

AN ABSTRACT OF THE THESIS OF

Olivia Duren for the degree of Master of Science in Botany and Plant Pathology presented on May 15, 2009.

Title: Chaparral History, Dynamics, and Response to Disturbance in Southwest Oregon: Insights from Age Structure.

Abstract approved:

Patricia S. Muir

Fuels management on Bureau of Land Management lands in SW Oregon, USA, is motivated by the needs to reduce fire hazard and restore ecosystems thought to be impacted by fire suppression. Chaparral is one of the most characteristic vegetation communities of SW Oregon's interior valleys, and extensive acreages within this system are targeted annually for fuels treatment. However, this community is also poorly understood. Little is known about its response to fire suppression, and the assumptions justifying the need for fuels reduction and on which treatment prescriptions are based are extrapolations from other ecosystems. I studied patterns in chaparral age structure of two obligate-seeding shrubs, *Arctostaphylos viscida* C. Parry and *Ceanothus cuneatus* (Hook.) Nutt., for insights into the influences of environment and the two dominant disturbances in SW Oregon, fire and grazing, on population structure and dynamics. My 31 low to mid-elevation study sites represent four chaparral 'types' and a range in times since fire (22 yr to > 114 yr). My study area is near the northernmost extension of the California chaparral vegetation type, and results indicate that SW Oregon chaparral populations diverge from studied California chaparral populations in several fundamental ways. All stands unburned for > 30 yr were uneven-aged due to prolific recruitment in the absence of fire and

appreciable fire survivorship. Relatively high shrub densities were associated with even-aged sites, but these sites were all young (< 30 yr) and density declined the longer stands were unburned. No relationships were detected between site environment or disturbance history and age structure in general, or the relative amount of fire-free recruitment or fire survivorship in particular. Results suggest that most, if not all, chaparral stands would over time develop uneven-aged structure across the range of environments represented in the study area.

Current fuels treatment prescriptions in SW Oregon chaparral are predicated on the assumption that fire suppression has replaced naturally high-frequency, low-severity fires with less frequent and higher-severity fires due to an unnatural accumulation of fuels. However, it appears that this model is not appropriate for chaparral vegetation. Chaparral has apparently experienced a fire regime that is distinct from that of adjacent vegetation communities, and fire suppression does not appear to have altered overall chaparral structure or fire severity. Current fuels treatments are unlikely to reproduce stand structures observed in mature chaparral or in post-wildfire stands. Rather, fuels treatments are likely to alter the trajectory of chaparral development that appears to have been in place for the last century. Results clearly illuminate that chaparral encompasses a wide range of structures and responses to environment and disturbance, and imply that precepts of chaparral ecology and management should be tailored on a geographic basis. Results also underscore the need for management objectives to recognize differences among vegetation communities in complex environments.

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Chaparral History, Dynamics, and Response to Disturbance in Southwest Oregon:
Insights from Age Structure

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Olivia Duren

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APPROVED:

Major Professor, representing Botany and Plant Pathology

Chair of the Department of Botany and Plant Pathology

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of the Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Olivia Duren, Author

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**Chaparral History, Dynamics, and Response to Disturbance in Southwest Oregon:
Insights from Age Structure**

Chaparral History, Dynamics, and Response to Disturbance in Southwest Oregon: Insights from Age Structure

Introduction

Fire has been a central force in shaping the nature and function of ecosystems in the Klamath region of southwestern Oregon and northern California, USA (Franklin and Dyrness 1973; Agee 1990, 1993; Atzet and Martin 1992). Most native species in the region are adapted to or dependent on fire (Barbour 1988, Atzet and Wheeler 1982, Kaufmann 1990), and the historic spatial and temporal variability of fires has played an essential role in maintaining the exceptional complexity and biodiversity of its landscapes (Agee 1991*b*, Martin and Sapsis 1991, Frost and Sweeney 2000, Taylor and Skinner 2003). However, a century of fire suppression policy has significantly reduced the area burned (Frost and Sweeney 2000), altering structure, composition, and ecological processes in many ecosystems (e.g., Taylor and Skinner 1998, 2003; Riegel et al. 1992; Whitlock et al. 2004). The resultant accumulation of ground fuels and increase in tree density can contribute to uncharacteristically intense, less controllable wildfires that damage property and ecosystems (Agee and Skinner 2005; Hessburg et al. 2005; Peterson et al. 2005). The situation is exacerbated by continued home building in the Wildland Urban Interface (WUI; Western Governors Association [WGA] 2001; Stephens and Roth 2005; Gude et al. 2008). The increasing fragmentation of wildlands and risk to human resources is a particularly acute concern in southwest Oregon, where the top two counties for wildfire risk (development area in the WUI) in the western U. S. are located (Gude et al. 2008).

Mitigating fire hazard to property and restoring ecosystems have become central objectives of fire policy both nationally (USDI-USDA 1995; National Wildfire Coordinating Group 2001; Healthy Forest

Restoration Act 2003) and regionally (WGA 2001). In accordance with these objectives, the Bureau of Land Management (BLM) has implemented landscape-scale fuels treatment programs in southwest Oregon wildlands, treating over 5,000 ha/yr since the mid-1990s (USDI 2004a). Chaparral shrubland, a Mediterranean-climate community of dense, evergreen, drought-tolerant shrubs, is one of the most characteristic ecosystems of southwest Oregon interior valleys, and extensive acreages within this system are targeted annually for fuels treatments. Yet, chaparral is one of the least understood ecosystems in the region (Franklin and Dyrness 1973; Hosten et al. 2006), and assessment of whether fire hazard reduction and ecosystem restoration objectives are being met by fuels treatments in chaparral is stymied by a lack of information. Little is known about the response of southwest Oregon chaparral to fire suppression, and the assumptions justifying the need for fuels treatments and on which treatment prescriptions are based are extrapolations from other ecosystems. Further, fuels treatments in chaparral may conflict with management objectives aimed at containing exotic plant invasion (Keeley et al. 2005a; Merriam et al. 2006; Perchamides et al. 2008), and conserving the regionally unique assemblage of flora and fauna, including several species of concern, which depend on chaparral (Hosten et al. 2006; Seavy et al. 2008; USFWS 2009). Information is needed on whether fuels treatments in chaparral are meeting restoration goals, on the response of chaparral to past disturbances, and on its current structure and dynamics.

Current structure and dynamics in chaparral may be a product, in part, of multiple human alterations of natural disturbance regimes. The impact of intense historic grazing on many ecosystems of the arid western U. S. may have been at least as important as fire suppression (Belsky and Blumenthal 1997). Grazing has the potential to influence chaparral age structure both directly and indirectly, and community effects are likely to differ from those caused by fire or fire suppression (Keeley et al. 2003). To what extent do current chaparral age structures appear to have been affected by grazing? Given that fuels

treatments are intended, in part, to restore communities impacted by fire suppression, it is important to unravel the individual influences of grazing and fire suppression on current ecosystem processes.

My primary objective was to answer these questions about chaparral structure, dynamics, and responses to fire and grazing disturbance by characterizing patterns in age structures and assessing their relationship to environment and disturbance history. Low- to mid-elevation chaparral in the Klamath region is dominated by whiteleaf manzanita (*Arctostaphylos viscida*) and buckbrush ceanothus (*Ceanothus cuneatus*), both non-sprouting obligate-seeder species that, in California chaparral, are reported to require fire-related cues for germination, thereby forming even-aged stands that date back to the last fire (e.g. Keeley 1991; Keeley et al. 2005). As this study area represents the northernmost extension of the chaparral vegetation type, I compared age structures in Oregon chaparral of *A. viscida* and *C. cuneatus* to age structures reported for these and other obligate-seeder species in California chaparral. Specifically, I asked:

- (1) Do chaparral shrub species exhibit even-age structure, as expected from what is known about California populations, or is there significant inter-fire recruitment or fire survivorship exhibited as uneven-aged structure? If significant inter-fire recruitment or fire survivorship occur, what mechanism(s) might enable them? If multiple age structures occur, what environmental variables are most strongly associated with different age structures?
- (2) Is there evidence that grazing disturbance has measurably influenced chaparral age structure?
- (3) What are the relationships of current age structures to wildfire disturbance history, and are differences in fire severity among chaparral stands related to their wildfire history or environment?

Implementing appropriate fire and fuels management is often hampered by the lack of regionally-specific information (Stephens and Ruth 2005). Most precepts of chaparral ecology are based on comprehensive study of the southern California portion of this community (Keeley 2007), while northern communities have received relatively little attention. Differences in climate, fire history, and burning conditions over the range of this vegetation type (Keeley and Keeley 1988; Keeley 2002; Moritz et al. 2004) suggest that regional variability in community processes and response to disturbance are likely to necessitate a geographically-tailored approach to management. My results clearly indicate that chaparral comprised of purportedly obligate-seeder shrub species produce a wide range of structures and responses to environment and disturbance. Results expand our understanding of the variability within the chaparral vegetation type as well as our knowledge of the diversity within Mediterranean-climate shrubland ecosystems worldwide.

Methods

Study area

The study area lies at the confluence of the Coast, Cascade, and Sierra mountain ranges in the Klamath region of southwestern Oregon (approx. 42°8' to 42°20' N and 122°53' to 123°12' W). Study sites fall within the steep, rugged lower Applegate River watershed, a landscape of remarkably complex topography and microclimates. Boundaries are often abrupt between plant communities of widely divergent composition and structure. My focus was on the low to mid-elevation (500 m to 1200 m) foothills of the interior valleys, within the BLM-managed Applegate Adaptive Management Area. This area has a Mediterranean climate of cool, wet winters and hot, dry summers, and is in the driest climatic zone of Klamath region (Atzet and Wheeler 1982). Mean annual precipitation at a centrally-located weather station is 654 mm, 45% of which falls November through April; July mean maximum temperature is 32.0°C and January mean minimum temperature is -1.3°C (Western Regional Climate Center [WRCC] 2008). A complex geological history has given rise to highly diverse soils formed in metasedimentary, metavolcanic, and weathered schist material (Natural Resources Conservation Service 2008). Generally, soils are relatively undeveloped, shallow to moderately deep loams with good drainage (Haploixerults, Haploixeralfs, and Xerochrepts; Franklin and Dyrness 1973).

Vegetation distribution in the study area is strongly influenced by soil, moisture regimes, and species drought tolerance (Hosten and Pfaff *in prep*). Drought-tolerant vegetation dominates the non-forested components of the landscape mosaic where water stress is relatively high. Chaparral of buckbrush ceanothus (*C. cuneatus*) and whiteleaf manzanita (*A. viscida*) is most important on relatively hot, dry

slopes, interspersed with grasslands. 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* Dougl.), and Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirbel) Franco.) (nomenclature follows Hickman 1993). The chaparral communities of southwest Oregon represent the furthest northern extent of the California chaparral system; these Oregon communities, however, have been isolated by the Siskiyou Mountains for more than 4,000 years (Detling 1961).

The disturbance history of the lower Applegate watershed is long and complex. Native Americans populated the watershed for at least 4,000 yr and probably actively managed parts of the land with fire (LaLande 1995, Pullen 1996). This practice began to falter in the late 1700s as populations declined from introduced diseases, and stopped when Native Americans were extirpated from the valley after the 1856 Rogue River Wars (LaLande 1995). Euro-Americans settled the area soon after gold was discovered in 1851; placer and hydraulic mining gave way to sheep and cattle ranching as the main livelihood in the late 1880s. In attempting to burn off the brush, ranchers probably increased the fire frequency above that maintained by the Native Americans (LaLande 1995). A policy of fire suppression was instituted in the first decades of the 1900s, but was probably not effective in the Applegate Valley until the late 1920s – early 1930s (LaLande 1995), nor influential regionally until the 1940s (Atzet 1996, Taylor and Skinner 1998, Frost and Sweeney 2000). Small timber mills active around the turn of the century were replaced by industrial logging that intensified in the post-WWII housing boom; logging, along with ranching at lower than historic densities, continues today.

Field methods

Thirty-one study sites were located in areas where the prevailing vegetation was chaparral, although oak and conifer trees were occasionally intermixed (Fig. 1). Sites were chosen to represent a range of times since fire (22 yr to \geq 114 yr), as recorded on BLM fire maps (USDI 2006), and four chaparral ‘types,’ as defined by species relative cover (buckbrush chaparral, manzanita chaparral, manzanita-oak chaparral, and open oak-chaparral; Pfaff 2007b). Buckbrush and manzanita chaparral types generally represented vegetation communities with few trees and in which *C. cuneatus* or *A. viscida* dominated cover; manzanita-oak and open-oak chaparral types generally had higher tree cover with *C. cuneatus* or *A. viscida* in small patches or in the understory (Appendix A). Sites were spread as evenly as possible across times since fire and the four chaparral types. Where possible, sites were located in areas previously treated with handcut-pile and burn fuels reduction to limit the need for destructive sampling (16/31 sites were in treated areas; treatments occurred 0 to 9 yr prior to sampling). Sites were on 117 - 301° aspects and 13 - 34% slopes.

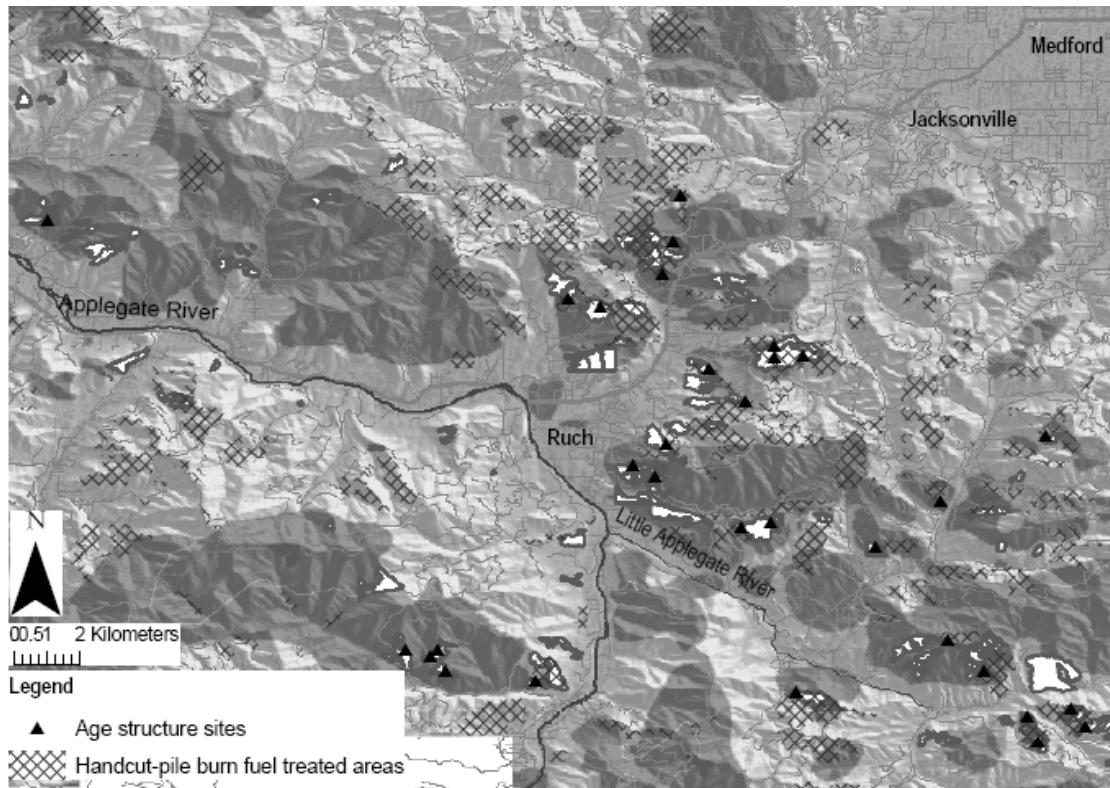


Figure 1. Location of study sites (n=31) in the Applegate Adaptive Management Area managed by the Bureau of Land Management, southwest Oregon. White polygons are chaparral and dark polygons are known historic fires (1896 – 2005).

