other than the high severity, moderate frequency regime we propose here may have prevailed. However, our evidence implies that chaparral within our study area probably experienced a fire regime that was distinct from the historically low or mixed severity, high frequency fires that characterized nearby conifer forests (e.g., Agee 1991, Sensenig 2002). Chaparral patches have also experienced different fire histories than the surrounding conifer matrix elsewhere (Nagel and Taylor 2005), perhaps because differences in fuel structure, continuity, and moisture prevent surface fire spread from forests to chaparral under moderate burning conditions, particularly when chaparral is young (Green 1981, Dieterich and Hibbert 1990, Cione *et al*. 2002, Taylor and Skinner 2003). Burning practices of early ranchers (e.g., Peterson 1916, LaLande 1995) and extensive livestock grazing are also likely to have influenced chaparral community structure and dynamics, but data to enable explicit assessment of the roles of these factors are lacking. Nonetheless, it is clear that uneven-aged structures, shrub fire survivorship, and recruitment in the absence of fire occur after the long absence of those practices.

Management Implications

Fire and fuels management in California chaparral has often been predicated on treatments developed in dry western conifer forests (Keeley 2002), and this is true of southwest Oregon interior valley chaparral as well (USDI 1998, 2004*b*). Yet, in contrast to dry forests, there is little evidence that chaparral stands in southwest Oregon or in California have experienced substantial structural change or shifts in fire severity in response to fire suppression (Keeley *et al.*1999, Moritz *et al.* 2004; debate continues on the extent to which suppression has altered landscape-scale patterns of fire size and frequency in southern California chaparral [e.g., Goforth and Minnich 2007, Keeley and Zedler 2009]).

Current hand-cut pile and burn fuel treatment prescriptions appear unlikely to reproduce stand structures observed in mature southwest Oregon interior valley chaparral. Residual canopy cover of woody species was 25% (SD = 18%) in treated stands, compared to the nearly complete cover documented in mature stands both before and after the onset of effective fire suppression (Peterson 1916, Perchemlides *et al*. 2008). Treatments also

seem unlikely to mimic fire effects on stand structure, as shrub cover retained by treatment is generally higher and less variable than would be left by fire. Treatments do not appear to duplicate the function of fire, as regeneration of shrub species characteristic of post-fire environments is 10 to >100 times lower in treated stands (Perchemlides 2006) than in stands burned by wildfire (Peterson 1916), substantially delaying recovery of shrub cover (Perchemlides *et al*. 2008). Because invasion and spread of non-native herbaceous species is facilitated by low shrub cover (Merriam *et al*. 2006, Perchemlides *et al*. 2008), shrub removal can contribute to an ecosystem state change from dominance by chaparral to dominance by annual or non-native vegetation (Jacobsen *et al*. 2004, Perchemlides *et al*. 2008).

The restoration potential of treatments that include a stand-level fire component is uncertain. Fire history records reveal that annual area burned in southwest Oregon interior valleys has been much reduced consequent to fire suppression, and many chaparral stands have had no recorded fire in at least 111 yr (Duren 2009). Whether fuels treatments that include stand-level fire may be justified to address seed bank attrition and other senescence risks (*sensu* Zedler 1995) in long-unburned chaparral is unclear, but very old (>90 yr) chaparral in California, at least, does not appear to be at risk of such degradation (Zedler 1995, Keeley *et al*. 2005*c*). Fire-free recruitment in southwest Oregon interior valley chaparral may allow population persistence under extended fire-free intervals. Research on the regeneration capacity of shrubs and herbs in long-unburned chaparral in southwest Oregon is needed to clarify whether fuels treatments may be useful in mitigating senescence risk in very old stands, and monitoring is needed in stands that have already been treated.

Fuels management objectives often prioritize fire hazard reduction, and our data do not address achievement of this goal. Our results do suggest, however, that fuels treatments, as currently implemented in southwest Oregon interior valley chaparral, are unlikely to accomplish restoration goals. Because high fuels and fire severity appear to have been, and continue to be, typical of chaparral, fuels management objectives to mitigate fire hazard and restore characteristic structures and processes may be incompatible.

