

Stand Structures of Oregon White Oak Woodlands, Regeneration, and their Relationships to the Environment in Southwestern Oregon

Authors: Gilligan, Laurie A., and Muir, Patricia S.

Source: Northwest Science, 85(2) : 141-158

Published By: Northwest Scientific Association

URL: <https://doi.org/10.3955/046.085.0206>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Stand Structures of Oregon White Oak Woodlands, Regeneration, and Their Relationships to the Environment in Southwestern Oregon

Abstract

Although Oregon white oak (*Quercus garryana*) woodlands are a characteristic landscape component in southwestern Oregon, little is known about their current or historical stand structures. Meanwhile, fuel reduction thinning treatments that change stand structures in non-coniferous communities are ongoing and widespread on public lands in this region; some of these treatments also have restoration objectives. Managers need baseline information on which to base prescriptions that have a restoration focus. We inventoried 40 Oregon white oak dominated woodlands across two study areas in southwestern Oregon, and describe here their stand characteristics and age structures. We assessed whether these varied systematically with site conditions or recorded fire history. Stands included various proportions of single- and multiple-stemmed trees and a range of tree densities and diameter- and age-class distributions. Variables that may indicate site moisture status were weakly associated with multivariate gradients in stand structure. Peak establishment of living Oregon white oaks generally occurred during 1850-1890, sometimes occurred in the early 1900s, and recruitment rates were low post-fire suppression (~1956). Recruitment of sapling-sized oak trees (<10 cm diameter at breast height, ≥ 1.3 m tall) was generally low and their ages ranged from 5 to 164 yr; they were not necessarily recent recruits. The observed wide range of variability in stand characteristics likely reflects the diversity of mechanisms that has shaped them, and suggests that a uniform thinning approach is unlikely to foster this natural range of variability.

Introduction

Woodlands dominated by Oregon white oak (*Quercus garryana*, also known as Garry oak) are characteristic of southwestern Oregon (Franklin and Dyrness 1973), yet their history and successional dynamics are largely unknown, challenging to study, and subject to debate (Agee 1993, Hosten et al. 2006). Some woodlands may be naturally occurring ecotones between mixed conifer forests and more xeric ecosystems such as grasslands, shrublands, or savanna (Wilson and Carey 2001, Hosten et al. 2006). In these, variations in Oregon white oak canopy cover and distribution are caused by disturbances, successional dynamics, and environmental factors such as edaphic limitations (Stein 1990, Murphy 2008). Dense oak woodlands in particular may be the product of decades of fire suppression that permitted atypically dense tree ingrowth into historical prairie or savanna (Thilenius 1968, Fritschle 2008). In the absence of fire, fuel loads may be unusually high, and may pose an increased risk of uncharacteristically high severity wildfire and conversion to a state that will not favor the long-term persistence of Oregon white oak populations (Reed and Sugihara 1987). Historical records provide

support for both long term oak woodland perpetuation and for transitions in vegetation cover from prairie, savanna, and shrubs (occasionally with scattered, open grown conifers) towards woodland and from woodland towards conifer-domination (e.g., Hickman 2005, Hosten et al. 2007b). To further complicate understanding of oak woodland history and dynamics, relatively recent anthropogenic disturbances and vegetation succession can mask effects of Native American management practices such as burning, acorn collection, pruning, and cutting (McCarthy 1993, Boyd 1999).

In addition to being characteristic landscape components, Oregon white oak ecosystems are valued because they support unique habitats, extraordinary biodiversity, and many species-at-risk (Whittaker 1960, Chiller et al. 2000, Fuchs 2001). However, many Oregon white oak communities across the species' range from British Columbia to northern California are declining and at risk of local extirpation without active management, due to anthropogenic influences and regeneration difficulties (Muick and Bartolome 1987, Thysell and Carey 2001, Gedalof et al. 2006). Concern about the decline of these valuable and threatened ecosystems has prompted woodland restoration efforts based on a model of assumed pre-European settlement stand structures, which were presumably heavily affected by a Native

¹Author to whom correspondence should be addressed. Email: laurie_gilligan@hotmail.com

American influenced regime of frequent low-severity fires that left widely-spaced trees (USDI 1998).

On southwestern Oregon public lands, fuels reduction treatments that remove shrubs and smaller diameter trees alter the current structure of oak woodlands. These treatments are often driven by the dual-directive to reduce the threat of severe wildfire in the wildland-urban interface and accomplish restoration (USDI 2007). To evaluate whether the fuels treatments are likely to restore historical oak woodland stand structures, however, more information is needed on their historical and current structures and the factors that influence them. Investigations of factors that influence non-coniferous stand structures, however, have largely been concentrated in regions other than southwestern Oregon (e.g., Tveten and Fonda 1999, Erickson 2002, Dunwiddie et al. 2011), or have focused primarily on relationships between the environment and plant associations rather than on stand structures and their drivers (Riegel et al. 1992, Atzet et al. 1996, Pfaff 2007a). To inform management and restoration objectives for Oregon white oak woodlands in southwestern Oregon, baseline data on current stand structures and regeneration status are required.

The primary objectives of this study were to characterize oak woodland stand structures in southwestern Oregon, assess which environmental and disturbance factors are related to those structures, and investigate apparent changes in structure over time by examining tree age and size distributions. We posed five specific questions: (1) What tree and stand structures characterize Oregon white oak-dominated woodlands and how do these vary over the landscape? (2) Do current stand structures relate systematically to environmental conditions? (3) Are stand structures and age structures related and, if so, how? (4) What is the status of Oregon white oak regeneration in the sampled stands and does it vary systematically with environmental conditions? (5) Do age and size distributions suggest that disturbance regimes in oak woodlands changed after European settlement or after fire suppression? We provide new information on the condition, environmental associations, and history of Oregon white oak populations in a little studied portion of their range. Results fill fundamental gaps in knowledge of Oregon

white oak woodlands and can inform the development of regionally-specific models for their management.

Study Area

Our study took place within the interior valleys and foothills of two areas in southwestern Oregon's Jackson County: Butte Falls Resource Area and the Applegate Valley within the Medford BLM district's Ashland Resource Area (Figure 1). These study areas are located

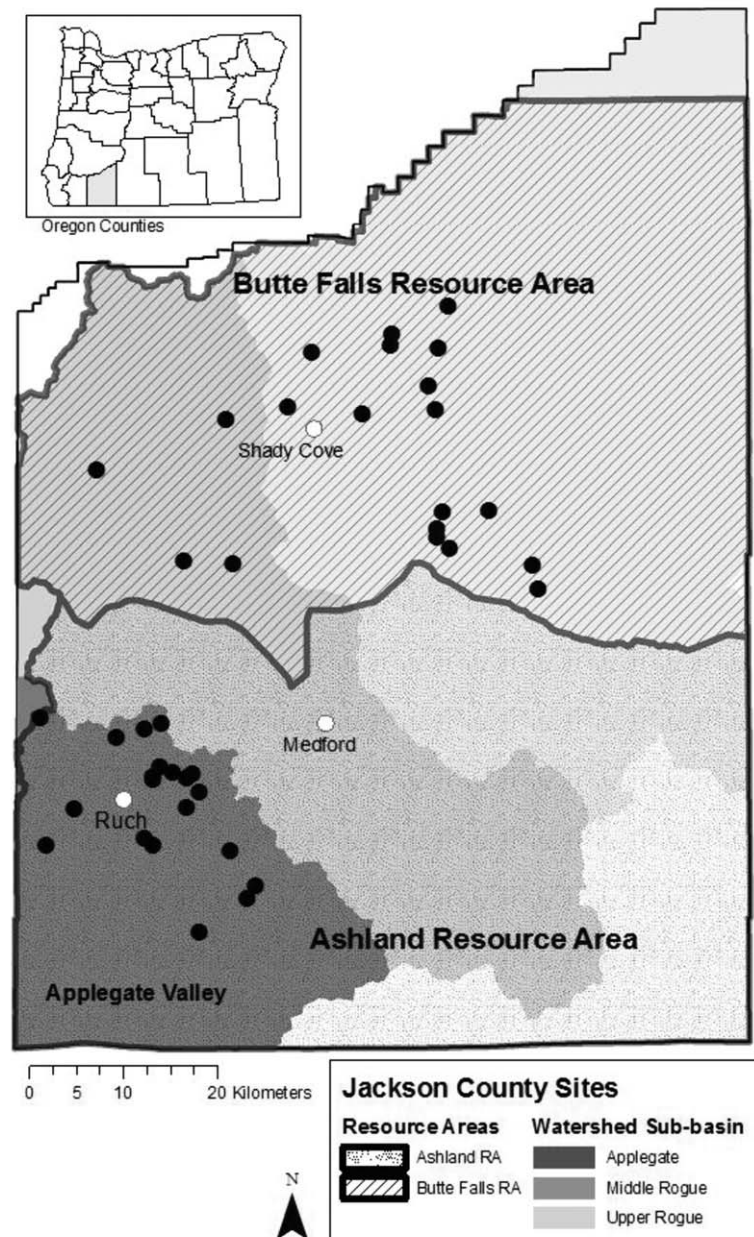


Figure 1. Study area in Jackson County, southwestern Oregon. Study sites are represented by circles and are located in Applegate Valley of the Ashland Resource Area and in the Butte Falls Resource Area, on USDI BLM land.

in the biologically diverse Klamath-Siskiyou ecoregion, and host a patchy mosaic of plant community types ranging from conifer-dominated, to oak savannas and woodlands, chaparral, and grassy openings (Hosten et al. 2006). The regional vegetation zone is classified as Interior Valley pine-oak-Douglas-fir (*Pinus-Quercus-Pseudotsuga*) (Franklin and Dyrness 1973). The climate is temperate Mediterranean with cool, moist winters and warm, dry summers.