Site centers in fuels-treated areas were designated in a geographic information system (GIS) as the centroid of an area defined by the coincidence of a fuels treatment unit with a particular chaparral type and time since fire; site centers in untreated areas were centroids of an area where a particular chaparral type and time since fire were coincident. In the fall of 2007, I sampled a total of 15–25 A. *viscida* and *C. cuneatus* individuals, across the two species, at each site. I established a 50 m x 4 m transect, which ran in a random direction from the site center. Sampled shrubs were randomly chosen every 3 m as those stumps (in treated stands) or living individuals (in untreated stands) closest to the tape that marked the transect center; the rare very rotten or excessively damaged stump, and shrubs that may have germinated after treatment (diameter near ground height < 1.6 cm), were excluded. In the

case of widely-spaced shrubs, additional transects were laid down parallel to and 10 m distant from the first transect until at least 15 samples were acquired. Shrubs were dug out to the point where the stems joined the roots in an effort to obtain the most accurate age possible; samples were taken at this point by cutting a thin cross-section of wood. In cases where there were multiple discrete stems, all stems were sampled. Shrub diameter at sampling height was recorded. Sites were characterized by pre-treatment (or current, for untreated sites) *A. viscida* and *C. cuneatus* shrub density (individuals ≥ 1.6 cm at ground height) and tree density (individuals ≥ 5 cm at diameter breast height), estimated by counting shrub and tree genets along the first transect.

Lab methods

Both *A. viscida* and *C. cuneatus* produce easily recognizable rings that are reliably laid down on an annual basis in southern CA (Keeley 1993). Shrub sections were sanded (120 - 240 grit) and growth rings counted under a dissecting microscope at 7 - 15x power. Ring counts were initially standardized by repeating the count with three independent observers; thereafter rings were counted by a single trained observer. 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 yr since treatment, and only samples older than the treatment were retained.

I gathered information on site environmental characteristics and disturbance history to assess their relationship with age structure. Aspect, elevation, and geographical coordinates were recorded with a compass and GPS on site (Appendix A). Aspect was transformed to reflect dryness by folding it about the NE – SW axis ($= |180-|aspect-225||$). Data on environmental variables thought likely to influence age

structure were taken from previously collected and processed GIS data (Pfaff 2007*a*), including annual precipitation; actual annual evapotranspiration; actual summer evapotranspiration; 6th field watershed; parent material; surface soil horizon depth; and soil percent clay, percent silt, percent sand, cation exchange capacity, and pH. I also obtained data on four wildfire disturbance variables (maximum fire-free interval, minimum fire-free interval, point fire frequency, and year of most recent fire, for fires > 40 ha, 1895 - 2005; USDI 2006). The site value for each variable was calculated as the average of the values sampled in GIS at the site center and at 50 m from center in each cardinal direction (Spatial Analyst, ArcGIS; ESRI 2006; Appendix A). Additional topographic variables (slope shape, percent slope, and topographic position index) were computed from a digital elevation model (USDI n. d. *a*) in GIS (Spatial Analyst, ArcGIS; ESRI 2006). Potential direct incident radiation and heatload, both indices of solar interception, were calculated in HyperNiche (McCune and Mefford 2004) from site latitude, slope, and aspect, using files available online (McCune 2007*a,b*).

Disturbances from historic and modern foraging activities of domestic livestock have the potential to markedly impact age structure, but have gone largely unrecorded. The absence of explicit historic records of livestock activities within the study area (apart from those under BLM grazing management since ca. 1970s) prevented a direct analysis of the impact of past disturbance. Therefore, I pursued the question of whether age structure was related to grazing by modeling the potential livestock utilization of sites and the association between age structure and known recent grazing history (since ca. 1970s; pers. comm. K. Hackett, Rangeland Management Specialist, Medford, OR, BLM). Cattle replaced sheep as the primary grazers in the mid-1910s (Borgias 2004); because cattle have been the primary grazers in the study area for the last century, analysis of current and historic livestock influence centers on cattle grazing behavior.

In complex terrain, such as is typical of the study area, the distribution of livestock across the landscape depends primarily on slope (e.g., Pinchak et al. 1991), proximity to water or roads (e.g., Hosten et al. 2007b), and the interaction of these factors. I assessed the potential for livestock utilization of each site based on its distance from the nearest road or trail, the average slope from the road to the site, distance to the nearest water source (seasonal/intermittent, seep/spring, or perennial), and the average slope from water to the site (Appendix A). Transportation and hydrology spatial datasets were acquired from USDI (n. d. b) and the Oregon Water Resources Dept. (2005), respectively. Distances were found using a GIS tool that calculates true overland distance accounting for topography (3D Analyst, ArcGIS; ESRI 2006). Average percent slopes were calculated from the difference in elevation from the study site to the nearest road or water and the horizontal distance between the same. Because livestock access to sites is controlled by the interaction of distance from access point and slope from the access point to the site, the assessment also included 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).

I described recent grazing history at each site (since ca. 1970s) using metrics for the number of years the site had been ungrazed; the seasonality of grazing (spring to early summer, spring to mid summer, and summer to late summer); and computing a grazing intensity index by multiplying the BLM-allotted Animal Unit Months (AUMs, where 1 AUM is an allotment for one cow and calf for one month) by the number of allotted grazing months, and then dividing by the area in each allotment (AUM data from USDI 2008).

Statistical methods

Shrub ages

Samples yielded either high-quality age counts (clear ring count from bark to pith), satisfactory age counts (nearly complete count with ≤ 10 yr estimated to be missing) or low-quality age counts (count compromised by center rot or insect damage, > 10 rings missing). Ages of some samples with low-quality counts (see Results) were estimated with non-parametric multiplicative regression (NPMR; McCune 2006). NPMR is similar to other regression techniques in that it allows a screening of predictor variables, an assessment of the strength of their relationship to the response, and an evaluation of the strength and significance of the model. However, NPMR differs from other regression techniques in that it includes all interactions between predictors automatically, and makes no assumptions about the shape of the response surface. This allows relationships between response and predictors, and of predictors to each other, to be complex, non-linear, asymmetric, and multi-modal.

NPMR regression models to predict shrub ages were built in HyperNiche (McCune and Mefford 2004) using high-quality samples; models were then used to estimate ages for poor-quality samples of each species separately. NPMR builds models by assessing all possible combinations of predictor variables on the basis of improvement of fit (leave-one-out cross-validated R^2 [xR^2]). The model then estimates the response at a particular target point in the predictor space by borrowing information from nearby areas in the predictor space (McCune 2006). Model building was implemented using local mean, Gaussian weights, and minimum average $N^* = 1$; age estimation was implemented using minimum $N^* = 1$ required for an estimate. The local mean is the average of the observed response values, where the influence of each value is weighted by its proximity to the target point in the predictor space. The rate at which a

predictor's influence diminishes with distance from the target is determined by a Gaussian curve smoothing parameter. The neighborhood size, N^* , is the amount of data used to make a prediction and is the sum of the Gaussian weights; minimum $N^* = 1$ requires that the sum of the weights be at least 1 to estimate a response at that point (McCune 2006).

Predictor variables available for each model were sample diameter; height at which sample was taken; time since last recorded fire (as an indicator of expected age of the dominant cohort); mean outer ring width, calculated from the combined width of rings across the last 20 yr, measured to the nearest mm (or the last 10 yr of growth for shrubs < 20 yr old); and chaparral 'type.' The response variable, sample age count, as well as the predictor variables sample diameter and height at cut, were log-transformed prior to analysis. Although NPMR does not make assumptions about the distribution of variable values, transformations can improve model fit by equalizing variance across the response surface so model fit is not overly dependent on a portion of the dataset.

Confirmation of annual ring deposition and estimation of age count error

I tested the assumption that *A. viscida* and *C. cuneatus* produce annual rings in southwest Oregon by assessing the correspondence between a 'marker ring' (an unusually narrow ring) and a known calendar year of unusually low precipitation. This also allowed me to derive error estimates for shrub age counts. These integrated error estimates include error in ring counting, error introduced by false or missing rings, and error introduced by any asynchronous responses among shrubs, such as when an individual's narrowest ring was a response to injury rather than drought.

Error estimates were derived for a subset of samples with high-quality counts ($n = 20$ each of *A. viscida* and *C. cuneatus*). Years of unusually low precipitation were identified from a weather station located centrally to the study sites. The year 1949 was used as the drought year for *A. viscida*, and 1976 was used as the drought year for *C. cuneatus*; precipitation in these years was 50.8% and 37.7% lower than the 65-year average, respectively (WRCC 2008). The earlier year was not used as the drought year for *C. cuneatus* because few samples were that old.

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 the shrub was cut and the drought year. The difference between the ring count and the elapsed time was taken as the integrated error estimate.

Patterns in age structure, relationships to environment, and shrub recruitment in the absence of fire

Quantification of the age structure in each stand allowed me to describe patterns in age structure, compare them among stands, and assess statistical relationships among age structures, environment and disturbance history. Each stand's age structure was characterized by six attributes of shrub age distribution: median age, skew, kurtosis, variance, coefficient of variation (CV), and range in ages divided by median age. When calculating age structure characteristics, I assumed that shrubs were alive when cut for fuels treatment. This assumption would lead to underestimation of ages for (years between shrub germination and sampling) shrubs that died prior to treatment. I tested the effect of this assumption on age structure characteristics by comparing characteristics between untreated stands, where only live shrubs were sampled, and treated stands of similar age. I found that the possible

inclusion of shrubs that were dead prior to treatment may have made age structures of treated stands more even-aged relative to age structures of untreated stands (e.g., CV and variance of shrub ages were 31% and 20% lower and kurtosis was 8x higher in treated stands) . This assumption may have introduced some noise into the age distribution data and prevented me from detecting weak relationships of age structure to environment and disturbance, but it is highly unlikely to affect inferences about age structure, and, in particular, unlikely to falsely make age distributions differ from the expected even-aged structure.

I mapped each stand in the space defined by its age structure attributes using nonmetric multidimensional scaling (NMS) ordination, implemented in PC-ORD (McCune and Mefford 2006). Ordination allows age structures to be considered on continuous scales rather than breaking them into age structure ‘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). NMS 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 site outliers were detected ($SD \geq 2.0$), but both were retained because no aspect of the ordination substantially changed when they were removed.

The relationship of stand age structure to variables describing site climate, topography, soils and stand structure of associated trees was examined by calculating the correlations between site variables and the ordination axes, and by inspecting joint plot overlays. Quantitative variables with skew > 1 were log-transformed to compress high values and spread low values, improving homogeneity of variance.

To explore a mechanism that could account for inter-fire recruitment (shrub \geq 20 yr younger than the last known fire in stands reported to be unburned for 30 – 72 yr) of the two reportedly obligate-seeder shrub species, I investigated the possibility of seed germination response to heat from sources other than fire. I measured mid-August soil temperatures at two depths (2.5 cm and 5.0 cm below soil surface) at 13 sites within the study area with standard soil thermometers. Temperatures were measured during the warmest part of the day (1230 – 1530 hr, air temperature 29 - 36.5°C) in gaps between shrubs (> 2 m from all shrub crowns), where cover of herbaceous litter was 60 - 100% but less than 3 cm thick. Three measurements were taken at each depth. These summer surface soil temperatures were compared to temperatures known to significantly increase germination of *A. viscida* and *C. cuneatus*.

I also regressed abundance of fire-free recruits was associated against environmental characteristics thought likely to be mechanistically related to seed germination and seedling survival: heatload; tree basal area and shrub density as indicators of soil heating; actual summer evapotranspiration as an indicator of seed desiccation and seedling water stress; and percent clay (*A. viscida* and *C. cuneatus* often do not successfully establish in high-clay soils due to shrink-swell damage to roots; Hosten and Pfaff *in prep*). The NPMR regression model was implemented using local mean, Gaussian weights, and minimum average $N^* = 1$.

Relationship of grazing disturbance to chaparral age structure and recruitment in the absence of fire

The relationship between stand age structure and grazer disturbance was assessed by calculating the correlations between grazer disturbance variables and ordination axes, as well as by examining joint plot overlays. Quantitative variables with skew > 1 were log-transformed. I determined whether age structure, as described by NMS ordination axis scores, was associated with grazing disturbance variables. Models

were assessed for each axis, using scores from the varimax-rotated solution, which maximized loadings of age characteristics on ordination axes. NPMR was implemented using local mean, Gaussian weights, and minimum average $N^*=1$. To account for the possibility that multiple ordination axes could make the 'grazer disturbance' signal too diffuse to detect, I also regressed ordination scores from stand age structure forced onto a single axis on grazing variables. As results did not differ substantially between the regressions, only results from regressions with the three-axis solution are reported.

Because grazing could facilitate fire-free recruitment by creating gaps in the shrub canopy necessary for soil heating or by mechanically scarifying seed, or impede it by damaging seedlings, I attempted to model the relationship between shrub density and grazing disturbance variables, and between the amount of fire-free recruitment and grazing disturbance variables. Variable selection and model evaluation was implemented with NPMR using specifications described previously.

Relationship of age structure to wildfire disturbance history and indicators of fire severity

I explored the possibility that observed age structures were the product of past fire history at each site, as far as it is known, using the wildfire history variables described previously. (This analysis did not explore whether the number of years since the last known fire was related to differences in age structure as this metric was correlated with stand age and was used to estimate some shrub ages.) The relationship of stand age structure to wildfire disturbance history was examined by calculating the correlation of each fire history variable with age structure ordination axes and by inspecting joint plot overlays. Quantitative variables with skew > 1 were log-transformed.

Fire severity is the magnitude of ecosystem effects of a fire and can influence post-disturbance recovery. As fire severity was not recorded for most historic fires, I used biotic indicators of fire severity in an attempt to detect the influence of topographic, fuels, and fire history variables on fire severity in sampled chaparral stands. The proportion of *A. viscida* and *C. cuneatus* shrubs that survived fires in each stand (shrubs \geq 20 yr older than last known fire in stands reported to be unburned for \leq 72 yr) was used as a proxy for wildfire severity. Both *A. viscida* and *C. cuneatus* are easily killed by fire (e.g., Keeley et al. 2008), and the presence of survivors suggests relatively low-severity fire. A regression model was used to assess whether the proportion of fire survivors was related to variables likely to influence fire severity, including topographic variables (percent slope and heatload), fuel variables (tree basal area, tree density, and shrub density), and fire history variables (point fire frequency, maximum interval between fires, and minimum interval between fires). Variable selection and model evaluation were implemented using NPMR as previously described.

Results

Shrub ages

A total of 485 shrubs were aged, with samples nearly evenly distributed between *A. viscida* and *C. cuneatus*. The largest *A. viscida* shrub sampled was 50 cm diameter near ground level, although an unsampled *A. viscida* measured 69 cm diameter near ground level. The largest *C. cuneatus* shrub sampled was 43 cm near ground level.

The oldest *A. viscida* sampled was > 146 yr old; 44 *A. viscida* samples were ≥ 100 yr. The oldest *C. cuneatus* sampled was > 114 yr old; three *C. cuneatus* were ≥ 100 yr. These minimum ages underestimate actual age, as sample centers for most of these individuals were rotted. Rot in samples of both species, and the stem axis-splitting growth pattern of old *C. cuneatus*, which obliterates the pith, makes it likely that samples from many more individuals were also older than their counted or estimated ages.