ACKNOWLEDGEMENTS

We thank B. McCune for statistical assistance, and B. McCune, D. Hibbs, and two anonymous reviewers for their careful criticisms and insightful comments on an earlier version of this paper. Thanks also to D. Maze and B. Hudson for tireless field and lab assistance. We appreciate the contribution of indispensable datasets from E. Pfaff, and from A. Parsons and K. Hackett of the Medford BLM, and acknowledge the Medford BLM for administrative and logistical support. Thank you also to P. Hosten for his commitment to both the ecosystems and the people of southwest Oregon, and for laying the foundation essential to getting this and many other projects off the ground. This work was funded by the Joint Fire Science Program (Project 06-3-1-35).

LITERATURE CITED

Agee, J.K. 1991. Fire history along an elevational gradient in the Siskiyou Mountains, Oregon. Northwest Science 65: 188-199.

Atzet, T., and D.L. Wheeler. 1982. Historical and ecological perspectives on fire activity in the Klamath Geological Province of the Rogue River and Siskiyou National Forests. Forest Service Publication R6-Range-102, Portland, Oregon, USA.

Biswell, H.H., and J.H. Gilman. 1961. Brush management in relation to fire and other environmental factors on the Tehama deer winter range. California Fish and Game 47: 357-389.

Christensen, N.L., and C.H. Muller. 1975. Effects of fire on controlling plant growth in *Adenostoma* chaparral. Ecological Monographs 45: 29-55. doi: 10.2307/1942330

Cione, N.K., P.E. Padgett, and E.B. Allen. 2002. Restoration of a native shrubland impacted by exotic grasses, frequent fire, and nitrogen deposition in southern California. Restoration Ecology 10: 376-384. doi: 10.1046/j.1526-100X.2002.02038.x

Delgado, J.A., J.M. Serrano, F. Lopez, and F.J. Acosta. 2001. Heat shock, mass-dependent germination, and seed yield as related components of fitness in *Cistus ladanifer*. Environmental and Experimental Botany 46: 11-20. doi: 10.1016/S0098-8472(01)00076-4

Detling, L.E. 1961. The chaparral formation of southwestern Oregon, with considerations of its postglacial history. Ecology 42: 348-357. doi: 10.2307/1932085

Deveny, A.J., and L.R. Fox. 2006. Indirect interactions between browsers and seed predators affect the seed bank dynamics of a chaparral shrub. Oecologia 150: 69-77. doi: 10.1007/s00442-006-0503-3

Dieterich, J.H., and A.R. Hibbert. 1990. Fire history in a small ponderosa pine stand surrounded by chaparral. Pages 168-173 in: J.S. Krammes, technical coordinator. Effects of fire management of southwestern natural resources. Forest Service General Technical Report RM-19, Fort Collins, Colorado, USA.

Duncan, D.A., N.K. McDougald, and S.E. Westfall. 1987. Long-term changes from different uses of foothill hardwood rangelands. Pages 367-372 in: Proceedings of the symposium on multiple-use management of California's hardwood resources. Forest Service General Technical Report PSW-100, Berkeley, California, USA.

Duren, O.C. 2009. Chaparral history, dynamics, and response to disturbance in southwest Oregon: insights from age structure. Thesis, Oregon State University, Corvallis, USA. <http://hdl.handle.net/1957/11909> Accessed 6 January 2010.

Enright, N.J., and D. Goldblum. 1999. Demography of a non-sprouting and resprouting *Hakea* species (Proteaceae) in fire-prone Eucalyptus woodlands of southeastern Australia in relation to stand age, drought and disease. Plant Ecology 144: 71-82. doi: 10.1023/A:1009839800864

Gauthier, S., Y. Bergeron, and J.P. Simon. 1996. Effects of fire regime on the serotiny level of jack pine. Journal of Ecology 84: 539-548. doi: 10.2307/2261476

Goforth, B.R., and R.A. Minnich. 2007. Evidence, exaggeration, and error in historical accounts of chaparral wildfires in California. Ecological Applications 17: 779-790. doi: 10.1890/06-0831

Green, L.R. 1981. Burning by prescription in chaparral. Forest Service General Technical Report PSW-51, Berkeley, California, USA.

Haidinger, T.L., and J.E. Keeley. 1993. Role of high fire frequency in destruction of mixed chaparral. Madroño 40: 141-147.