Native Americans inhabited this area for thousands of years prior to Euro-American settlement. Following settlement, an array of novel anthropogenic disturbances such as mining, grazing, farming, and introduction of exotic species occurred. Although site-specific historical data on most individual disturbances are lacking, temporal patterns in oak recruitment in the overall study area may have been particularly affected by the following events. Completion of the Applegate Trail in 1846 opened a passage for steady Euro-American settlement (Lawrence 1971). Following the end of the Rogue River Indian Wars in the 1850s, most surviving Native Americans were displaced away from this region, as settlement populations boomed and land uses shifted (Boyd 1999a). Ethnographic accounts of Native American burning practices in this region are sparse compared with depictions of the practices of other northwest Native American tribes (Boyd 1999a). Limited anecdotal interviews suggest that fires were set as often as annually in the more productive valleys; in the mid-elevation mountains, fires were less frequent, more localized, and more often attributed to lightning than to Native Americans (Boyd 1999a). Our study sites in the foothills were likely influenced by both valley and mid-elevation fire dynamics. It is quite certain that Euro-American settlers used fire extensively immediately following settlement, and their burning practices were likely more widespread and indiscriminate across vegetation types and seasons than were those of the Native Americans (LaLande 1995, Boyd 1999a). However, reductions in Native American burning may have occurred in the 1770s or earlier, as introduced infectious disease decreased Native American populations (Boyd 1999b). Fire suppression policies began in the early 1900s, and mechanized fire suppression was initiated in 1920, when helicopters were used to scout for wildfires (Pyne 1982). However, fire suppression efforts are unlikely to have substantially affected wildfire behavior in the area until fire-fighting technology advanced in the mid-1900s, and specifically when airplanes began dropping fire retardant in 1956 (Pyne 1982, Frost and Sweeney 2000).

The Applegate and Butte Falls study areas were chosen to investigate similarities and differences among oak woodlands across a range of site conditions in southwestern Oregon and to expand upon previous vegetation studies in non-coniferous ecosystems within the region's wildland-urban interface (e.g., Hosten et al. 2007b, Pfaff 2007a, Perchemlides et al. 2008, Sikes and Muir 2009, Duren and Muir 2010). Study sites were spread over a 68 x 53 km area.

The Applegate Valley study sites are located in and around the unincorporated community of Ruch (42°14' N, 123°2' W). Long-term mean annual temperature is 11.5 °C and mean annual precipitation is 646 mm (Western Regional Climate Center [WRCC] 2009). Butte Falls sites are near the city of Shady Cove (42°32' N, 123°33' W). Long-term mean annual temperature from the closest weather station (Lost Creek Dam) is 11.5 °C and mean annual precipitation is 853 mm (WRCC 2009). Several soil types occur in both study areas, although sandy and silty loams are more common in the Applegate sites, and most Butte Falls sites have soils with a clay or cobbly clay component (Johnson 1994).

Methods

Study Site Selection and Plot Layout

We planned to sample Oregon white oak woodlands on 20 sites in each resource area in summer, 2008 (Figure 1). These oak woodlands, in contrast to savannas and forests, were defined as community types where Oregon white oak was the dominant woody species and tree canopy cover was $\geq 25\%$. We randomly selected site locations in the two study areas with the GIS extension Hawth's Analysis Tools (Beyer 2004) using GIS layers that identified Oregon white oak-dominated vegetation (Ecoshare 2008, Pfaff 2007b), stratified across 16 soil types to represent the range of soils on which these oak communities occur and constrained to avoid known disturbances such as fuels treatments or logging. Reliable short or long term data on livestock grazing history are not available; it is likely that most or all sites had experienced grazing at some time. If the location identified using the pre-selected GPS coordinates was too small to contain a plot, or did not meet the oak woodland community type criteria and sampling constraints (if sites landed in fuels-treated areas with outdated map boundaries, or if signs of logging were evident) in the field, the site was relocated to the nearest oak woodland patch of sufficient size, and sampling was centered on a randomly chosen point within the woodland patch. The forty study sites encompassed

all aspects and a wide range of topographic positions (396 – 1257 m in elevation, slopes of 4 – 80%), and supported woodlands ranging from 25-85% canopy cover. After data collection, it was determined that four sites (three from Applegate, one from Butte Falls) may have experienced a prescribed burn within the previous 9 yr, and that two of these sites may also have experienced a hand-cut pile and burn fuels treatment. Data from these sites were excluded from most analyses but were retained for Oregon white oak tree age predictions. There were recorded wildfires (back to 1910) for many sites, but wildfires were recorded for only two sites after 1936.

One stand was sampled on each site using: (1) a “large plot” (the stand) for recording presence/absence of relict trees visible from the stand’s center; (2) a circular 0.1 ha plot in which tree, sapling, and shrub data were recorded; and (3) three randomly located 0.033 ha subplots nested within each 0.1 ha plot in which data on seedling-sized tree regeneration were recorded. Relict trees were defined as having a size and form indicative of open-grown conditions and establishment before European settlement, with a large diameter at breast height (dbh; 1.3 m), low-to-ground large limbs present or evident from branch stubs, and a broad crown.

Stand Structure Data

Relict tree data included frequency (0-4; number of large plot quadrants in which relicts occurred) and a constrained relict count (0-8; number of relicts visible in each large plot quadrant, up to a maximum of two per quadrant; this constraint avoided inflated counts on relatively open sites where more relicts could be seen). In the 0.1 ha plot, we visually estimated percent cover of trees and shrubs at life form and species levels from plot center. We recorded data on trees (≥ 10 cm dbh), including species, dbh, height, height to base of live crown, multiple-stem number (count of stems per tree separating at or below ground level), and health (3 = tree healthy, 2 = unhealthy, 1 = nearly dead, 0 = dead). The smallest and largest living trees (≥ 10 cm dbh) of each conifer species, when present, were cored at a height of 1.3 m to provide insight into conifer recruitment in these oak woodlands. Sapling data included number of stems, species, and height for all live tree species ≥ 1.3 m tall and < 10 cm dbh. In the regeneration subplots, we recorded the species and number of stems for regeneration (all living tree species < 1.3 m tall), and tallied separately the number of Oregon white oak regeneration stems that occurred

under and outside of Oregon white oak tree driplines. Because the distinction between seedlings and sprouts was often not clear, they were lumped as seedling-sized regeneration.

Additional data were recorded on Oregon white oaks only. A subsample of 6-10 living Oregon white oak trees per plot, selected to represent the range of tree (≥ 10 cm dbh) sizes in each stand, were cored at ca. 0.8 m with an increment borer to determine tree age. The largest stem of multiple-stemmed trees was cored. We cored all stems from five multiple-stemmed trees across three sites to estimate the age range encompassed by multiple stems of the same tree. Six stands from each study area, selected to span the range of Oregon white oak sapling densities observed across all stands that supported saplings, were revisited in the summer of 2009. At that time, all (or a maximum of 10, when more than 10 were present) Oregon white oak saplings (≥ 1.3 m tall and < 10 cm dbh) that occurred within the 0.1 ha center plot in each stand were cored at 0.8 m or cut at ground-level for aging, and their heights and dbh were measured. The smallest diameter sapling was sampled, and the remaining sampled saplings were selected randomly when > 10 saplings were present.

Environmental attributes recorded onsite included slope, aspect, elevation, topographic position, and evidence of fire or other disturbance. Environmental variables compiled from GIS layers included: parent geology; soil type, texture and depth; mean spring precipitation (March – May total, mm); recorded fire years (back to 1910), and presence or absence of recorded fires (USDA NRCS 2009, Oregon Geospatial Enterprise Office 2009, Pfaff 2007a).

Increment Core and Cross Section Preparation

Cores were glued onto grooved wood, belt-sanded using coarse grit, and finished with a 400 or 600 grit paper hand-sanding as needed. We counted annual rings using a binocular microscope (up to 40x). When a core missed the tree pith, the number of missing rings was estimated based on the average width of the most interior visible 5–10 annual rings, using a transparency overlay of similar ring widths that lined up with the tree core’s ring curvature (Villalba and Veblen 1997). Minimum age was recorded for tree cores that did not hit center due to rot. Age counts with relatively high uncertainty due to very small rings, rot, or anomalies such as multiple piths were not used to create equations for predicting ages of uncored trees (see below), but were used for calculating stand age structure parameters.