Sixty four percent of samples had clear, reliable ring counts from bark to pith; their ages were not estimated. NPMR satisfactorily modeled ages for samples of both species (*A. viscida*: $xR^2 = 88\%$, $p = 0.047$; selected predictors included sample diameter and mean ring width of last 20 yr; *C. cuneatus*: $xR^2 = 69\%$, $p = 0.047$; selected predictors included sample diameter, chaparral ‘type’, and expected stand age from fire history maps; Fig. 2). Ages were estimated for 13% of samples (12% *A. viscida*, 1% *C. cuneatus*) using NPMR models. Estimated ages averaged 13 yr older than ring count ages for these

samples. For samples that yielded poor quality counts and where age estimated by the regression models was less than ring count, the ring count age was not adjusted (23% of samples).

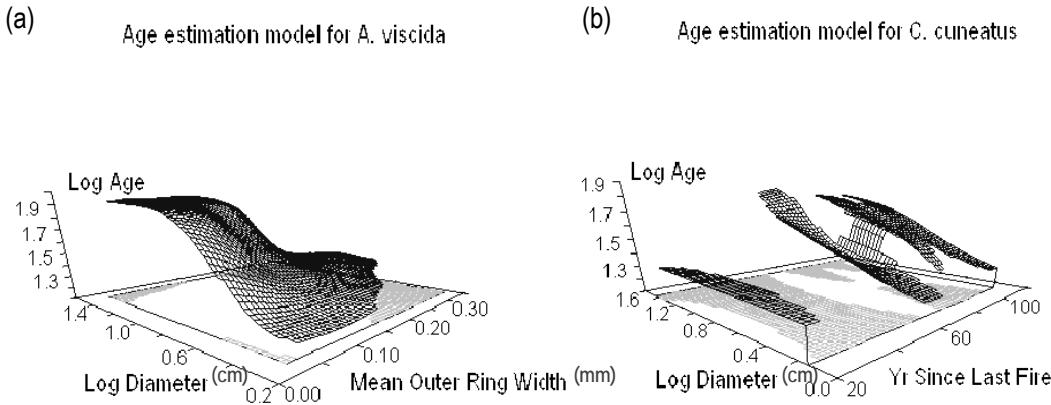


Figure 2. NPMR models used to estimate ages for shrub samples with incomplete age counts for (a) *A. viscida* and (b) *C. cuneatus*. Chaparral 'type' was also an important predictor in the age estimation model for *C. cuneatus*, but is not represented. Grey space in the grid indicates absence of data.

Confirmation of annual ring deposition and estimation of age count error

Counts to narrow rings in samples of *A. viscida* missed the 1949 drought year by a maximum of ± 8 yr (mean ± 2.1 yr based on the absolute value of years missed). Counts to narrow rings in samples of *C. cuneatus* missed the 1976 drought year by a maximum of ± 5 yr (mean ± 2.6 yr based on the absolute value of years missed). Therefore, I estimated a maximum integrated error of $\sim \pm 8$ yr per 60 yr age count in *A. viscida* (a maximum of 19 yr error in the oldest sample), and a maximum integrated error of $\sim \pm 5$ yr per 30 yr age count in *C. cuneatus* (a maximum of 18 yr in the oldest sample). Errors were slightly larger for *C. cuneatus* than for *A. viscida* because ring widths seemed relatively insensitive to annual differences in precipitation, and because growth patterns such as fluting that are common in *Ceanothus* appeared to have a greater effect on ring width than did precipitation. Age count overestimation and underestimation were equally likely for both species, suggesting that neither false

nor missing rings, if present, were more common. The error introduced from asynchrony in ring width response to precipitation probably outweighed that from counting mistakes or missing and false rings in the integrated error estimates. Because this method depends on synchrony, it probably overestimates actual error rates. Potential maximum errors were not large enough to affect inferences about age structure.

The integrated error estimate was incorporated into age structure analysis by generously defining even-aged stands to be those in which the ages of all shrubs sampled were within 20 yr of each other, fire-free recruits as ≥ 20 yr younger than the last known fire, and fire survivors as shrubs ≥ 20 yr older than the last known fire.

Patterns in age structure, relationships to environment, and shrub recruitment in the absence of fire

Stands were mostly uneven-aged, showing either prolonged fire-free recruitment, substantial fire survivorship, or both (Fig. 3; see Appendix B for age distributions of all 31 stands). Only 8 of 31 stands (26%) were even-aged (all sample ages within a 20 yr span), and all of these had median age < 30 yr. Age structures retained their even-aged or uneven-aged nature even when samples with estimated or poor-quality ages were disregarded. Recruitment of reputedly obligate-seeder shrubs was prolific in the absence of fire. Fire-free recruits comprised 16.1% of shrubs sampled in stands unburned for 30 – 72 yr; 24% of recruits were *A. viscidula*, and 76% *C. cuneatus*. (Shrubs of both species, particularly older individuals, were occasionally observed to produce adventitious roots and proliferate by layering; some shrubs much younger than the last known fire may have been the result of vegetative recruitment, but ramets were relatively uncommon and easily distinguished from genets in most cases.) Recruitment appeared to be prolonged, often lasting several decades. However, despite much higher fire-free

recruitment than expected, recruitment contributed only 4 – 71 new shrubs per ha per decade (mean 32 shrubs). Fire survivors comprised 5.4% of shrubs sampled in stands unburned for \leq 72 yr; 86% of survivors were *A. viscida* and 14% were *C. cuneatus*. Assuming that mean canopy cover of an *A. viscida* individual was 1.5 m² (Howard 1992), fires apparently left mean canopy cover of 56 m²/ha (range 0 – 288 m²/ha). These data on fire survivorship and fire-free recruitment include only stands burned \leq 72 yr prior to sampling, due to the lower reliability of older fire maps. Data on fire-free recruitment are further constrained to include only stands burned 30 to 72 yr prior to sampling, due to the criteria used to define recruits and the sampling avoidance of shrubs < 1.6 cm (= ~ 10 yr). Designation of a stand as even-aged is independent of whether fire-free recruits were detected. Patterns of recruitment and survivorship in older stands (last known burn 73 to > 112 yr prior to sampling), although less reliable, appeared to be similar to those observed in younger stands, with the exception that the proportion of shrubs sampled that were recruits nearly doubled, probably due to longer recruitment periods. The relative abundance of fire-free recruits and fire survivors was similar whether or not samples with poor or estimated ages were included.

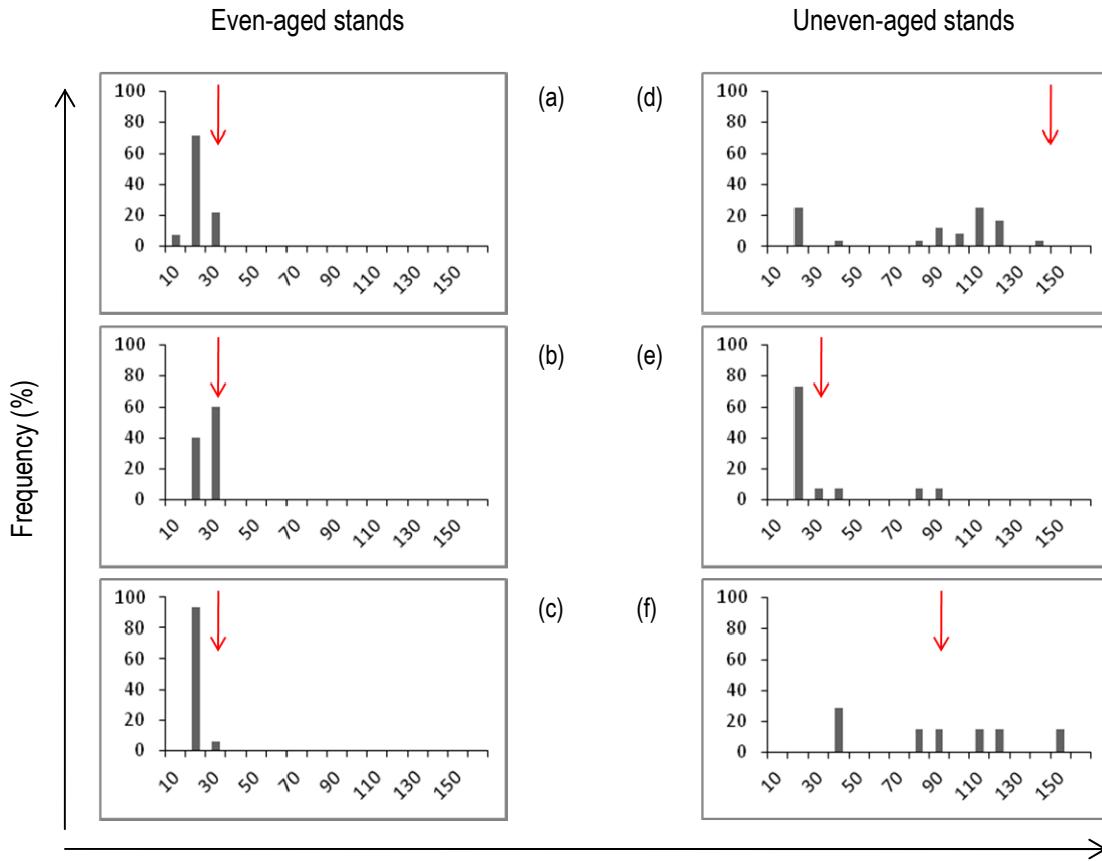


Figure 3. Selected age distributions for chaparral study sites showing representative even-aged stands (a – c) and representative stands that are uneven-aged due to (d) shrubs that recruited in the absence of fire (≥ 20 yr younger than last known fire), (e) shrubs that survived the last known fire (≥ 20 yr older than last known fire), or (f) both. Arrows indicate year of last known fire.

NMS ordination of stands in the space defined by their age distribution characteristics yielded a strong solution (99.4% cumulative R^2 over three axes; varimax rotated) with low stress (stress = 2.54, 54 iterations) and low instability (instability < 0.00001). All three dimensions (axes) provided significantly more reduction in stress than expected by chance ($p \leq 0.01$, Monte Carlo test with 250 randomized runs). Together, Axes 1 and 2 represented 42.3% of the variation in the data. These axes primarily separated even-aged stands from uneven-aged stands; stands with low relative range, variance, or coefficient of variation in shrub ages were distributed toward the bottom of both axes (Table 1, Fig. 4).

Stands with relatively low median ages were also positioned toward the bottom of Axis 2, as even-aged stands tended to be young. Axis 3 represented 57.1% of the variation, and separated stands in terms of age distribution kurtosis and skew. Stands near the top of this axis generally had more negative kurtosis and positive skew, and tended to have 'flatter' age distributions with heavier recent recruitment with fewer old shrubs relative to stand median age. Stands near the bottom of this axis generally had more positive kurtosis and negative skew, and tended to have 'peaky' age distributions with more old shrubs, relative to stand median age, and fewer recent recruits. Because skew and kurtosis are exaggerated for stands with a small spread in ages, this interpretation for Axis 3 is more applicable to older stands than to relatively young stands.

Table 1. Correlations (Pearson's r) of age distribution characteristics with NMS ordination axes. Only correlations with $r > |0.500|$ are shown. Relative age range is range in ages divided by median age.

Axis:	1	2	3
% Variation represented	26.5	15.8	57.1
Skew	0.787	-	0.755
Kurtosis	-	-	-0.893
Variance	-	0.950	-
Relative age range	0.919	-	-
Coefficient of variation	0.818	0.625	-
Median age	-	0.637	-

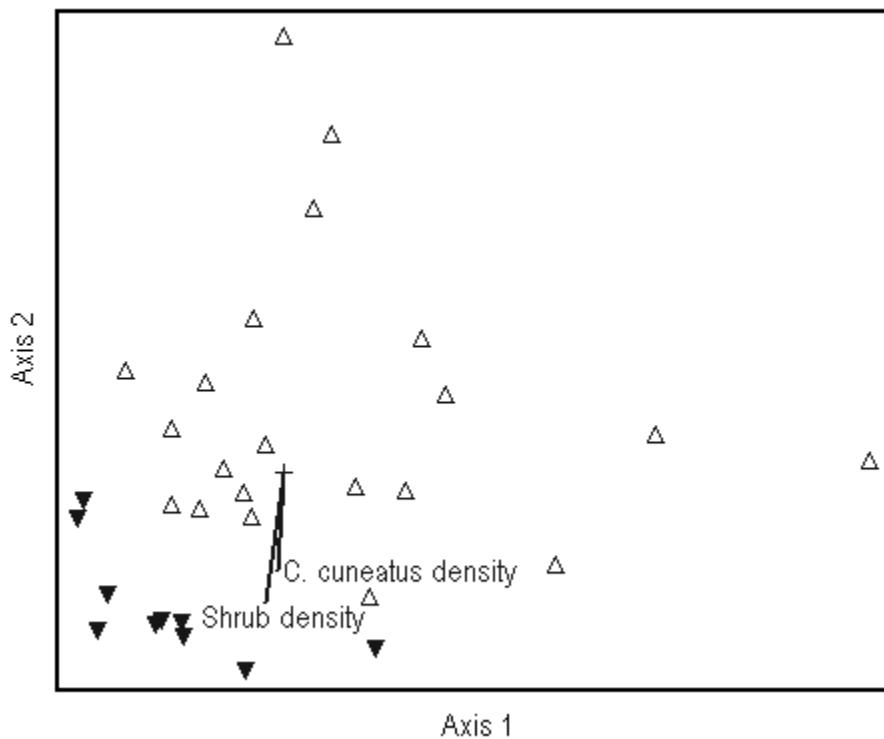


Figure 4. Representative NMS ordination of stands in the space defined by the characteristics of their age distribution. Closed triangles represent even-aged stands (ages of all shrubs sampled within 20 yr of each other) and open triangles represent uneven-aged stands (age range > 20 yr of each other). The joint plot overlay shows the relationship of shrub density of *C. cuneatus* (genets/m²) alone, and density of both *C. cuneatus* and *A. viscida* together (genets/m²), to axes (length and angle of the overlay lines indicate the strength and direction of the relationships).

Study sites represented a considerable range in climatic, topographic, edaphic, and tree structure characteristics that seemed likely to influence age structures (see Appendix A for complete site characteristics). Sites were particularly widespread in elevation (520 - 1140 m), aspect (117 - 301°), annual precipitation (655 - 841 mm), surface soil horizon depth (36 - 85 cm), and tree basal area (0 - 36 m²/ha). Despite the range in environmental variables across sites, only two inter-related variables of the 34 considered were substantially related to patterns in age structure: density of *C. cuneatus* (genets/m²) alone and density of *A. viscida* and *C. cuneatus* together (genets/m²) were correlated with Axis 2

($r = -0.500$ and $r = -0.573$ respectively; Fig. 4). Stands with higher shrub density tended to be more even-aged, and were also relatively young (fewer years since last fire; Fig 5). Correlations of other variables with any axis were weak ($|r| < 0.450$).