Healthy Forest Restoration Act. 2003. Public Law no. 108-148. United States Statutes at Large 117: 1887-1915.

Hessburg, P.F., J.K. Agee, and J.F. Franklin. 2005. Dry forests and wildland fires of the inland northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management 211: 117-139. doi: 10.1016/j.foreco.2005.02.016

Hosten, P.E., O.E. Hickman, F.K. Lake, F.A. Lang, and D. Vesely. 2006. Oak woodlands and savannas. Pages 63-96 in: D. Apostol and M. Sinclair, editors. Restoring the Pacific northwest: the art and science of ecological restoration in Cascadia. Island Press, Washington, D.C., USA.

Hosten, P.E., H. Whitridge, D. Schuster, and J. Alexander. 2007. Livestock on the Cascade-Siskiyou National Monument: a summary of stocking rates, utilization, and management. Bureau of Land Management, Medford, Oregon, USA.

Howard, J.L. 1992. *Arctostaphylos viscida.* Fire effects information system online database. Forest Service. <http://www.fs.fed.us/database/feis/plants/shrub/arcvis/all.html>. Accessed 7 February 2007.

Jacobsen, A.L., S.D. Davis, and S.L. Babritius. 2004. Fire frequency impacts non-sprouting chaparral shrubs in the Santa Monica Mountains of southern California. Pages 1-5 in: M. Arianoutsou and V.P. Panastasis, editors. Ecology, conservation and management of Mediterranean climate ecosystems. Millpress, Rotterdam, Netherlands.

Jones, A. 2000. Effects of cattle grazing on North American arid ecosystems: a quantitative review. Western North American Naturalist 60: 155-164.

Kauffman, J.B., and R.E. Martin. 1991. Factors influencing the scarification and germination of three montane Sierra Nevada shrubs. Northwest Science 65: 180-187.

Keeley, J.E. 1987. Role of fire in seed germination of woody taxa in California chaparral. Ecology 68: 434-443. doi: 10.2307/1939275

Keeley, J.E. 1991. Seed germination and life history syndromes in the California chaparral. The Botanical Review 57: 81-116. doi: 10.1007/BF02858766

Keeley, J.E. 1992. Demographic structure of California chaparral in the long-term absence of fire. Journal of Vegetation Science 3: 79-90. doi: 10.2307/3236001

Keeley, J. E. 1993. Utility of growth rings in the age determination of chaparral shrubs. Madroño 40: 1-14.

Keeley, J.E. 2002. Fire management of California shrubland landscapes. Environmental Management 29: 395-408. doi: 10.1007/s00267-001-0034-Y

Keeley, J.E. 2007. Chaparral and fire. Fremontia 35: 16-21.

Keeley, J.E., and C.J. Fotheringham. 2001. Historic fire regime in southern California shrublands. Conservation Biology 15: 1536-1548. doi: 10.1046/j.1523-1739.2001.00097.x

Keeley, J.E., C.J. Fotheringham, and M. Baer-Keeley. 2005*a*. Determinants of postfire recovery and succession in Mediterranean-climate shrublands of California. Ecological Applications 15: 1515-1534. doi: 10.1890/04-1005

Keeley, J.E., C.J. Fotheringham, and M. Morais. 1999. Reexamining fire suppression impacts on brushland fire regimes. Science 284: 1829-1832. doi: 10.1126/science.284.5421.1829

Keeley, J.E., T.W. McGinnis, and K.A. Bollens. 2005*b*. Seed germination of Sierra Nevada post-fire chaparral species. Madroño 52: 175-181. doi: 10.3120/0024-9637(2005)52[175:SGOSNP]2.0.CO;2

Keeley, J.E., A.H. Pfaff, and H.D. Safford. 2005*c*. Fire suppression impacts on post-fire recovery of Sierra Nevada chaparral shrublands. International Journal of Wildland Fire 14: 255-265. doi: 10.1071/WF05049

Keeley, J.E., and P.H. Zedler. 2009. Large, high intensity fire events in southern California shrublands: debunking the fine-grained age-patch model. Ecological Applications 19: 69-94. doi: 10.1890/08-0281.1

LaLande, J. 1995. An environmental history of the Little Applegate River watershed, Jackson County, Oregon. Forest Service, Medford, Oregon, USA.