Statistical Analysis

Patterns in Stand Structure – To examine patterns in oak woodland stand structure across all sites, and their relationships to environmental attributes or disturbance history, we used nonmetric multidimensional scaling ordination (NMS; Kruskal 1964, Mather 1976). Attributes measured at the individual tree or shrub level were converted to plot means to characterize overall stand structures in a 26-variable matrix. Stand structure variables were square root or log transformed if their skew was > 1 and if transforming decreased the skew (McCune and Grace 2002). Values for each variable were relativized by their standard deviate.

One stand was identified as an outlier (mean plot distance > 2 standard deviations from the grand mean) in the 36-stand analysis. Deleting the outlier from the analysis had little effect on the relative positions of stands in stand structural space and there was high heterogeneity among stands, such that the initial outlier deletion produced new outliers in the following analyses. Because of these consequences and because the individual stand variables were not ecologically anomalous, the outlier was retained in analyses.

A secondary matrix included 17 environmental and disturbance history variables for each site. Variables included resource area, mean spring precipitation, elevation, heat load (McCune 2007), topographic position, shrub cover, mean shrub basal diameter, soil textures and depth, soil type, parent geology, vegetation cover type, fire occurrence history ($=0/1$, back to 1910; sites with no recorded fire but with externally visible fire scars or charcoal on at least one tree also $=1$), years since wildfire (back to 1910), and distance from nearest road. Topographic positions were ranked by mesoslope position and degree of protection, with the gradient ranging from bottomlands ($=1$) to draws, slopes, and exposed ridgetops ($=8$) (modified from Whittaker 1960).

The NMS ordination was carried out using PC-ORD v. 6.93 beta (McCune and Mefford 2009) with a random starting configuration in the conservative “slow and thorough” autopilot option. We used Euclidean distance because there were negative numbers in the data set. The ordination solution was orthogonally rotated to maximize correlations between stand structural axes and the environmental and disturbance variables, using the number of dimensions recommended by PC-ORD. We investigated relationships between gradients in stand structure and environmental and disturbance variables using Pearson’s r correlation coefficients and visual overlays.

Tree Age Predictions—To describe age structures of living trees, assess their relationships to stand structure, and make inferences about stand history, ages were predicted for non-cored and partially cored Oregon white oak tree stems using nonparametric multiplicative regression (NPMR; McCune 2006; implemented in Hyperniche v. 2.60 [McCune and Mefford 2008]; n stems = 1748; n = 994 in Applegate, n = 754 in Butte Falls) with tree and environmental data as potential predictors. NPMR does not make assumptions about the shape of the response variable, allows for multiplicative interactions between predictors, and thus was useful for evaluating the importance of tree and environmental predictors potentially associated with tree age. We used scatterplots to examine relationships between candidate predictor variables and known tree ages, choosing variables for potential inclusion in the NPMR analysis if the scatter appeared non-random. Variables with skew > 1 were log-transformed if transforming decreased the skew (McCune and Grace 2002).

Site-level variables chosen for potential tree age predictor matrices included resource area, spring precipitation, heatload, percent tree cover, and tree cover type (*open oak* – total tree cover $< 50\%$, Oregon white oak $< 50\%$, ponderosa pine (*Pinus ponderosa*) $\leq 10\%$; *oak woodland* – Oregon white oak cover $\geq 50\%$, ponderosa pine $\leq 10\%$; *mixed oak* – total tree cover $\geq 50\%$, non-Oregon white oak trees $> 10\%$; and *oak-madrone* – total tree cover $\geq 50\%$, madrone (*Arbutus menziesii*) $\geq 20\%$; cover types were delineated in the field). Variables at the plot-level included stand stem density (of all tree species), sapling density (of all tree species), mean live crown ratio (live crown length/tree length), mean Oregon white oak dbh and height (both log-transformed), and mean number of multiple-stems/tree. Variables at the individual-tree level included number of stems, log(tree height), log(dbh), and crown ratio. Due to age variation between stems of the same tree, ages for multiple-stemmed trees were predicted at the stem-level (rather than tree-level). The response variable was (log)age.

We developed age prediction models for each resource area separately because these were more powerful than a combined model. Age models were built using tree cores with known ages and confident counts (using adjusted counts from transparency overlays if the core narrowly missed the pith); $n = 117$ trees for model building from Butte Falls and 106 trees from Applegate. Butte Falls model building also included one partial age from the oldest cored tree (> 429 yr) to guide extrapolated age predictions. No high quality cores were in the 400-yr

range and no complete cores from the Applegate approached that age. The local-linear model setting with default minimum neighborhood sizes was selected because it enabled more accurate estimates of both old and young trees. Selected models optimized the xR^2 , a measure of the residual to total sum of squares similar to the conventional R^2 statistic with “leave-one-out cross-validation,” which calculates sums of squares excluding the data point used to estimate the response at its respective point. Models were assessed for statistical significance with 100 runs of a randomization test, and then applied to predict ages of all non-cored Oregon white oak trees ≥ 10 cm dbh.

We compared known age counts to those predicted by the model; mean absolute residuals were 9 yr in the Applegate and 12 yr in Butte Falls (with 9% and 16% of error > 20 yr for the two study areas, respectively). Potential error of predicted ages was also examined with a separate validation data set from tree cores that did not reach the pith and whose counted ages thus were minimum ages. For these, models should have predicted an age older than counted, and this was true for 80% of predicted ages from the Applegate and for all predictions from Butte Falls. For the Applegate trees, underestimates ranged from 1–58 yr lower than minimum counts, with a median of 9 yr. The error is similar to those indicated by the model residuals, but actual prediction error may be larger if the minimum age estimates from trees whose core did not reach the pith are in fact substantially younger than actual ages. In particular, old trees often had larger residuals in the NPMR models than did younger trees. This probably resulted at least in part from having few tree cores to predict ages of old trees, due to rot. Thus, ages of trees predicted to be > 200 yr are less certain than those for younger trees, and are probably disproportionately underestimated. Nevertheless, they probably established before Euro-American settlement. Predicted tree ages are useful for broad characterizations of age structure and dynamics, but are not at a resolution that enables discerning regeneration dynamics within a few years.

Stand Age Structures, Regeneration, and Changes over Time—When predicted ages were less than counted ages for trees with partial cores, the counted age was used in age structure analyses. We grouped trees in 20-yr age bins; this resolution was appropriate given error rates associated with age predictions. Oregon white oak tree age structures (based on actual and predicted ages) were summarized into types for descriptive purposes and to provide insights into stand dynamics; these structures were illustrated graphically. Six years were added to

counted or predicted ages (if cored at 0.8 m), based on the mean number of years required for saplings to reach the core height of 0.8 m (Gilligan 2010). While ages for most saplings were not available, and could not be predicted satisfactorily based on our relatively small sample of sapling ages and available data, it was important to include sapling-sized individuals in age structure reconstructions. We did this by assessing the continuity of sapling heights and dbhs (when recorded) and by incorporating available sapling ages. Two sapling height groups (≤ 4 m and > 4 m) were included in age structure graphs, to facilitate a coarse assessment of their contribution to age structures and dynamics.

We examined apparent changes in Oregon white oak stand age structures over time by categorizing proportions of surviving trees that established in various time spans: pre-1851 (largely pre-Euro-American settlement); from 1851 until 1956 (post-Euro-American settlement, pre-aerial fire retardant application and effective fire suppression); and 1956 or later (post-effective fire suppression).

We used sapling to tree ratios (S:T) to examine apparent levels of Oregon white oak regeneration for each stand. Use of such ratios is based on the assumption that sapling-sized oak trees (≥ 1.3 m and < 10 cm dbh) are younger than larger trees (White 1966, Lathrop and Arct 1987). Although some sapling-sized individuals were as old as individuals ≥ 10 cm dbh (see Results), the ratios nevertheless may provide coarse insights into levels of stand regeneration (Muick and Bartolome 1987). Regeneration levels were classified from very low to high, using the following categories (after Muick and Bartolome 1987): very low, $S:T \leq 0.1$; low, $0.1 < S:T < 0.5$; medium, $0.5 \leq S:T < 1$; high, $S:T \geq 1$. Ratios are based on a definition of “tree” that includes both single- and multiple-stemmed individuals.

Results

Tree and Shrub Species Composition

The 36 sampled oak woodlands had tree cover ranging from 25–85% with Oregon white oak cover ranging from 15–70%. Ponderosa pines were commonly associated with Oregon white oaks, occurring in 69% of stands; the oldest sampled ponderosa pine was 175 yr at dbh. Douglas-fir (*Pseudotsuga menziesii*) occurred in 58% of stands, across the full range of precipitation levels and soil depths. The oldest sampled Douglas-fir was 125 yr at dbh. Oregon white oak comprised $>95\%$ of tree cover in 17 stands, while in other stands, other hardwoods were codominant with Oregon white oak.

California black oak (*Quercus kelloggii*) occurred in 47%, madrone in 36%, and incense-cedar (*Calocedrus decurrens*) in 17% of stands.