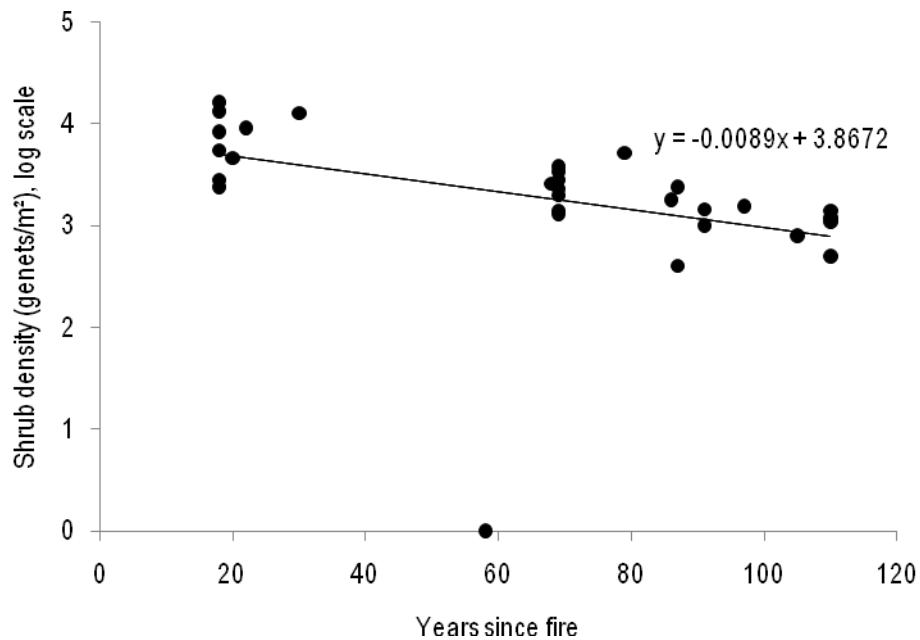


Figure 5. Chaparral shrub density declines with time since fire, despite continual low-level recruitment in the absence of fire.

Soil temperatures were high enough to stimulate germination of these reportedly obligate-seeder shrub species in the absence of fire. Maximum recorded summer soil temperature in gaps between shrubs was 68.5°C in the upper 2.5 cm of soil (mean 52.9°C; maximum soil temperature at 5.0 cm was 55.0°C, mean 42.5°C; air temperature range 29.5°C - 36.5°C). Differences in fire-free recruitment between sites were not associated with differences in site environmental characteristics thought likely to be mechanistically related to fire-free recruitment (best NPMR models $xR^2 < 0$). This analysis is somewhat unsatisfactory, however, because data on fire-free recruitment were constrained to include

only stands burned 30 to 72 yr prior to sampling, for reasons given above. In practice, only stands unburned 66 – 71 yr were available for this analysis ($n = 8$). Relationships between environment and recruitment are likely to be more detectable in a larger and less homogeneous sample of stands.

Relationship of grazing disturbance to chaparral age structure and recruitment in the absence of fire

Study sites represented a considerable range in potential livestock utilization. Some were on level ground close to roads, trails, or water, while others would likely be accessed by livestock only with great difficulty (site distance to nearest road or trail 16 - 578 m, mean 211 m; slope from road to site 68% downhill to 38% uphill, mean |24.7%|; site distance to nearest seasonal or perennial water 118 - 2052 m, mean 411 m; slope from water to site 7% to 57% uphill, mean 28% uphill; Appendix A). Steep slopes and extensive overland distances to the nearest water suggest that only 3 of 31 sites were likely to have seen substantial grazing activity historically or currently, given what is known about cattle foraging behavior. Specifically, although some sites were relatively close to water or roads, few were both within 800 m of water and had $\leq 10\%$ slope between road or water and the site (criteria from Mueggler 1965; Gillen et al. 1984; Pinchak et al. 1991). Sites also differed markedly in known grazing history. Most sites had been ungrazed by livestock for ≥ 27 yr ($n = 25$), one site was ungrazed for 23 yr, three sites were ungrazed for 11 yr, and two sites were actively grazed. The grazing intensity index differed more than 16-fold across sites. Sites also differed in seasonality of grazing (spring to early summer, spring to mid summer, and summer to late summer grazing regimes were included). Nonetheless, differences in inferred potential grazing disturbance between sites were not related to patterns in age structure as revealed by correlations between grazer disturbance variables and NMS ordination axes ($r < |0.350|$) or relationship between grazing disturbance variables and age structure ordination scores ($xR^2 < 0.16$).

for the best NPMR models), fire-free recruitment ($xR^2 < 0.35$ and $p > 0.5$ for the best NPMR models), or shrub density ($xR^2 < 0.19$ for the best NPMR models).

Relationship of age structure to wildfire disturbance history and indicators of fire severity

Chaparral study sites varied widely in fire history experienced over the last century. Some stands had experienced three fires while others had experienced none, and some had burned within the last decade while others weren't known to have had a fire in ≥ 112 yr. However, differences in site fire history were not related to patterns in stand age structures ($r \leq |0.26|$ for correlations of fire history variables with NMS ordination axes; excludes years since last fire). Further, no topographic, fuel, or fire history variables were related to differences in fire severity between chaparral stands, as described by shrub survivorship (best NPMR models $xR^2 < 0.12$).

Discussion

Patterns in age structure, relationships to environment, and shrub recruitment in the absence of fire

Age structures observed in southwest Oregon chaparral sites are unusual relative to age structures reported for obligate-seeder species in California chaparral. The shrub species that comprise low- and mid-elevation southwest Oregon chaparral (*A. viscida* and *C. cuneatus*) are both reported to be obligate-seeders in California that require fire-related cues for germination and lack the ability to expand their populations in the absence of fire (e.g. Keeley 1991; Keeley et al. 2005c). Age structure studies of California chaparral report that obligate-seeder species in stands of all ages form even-aged stands (almost all within 1 yr; Keeley 1988) dating back to the most recent fire (e.g., Keeley 1992, Zammit and Zedler 1993). In contrast, all of my stands > 30 yr were uneven-aged due to prolific fire-free recruitment, appreciable fire survivorship, and possibly some vegetative recruitment by layering. Here I focus on the contribution of fire-free recruits in understanding northern chaparral stand dynamics; the role of fire survivors is discussed below in the context of grazing and fire disturbance.

Fire-free recruitment of species with mostly refractory seeds can be facilitated by solar heating of the soil surface (Christensen and Muller 1975). Soil heating is a plausible mechanism for stimulating seed germination in my study sites, as surface soil temperatures measured in gaps were comparable to temperatures known to significantly increase seed germination of *C. cuneatus* (Keeley 1987). (I expect soil temperatures to commonly exceed those measured, as air temperatures are often higher than those that prevailed during field trials.) Most fire-free recruits were *C. cuneatus*, which is consistent with

the observation that *Ceanothus* seeds are more sensitive to heat stimulation than are those of *Arctostaphylos* (e.g., Kauffman and Martin 1991, Keeley 1991).

Differences in the proportion of fire-free recruits among stands, however, were not related to characteristics that influence soil heating and that were thought likely to be mechanistically related to recruitment, although the analysis was circumscribed by a small, relatively homogenous sample. Stands in which fire-free recruitment was lacking had higher shrub density, but all such stands were young (< 30 yr) and density covaries with age in southwest Oregon chaparral and elsewhere (e.g., Schlesinger and Gill 1980, Zammit and Zedler 1993). The lack of a relationship between even-agedness and other site characteristics, and the absence of older even-aged stands, suggest that most, if not all, unburned chaparral stands would eventually develop uneven-aged structure across the range of environments represented in the study area.

Occasional seedlings of obligate-seeding species of *Ceanothus* and *Arctostaphylos* in long-unburned chaparral have been noted elsewhere in response to anthropogenic clearing (Kauffman and Martin 1991, Moreno and Oechel 1991, Keeley 1992). Seedlings of *C. cuneatus*, but not *A. viscida*, have also been reported in apparently undisturbed chaparral in the Sierra Nevada foothills (Biswell and Gilman 1961), in maritime chaparral (Carroll et al. 1991), in stands of edaphically-mediated low density (Safford and Harrison 2004), and within grazing exclosures (Duncan et al. 1987; Deveny and Fox 2006). While a few percent of seeds are non-refractory and can produce seedlings in the absence of fire (Keeley 1987), seedlings generally do not establish successfully in intact chaparral (Biswell and Gilman 1961, Christensen and Muller 1975, Keeley 1987, Zammit and Zedler 1988). In contrast, my observations show that, although fire-free recruits showed evidence of suppressed growth rates (mean ring width of the last 20 yr of growth was only 70% that of cohort dominants), they persisted to at least 46 yr of age.

Documentation of significant recruitment of obligate-seeder species in the absence of disturbance in some chaparral populations, but not others, raises the obvious question of why demographic dynamics appear to differ between populations, even in stands composed of the same species. Within the range of the chaparral vegetation type, areas conducive to fire-free recruitment may have both greater soil heating and greater summer soil moisture, which may interact to promote seed germination and seedling survival, compared to areas that lack fire-free recruitment. The coincidence of heat and moisture increases germination rates of *Ceanothus* and lowers temperatures at which germination is stimulated (Kauffman and Martin 1991). Mean summer precipitation (Jun – Aug) at southwest Oregon sites is generally greater than summer precipitation in California regions in which obligate-seeder chaparral has been reported to produce even-age structure (e.g., Montygied-Loyba and Keeley 1987; Keeley 1992, 1993; Zammit and Zedler 1993; see Appendix C). How chaparral populations differ in opportunities for soil heating are less clear, as southwest Oregon sites support shrub densities within the range reported for chaparral elsewhere (e.g., Keeley et al. 2008), and stand-level shrub cover is high (91 – 98% in stands unburned 43 to ≥ 112 yr [Perchmlides et al. 2008], stand ages from fire history maps [USDI 2006]). On a microsite scale, however, canopy gaps are apparently sufficient to allow soil heating and seed germination. Incomplete shrub cover was also thought to be related to fire-free recruitment of obligate-seeders on a serpentine chaparral site (Safford and Harrison 2004).

Higher summer moisture and shrub gaps may interact to allow seedling survival by alleviating resource limitations. Acute competition for limited soil moisture, particularly in younger shrubs with less well-developed root systems, drives shrub thinning in southern California chaparral (Schlesinger and Gill 1980, Zammit and Zedler 1993), and shrubs on more xeric aspects have lower rates of growth and canopy recovery (Zammit and Zedler 1993; Keeley et al. 2005b). In contrast, neither shrub growth rates (mean ring width over the first or last 20 yr of growth), nor shrub density were related to aspect in my

study sites ($r^2 < 0.07$), suggesting that moisture may be less physiologically restricting than in drier areas. Though these patterns offer some tacit support for the idea that soil heating and summer moisture positively influence successful fire-free recruitment, further data are needed to assess the validity of this suggestion.

Differences in seed pools among sites may present another possible explanation for differences in chaparral demographic dynamics. Obligate-seeder species often have polymorphic seed pools comprised of both refractory and non-refractory seeds (Keeley 1991). Fire-free recruitment in relatively isolated populations may be the result of a greater proportion of non-refractory seeds in these seed pools (Carroll et al. 1991; Odion 2000). The 4,000 yr segregation of Oregon chaparral from chaparral to the south (Detling 1961) could enable biological divergence in seed germination biology between populations. However, the age structure of chaparral across much of northern California is unknown, and occasional reports from this region of fire-free recruitment of *C. cuneatus* (Biswell and Gilman 1961; Duncan et al. 1987; Safford and Harrison 2004; Deveny and Fox 2006), imply the possibility of demographic dynamics similar to those observed in southwest Oregon.

Relationship of grazing disturbance to chaparral age structure, recruitment in the absence of fire, and fire survivorship

Grazing has been one of the most intense, extensive, and pervasive historic disturbances in the Applegate Valley. This area was considered the prime cattle-raising area of the Pacific Northwest (LaLande 1995), and was grazed in such numbers from settlement to the 1920s that the entire range was “practically ruined” (Gribble 1916). Sheep, goats, and hogs free-roamed the landscape early in the settlement period, but their presence was relatively short-lived (LaLande 1995). Cattle, on the other hand, were introduced at the time of Euro-American settlement and persist today on many allotments

within the study area. Therefore, I discuss potential livestock impacts on age structure in terms of cattle grazing, asking whether the unusual age structure dynamics documented in my sites are intrinsic to southwest Oregon chaparral, or if fire-free recruitment and fire survivorship might simply be products of grazing disturbance.

Cattle grazing could impact chaparral age structure both directly and indirectly. *Arctostaphylos viscida* and *C. cuneatus* are generally considered unpalatable by grazers (e.g., USDA 1937), but *C. cuneatus* is browsed by cattle under ‘forced’ conditions such as early-season grazing, drought, or overstocked pastures (Peterson 1916; Hosten et al. 2007b). Such conditions predominated in the study area from about 1914 to the early 1920s (LaLande 1995). Because browsing is associated with a decline in *Ceanothus* seed production (Deveny and Fox 2006), cattle could have directly altered chaparral regeneration dynamics, as well as relative proportions of *A. viscida* and *C. cuneatus* where the two species co-exist. However, the time period of overstocking pre-dates the origin of most of my sampled shrubs. Under the lower stocking densities that predominated over most of the past century, indirect impacts on demography would have been more likely. Cattle could have modified chaparral age structure by physically damaging mature shrubs and trampling seedlings (Deveny and Fox 2006; Christian et al. 2008). They could have also altered shrub germination and recruitment microenvironments by mechanically scarifying seed; disturbing soil and modifying seedbed properties or altering soil heating by changing vegetative cover (Belsky and Blumenthal 1997, Jones 2000); modifying plant composition and traits of competitors (e.g., perennial v. annual, native v. exotic; Belsky and Blumenthal 1997; Keeley et al. 2003); and decreasing populations of seedling herbivores (Mills 1983, Deveny and Fox 2006).

Cattle utilization is likely to have varied widely among study sites, as sites differed considerably in both potential livestock utilization and recent grazing history. However, I found no relationship between inferred grazing impact and chaparral age structure or fire-free recruitment. There are at least three possible interpretations of these results: 1) Conceivably, historic livestock disturbance was pervasive across all sites and impacted extant age structure and fire-free recruitment similarly at all sites. Some utilization of even unfavorable sites would have been possible during the extremely high stocking levels of 1914 to the early 1920s (Cook 1966, LaLande 1995). 2) Alternatively, the absence of a grazing signal may indicate minimal livestock disturbance in both accessible and inaccessible sites, and across sites that differed in recent grazing management. Cattle are reported to avoid brushy portions of otherwise high-use allotments, even where preferred forage is plentiful (Peterson 1916; Cook 1966; Owens et al. 1991). 3) Livestock impacts on age structure and fire-free recruitment may have differed among sites, but dissimilarities were not detectable with the methods used. The model of likely grazer disturbance could have been incomplete, or relatively small sample sizes could have prevented detection of subtle relationships. Further, the ‘legacy effect’ of historic grazing may be more influential on modern community structure and composition than recent grazing regimes (Borman 2005), but I could not account for the potentially confounding factor of changing grazing regimes over time. This retrospective study might obscure interactions between changes in ecosystem processes associated with grazing and changes in other processes that were concurrent with the onset of grazing, such as the decline of native ungulates and rodents that browse on shrubs (LaLande 1995; Hosten et al. 2007b).

Though no direct livestock disturbance signal was detected in current age structures, shrub densities and age structures may have been impacted by altered fire regimes associated with early grazing practices. Early stockmen were intent on improving access and converting the disagreeable ‘brush’ into cattle forage by targeting low- and mid-elevation chaparral stands for frequent burning (ca. every 6 yr;

Peterson 1916), a practice which probably lasted half a century (ca. 1860 – 1920; LaLande 1995).

Arctostaphylos viscida starts producing seeds at about age ten (Howard 1992). *Ceanothus cuneatus* can produce seeds at about age five under ideal conditions, but appreciable seed production may be delayed fifteen years or more as shrubs are a preferred browse of deer (Biswell and Gilman 1961).

Because these species and those with similar life history traits require 20 – 30 yr without disturbance to adequately replenish soil seedbanks (Biswell and Gilman 1961, Keeley and Fotheringham 2006), high-frequency fire depletes seedbanks and impairs chaparral recovery, and is associated with expansion of fine fuels (Zedler et al. 1983; Duncan et al. 1987; Freudenberger et al. 1987; Haidinger and Keeley 1993; Jacobsen et al. 2004; Syphard et al. 2006). Decreased fire intensity associated with altered fuel structure and loading could have contributed to the fire survival of some individuals, and patchy shrubs could have enabled greater exposure of the soil to solar heating, perhaps facilitating fire-free recruitment. The association between early grazing practices and fire survivors and fire-free recruits in southwest Oregon chaparral is uncertain, but it is clear that survivorship and fire-free recruitment persist in the long absence of those practices.