League, K.R. 2005. *Ceanothus cuneatus.* Fire effects information system online database. Forest Service. < http://www.fs.fed.us/database/feis/plants/shrub/ceacun/all.html>. Accessed 12 February 2007.

McCune, B. 2006. Non-parametric habitat models with automatic interactions. Journal of Vegetation Science 17: 819-830. doi: 10.1111/j.1654-1103.2006.tb02505.x

McCune, B. 2007. Improved estimates of incident radiation and heat load using non-parametric regression against topographic variables. Journal of Vegetation Science 18: 751-754. doi: 10.1111/j.1654-1103.2007.tb02590.x

McCune, B., and J.B. Grace. 2002. Analysis of ecological communities. MjM Software, Gleneden Beach, Oregon, USA.

Merriam, K.E., J.E. Keeley, and J.L. Beyers. 2006. Fuel breaks affect nonnative species abundance in Californian plant communities. Ecological Applications 16: 515-527. doi: 10.1890/1051-0761(2006)016[0515:FBANSA]2.0.CO;2

Montygierd-Loyba, T.M., and J.E. Keeley. 1987. Demographic structure of *Ceanothus megacarpus* chaparral in the long absence of fire. Ecology 68: 211-213. doi: 10.2307/1938821

Moritz, M.A., J.E. Keeley, E.A. Johnson, and A.A. Schaffner. 2004. Testing a basic assumption of shrubland fire management: how important is fuel age? Frontiers in Ecology and Environment 2: 67-72. doi: 10.1890/1540-9295(2004)002[0067:TABAOS]2.0.CO;2

Nagel, T.A., and A.H. Taylor. 2005. Fire and persistence of montane chaparral in mixed conifer forest landscapes in the northern Sierra Nevada, Lake Tahoe basin, California, USA. Journal of the Torrey Botanical Society 132: 442-457. doi: 10.3159/1095-5674(2005)132[442:FAPOMC]2.0.CO;2

Natural Resources Conservation Service [NRCS]. 2008. Data download portal for Oregon soil survey data, OR632 Jackson County area. <http://soildatamart.nrcs.usda.gov>. Accessed 24 September 2008.

Odion, D.C., and F.W. Davis. 2000. Fire, soil heating, and the formation of vegetation patterns in chaparral. Ecological Monographs 70: 149-169. doi: 10.1890/0012-9615(2000)070[0149:FSHATF]2.0.CO;2

Odion, D.C., E.J. Frost, J.R. Strittholt, H. Jiang, D.A. DellaSalla, and M.A. Moritz. 2004. Patterns of fire severity and forest conditions in the western Klamath Mountains, California. Conservation Biology 18: 927-936. doi: 10.1111/j.1523-1739.2004.00493.x

Ooi, M.K.J., R.J. Whelan, and T.D. Auld. 2006. Persistence of obligate-seeding species at the population scale: effects of fire intensity, fire patchiness and long fire-free intervals. International Journal of Wildland Fire 15: 261-269. doi: 10.1071/WF05024

Perchemlides, K.A. 2006. Impacts of fuel reduction thinning treatments on oak and chaparral communities of southwestern Oregon. Thesis, Oregon State University, Corvallis, USA.

Perchemlides, K.A., P.S. Muir, and P.E. Hosten. 2008. Responses of chaparral and oak woodland plant communities to fuel-reduction thinning in southwestern Oregon. Rangeland Ecology and Management 61: 98-109. doi: 10.2111/07-026R1.1

Peterson, L.J. 1916. Ecological survey of brush areas: report on brush and grazing conditions. Forest Service, Medford, Oregon, USA.

Pfaff, E. 2007*a*. Climate, topography, soils, and wildfire spatial datasets. Thesis, Southern Oregon University, Ashland, USA.

Pfaff, E. 2007*b*. Patterns of grassland, shrubland, and woodland vegetation abundance in relation to landscape-scale environmental and disturbance variables, Applegate watershed, southwest Oregon. Thesis, Southern Oregon University, Ashland, USA.

Pinchak, W.E., M.A. Smith, R.H. Hart, and J.W. Waggoner. 1991. Beef cattle distribution patterns on foothill range. Journal of Range Management 44: 267-275. doi: 10.2307/4002956

PRISM Climate Group. 2006. United States average monthly or annual precipitation, 1971 - 2000. <http://www.prism.oregonstate.edu>. Accessed 5 May 2009.