All stands supported shrubs, with shrub cover ranging from 2–75%. Poison oak (*Toxicodendron diversilobum*) was the most common shrub species, occurring in 81% of stands with a mean cover of 13% when present. Other commonly occurring shrub species in descending frequency of occurrence (from 69–22% of stands) included whiteleaf manzanita (*Arctostaphylos viscida*), buckbrush ceanothus (*Ceanothus cuneatus*), birchleaf mountain mahogany (*Cercocarpus betuloides*), deerbrush (*Ceanothus integerrimus*), Saskatoon serviceberry (*Amelanchier alnifolia*), and hollyleaved barberry (*Mahonia aquifolium*).

Patterns in Stand Structures and Relationships to Environment

Stand structures ranged widely across sampled stands (Table 1). The inventory included 2547 tree- and 969 sapling-sized individuals. Stands included variable proportions of single and multiple-stemmed Oregon white oaks; 28% of Oregon white oak trees across all size classes were multiple-stemmed, 10% ≥ 30 cm dbh were multiple-stemmed, and none ≥ 50 cm dbh were multiple-stemmed. Oregon white oak diameters ranged widely across stands; one stand had none > 13 cm dbh, in another all were ≥ 16 cm, and the largest across all stands was 73 cm. Ten stands had no relict trees within the 0.1 ha plot, and four of those had no relicts in sight.

NMS ordination revealed two strong and interpretable gradients in stand structure across all stands, along with a third but weaker gradient. The ordination had a 3-dimensional solution, final instability < 0.0001 , and all randomized runs with stress $<$ observed stress ($P = 0.004$, Monte Carlo tests with 250 runs). The ordination accounted for 88.5% of the variability in stand structure data (final stress = 11.1; 64 iterations).

A strong structural gradient along Axis 2, which represented 33.7% of variability in the data, was proportion of the stand in small versus large dbh classes (Figure 2, Table 2). Stands with relatively high proportions of Oregon white oaks in smaller dbh classes and higher sapling densities, and higher stand densities (# of tree + sapling stems)

TABLE 1. Stand structure attributes for trees and saplings across sampled stands ($n = 36$ stands, 2547 trees and 969 saplings).

Stand Structure Attribute	Min.	Max.	Mean
Stem density (tree+sapling stems ha^{-1})	150	1810	990
Tree density (ha^{-1})	90	1100	711
Tree basal area ($\text{m}^2 \text{ha}^{-1}$)	4.5	42.4	19.5
QUGA sapling density (ha^{-1})	0	560	150
QUGA relict tree density ^a (ha^{-1})	0	60	21
QUGA height (tree+sapling, mean, m)	5.1	9.1	7.4
QUGA % multi-stemmed trees	0	66	28

Species code QUGA = *Quercus garryana*.

^aRelict mean is for stands where relicts were present.

and cover were towards the low end of Axis 2; stands with relatively high proportions of Oregon white oaks in larger dbh classes, abundant relicts, and lower stand densities and cover were towards its upper end.

Axis 3 (41.4% of the variance in the data) grouped stands with lower proportions of multiple-stemmed but

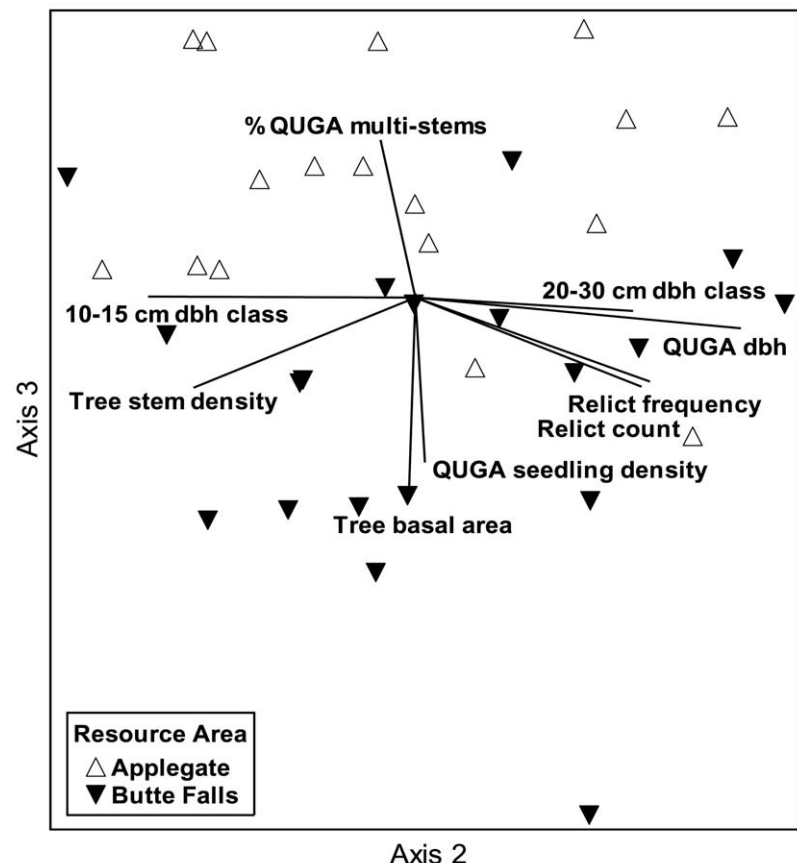


Figure 2. NMS ordination of all plots (triangles) in stand structural space (2 of 3 dimensions shown). Vectors represent the strongest gradients ($r^2 \geq 0.4$) in stand structure along Axes 2 and 3. QUGA = *Quercus garryana*. See Table 1 for variable definitions and units.

TABLE 2. Correlation (Pearson's r) of stand structural and environmental variables with NMS ordination axes. Correlations with stand structural or environmental variables are reported if $|r| \geq 0.45$ with one or more axes (in bold).

	Axis 1	Axis 2	Axis 3
% variance explained by axes	13.4%	33.7%	41.4%
Environmental or structural attribute			
Soil silt (%)	-0.27	-0.36	0.59
Stand stem density (tree+sapling stems ha ⁻¹)	0.18	-0.73	-0.47
Tree cover (across species, %)	0.16	-0.51	-0.53
Tree basal area (m ² ha ⁻¹)	-0.15	-0.12	-0.67
Tree height (mean, m)	0.56	-0.02	-0.59
QUGA tree density (trees ha ⁻¹)	-0.57	-0.37	-0.19
QUGA cover (trees+saplings+regeneration, %)	-0.54	-0.21	-0.42
QUGA tree height (mean, m)	0.36	0.14	-0.57
QUGA tree mortality (% dead)	-0.14	0.44	-0.45
QUGA # stems/tree (mean)	-0.21	-0.30	0.60
QUGA % multi-stemmed trees	-0.25	-0.29	0.63
QUGA sapling height (mean, m)	0.56	-0.32	-0.14
QUGA sapling density (saplings ha ⁻¹)	0.49	-0.58	-0.39
Sapling:Tree	0.70	-0.22	-0.24
PSME saplings (%)	0.59	-0.17	-0.33
PSME tree mortality (% dead)	0.18	-0.23	-0.48
QUGA seedling-sized regeneration density	-0.12	0.15	-0.64
Tree health score (mean)	0.04	0.07	0.58
QUGA % in 10-15 cm dbh size class	0.50	-0.81	0.05
QUGA % in 15-20 cm dbh size class	-0.64	0.43	0.04
QUGA % in 20-30 cm dbh size class	-0.40	0.73	-0.18
QUGA % in 30-40 cm dbh size class	0.04	0.58	-0.16
QUGA % in 40+ cm dbh size class	-0.13	0.57	-0.42
QUGA tree dbh (mean, cm)	-0.35	0.89	-0.27
Relict tree frequency	-0.09	0.76	-0.46
Relict tree constrained count	-0.19	0.74	-0.47

Species codes: QUGA = *Quercus garryana*, PSME = *Pseudotsuga menziesii*. Tree health was scored from 3-0 (3=healthy, 2=unhealthy, 1=nearly dead, 0=dead). PSME % sapling value compared number of PSME saplings to sum of QUGA and PSME saplings. QUGA seedling-sized regeneration density units = stems/0.01 ha.

relatively tall trees, lower tree health values, and higher Oregon white oak seedling-sized regeneration densities towards the low end of the axis. Stands located lower on Axis 3 also had relatively high basal areas, tree cover, stand densities, Douglas-fir mortality, and more abundant relicts. Although the two study areas were intermixed along this gradient, stands from the Applegate generally fell higher on Axis 3 than those from Butte Falls. Axis 1 (represented 13.4% of variability in the data) described a gradient from higher to lower Oregon white oak tree densities and percent cover, increasing sapling to tree

ratios and Douglas-fir sapling relative densities, and taller Oregon white oak saplings.

Percent soil silt was the only environmental variable strongly correlated with patterns in stand structure across study areas ($r = 0.59$ with Axis 3; Table 2, maximum $|r|$ for other variables = 0.40). Correlations of other environmental variables with Axis 3 were weaker, but collectively appeared to reflect xeric and harsher conditions in the Applegate than in Butte Falls. Higher elevations, more exposed topographic positions, higher percent soil sand, and shallower soils were all

positioned higher on Axis 3; and in contrast, higher precipitation levels were positioned lower on Axis 3.