Relationship of age structure to wildfire disturbance history and indicators of fire severity

Age structures of chaparral in my study area indicate that all stands, including those with shrub survivors, had experienced high-severity fires that killed $\geq 97\%$ aboveground vegetation since at least the mid-1930s (accurate assessment of severity before this time from age structures is limited by the quality of older fire maps). High-severity fires are also characteristic of chaparral in the California South Coast, Sierra Nevada, and Klamath regions (e.g., Keeley 2006; van Wagendonk and Fites-Kaufman 2006; Skinner et al. 2006). Unlike other vegetation types in which high-severity disturbance can strongly alter community structure and processes, high-severity fire often favors the persistence of chaparral

within the vegetation mosaic by clearing encroaching trees (Taylor and Skinner 1998, Nagel and Taylor 2005) and stimulating seed germination of obligate-seeder species (Moreno and Oechel 1991, Odion and Davis 2000).

Shrub fire survivors have occasionally been noted in California chaparral (e.g., Nagel and Taylor 2005), but, to my knowledge, no measure of the extent of survivorship exists with which I can compare my results. The appreciable number of shrub survivors in many southwest Oregon chaparral stands may imply that, relative to South Coast and Sierra Nevada chaparral, fires in southwest Oregon chaparral burn with comparatively higher spatial complexity. Most survivors were *A. viscida*, which is considered less flammable than *C. cuneatus* (Weatherspoon and Skinner 1995). Fire severity is higher in sites with greater stand density and radiation interception in chaparral on a regional scale (Keeley et al. 2005d). My analysis did not detect that these or other environmental, topographic, or fuel characteristics were related to differences in fire severity among sites in the post-suppression era, as inferred by percent of fire survivors.

Management implications

Fuel reduction efforts on BLM lands are motivated by the needs to reduce fire hazard and to restore ecosystems (USDI 1998, USDI 2004b). The lack of basic information about southwest Oregon chaparral structure, dynamics, and response to environment and disturbance has stymied evaluation of the extent to which fuels treatments mimic natural disturbance regimes, and, thus, work towards accomplishment of restoration objectives. This study aimed to characterize chaparral attributes, response to disturbances, and structural change over time to inform management decision-making and effective allocation of limited resources. The ability to satisfactorily evaluate the efficacy of fuels

treatments is particularly important in light of their substantial impact on the landscape, potential conflict with other management objectives, and high expense.

Results of this study suggest that Oregon chaparral populations differ from studied California chaparral populations in several fundamental ways, including the degree to which they depend on fire for recruitment of new individuals, and possibly the nature of fire disturbance. These observations imply that precepts of chaparral ecology and management should be tailored on a geographic basis. For example, fuel-related predictors of fire behavior in southern California chaparral are not likely to be directly applicable to southwest Oregon chaparral. Fuel moisture in live and dead fuels, proportion of dead fuels, standing biomass, surface fuelbeds, fuel continuity, and chemical content of fuel are all important characteristics in determining chaparral fire behavior (Green 1981, Conrad and Regelbrugge 1994). Values for these parameters are likely to vary considerably over the range of climate, topography, species composition, and stand structure evident over the extent of the chaparral vegetation type. Predictions of increased fire hazard with stand age (e.g., Rothermel and Philpot 1973, Green 1981) have been questioned in southern California chaparral (Keeley and Fotheringham 2001; Moritz et al. 2004), and are likely to be even more problematic in southwest Oregon obligate-seeder chaparral stands where time since last fire is not indicative of shrub ages and where concurrent stand thinning and fire-free recruitment may influence stand-level fuel moisture, proportion of dead fuels, biomass, and other characteristics. In the Klamath region, limited evidence suggests that, as in southern California, fuels treatments in chaparral may not necessarily alter fire effects in wildfires that burn under extreme conditions (Hosten *in prep*), perhaps because exogenous environmental conditions associated with naturally higher fire severity on south-facing slopes (e.g., higher heatload, lower fuel moisture) could make treatments in these areas less effective at modifying fire behavior (Alexander et al. 2006). Certainly more regionally-specific information is needed on fire behavior in both treated and

untreated southwest Oregon chaparral, across a range of weather and site conditions, to assess whether fuels treatments meet fire hazard mitigation objectives.

Using fuels treatments to meet restoration objectives in chaparral is predicated on the supposition that fire suppression has replaced naturally high-frequency, low-severity fires with uncommon fires that are higher-severity due to an unnatural accumulation of fuels (USDI 1998, 2004b). While available information is not likely to allow a precise characterization of pre-Euro-American settlement fire regimes in southwest Oregon chaparral, or a complete analysis of the effects of fire suppression on former fire regimes, evidence suggests that the assumptions underlying fuels treatments have limited relevance to chaparral. For example, Oregon chaparral probably experienced a fire regime that was distinct in both severity and frequency from that of adjacent conifer forests and oak woodlands. Fire severity in nearby conifer forests has been mixed but most often low-severity, leaving most large trees living, both prior to the 1900s (Agee 1991a, 1993; Sensenig 2002) and in recent decades (Odion et al. 2004; Knapp et al. 2008). In contrast, high-severity fire has been characteristic of low- to mid-elevation chaparral stands before and after the onset of effective fire suppression. In recent fires burning at higher elevations, xeric aspects and the shrub communities often found on them have commonly burned with higher severity than other areas, killing almost all above-ground vegetation (Taylor and Skinner 1998; Odion et al. 2004; Alexander et al. 2006; Knapp et al. 2008).

Fire frequency also may have differed in chaparral from that in adjacent conifer and oak woodlands during pre-settlement times. Reconstructions of fire history in nearby conifer stands document average frequencies of 9 – 16 yr (3 – 35 yr range) prior to 1900 (2 – 8 ha stands; Agee 1991a, Sensenig 2002). However, pre-settlement fires in chaparral probably burned no more often than 20 - 30 yr, as fires more frequent than this have been observed to deplete shrub seedbanks and impair recovery of *A. viscida*

and *C. cuneatus* (Biswell and Gilman 1961). Frequently recurrent fires can quickly reduce cover, or even eliminate, chaparral of *A. viscida* and *C. cuneatus* and other species with similar life history traits (Zedler et al. 1983; Duncan et al. 1987; Freudenberg et al. 1987; Haidinger and Keeley 1993; Jacobsen et al. 2004; Syphard et al. 2006). This scenario is contrary to the widespread existence of dense chaparral in the study area that was documented by the first settlers (Pullen 1996) and in early land surveys associated with the General Land Office (1857; LaLande 1995) and the 2nd Forest Homestead Act (1906; Hosten et al. 2007a). Episodes of high-frequency fire on a local scale are certainly possible, but as a single recurrent fire on a very short interval can nearly extirpate chaparral (Zedler et al. 1983; Jacobsen et al. 2004) longer intervals likely predominated in most of this vegetation type. The prevalence of stands already 35 yr old or older (40% of chaparral area) by the early decades of the 20th century, and notes that three 1915 fires all burned 30 yr old chaparral (Peterson 1916), also suggest somewhat longer fire frequencies in chaparral than have been recorded in adjacent vegetation communities. Longer fire return intervals in chaparral patches compared to those in the surrounding conifer matrix were recorded in the Sierra Nevadas (Nagel and Taylor 2005). Although relatively high fire frequencies in adjacent conifer stands (Agee 1991a, Sensenig 2002) suggest that sources of ignition in chaparral were undoubtedly common, chaparral stands younger than 20 yr are generally thought to not carry fire well, outside of extreme fire weather, due to relatively high live fuel moisture and low proportion of dead fuels (Green 1981, Dieterich and Hibbert 1990). Surface fire spread between vegetation communities may also be halted under moderate burning conditions by changes in fuel structure, continuity, and moisture (Riegel et al. 1992; Cione et al. 2002; Taylor and Skinner 2003). The fire regime under which southwest Oregon chaparral developed prior to Euro-American settlement is uncertain, and other regimes are possible besides the one advocated here. However, taken together, I suggest that the available evidence implies that the model of frequent and low severity burns, resulting

in a relatively homogeneous landscape featuring mostly scattered shrubs and trees, is probably not appropriate for chaparral vegetation.

Vegetation communities with different fire regimes may also be differentially impacted by fire suppression. Fire suppression has led to un-historic increases in density in many conifer forests (Sensenig 2002, Taylor and Skinner 2003) and oak savannas (Sugihara and Reed 1987; Riegel et al. 1992). Such changes in forest structure may justify fuel removal treatments as restoration (USDI 1998). In chaparral, however, documentation of nearly complete shrub cover in chaparral prior to fire suppression (Peterson 1916) as well as after suppression (Perchemlides et al. 2008) may indicate that suppression has had little effect on overall chaparral structure. (Scattered *A. viscida* and *C. cuneatus* also form open understories in oak and conifer-dominated communities [Pfaff 2007b], but these communities are not considered to be chaparral and are outside the scope of this study.) The exact nature of stand structure in southwest Oregon chaparral prior to Euro-American settlement is unknown, but available evidence suggests that continuous canopies are likely characteristic of southwest Oregon chaparral, as is typical elsewhere (Keeley and Keeley 1988). Results show that shrub density in chaparral declines the longer a stand is unburned, but data is needed on how total fuel loadings and other determinants of fire hazard change with stand development.

As with structure, fire suppression may not have altered chaparral fire severity. For example, I found unmistakable fire survivors in chaparral that burned in 1987, suggesting that fires that leave shrub survivors are possible in chaparral even after 40 – 50 yr of effective fire suppression. Because chaparral likely historically burned more severely and somewhat less frequently than other parts of the landscape, fire suppression may have modified chaparral less than other vegetation types in the study area. This is consistent with the finding that the proportion of the landscape dominated by low- and mid-

elevation chaparral has largely been stable since the early 1900s, while the importance of other vegetation types has changed (DiPaolo and Hosten *in prep*).

Results suggest that current fuel treatment prescriptions produce post-treatment chaparral structure that does not mimic either mature chaparral or chaparral recently disturbed by wildfire, and prescriptions therefore are unlikely to meet restoration objectives. On the one hand, treatments are unlikely to reproduce stand structures observed in mature chaparral, as the cover of widely-spaced shrub clumps left by treatment is generally an order of magnitude lower than shrub cover in mature natural stands. For example, shrub cover in chaparral unburned 43 to ≥ 112 yr was 91 – 98% (Perchelides et al. 2008; ages from fire history maps, USDI 2006), whereas a prescription implemented in part of the study area called for retaining about 4.6 – 13% shrub cover, based on size and spacing of leave patches (USDI 2004b). On the other hand, treatments also seem unlikely to mimic fire disturbance in effects on post-treatment structure and ecological processes. Shrub cover retained by fuel treatments (4.6% - 13% cover; USDI 2004b) is generally greater and less variable than would be left by fire (average 0.56% shrub cover [range 0% to 2.9% cover] after wildfires burning in the last 72 yr). In addition, treatments do not mimic natural disturbance, as regeneration of both chaparral shrub species and native forbs characteristic of post-fire environments is much lower in treated stands relative to stands burned by wildfire (Perchelides et al. 2008). For example, shrub regeneration was only 560 seedlings/ha at sites post- pile and burn treatment (Perchelides 2006), compared to 10,000 - 76,000 seedlings/ha noted after wildfires in the study area (Peterson 1916). Recovery of shrub cover also appears to be severely delayed in treated stands relative to chaparral burned by wildfire (Perchelides et al. 2008). Because invasion of exotic species is facilitated by low shrub cover (Keeley et al. 2005a; Merriam et al. 2006; Perchelides et al. 2008), sparse shrub regeneration can reinforce the trend initiated by removal of shrubs, contributing to an ecosystem state change from dominance by chaparral

to dominance by annual or exotic vegetation (Jacobsen et al. 2004; Perchemlides et al. 2008). I reiterate the suggestion of Perchemlides and others (2008) that, where treatment is deemed necessary and restoration is an objective, prescriptions should include follow-up prescribed burning to renew shrub regeneration; renewed shrub cover may help suppress the expansion of annuals and exotics likely to be stimulated by treatment. Cutting and burning treatments should not be applied less than 20 – 30 yr apart to avoid degrading chaparral through high-frequency disturbance.

Although it appears that chaparral in the Applegate Valley may not have been affected by fire suppression in ways similar to other vegetation communities (e.g., structure and fire severity do not appear to have been altered), the question remains as to whether the several-fold reduction in area burned since the onset of effective fire suppression (Appendix D, Fig. 1) has impacted this fire-dependent system. Nearly 40% of chaparral area in this region of southwest Oregon has not had a recorded fire in at least 112 yr. In California chaparral, at least, this lengthy absence of fire may be outside the historic range of variability (Keeley et al. 2005a). Even though seeds of some chaparral shrub species are long-lived (e.g., *C. cuneatus*; Quick and Quick 1961), seedbanks of shrubs and the transitory herbs associated with post-fire chaparral could presumably experience attrition (Zammit and Zedler 1988). However, this ‘senescence risk’ (*sensu* Zedler 1995) is probably important only for short-lived species and very long intervals between fires (Zedler 1995). For example, in long-unburned Sierra Nevada chaparral stands, some degradation of the seedbank was suggested by lower post-fire seedling density of *C. cuneatus* in ancient stands (unburned for > 100 yr) than in mature stands (unburned for 50 – 60 yr). Nonetheless, regeneration of shrubs was still at replacement level, and diversity and abundance of post-fire endemic annuals was not affected by the elongated time since fire (Keeley et al. 2005a). Research on the regeneration capacity of shrubs and herbs in long-unburned chaparral in southwest Oregon is needed to clarify whether fuels treatments can be justified as

restoration to address senescence risk in very old stands, and monitoring is needed in stands that have already been treated. Until the role of fuels treatments in chaparral restoration is better understood, I suggest, where restoration is an objective, that treatments in chaparral be suspended and resources redirected to treat those conifer and oak systems known to have been substantially altered by fire suppression.

Chaparral is thought to have persisted in the study area for more than 8,000 yr (Detling 1961). Chaparral seems to have been resilient to past disturbances, and the importance of chaparral on low- and mid-elevation south-facing slopes within the Applegate Valley appears to have been largely stable since the early 1900s (DiPaolo and Hosten *in prep*). The work reported here shows that many shrubs can attain great age, and that most chaparral stands pre-date the era of effective fire suppression. Chaparral is a keystone community that supports a regionally unique assemblage of wildlife and numerous special-status plants and animals. The unique way in which fire appears to interact with chaparral is likely to further landscape-level variability that is important in sustaining the complexity and diversity for which the Klamath region is known (Martin and Sapsis 1991). Fuels treatments in chaparral seem unlikely to meet restoration objectives, and are likely to replace the trajectory of chaparral development that appears to have been in place for the last century. Given the interdependency between biodiversity and the diversity of fire's spatial and temporal characteristics, it makes little sense to impose the same fire management policy on different vegetation types (Martin and Sapsis 1991). I suggest that management objectives be developed that promote chaparral as an integral part of the southwest Oregon landscape to sustain landscape-level heterogeneity and species conservation.

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Appendices

Appendix A

Characteristics of sampled chaparral stands. Chaparral 'types' were previously defined by Pfaff (2007b) by grouping together areas of similar plant species composition, assessed in ground surveys, with hierarchical agglomerative clustering. Tree and shrub composition and cover within a chaparral type represent the mean conditions across all stands in the study area in that type, and therefore represent general vegetation conditions rather than conditions specific to stands sampled in this study. Environment and disturbance characteristics, on the other hand, are specific to the indicated stand. Definitions, notes, and data sources on stand characteristics are in Table 13 for climate and topography variables, Table 14 for soil and stand structure variables, and Table 15 for disturbance variables.