Safford, H.D., and S. Harrison. 2004. Fire effects on plant diversity in serpentine vs. sandstone chaparral. Ecology 85: 539-548. doi: 10.1890/03-0039

Schlesinger, W.H., and D.S. Gill. 1978. Demographic studies of the chaparral shrub, *Ceanothus megacarpus,* in the Santa Ynez Mountains, California. Ecology 59: 1256-1263. doi: 10.2307/1938239

Schlesinger, W.H., and D.S. Gill. 1980. Biomass, production, and changes in the availability of light, water, and nutrients during the development of pure stands of the chaparral shrub, *Ceanothus megacarpus,* after fire. Ecology 61: 781-789. doi: 10.2307/1936748

Sensenig, T.S. 2002. Development, fire history and current and past growth of old-growth and young-growth forest stands in the Cascade, Siskiyou and mid-coast mountains of southwestern Oregon. Dissertation, Oregon State University, Corvallis, USA.

Sugihara, N.G., J.W. van Wagtendonk, K.E. Shaffer, J. Fites-Kaufman, and A.E. Thode, editors. 2006. Fire in California's ecosystems. University of California Press, Berkeley, USA.

Syphard, A.D., J. Franklin, and J.E. Keeley. 2006. Simulating the effects of frequent fire on southern California coastal shrublands. Ecological Applications 16: 1744-1756. doi: 10.1890/1051-0761(2006)016[1744:STEOFF]2.0.CO;2

Taylor, A.H., and C.N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecology and Management 111: 285-301. doi: 10.1016/S0378-1127(98)00342-9

Taylor, A.H., and C.N. Skinner. 2003. Spatial patterns and controls on historic fire regimes and forest structure in the Klamath Mountains. Ecological Applications 13: 704-719. doi: 10.1890/1051-0761(2003)013[0704:SPACOH]2.0.CO;2

Tieu, A., K.W. Dixon, K.A. Meney, K. Sivasithamparam, and R.L. Barrett. 2001. Spatial and developmental variation in seed dormancy characteristics in the fire-responsive species *Anigozanthos manglesii* (Haemodoraceae) from western Australia. Annals of Botany 88: 19-26. doi: 10.1006/anbo.2001.1424

United States Department of the Interior [USDI]. 1998. Ecosystem restoration in the Ashland Resource Area. United States Department of the Interior, Medford, Oregon, USA.

United States Department of the Interior [USDI]. 2004*a*. Annual program summary and monitoring report for fiscal year 2004. United States Department of the Interior, Medford, Oregon, USA.

United States Department of the Interior [USDI]. 2004*b*. Little Applegate fuel hazard reduction project. Categorical exclusion/decision record CE-OR116-04-5. United States Department of the Interior, Medford, Oregon, USA

United States Department of the Interior [USDI]. 2006. Fuels treatment and wildfire spatial dataset, maintained by Medford District Bureau of Land Management staff A. Parsons. United States Department of the Interior, Medford, Oregon, USA

United States Department of the Interior [USDI]. 2008. Grazing history dataset. United States Department of the Interior, Bureau of Land Management, Medford, Oregon, USA.

United States Fish and Wildlife Service [USFWS]. 2009. Federally listed, proposed, candidate species, and species of concern under the jurisdiction of the Fish and Wildlife Service which may occur within Jackson County, Oregon. United States Department of the Interior, Portland, Oregon, USA. <http://www.fws.gov/oregonfwo/Species/Lists/Documents/County/JACKSON%20COUNTY.pdf>. Accessed 4 April 2009.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research 21: 414-416. doi: 10.1139/x91-053

Zammit, C.A., and P.H. Zedler. 1993. Size structure and seed production in even-aged populations of *Ceanothus greggii* in mixed chaparral. Journal of Ecology 81: 499-511. doi: 10.2307/2261528

Zedler, P.H. 1995. Fire frequency in southern California shrublands: biological effects and management options. Pages 101-112 in: J.E. Keeley, and T. Scott, editors. Brushfires in California wildlands: ecology and resource management. International Association of Wildland Fire, Fairfield, Washington, USA.