Stand Age Structures and Changes Over Time

Tree Ages—Counted ages of Oregon white oak trees (≥ 10 cm at dbh) ranged from 59 to over 429 yr (minimum age for the oldest tree, which was not cored to pith). True ages beginning at establishment/sprout date could be substantially older than reported ages if seedlings or sprouts were browsed or did not have a single dominant stem dating to establishment (Hibbs and Yoder 1993). Cores from 223 trees yielded nearly complete counts to pith. Using transparencies, we estimated ≤ 1 additional yr for 46% and ≤ 10 additional yr for 95% of these cores. Cores from 57 trees ($n = 40$ in Applegate, $n = 17$ in Butte Falls) yielded partial age counts due to heart rot. The age range for multiple-stems that appeared to represent a single tree was from 3–50 yr. Although many of these stems probably originated from basal sprouts, some might have originated from animal caches; these were not distinguished by our methods.

The mean age count for Oregon white oaks in the smallest tree dbh class (10.0–10.9 cm) was 113 yr. This class, however, included trees that ranged from 59 to 162 yr old (Figure 3). Thus, the presence of sapling-sized individuals (< 10 cm dbh) in a stand does not necessarily indicate recent regeneration. Therefore, ‘successful’ and ‘moderate’ regeneration levels (as described by high or medium S:T ratios, below) should be interpreted cautiously.

Approximately 75% of sampled Oregon white oak trees were between 10–20 cm dbh. The median 1-cm dbh class encountered across all sites (15–15.9 cm) had a similar counted age range (84–150 yr) to that of 10.0–10.9 cm dbh trees. All trees ≥ 40 cm dbh whose ages could be counted to the pith were > 200 yr, but trees in the 30–40 cm dbh class included both younger (≥ 137 yr), and older trees (> 200 yr).

Sapling Ages—Ages of cored Oregon white oak saplings ($n = 85$; ≥ 1.3 m tall, < 10 cm dbh) spanned from 8–164 yr. The mean sapling age was 83 yr; this mean is probably low because sampling deliberately included the single smallest diameter sapling per site. Aged saplings > 4 m tall established prior to pre-estimated fire suppression (1956), but saplings ≤ 4 m established across a broader range of years (both pre- and post-fire suppression). In 10 of the 12 stands in which saplings

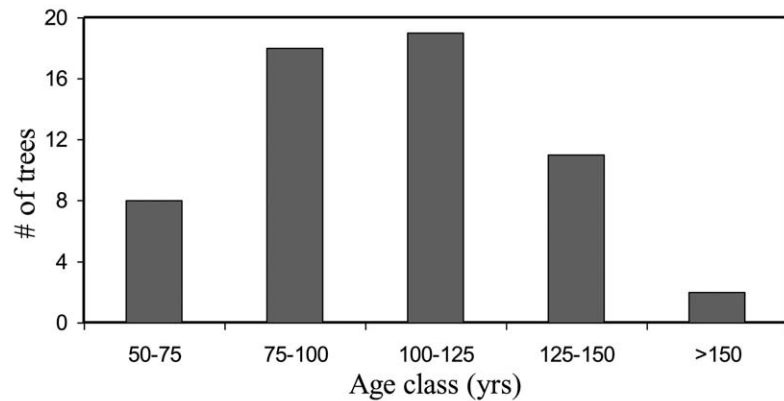


Figure 3. Age class distribution of small (10.0–10.9 cm dbh) cored Oregon white oak trees ($n = 58$).

were aged, at least one sapling was younger than the sampled Oregon white oak trees, but only half had saplings with establishment dates after 1956. Sapling ring widths were often narrow in the sapwood; as many as 70 annual rings/cm were common.

Regeneration—Oregon white oak seedling-sized regeneration (individuals < 1.3 m tall) occurred in all stands. Most Oregon white oak seedling-sized regeneration occurred under an Oregon white oak drip line (92% of 1707 stems). Douglas-fir regeneration (seedlings) occurred in eight stands, of which seven also supported Douglas-fir saplings.

Nearly two-thirds of stands (23 of 36) had low or very low Oregon white oak sapling to tree ratios (Table 3). Ratios in half of the Applegate stands were in the very low category. Even though S:T ratios are based solely on dbh and some saplings were as old as trees, they probably give a rough approximation of age class ratios; there was a strong positive correlation between dbh and age for Oregon white oak saplings across study areas (NPMR; $xR^2=0.80$, $P \leq 0.01$).

Tree Age Predictions from Stand Structural Variables—NPMR successfully predicted ages for non-cored and

TABLE 3. Oregon white oak regeneration levels indicated by sapling to tree (S:T) ratios (after Muick and Bartolome 1987), broken down by study area. Data are numbers of stands. The four stands that may have experienced prescribed burning or manual thinning within the 9 yr prior to sampling are excluded from these data.

Regeneration level	S:T	Applegate Valley	Butte Falls	Total
Very low	$S:T \leq 0.1$	8	3	11
Low	$0.1 < S:T < 0.5$	5	7	12
Medium	$0.5 \leq S:T < 1$	2	4	6
High	$S:T \geq 1$	2	5	7

TABLE 4. Nonparametric multiplicative regression age prediction models for each study area.

Study Area	Applegate	Butte Falls
Cumulative xR^2	0.79	0.81
Average N^*	6.4	6.1
Min. model N^*	5.3	5.8
Min. estimate N^*	1.3	1.5
Tolerances		
Dbh (log, cm)	0.215	0.187
Mean # of stems/tree	0.340	0.090
Heat load	3.32	-
Spring precipitation	-	10.0
Tree cover (%)	9.00	-
Stand stem density (stems ha^{-1})	-	18.5
Sensitivities		
Dbh (log, cm)	0.44	0.38
Mean # of stems tree $^{-1}$	0.43	0.18
Heat load	0.73	-
Spring precipitation	-	0.36
Tree cover (%)	0.58	-
Stand stem density (stems ha^{-1})	-	0.24

Tolerance = the range of predictor space from nearby predictor values used to estimate response; predictors with narrow tolerances do not have an evenly linear relationship through range; predictors with broad tolerances have either strong linear relationships or smaller effects on model. Sensitivity = the magnitude of change in response value from changing a predictor value; if a shift in predictor causes a shift in the response of equal magnitude on average, sensitivity = 1. N^* = Neighborhood size of data points to predict response. Mean # of stems/tree is of Oregon white oaks, and tree cover and stem density refer to cover and density of all tree species.

partially cored Oregon white oak stems (Monte Carlo tests, 100 randomized iterations, $P \leq 0.01$; Table 4). The predictive power of models based only on dbh was modest ($xR^2=0.46$ and 0.50 for Applegate and Butte Falls, respectively). Inclusion of predictors pertaining to stand structure and apparent indicators of potential site moisture status, however, substantially increased the models' predictive power. For the Applegate, the full NPMR model gave a xR^2 of 0.79 , and identified four predictors for tree age: (log)dbh, heatload, tree cover, and the mean number of stems/Oregon white oak tree. The full Butte Falls model gave a xR^2 of 0.81 , and also identified four predictors: (log)dbh, spring precipitation, the mean number of stems/Oregon white oak tree, and stand density (# of tree + sapling stems of all tree species).

Age Structures—The stand age structures of surviving Oregon white oak trees (Figure 4; stands depicted were selected to illustrate types described below) suggest a tendency towards pulsed regeneration, with limited

recruitment since the 1930s or earlier. In 44% of stands, trees likely established from one or two major pulses of establishment, with few or no trees in other age classes (Figure 4a). In 28% of stands, there was evidence of historical continuous or frequent pulses of recruitment, but few or no saplings were present (Figure 4b). Trees occurred in most age classes, showing continuous or frequent pulses of recruitment, with saplings present in 22% of stands (Figure 4c). In the remaining 6% of stands, there was fairly gradual infilling over the past 100-140 yr, with no old trees present (Figure 4d). There was clear potential for conversion to Douglas-fir dominance in 14% of stands (e.g., Figure 4d), indicated by substantial recent Douglas-fir regeneration (sapling size class) and a relative paucity of Oregon white oak saplings.

In many stands, the highest rates of establishment for currently surviving Oregon white oak trees occurred after Euro-American settlement (~1851), and recruitment decreased or even stopped after fire suppression became particularly effective (~1956). For example, nearly half of stands (17 of 36) supported ≤ 2 surviving Oregon white oaks (saplings or trees) that established after ~1956, and only 6% of stands had age structures that suggest that most recruitment into Oregon white oak tree size classes occurred after ~1956. However, the other 19 stands did support sapling-sized individuals < 4 m tall (in low to high numbers), at least some of which originated after 1956. Although wildfire can erase evidence of pre-fire tree density and establishment, no recent wildfires were recorded in the stands that appeared to support little regeneration after ~1956. All surviving aged Douglas-firs ($n = 40$) established post-settlement, and recruitment increased after estimated effective fire suppression. Ponderosa pines established both post- and pre-settlement, with higher rates of surviving tree recruitment post-settlement.

Across all sites, there was markedly abundant establishment of currently surviving Oregon white oak trees during 1850–1890 (Figure 5). Elevated regeneration also apparently occurred between 1910 and 1930 in some stands, a time during which several large wildfires occurred. Small numbers of surviving trees that established before 1850 in scattered age classes were present in 56% of stands.