Table 1. Tree and shrub composition and mean % cover in the buckbrush chaparral type.

	Common name	Scientific name	Mean % cover	Total % cover
Trees	Pacific madrone	<i>Arbutus menziesii</i>	1.4	6.8
	ponderosa pine	<i>Pinus ponderosa</i>	1.0	
	Oregon white oak	<i>Quercus garryana</i>	4.4	
Shrubs	whiteleaf manzanita	<i>Arctostaphylos viscida</i>	2.5	47.2
	buckbrush ceanothus	<i>Ceanothus cuneatus</i>	31.1	
	birchleaf mountain mahogany	<i>Cercocarpus betuloides</i>	2.6	
	bearbrush	<i>Garrya fremontii</i>	2.6	
	Klamath plum	<i>Prunus subcordata</i>	3.0	
	poison oak	<i>Toxicodendron diversilobum</i>	5.5	

Table 2. Tree and shrub composition and mean % cover in the manzanita chaparral type.

	Common name	Scientific name	Mean % cover	Total % cover
Trees	Pacific madrone	<i>Arbutus menziesii</i>	2.9	15.9
	ponderosa pine	<i>Pinus ponderosa</i>	4.7	
	Douglas-fir	<i>Psuedotsuga menziesii</i>	1.0	
	Oregon white oak	<i>Quercus garryana</i>	4.4	
	California black oak	<i>Quercus kelloggii</i>	3.0	
Shrubs	whiteleaf manzanita	<i>Arctostaphylos viscida</i>	48.9	61.2
	buckbrush ceanothus	<i>Ceanothus cuneatus</i>	2.1	
	deerbrush	<i>Ceanothus integerrimus</i>	1.7	
	pink honeysuckle	<i>Lonicera hispidula</i>	1.1	
	poison oak	<i>Toxicodendron diversilobum</i>	7.3	

Table 3. Tree and shrub composition and mean % cover in the manzanita-oak chaparral type.

	Common name	Scientific name	Mean % cover	Total % cover
Trees	Pacific madrone	<i>Arbutus menziesii</i>	7.4	30.3
	ponderosa pine	<i>Pinus ponderosa</i>	3.8	
	Douglas-fir	<i>Psuedotsuga menziesii</i>	1.8	
	Oregon white oak	<i>Quercus garryana</i>	14.1	
	California black oak	<i>Quercus kelloggii</i>	3.2	
Shrubs	whiteleaf manzanita	<i>Arctostaphylos viscida</i>	15.4	31.8
	buckbrush ceanothus	<i>Ceanothus cuneatus</i>	4.9	
	deerbrush	<i>Ceanothus integerrimus</i>	2.0	
	pink honeysuckle	<i>Lonicera hispidula</i>	2.3	
	poison oak	<i>Toxicodendron diversilobum</i>	7.1	

Table 4. Tree and shrub composition and mean % cover in the open-oak chaparral type.

	Common name	Scientific name	Mean % cover	Total % cover
Trees	Pacific madrone	<i>Arbutus menziesii</i>	1.1	28.0
	ponderosa pine	<i>Pinus ponderosa</i>	3.1	
	Douglas-fir	<i>Psuedotsuga menziesii</i>	1.4	
	Oregon white oak	<i>Quercus garryana</i>	22.4	
Shrubs	whiteleaf manzanita	<i>Arctostaphylos viscida</i>	2.6	26.4
	hollyleaved barberry	<i>Berberis piperiana</i>	1.4	
	buckbrush ceanothus	<i>Ceanothus cuneatus</i>	7.9	
	deerbrush	<i>Ceanothus integerrimus</i>	0.9	
	birchleaf mountain mahogany	<i>Cercocarpus betuloides</i>	8.7	
	poison oak	<i>Toxicodendron diversilobum</i>	4.9	

Table 5. Environmental characteristics of stands in the buckbrush chaparral type (n = 8). * No live trees on site.

	Yr of last fire	1895 or earlier	1895 or earlier	1914	1936	1936	1936	1987	1987
Climate	Actual annual evapotranspiration (mm)	509	490	489	482	497	493	485	488
	Summer actual evapotranspiration (mm)	130	96	98	91	104	109	91	93
	Annual precipitation (mm)	841	675	722	718	714	712	691	699
Topography	Elevation (m)	1138	899	867	798	1107	1026	739	840
	Folded aspect (°)	251	166	279	117	261	271	192	214
	Topographic position index	8.6	7.6	9.2	6	10	8.8	6.6	9.6
	% Slope	24	31	22	25	24	34	23	26
	Slope shape	10.6	9.3	12.3	10.0	10.8	10.1	10.1	10.4
	Potential direct incident radiation (MJ/cm ² · yr)	0.83	0.97	0.74	0.85	0.79	0.72	0.95	0.93
	Heatload	0.94	0.86	0.88	0.69	0.92	0.91	0.93	0.96
Soils	6th field watershed membership	12	9	9	13	12	9	12	12
	Parent material	42	12	42	42	42	42	42	42
	Surface horizon depth (cm)	36	85	56	37	56	75	40	65
	% Clay	16	8	13	16	13	10	17	11
	% Sand	27	13	21	26	21	16	24	19
	% Silt	25	13	20	25	21	15	27	18
	pH	4	2	3.2	4.2	3.2	2.4	5	2.8
Stand structure	Cation exchange capacity (mEq/100 g)	16	5	12	15	12	7	10	9
	Tree basal area (m ² /ha)	4.2	5.5	11.6	5.8	8.4	1.1	0.3	1.0
	Pre-treatment shrub density (genets/m ²)	0.5	0.1	0.3	0.5	0.9	0.2	0.6	1.6
	% Multi-stemmed hardwoods	80	70	95	96	100	50	NA*	100

Table 6. Disturbance characteristics of stands in the buckbrush chaparral type (n = 8)

	Yr of last fire	1895 or earlier	1895 or earlier	1914	1936	1936	1936	1987	1987
Wildfire Disturbance History (recorded fires > 40 ha, 1895-2005)	Point fire frequency	0	0	1	1	1	1	3	2
	Yr since last fire	≥112	≥112	93	72	72	72	21	21
	Maximum fire interval (yr)	≥112	≥112	100	100	100	100	73	73
	Minimum fire interval (yr)	≥112	≥112	0	0	0	0	22	73
Potential human and livestock disturbance	Distance from nearest road or trail (m)	176	40	224	73	310	16	538	205
	% Slope from road or trail to site	31	-66	20	-54	25	0	-22	0
	Distance from nearest water to site (m)	543	484	455	118	494	546	163	235
	% Slope from water to site	35	36	37	10	57	35	27	56
	Road access index	5400	-2600	4500	-4000	7800	0	-11800	100
	Water access index	19000	17400	16600	1200	28100	19100	4300	13000
	Yr ungrazed	27	23	27	27	27	27	27	27
	Grazing intensity index	0.02	0.12	0.02	0.02	0.02	0.02	0.23	0.23
	Season grazed	3	2	3	3	3	3	2	2

Table 7. Environmental characteristics of stands in the manzanita chaparral type (n = 6).

	Yr of last fire	1895 or earlier	1895 or earlier	1900	1936	1936	1936
Climate	Actual annual evapotranspiration (mm)	493	490	484	485	483	483
	Summer actual evapotranspiration (mm)	108	103	93	87	90	90
	Annual precipitation (mm)	765	741	727	771	673	663
Topography	Elevation (m)	891	887	790	521	679	618
	Folded aspect (°)	195	270	213	124	176	202
	Topographic position index	7.2	8.4	6.6	5.2	4.4	6.6
	% Slope	22	20	22	13	26	28
	Slope shape	10.1	10.4	10.5	9.9	11.0	9.6
	Potential direct incident radiation (MJ/cm ² ·yr)	0.95	0.77	0.92	0.85	0.97	0.96
	Heatload	0.93	0.89	0.95	0.77	0.90	0.95
Soils	6th field watershed membership	13	13	12	2	6	6
	Parent material	42	42	42	42	42	42
	Surface horizon depth (cm)	40	40	40	41	49	67
	% Clay	17	17	17	17	15	12
	% Sand	24	24	24	22	22	17
	% Silt	27	27	27	28	24	19
	pH	5	5	5	4.4	4.4	3.2
Stand Structure	Cation exchange capacity (mEq/100 g)	10	10	10	10	9	7
	Tree basal area (m ² /ha)	5.8	17.8	2.9	1.3	0.2	2.9
	Pre-treatment shrub density (genets/m ²)	0.1	0.2	0.2	1.3	0.1	0.3
	% Multi-stemmed hardwoods	46	26	100	92	0	100

Table 8. Disturbance characteristics of stands in the manzanita chaparral type (n = 6)

	Yr of last fire	1895 or earlier	1895 or earlier	1900	1936	1936	1936
Wildfire Disturbance History (recorded fires > 40 ha, 1895-2005)	Point fire frequency	0	0	1	1	1	1
	Yr since last fire	≥112	≥112	107	72	72	72
	Maximum fire interval (yr)	≥112	≥112	100	100	100	100
	Minimum fire interval (yr)	≥112	≥112	0	0	0	0
Potential human and livestock disturbance	Distance from nearest road or trail (m)	407	210	364	191	320	39
	% Slope from road or trail to site	23	-4	10	7	32	-69
	Distance from nearest water to site (m)	213	465	511	119	141	474
	% Slope from water to site	24	23	24	19	42	7
	Road access index	9400	-900	3800	1300	10300	-2700
	Water access index	5100	10600	12000	2200	6000	3200
	Yr ungrazed	11	27	27	active	27	27
	Grazing intensity index	0.03	0.02	0.02	0.04	0.23	0.02
	Season grazed	3	3	3	2	2	3

Table 9. Environmental characteristics of stands in the manzanita-oak chaparral type (n = 9).

	Yr of last fire	1895 or earlier	1895 or earlier	1900	1914	1914	1936	1936	1987	1987
Climate	Actual annual evapotranspiration (mm)	489	477	490	481	495	473	478	495	494
	Summer actual evapotranspiration (mm)	103	83	101	90	98	89	86	96	96
	Annual precipitation (mm)	755	661	789	677	678	685	660	700	702
Topography	Elevation (m)	851	595	806	666	693	709	761	843	743
	Folded aspect (°)	204	192	201	236	133	233	197	206	227
	Topographic position index	8.4	6	7.8	9	6	6.6	6.6	6.6	4.4
	% Slope	20	17	19	23	24	24	23	25	24
	Slope shape	9.8	10.5	10.3	10.9	9.7	10.6	9.6	10.0	10.1
	Potential direct incident radiation (MJ/cm ² ·yr)	0.93	0.92	0.93	0.87	0.90	0.88	0.95	0.94	0.90
	Heatload	0.93	0.90	0.93	0.95	0.75	0.96	0.93	0.95	0.96
Soils	6th field watershed membership	13	7	12	9	9	12	4	7	7
	Parent material	42	42	42	42	42	42	42	42	42
	Surface horizon depth (cm)	40	40	40	39	38	39	40	36	36
	% Clay	17	17	17	17	17	17	17	16	16
	% Sand	24	24	24	25	25	24	24	27	27
	% Silt	27	27	27	27	26	27	27	25	25
	pH	5	5	5	4.8	4.6	4.8	5	4	4
Stand Structure	Cation exchange capacity (mEq/100 g)	10	10	10	11	12	11	10	16	16
	Tree basal area (m ² /ha)	9.5	21.2	28.1	18.9	12.2	9.2	8.8	16.0	36.2
	Pre-treatment shrub density (genets/m ²)	0.1	0.1	0.1	0.1	0.1	0.3	0.1	1.3	0.2
	% Multi-stemmed hardwoods	82	39	49	27	15	62	39	94	88

Table 10. Disturbance characteristics of stands in the manzanita-oak chaparral type (n = 9).

	Yr of last fire	1895 or earlier	1895 or earlier	1900	1914	1914	1936	1936	1987	1987
Wildfire Disturbance History (recorded fires > 40 ha, 1895-2005)	Point fire frequency	0	0	1	2	2	1	1	2	2
	Yr since last fire	≥112	≥112	107	93	93	72	72	21	21
	Maximum fire interval (yr)	≥112	≥112	100	4	4	100	100	73	73
	Minimum fire interval (yr)	≥112	≥112	0	4	4	0	0	73	73
Potential human and livestock disturbance	Distance from nearest road or trail (m)	464	331	21	253	425	305	69	80	38
	% Slope from road or trail to site	17	28	9	38	-26	11	-32	-39	0
	Distance from nearest water to site (m)	348	308	322	361	356	242	411	166	749
	% Slope from water to site	12	12	25	38	14	31	22	33	20
	Road access index	8000	9100	200	9500	-11200	3400	-2200	-3100	0
	Water access index	4200	3700	8100	13600	4800	7400	9000	5500	14900
	Yr ungrazed	11	27	27	27	27	active	27	27	27
	Grazing intensity index	0.03	0.00	0.02	0.00	0.00	0.06	0.00	0.00	0.00
	Season grazed	3	1	3	1	1	2	1	1	1

Table 11. Environmental characteristics of stands in the open-oak chaparral type (n = 8).

	Yr of last fire	1895 or earlier	1895 or earlier	1914	1936	1936	1936	1987	1987
Climate	Actual annual evapotranspiration (mm)	483	491	485	485	490	480	489	494
	Summer actual evapotranspiration (mm)	96	101	96	91	98	94	91	96
	Annual precipitation (mm)	734	733	722	655	683	697	692	717
Topography	Elevation (m)	774	785	716	799	781	723	782	848
	Folded aspect (°)	301	212	164	282	289	250	126	220
	Topographic position index	6	4.4	6	6.8	9.4	7.2	8.4	9
	% Slope	22	23	20	28	24	21	27	27
	Slope shape	10.6	9.5	9.7	11.0	10.6	10.7	10.3	10.5
	Potential direct incident radiation (MJ/cm ² · yr)	0.66	0.93	0.94	0.70	0.69	0.83	0.88	0.92
	Heatload	0.81	0.95	0.86	0.87	0.85	0.93	0.72	0.97
Soils	6th field watershed membership	13	9	9	4	9	9	7	7
	Parent material	42	42	42	42	42	42	42	42
	Surface horizon depth (cm)	36	37	49	36	39	38	38	36
	% Clay	16	16	15	16	17	16	16	16
	% Sand	26	26	22	27	23	25	26	27
	% Silt	26	25	24	25	27	26	26	25
	pH	4	4.2	4.4	4	4	4.4	4.4	4
Stand Structure	Cation exchange capacity (mEq/100 g)	16	15	9	16	12	14	14	16
	Tree basal area (m ² /ha)	25.8	15.4	9.8	15.0	19.5	16.0	14.2	16.9
	Pre-treatment shrub density (genets/m ²)	0.0	0.0	0.2	0.2	0.2	0.4	0.8	0.3
	% Multi-stemmed hardwoods	18	39	65	0	67	61	42	55

Table12. Disturbance characteristics of stands in the open-oak chaparral type (n = 8).

	Yr of last fire	1895 or earlier	1895 or earlier	1914	1936	1936	1936	1987	1987
Wildfire Disturbance History (recorded fires > 40 ha, 1895-2005)	Point fire frequency	0	0	1	1	1	1	2	2
	Yr since last fire	≥112	≥112	93	72	72	72	21	21
	Maximum fire interval (yr)	≥112	≥112	100	100	100	100	73	73
	Minimum fire interval (yr)	≥112	≥112	0	0	0	0	73	73
Potential human and livestock disturbance	Distance from nearest road or trail (m)	35	408	428	202	37	48	51	225
	% Slope from road or trail to site	-33	-39	26	-41	8	21	-8	27
	Distance from nearest water to site (m)	227	151	418	140	2052	425	576	530
	% Slope from water to site	32	7	26	21	16	41	43	50
	Road access index	-1200	-15800	10900	-8200	300	1000	-400	6000
	Water access index	7400	1000	10800	3000	32600	17400	24700	26800
	Yr ungrazed	11	27	27	27	27	27	27	27
	Grazing intensity index	0.03	0.02	0.02	0.00	0.02	0.02	0.00	0.00
	Season grazed	3	3	3	1	3	3	1	1

Table 13. Definitions, notes and sources for climate and topography characteristics.

	Notes	Source
Chaparral type	Defined by species relative cover	Pfaff 2007b
Yr of last fire	Recorded fires > 40 ha, 1895-2005	USDI 2006
Climate	Actual annual evapo-transpiration (mm)	Data previously collected and processed; Pfaff 2007a
	Summer actual evapo-transpiration (mm)	Data previously collected and processed; Pfaff 2007a
	Annual precipitation (mm)	Data previously collected and processed; Pfaff 2007a
Topography	Elevation (m)	Collected in field with GPS
	Folded aspect (°)	Aspect collected in field with compass, then folded to reflect 'xeric-ness' ($= 180- \text{aspect}-225 $)
	Topographic position index	Calculated in GIS from a digital elevation model (DEM; USDI n. d. a)
	% Slope	Calculated in GIS from a DEM; USDI n. d. a
	Slope shape	Calculated in GIS from a DEM; USDI n. d. a
	Potential direct incident radiation (MJ/cm ² · yr)	Calculated from online files; McCune 2007a
	Heatload	Calculated from online files; McCune 2007a
	6th field watershed membership	Data previously collected and processed; Pfaff 2007a

Table 14. Definitions, notes and sources for soil and stand structure characteristics.

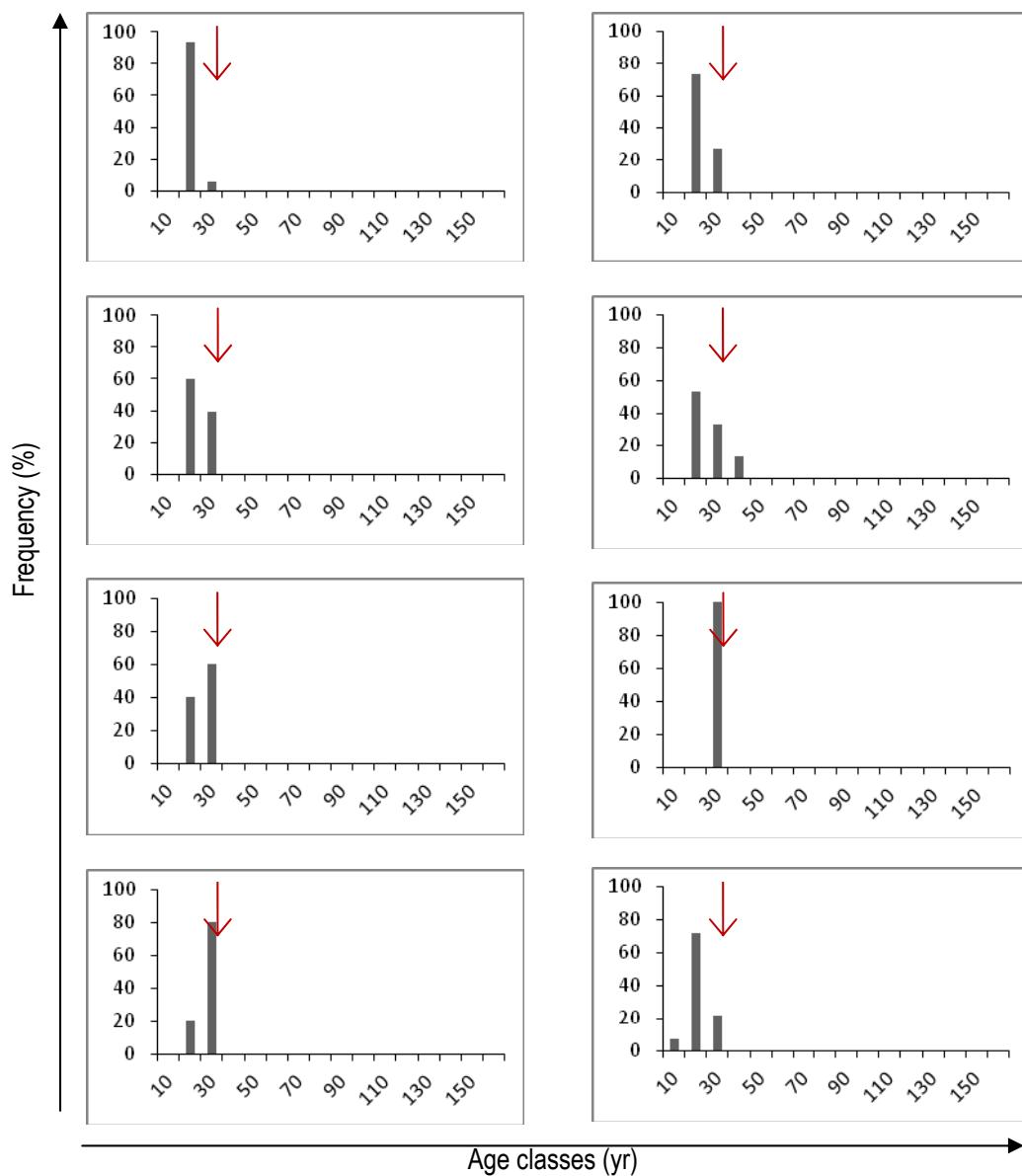
		Notes	Source
Soil	Parent material Surface horizon depth (cm) % Clay % Sand % Silt pH Cation exchange capacity (mEq per 100 g)		Data previously collected and processed; Pfaff 2007a Data previously collected and processed; Pfaff 2007a
Stand structure	Tree basal area (m ² /ha) Pre-treatment shrub density (genets/m ²) % Multi-stemmed hardwoods	Includes <i>A. viscosa</i> and <i>C. cuneatus</i> only	Field data; see Methods Field data; see Methods Field data; see Methods

Table 15. Definitions, notes and sources for disturbance characteristics.

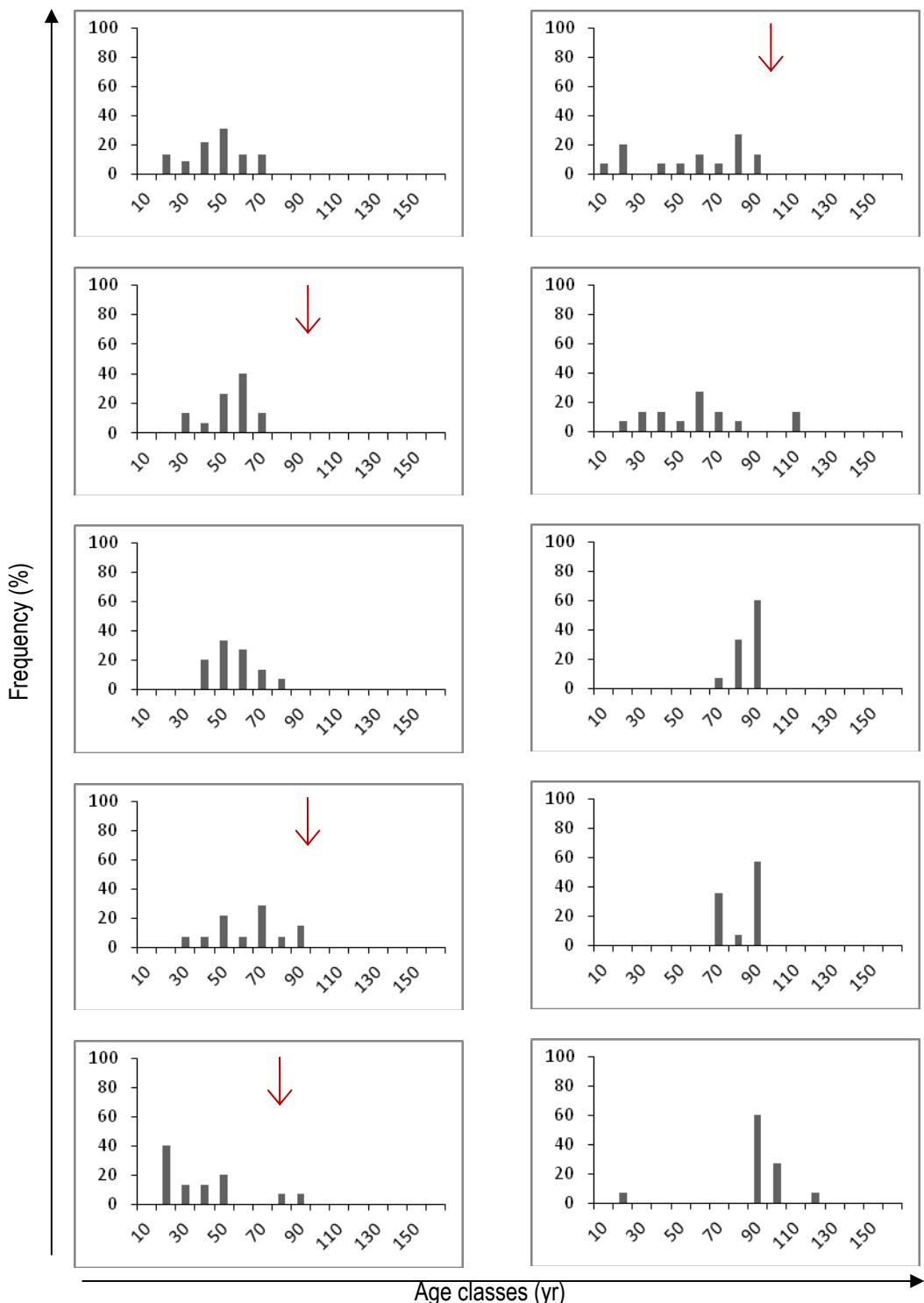
		Notes	Source
Wildfire	Point fire frequency	Point = 30m x 30m; recorded fires > 40 ha, 1895-2005	USDI 2006; collected and processed by Pfaff 2007a
	Yr since last fire	Relative to 2005; recorded fires > 40 ha, 1895-2005	USDI 2006; collected and processed by Pfaff 2007a
	Maximum fire interval (yr)	recorded fires > 40 ha, 1895-2005	Sites burned once were assigned a max. fire interval of 100 yr. USDI 2006; collected and processed by Pfaff 2007a
	Minimum fire interval (yr)	recorded fires > 40 ha, 1895-2005	Sites burned once were assigned a min. fire interval of 0 yr. USDI 2006; collected and processed by Pfaff 2007a
Potential human and livestock disturbance	Distance from nearest road or trail (m)		Calculated in GIS from transportation spatial files; USDI n. d. b
	% Slope from road or trail to site		Calculated in GIS from transportation spatial files; USDI n. d. b
	Distance from nearest water to site (m)		Calculated in GIS from hydrology spatial files; Oregon Water Resources Dept. 2005
	% Slope from water to site		Calculated in GIS from hydrology spatial files; Oregon Water Resources Dept. 2005
	Road access index	(Distance from road to site) x (slope from road to site)	Calculated in GIS
	Water access index	(Distance from water to site) x (slope from water to site)	Calculated in GIS
	Yr ungrazed	Relative to 2008	USDI 2008
	Grazing intensity index	(Animal Unit Month allotment) x (number allotted grazing months)	Calculated from USDI 2008
	Season grazed	1 = spring to early summer; 2 = spring to mid summer; 3 = summer to late summer	USDI 2008

Appendix B

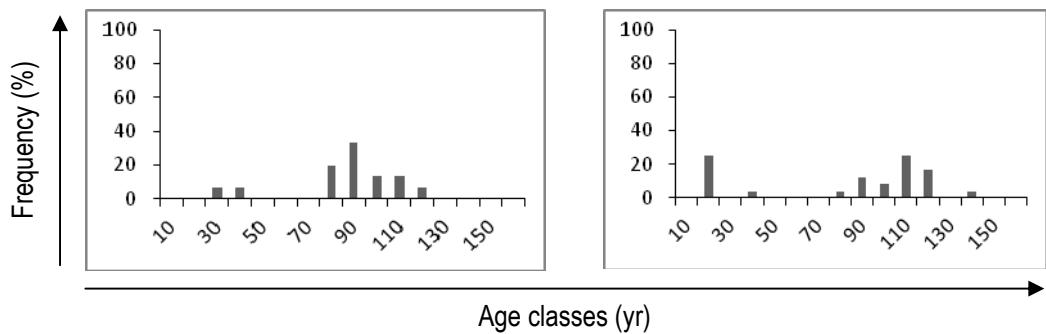
Age distributions for shrubs in chaparral study sites (15–25 samples of *A. viscida* and *C. cuneatus*, together, per site). (a) Eight of 31 chaparral sites were even-aged (all sample ages within 20 yr); all even-aged sites burned < 30 yr ago. All sites > 30 yr were uneven-aged due to (b) obligate-seeder 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. Age distributions retained even-aged or uneven-aged character even when samples with estimated or poor-quality ages were disregarded. Arrows mark yr of last known fire recorded on BLM fire history maps (USDI 2006). Stands without arrows have not had a recorded fire in at least 112 yr. Comparison of age structures with burn maps suggest that maps are often less accurate for older fires.



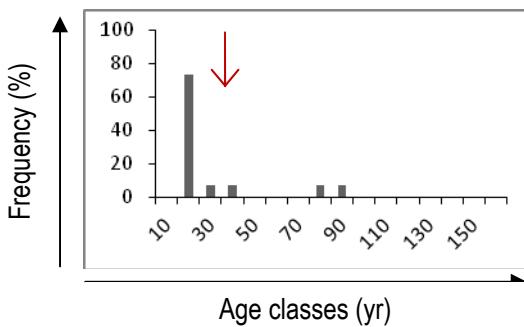
(a) Stands with even-aged structure.