Discussion

Overview

Tree and sapling age and size distributions in sampled woodlands suggest that age structure and recruitment dynamics may have shifted shortly after Euro-American

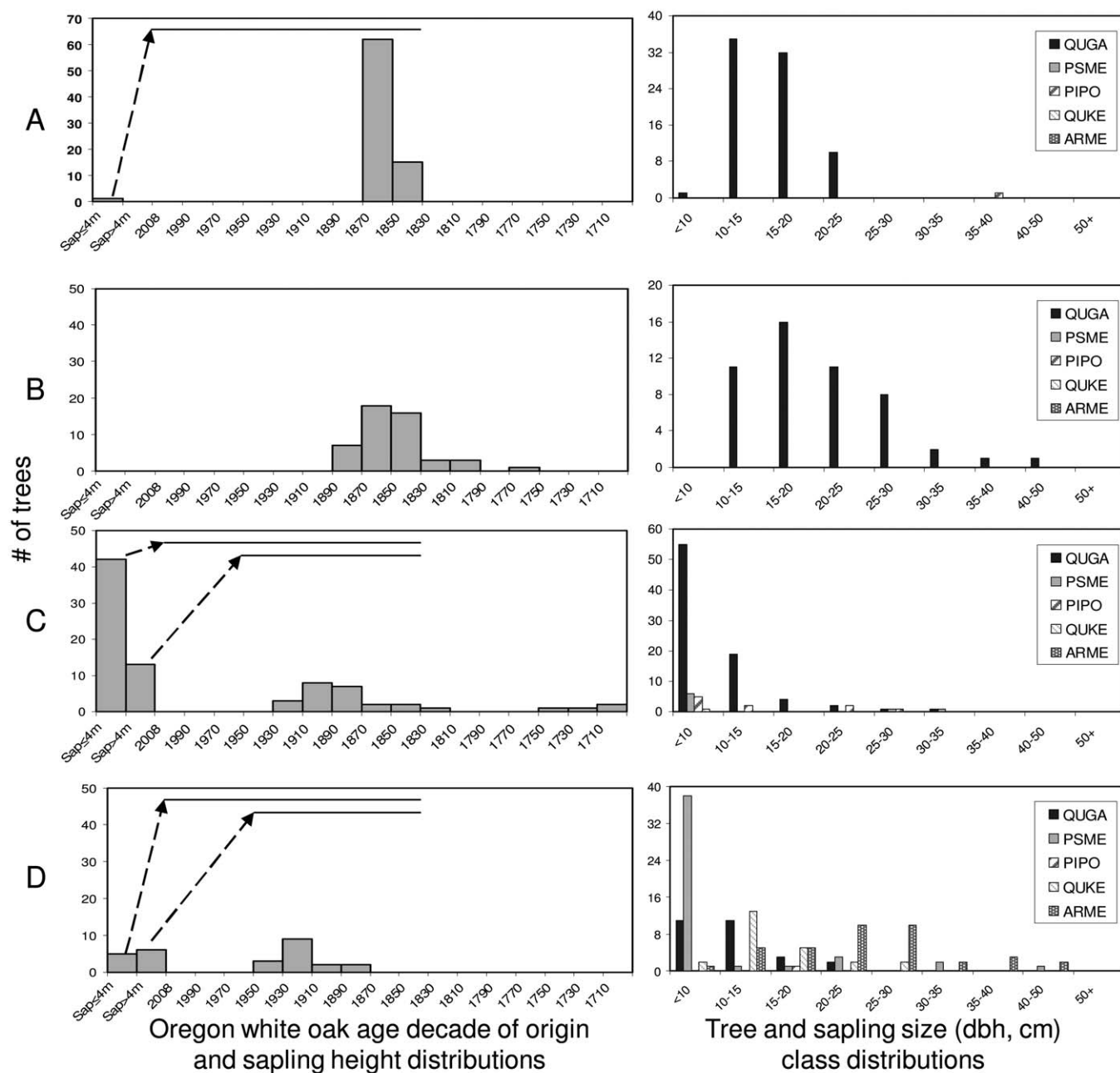


Figure 4. Representative Oregon white oak age (year of origin in 20-yr bins based on both counted and predicted ages) and sapling height (Sap) distributions paired with diameter distributions across species for the same stands. To enable estimates of sapling ages based on heights, arrows show observed age range of sapling height classes across all stands in which saplings were aged. Stand A illustrates single pulse recruitment. Stand B illustrates relatively continuous or frequent pulses of historical recruitment with no saplings present. Stand C illustrates continuous or frequent pulses of recruitment and apparently recent regeneration. Stand D illustrates apparently recent Oregon white oak infilling, and potential for stand conversion to Douglas-fir. Species codes: QUGA = *Q. garryana*, PSME = *P. menziesii*, PIPO = *P. ponderosa*, QUKE = *Q. kelloggii*, ARME = *A. menziesii*.

settlement and again after fire suppression became more effective. For example, stands often had apparently low current rates of regeneration success (based on sapling to tree ratios of surviving individuals); sapling-sized

individuals were present in some sites but 82% of those sampled established pre-1956. Few sites showed evidence of continuous recruitment, and many experienced an unusually large oak regeneration flush between

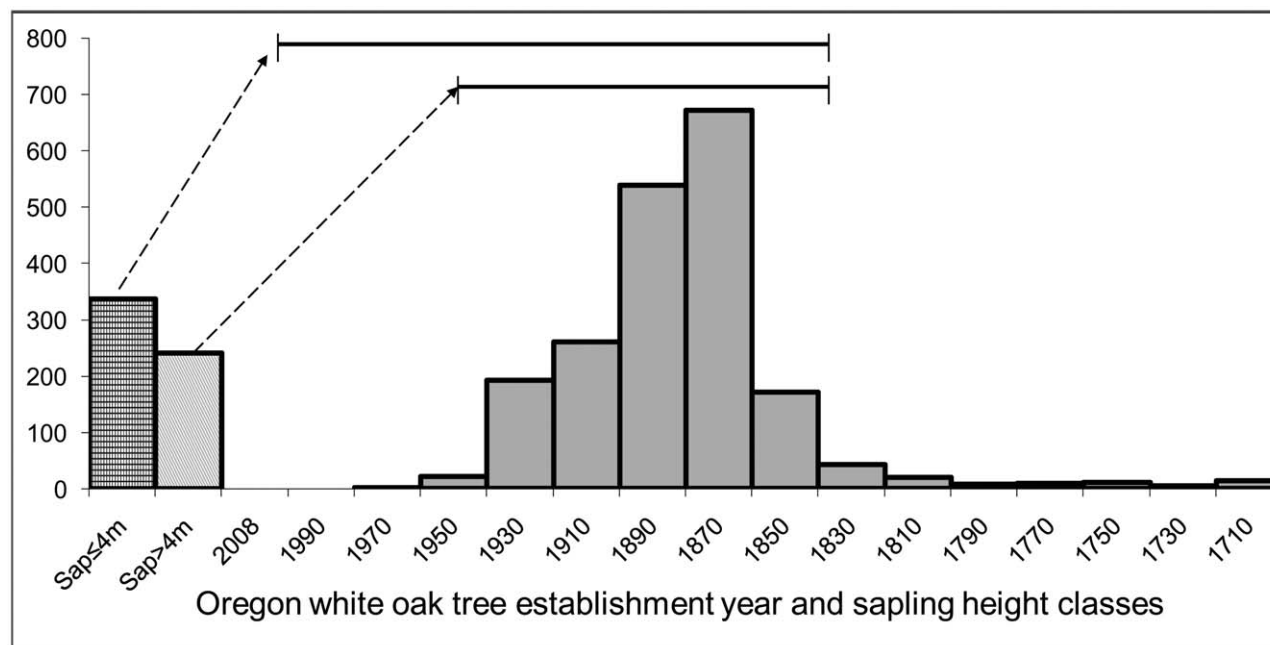


Figure 5. Distribution of Oregon white oak tree and sapling (Sap) year of origin across all stands. Data include both actual (cored) and estimated (using non-parametric multiplicative regression) tree ages. Sapling abundances are reported by height classes. Horizontal bars associated with sapling height classes show ranges of establishment years for each class, based on the subset of saplings that were aged.

~1850 and 1890, based on surviving trees. There was a broad range in ages of small diameter Oregon white oak trees and saplings among stands, but these were often >100 yr old, and nearly all tree-sized oaks established before estimated “effective” fire suppression (~1956).

Tree and Shrub Species Composition and Density

The sampled southwestern Oregon oak woodlands were more similar to drought-tolerant oak woodland plant associations of northern California than to oak communities farther north in the Willamette Valley. Similarities with northern California associations included both tree and shrub species compositions, with large chaparral shrub species present in all sampled stands (Riegel et al. 1992).