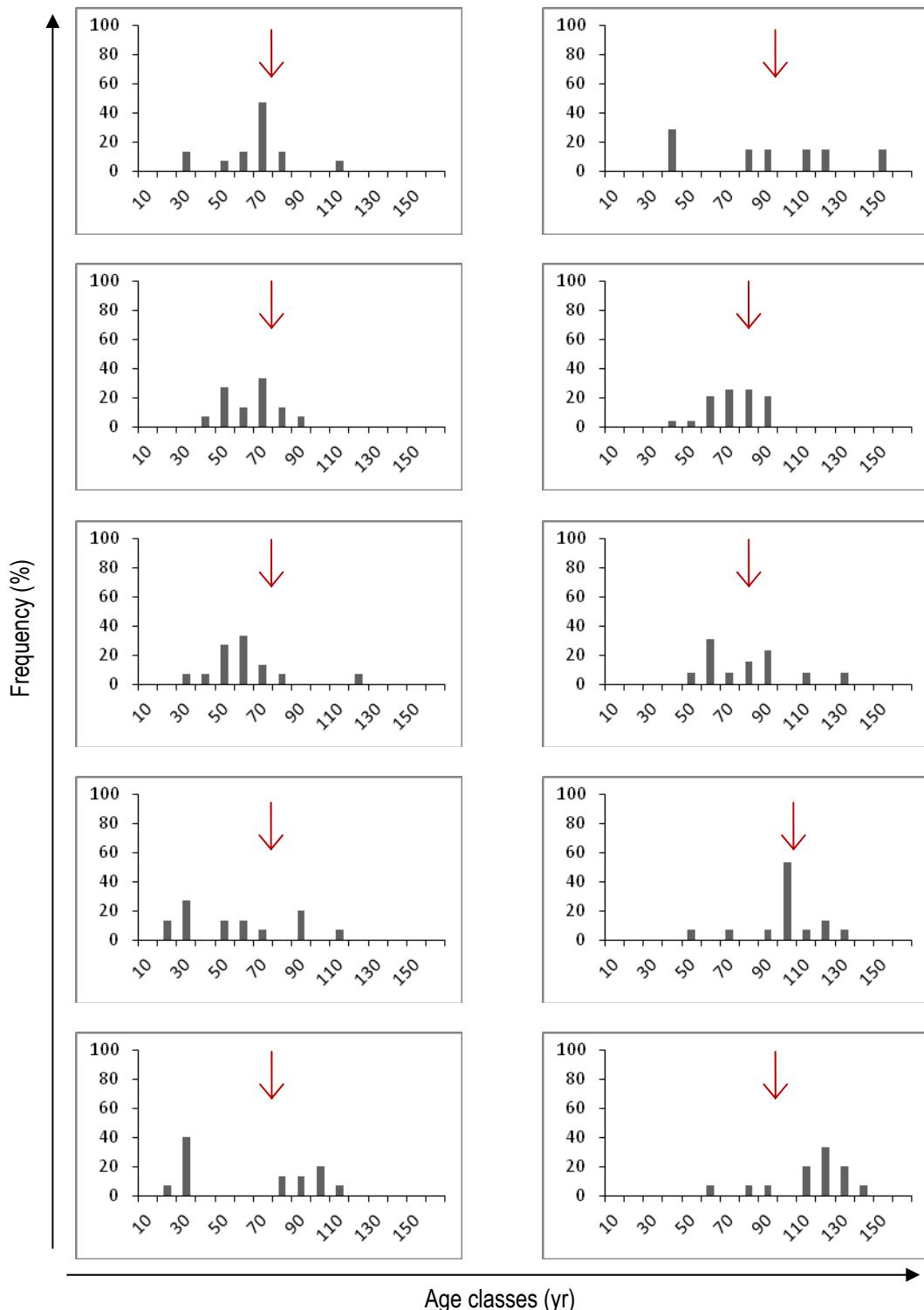
(b) Stands with uneven-aged structure with fire-free recruits



b) Stands with uneven-aged structure with fire-free recruits (cont.)



(c) Stands with uneven-aged structure with fire survivors



(d) Stands with uneven-aged structure with fire-free recruits and fire survivors

Appendix C

Characteristics of stands with even-aged structure (Table 1) and uneven-aged structure (Table 2) in which obligate-seeder shrub species were a major component. Sites were presumed to be undisturbed. When site location coordinates were not reported in the text, I estimated locations using 1:24,000 topographic maps. Precipitation data are from WRCC 2008, averaged across 1971-2000. See References for full citations of data sources.

Table 1. Site characteristics of stands > 30 yr reported to have even-aged structure. Stand age is the number of years since the last known fire. Whether summer precipitation and shrub density in stands reported to have even-aged structure are broadly representative of those characteristics in other even-aged stands is unknown.

Source	Chaparral composition	Lat (N)	Long (W)	Stand age (yr)	Summer precipitation (Jun-Aug; mm)	Shrub density (genets/ha)
Keeley 1992	mixed	37°56'	122°33'	≥ 61	15.0	29,500
Montgierd-Loyba and Keeley 1987	Mixed with <i>Ceanothus megacarpus</i>	~34°05'	~118°59'	55	5.1	13,887
Keeley 1992	mixed	34°20'	118°08'	89	13.5	13,280
Keeley 1992	mixed	37°56'	122°34'	≥ 93	15.0	12,960
Keeley 1992	mixed	34°05'	118°58'	56	1.5	10,940
Keeley 1992	mixed	34°06'	118°58'	56	1.5	9,160
Keeley 1992	mixed	33°45'	117°33'	118	3.0	8,450
Keeley 1992	mixed	39°09'	122°45'	74	9.1	7,880
Keeley 1992	mixed	36°28'	118°46'	102	12.4	7,060
Keeley 1992	mixed	33°22'	116°42'	66	30.7	5,470
Keeley 1992	mixed	34°12'	117°51'	66	13.7	5,400
Keeley 1992	mixed	33°17'	116°37'	76	30.7	4,960
Zammit and Zedler 1993	Mixed with <i>C. greggii</i>	34°23'	117°48'	57	56.9	2,871
Keeley 1993	mixed	36°28'	118°46'	83	12.4	1,860
Zammit and Zedler 1993	Mixed with <i>C. greggii</i>	35°23'	118°48'	82	4.1	1,143

Table 2. Site characteristics of stands > 30 yr in which stands had uneven-aged structure (as reported in this thesis; characteristics were averaged across stands of the same age), or stands in which recruitment of obligate-seeder species was reported (fire-free recruits were *Ceanothus cuneatus* in every case). Stand age is the number of years since the last known fire. It is unknown whether summer precipitation and shrub density in stands in which fire-free recruitment has been reported are broadly representative of those characteristics in other stands in which recruitment is present but has not been reported.

Source	Chaparral composition	Lat (N)	Long (W)	Stand age (yr)	Summer precipitation (Jun-Aug; mm)	Shrub density, mean and range (genets/ha)
Duren thesis, 2009	<i>Arctostaphylos viscida</i> and <i>Ceanothus cuneatus</i>	42°14'	123°02'	71	52.8	4,170 (1,300 – 12,850)
Peterson 1916	<i>A. viscida</i> and <i>C. cuneatus</i>	~42°15'	~123°05'	40	52.8	1,960
Duren thesis, 2009	<i>A. viscida</i> and <i>C. cuneatus</i>	42°14'	123°02'	93	52.8	1,712 (1,000-1,800)
Duren thesis, 2009	<i>A. viscida</i> and <i>C. cuneatus</i>	42°14'	123°02'	≥ 112	52.8	1,525 (0-5,200)
Duren thesis, 2009	<i>A. viscida</i> and <i>C. cuneatus</i>	42°14'	123°02'	107	52.8	1,175 (800-1,500)
Duncan et al. 1986	<i>Quercus douglasii</i> and <i>C. cuneatus</i>	~37°10'	~119°80'	50	6.4	not reported
Safford and Harrison 2004	Mixed serpentine	38°51'	123°30'	not reported	8.9	not reported, but recruitment attributed to relatively low cover
Deveny and Fox 2006	Maritime with <i>C. cuneatus</i> var. <i>rigidus</i>	~36°58'	~122°04'	not reported	10.9	not reported

Appendix D

Study area wildfire history 1910 – 2007 for chaparral vegetation and across all vegetation.

An understanding of past wildfire regimes and the impact of nearly a century of fire suppression is of particular interest to managers seeking to understand the effects of altered disturbance regimes on landscape pattern and function. I summarized fire history records available for the study area for the period 1910 – 2007 (USDI n. d. *c*) and compared fire regimes between the pre-suppression (1910 – 1939) and post-suppression (1940 - 2007) periods in chaparral and across all vegetation. (The polygon format dataset used here overlapped, and was congruent to, the raster format dataset used to derive study site fire history characteristics analyzed in relation to chaparral age structure. Although the polygon format dataset was missing the earliest fire records [1895 – 1909], this format was more suitable for the present purpose as it allowed burned areas to overlap.) Fire history characterizations presented here are not intended to represent ‘natural’ fire regimes of either chaparral or other vegetation, as this area had been settled by Euro-Americans for about 60 yr at the time of the earliest fire history records. Nonetheless, comparison of fire history trends before and after fire suppression may be instructive.

I adopted 1940 as the date of effective fire suppression for this comparison, as the regional influence of suppression was noted around this time period (Atzet 1996, Taylor and Skinner 1998, Frost and Sweeney 2000); this date also facilitates comparison with regional trends in pre- and post-suppression wildfire history summarized by Frost and Sweeney (2000). Within the study area, no fires were recorded 1937 – 1954, so adopting any date of effective suppression within this time period would not

alter conclusions. Nonetheless, the date chosen to mark effective suppression does influence the detection of apparent trends in wildfire history for the relatively limited extent of my study area. For instance, assuming suppression was effective around 1900, as was noted in tree fire scars within the watershed (Sensenig 2002), or in the late 1920s – early 1930s, as suggested by LaLande (1995), would alter conclusions concerning the effect of fire suppression in the study area.

Study area fire records suffer from bias against recording small fires (< 40 ha) and are of suspect accuracy for the earliest time periods (USDI 2006). For instance, ranchers were thought to have frequently set fires for forage production to such an extent that fire frequency during the ranching period (late 1800s – late 1920s or early 1930s) was probably greater than that maintained by earlier Native Americans (LaLande 1995). This implies that, over the landscape of the study area (100,930 ha), at least one fire would be expected to burn more or less annually. Yet, no fires were recorded in the study area for prolonged periods (e.g., 1915 – 1935) in the pre-suppression area. Errors of omission in the fire records are more likely for early time periods, suggesting that area burned and fire occurrence in the pre-suppression period may be somewhat underestimated. Despite these problems with the fire history records, they are the most complete records available.

Study area fire history records suggest that fire suppression has largely have been effective in both chaparral vegetation (Fig. 1, Table 1) and across all vegetation in the lower Applegate watershed (Fig. 2, Table 2). Mean area burned per year after fire suppression was an order of magnitude less than pre-suppression area burned in chaparral and across all vegetation, and fire occurrence (# fires/yr) was reduced five times or more. A review of fire history records for the entire Klamath region, inclusive of the study area as well as six surrounding national forests, revealed a similar trend in reduced area burned post-suppression, though fire occurrence showed no clear trend (Frost and Sweeney 2000). In

the lower Applegate Valley prior to suppression, area burned annually in chaparral, as a proportion of total area, appears to have been similar to annual proportional area burned in the study area as a whole (Table 3). It appears that fire suppression may have reduced area burned and fire occurrence more in chaparral than in the study area as a whole, but it is unclear if this trend is worth interpreting or is simply an artifact of inaccuracies in the fire history records.

Within the study area, fire suppression does not appear to be associated with changes in mean fire size in either chaparral or across all vegetation, contrary to the expectation that fuels accumulation in the absence of fire would result in larger burns in the post-suppression era (e.g., USDI 1998, 2004b). Across the entire Klamath region, average fire size was smaller post-suppression, but trends varied in individual forests as larger fires were more common in some areas but less common in other areas (Frost and Sweeney 2000).

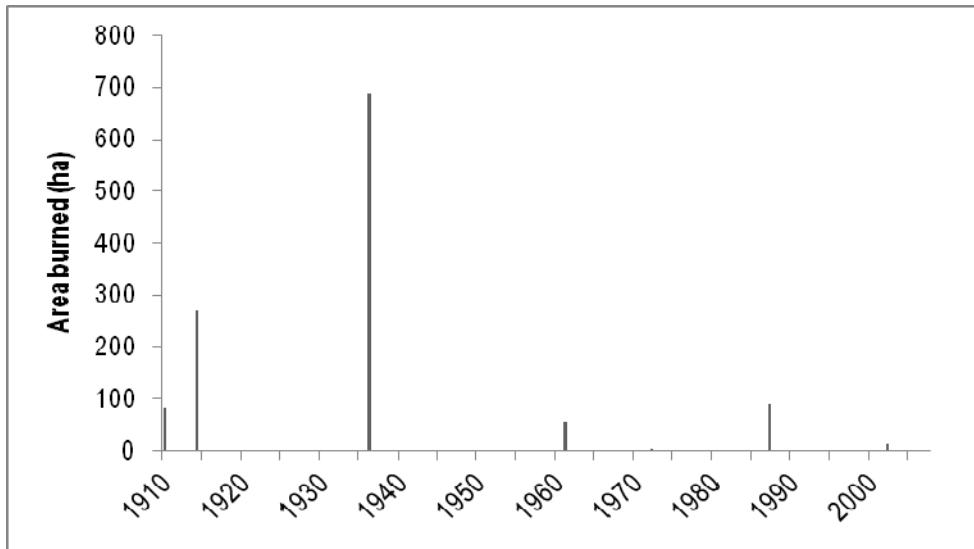


Figure 1. Fire history in chaparral of the lower Applegate Watershed, 1910 – 2007.

Table 1. Comparison of fire history attributes in chaparral of the lower Applegate Watershed before and after 1940, used here as the date when effective fire suppression began.

	Pre-suppression (1910 – 1939)	Post-suppression (1940 – 2007)	Ratio
Mean area burned per yr (ha)	36	2	18 : 1
# Fires per yr	0.8	0.1	8 : 1
Mean fire size (ha)	45	23	2 : 1

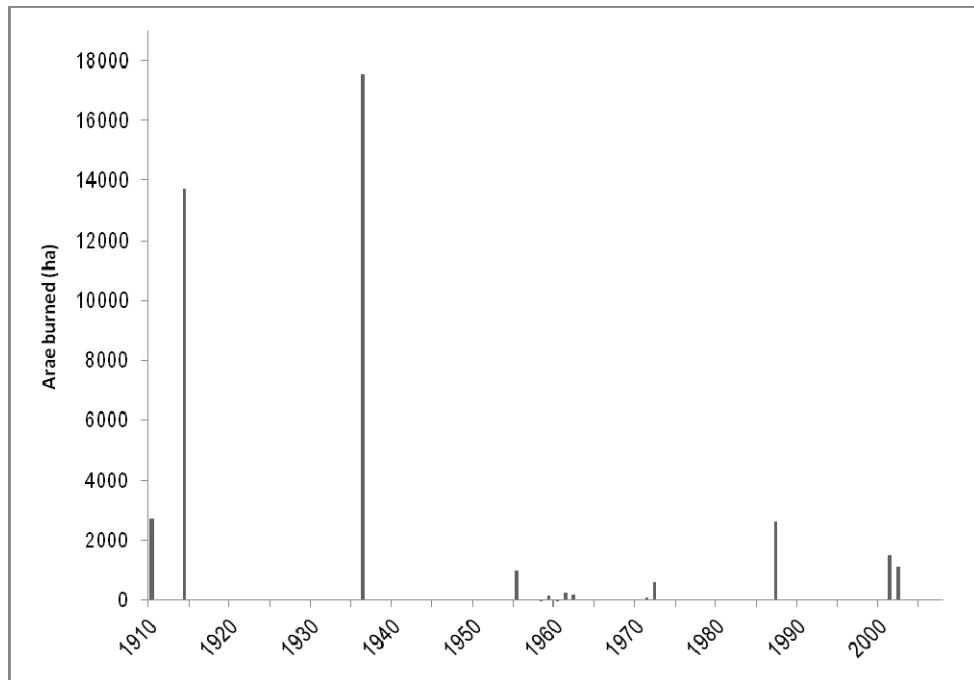


Figure 2. Fire history across all vegetation of the lower Applegate Watershed, 1910 – 2007.

Table 2. Comparison of fire history attributes across all vegetation of the lower Applegate Watershed before and after 1940, used here as the date when effective fire suppression began.

	Pre-suppression (1910 – 1939)	Post-suppression (1940 – 2007)	Ratio
Mean area burned per yr (ha)	1174	114	10 : 1
# Fires per yr	2.0	0.4	5 : 1
Mean fire size (ha)	587	318	2 : 1

Table 3. Comparison of pre-suppression (1910 - 1939) fire history between chaparral and across all vegetation.

	Pre-suppression (1910 - 1939)		Post-suppression (1940 - 2007)	
	Across all vegetation in study area		Across all vegetation in study area	
	Chaparral		Chaparral	
Mean % area of vegetation type burned per yr	2.30	1.16	0.15	0.13
# Fires per yr/area in vegetation type	0.000500	0.000020	0.000070	0.000004