Douglas-fir encroachment appeared to be ongoing over the > 50 years since fire suppression became particularly effective; several stands supported zero-to-few Oregon white oak saplings and several-to-many Douglas-fir saplings. Stands of Douglas-firs that dominated and overtopped large oaks were observed in both study areas, but were excluded from this study. Relict tree densities were only about one-tenth of those observed in the northernmost part of Oregon white oak’s historical range in British Columbia in an Oregon white oak study area located across a prairie-savanna-woodland

gradient (Gedalof et al. 2006), but appear to be higher than relict densities reported from Willamette Valley oak woodlands (that were historically more open oak communities), although the latter comparison is uncertain owing to inconsistencies in relict definitions (Thilenius 1968; Table 5). In general, ranges in tree densities in the stands we sampled overlapped with those documented for Oregon white oak-dominated communities both to the north and south (e.g., Thilenius 1968, Sugihara and Reed 1987, Thysell and Carey 2001, Gedalof et al. 2006). However, the highest stand densities that we encountered far exceeded the highest stand densities documented farther north in Vancouver Island, British Columbia, where oak communities were formerly open prairie-oak (Gedalof et al. 2006), and also exceeded those reported for oak communities in the Puget Trough, Washington (Thysell and Carey 2001). Observed stand densities were also, however, far lower than the 4500-12000 stems/ha observed in young stands that developed after high intensity fires in the 1940s in the Bald Hills of northern California (Sugihara and Reed 1987).

Patterns in Stand Structure and Relations to the Environment

Individual environmental variables were weakly correlated with gradients in stand structure. The strongest correlations across study areas related to edaphic

TABLE 5. Stand structure attributes reported from studies of Oregon white oak communities that were selected to represent geographical variability along the south to north gradient of the species range.

Region	Relict tree densities Range (mean) ha ⁻¹	Stand densities Range (mean) ha ⁻¹	DBH range : Age range Comparison of cm : yr
Bald Hills, CA¹:		60-530 (stems in all-aged stands) 740-2550 (stems in clustered multiple-stemmed even aged stands) 4500-12000 (stems in dense even-aged stands)	<12 : 34-37 10-30 : 70-100
Southwestern OR²:	<10-60 (21)	50-1080 (370) QUGA trees 90-1100 (711) trees 150-1810 (990) sapling+tree stems	<12 : 5-260 10-30 : 53-279
Willamette Valley, OR³:	3-15	17 (mean no. of trees in savanna plots) 702-841 (mean no. of trees in woodland plots) 1054 (mean no. of trees in forest plots)	
Puget Trough, WA⁴:	105-450 (254)	QUGA trees	
Vancouver Island, B.C.⁵:	210	300 (mean no. of trees in plots transitional between savanna and woodland) 390 (mean no. of trees in woodland plots) 460 (mean no. of trees in oak plots with snags present)	76-94 : 257-308

Species code: QUGA = *Quercus garryana*. ¹Sugihara and Reed 1987, ²Gilligan and Muir (this study), ³Thilenius (1968), ⁴Thysell and Carey 2001, ⁵Gedalof et al. 2006.

characteristics, and within study areas, to potential site moisture status or fire history, depending on the study area (see Gilligan 2010 for analyses within study areas). Collectively these represented a gradient from the harshest, driest sites in the Applegate study area to more productive sites in the Butte Falls study area. The general lack of strong correlations between stand structures and measured environmental or disturbance variables probably indicates complex interactive influences of such variables in concert with variations in site history. Wildfire did not appear to have a consistent effect on stand structures across study areas, but most stands had not experienced recorded fire in the last ~70 years. The lack of correlation between fire history and stand structures may be influenced by the facts that the recorded fire data dates back only to 1910, and that recorded fires may not comprehensively include all wildfires.

Other studies across Oregon white oak's range have also identified associations between stand structures and moisture stress (e.g., Riegel et al. 1992, Erickson 2002, Devine and Harrington 2007, Maertens 2008), soil limitations (Erickson 2002, Murphy 2008) and oak resilience to (prescribed) fire effects (Regan and Agee 2004, Fry 2008).

Oregon White Oak Diameter and Age Structure

Oregon white oak trees from southwestern Oregon were smaller in diameter than trees of similar ages reported from areas both to the south and to the north of our study area (e.g., Thilenius 1968, Sugihara and Reed 1987; Table 5). Sapling-sized Oregon white oak age ranges overlapped with those of tree-sized oaks, suggesting that it is not universally appropriate to use the sapling size class as an age proxy to interpret recent regeneration dynamics, as is sometimes done (e.g., Thilenius 1968, Muick and Bartolome 1987, Jackson et al. 1998, Gedalof et al. 2006); such use should be based on understanding of age-size relationships for the study area in question.

Oregon white oak tree ages were best predicted by models that incorporated both dbh and site variables. The modest predictive power of dbh alone was probably influenced by the fact that sampling encompassed a wide range of tree densities and site conditions, and both even-and uneven-aged stands. Age-growth dynamics are likely to differ across such a range of stand and site conditions. Trees with the same diameters were younger in some relatively low density stands than in those with higher densities, suggesting possible competitive effects in denser stands. Many saplings had

very narrow annual rings in the sapwood, supporting the possibility that competition may affect tree growth in some stands.

Regeneration

Low levels of oak regeneration have been noted and investigated in oak communities in the western United States for the past century (Bartolome et al. 1987) and for even longer in oak communities of the eastern United States (Clark 1993). However, there is a paucity of data on Oregon white oak regeneration rates in southwestern Oregon, and the limited information that is available has attributed apparently low regeneration rates to unnaturally high stand densities caused by fire suppression (Riegel et al. 1992). We found low Oregon white oak sapling to tree ratios in many stands, which coupled with the old ages of many saplings, may suggest that current sapling recruitment rates are also low in southwestern Oregon. Causes for slowed or halted regeneration here, if current regeneration rates are anomalously low, are uncertain. Conifer encroachment is considered the largest threat to persistence of Oregon white oak ecosystems (e.g., Reed and Sugihara 1987, Gedalof et al. 2006, Devine and Harrington 2006), aside from land conversion (Fuchs 2001), but this is unlikely to be a primary factor limiting sapling recruitment in the Oregon white oak-dominated stands that we selected.

Seedling-sized oak regeneration was present in all stands, and often abundant. Therefore, lack of oak establishment does not appear to be a cause of the paucity of saplings observed in many stands. Seedling-sized regeneration densities were often highest on sites that supported relatively high tree stocking (tree density, cover, or basal area). This association may be caused by relatively abundant regeneration sources on such sites (e.g., acorns or root sprouts), and facilitated by presence of oak-associated mycorrhizae (Frank et al. 2009). Relatively benign site quality may also explain the positive association of seedling-sized regeneration with Oregon white oak driplines; adult tree presence indicates site or microsite suitability, and the trees may ameliorate the harshness of microsite conditions (Carvell and Tryon 1961).

There is uncertainty about the effects of low or diminishing oak sapling recruitment on long-term oak persistence (Lorimer 1993), and low regeneration rates may be normal if stands are fully stocked due to lack of disturbance, driven by limitations in available rooting area, light, moisture, or other resources. In this case, low recruitment of currently surviving saplings over the last ~100 yr may not necessarily be problematic

for oak persistence. Concerns about apparently low regeneration rates might also be tempered by the long life span of Oregon white oaks (>400 yr), and the likelihood that a disturbance will occur at some point in the lifespan, triggering sprouting (Agee 1996) and increasing resource availability.

Numerous natural and anthropogenic influences may inhibit sapling recruitment in southwestern Oregon, and these can have complex and interacting effects. Some potential explanatory factors include a lengthy seedling-to-sapling transition that can be prolonged by browsing or herbivory by small mammals (Hibbs and Yoder 1993, MacDougall et al. 2010); competition from exotic grasses (Barnhart et al. 1996, Thysell and Carey 2001); historical and possibly current livestock grazing (Jackson et al. 1998, Hedrick and Keniston 1966); and competition for soil water (Devine and Harrington 2007, Devine et al. 2007).

Changes in Stand Structure Over Time

Most surviving Oregon white oaks in our study areas established in the mid-late 1800s, after Euro-American settlement, although recruitment trends varied across stands. This timing is consistent with abundant regeneration of Oregon white oak in other parts of its range, and that of similar oak species in California (White 1966, Thilenius 1968, Gedalof et al. 2006, Dunwiddie et al. 2011).

If fire use by settlers was frequent and widespread (e.g., LaLande 1995), human-set fires that top-killed oaks and stimulated resprouting may be responsible, at least in part, for the apparent post-Euro-American settlement origins of many surviving trees (Regan and Agee 2004). Although our study design avoided sites with signs of logging, even if no signs (such as stumps) were evident, it is possible there was logging and clearing following Euro-American settlement that resulted in even-aged stands due to sprouting. Alternatively, the cessation of Native American burning with Euro-American settlement as observed in other regions (e.g., Sprenger and Dunwiddie 2011) could have allowed both oak ingrowth into prairie and increased survivorship of oak seedlings in formerly frequently burned oak savanna. Relatively abundant oak recruitment also coincided with high livestock stocking levels in southwestern Oregon (LaLande 1995, Hosten et al. 2007a) and with other land use changes associated with Euro-American settlement (e.g., MacDougall 2008). Reports on effects of both Euro-American settler and Native American burning and other practices on southwestern Oregon oak communities are, however, largely speculative and

anecdotal. The oak recruitment flush also corresponded with increased tree growth rates and recruitment in nearby mixed conifer riparian areas after a climatic transition from extended drought during ~1815-1850 to wetter and cooler conditions (Messier 2009).

It remains unknown whether tree densities in oak woodlands changed after Euro-American settlement. It is commonly assumed that Oregon white oak tree densities were lower before than after Euro-American settlement (e.g., Stein 1990, Riegel et al. 1992, Fuchs 2001), and the structures of the 6% of stands dominated by < 150 year old trees with no relict trees, and of the 22% of stands with probable continuous recruitment that we surveyed are consistent with this conception. Historical records (e.g., General Land Office [GLO] surveys), however, document that dense oak woodlands occupied substantial portions of the landscape in southwestern Oregon during the 1850s (Hickman 2005, Hosten et al. 2007b). Ponderosa pine-oak and oak woodlands formed the most dominant vegetation class recorded in southwestern Oregon GLO surveys, in contrast with surveys from the Willamette Valley where prairie was the most dominant class (Hickman 2005, Christy and Alverson 2011). It is likely that there was a great deal of landscape patchiness in the past, which included both historical woodlands and open-oak patches. Some sites supported a large proportion of multiple-stemmed trees with stems originating shortly after Euro-American settlement; the parent trees were probably present prior to settlement.

Research and Management Implications

Current stand structures and histories of Oregon white oak woodlands varied widely across our southwestern Oregon study sites. Both current and historical recruitment trends varied among stands, ranging from a single large recruitment pulse to continuous and ongoing recruitment. This variability suggests that management with a uniform thinning prescription across sites, as has been the practice on treated BLM lands in our study region, may not benefit oak woodlands on the landscape scale. Varied management prescriptions could maintain or enhance diversity in stand and age structures across the landscape, and treatments such as broadcast burning that mimic historic natural and

anthropogenic disturbances may be preferable to other thinning techniques (Sugihara and Reed 1987).

Additional research is needed on the relationship of site moisture status to stand structures and oak recruitment in southwestern Oregon. Results would help to discern whether site-to-site variation in regeneration levels is due to unique (and slow to change) site characteristics, such as soil or microclimate, or to attributes that can benefit from management. Improved understanding of the relationships between oak regeneration and site moisture status may be particularly important as climate change becomes more influential and land managers are confronted with taking those changes into account in their ecosystem management plans. The need for enhanced understanding of Oregon white oak's response to site moisture is particularly pressing in southwestern Oregon, which is the driest end of the species' range (Franklin and Dyrness 1973).

Although a large proportion of Oregon white oak-dominated communities has been lost across the species' range, large tracts of public lands in southwestern Oregon continue to support such communities, many of which are woodlands. Oak ecosystem histories in southwestern Oregon are not well understood and active fuels management is taking place in oak systems in this region. Together, these lend urgency to the need for knowledge that can be gained from sustained monitoring of Oregon white oak communities after fuels treatments. Such knowledge can identify treatments that are most likely to support long-term oak community persistence and maintain variability in oak-dominated systems across the landscape.

Acknowledgements

This study was made possible by funding and support from Joint Fire Sciences Program, Oregon State University, and the Bureau of Land Management. Special thanks to Paul Hosten from the BLM for sharing resources and guidance; and also to Marcia Wineteer, Alan Mason, and Paul LeBlanc. Bruce McCune, David Hibbs, and Olivia Duren from Oregon State University provided comments on this manuscript, and Emily Straus and Hannah Goodwin assisted with field work. The manuscript benefited greatly from the comments of the Special Issue Editor and two anonymous reviewers.

Literature Cited

- Agee, J. K. 1993. *Fire Ecology of Pacific Northwest Forests*. Washington D.C., Island Press.
- Agee, J. K. 1996. Fire in restoration of Oregon white oak woodlands. In C. C. Hardy and S. F. Arno, (editors), *The Use of*

- Fire in Forest Restoration*. USDA Forest Service General Technical Report INT-GTR-341, Intermountain Research Station. Ogden, UT. Pp. 72-73.
- Atzet, T., D. E. White, L. A. McCrimmon, P. A. Martinez, P. R. Fong, and V. D. Randall. 1996. *Field guide to the forested plant associations of southwestern Oregon*. USDA Forest

- Service PNW Regional Technical Paper R6-NR-ECOL-TP-17-96, Portland, OR.
- Barnhart, S. J., J. R. McBride, and P. Warner. 1996. Invasion of northern oak woodlands by *Pseudotsuga menziesii* (Mirb.) Franco in the Sonoma mountains of California. *Madrono* 43:28-45.
- Bartolome, J. W., P. C. Muick, and M. P. McClaran. 1987. Natural regeneration of Californian hardwoods. In T. R. Plumb and N. H. Pillsbury (editors), *Proceedings of the Symposium on Multiple-Use Management of California's Hardwood Resources*. USDA Forest Service General Technical Report PSW-100, Southwest Forest and Range Experiment Station, Berkeley, CA. Pp. 26-31.
- Beyer, H. L. 2004. *Hawth's Analysis Tools for ArcGIS v. 3.27*. Available online at <http://www.spatialecology.com/htools/> (Accessed May 2008).
- Boyd, R. 1999a. *Indians, Fire and the Land in the Pacific Northwest*. Oregon State University Press, Corvallis.
- Boyd, R. 1999b. The coming of the spirit of pestilence. Introduced infectious diseases and population decline among northwest coast Indians, 1774-1874. University of Washington Press, Seattle.
- Carvell, K. L., and E. H. Tryon. 1961. The effect of environmental factors on the abundance of oak regeneration beneath mature oak stands. *Forest Science* 7:98-105.
- Chiller, D. G., D. G. Vesely, and W. I. Dean. 2000. Assessment of oak woodland resources in BLM's Eugene District, Lane County, Oregon. USDI BLM Technical Note 406. Bureau of Land Management, Eugene, OR.
- Clark, F. B. 1993. A historical perspective of oak regeneration. In D. L. Loftis and C. E. McGee (editors), *Proceedings of the Symposium on Oak Regeneration: Serious Problems, Practical Recommendations*. USDA Forest Service General Technical Report SE-84. Southeastern Forest Experiment Station, Asheville, NC. Pp. 3-13.
- Christy, J. A., and E. R. Alverson. 2011. Historical vegetation of the Willamette Valley, Oregon, circa 1850. *Northwest Science* 85:93-107.
- Devine, W. D., and C. A. Harrington. 2006. Changes in Oregon white oak (*Quercus garryana* Dougl. ex Hook.) following release from overtopping conifers. *Trees* 20:747-756.
- Devine, W. D., and C. A. Harrington. 2007. Release of Oregon white oak from overtopping Douglas-fir: effects on soil water and microclimate. *Northwest Science* 81:112-124.
- Devine, W. D., C. A. Harrington, and L. P. Leonard. 2007. Post-planting treatments increase growth of Oregon white oak (*Quercus garryana* Dougl. ex Hook.) seedlings. *Restoration Ecology* 15:212-222.
- Dunwiddie, P. W., J. D. Bakker, M. Almaguer-Bay, and C. Sprenger. 2011. Environmental history of a Garry oak/Douglas-fir woodland on Waldron Island, Washington. *Northwest Science* 85:130-140.
- Duren, O. C., and P. S. Muir. 2010. Does fuels management accomplish restoration in southwest Oregon, USA, chaparral? *Insights from age structure*. *Fire Ecology* 6:76-96.
- Ecoshare. 2008. *Interagency Clearinghouse of Ecological Information - Pacific Northwest*. Available online at <http://www.reo.gov/ecoshare/gis/> (Accessed May 2008).
- Erickson, W. R. 2002. Environmental relationships of native Garry oak (*Quercus garryana*) communities at their northern margin. In R. B. Standiford, D. McCreary, and K. L. Purcell (editors), *Proceedings of the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape*. USDA Forest Service General Technical Report PSW-GTR-184, Pacific Southwest Research Station, Albany, CA. Pp. 179-190.
- Franklin, J. F., and C. T. Dyrness. 1973. *Natural Vegetation of Oregon and Washington*. General Technical Report PNW-8. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.
- Fritschle, J. A. 2008. Reconstructing historic ecotones using the public land survey: The lost prairies of Redwood National Park. *Annals of the Association of American Geographers* 98:24-39.
- Frank, J. L., S. Anglin, E. M. Carrington, D. S. Taylor, B. Viratos, and D. Southworth. 2009. Rodent dispersal of fungal spores promotes seedling establishment away from mycorrhizal networks on *Quercus garryana*. *Botany* 87:821-829.
- Frost, E. J., and R. Sweeney. 2000. *Fire Regimes, Fire History and Forest Conditions in the Klamath-Siskiyou Region: An Overview and Synthesis of Knowledge*. World Wildlife Fund, Klamath Siskiyou Ecoregion Program, Ashland, OR.
- Fry, D. L. 2008. Prescribed fire effects on deciduous oak woodland stand structure, Northern Diablo Range, California. *Range-land Ecology and Management* 61:294-301.
- Fuchs, M. A. 2001. *Towards a Recovery Strategy for Garry oak and Associated Ecosystems in Canada: Ecological Assessment and Literature Review*. Technical Report GBEI/EC-00-030. Environment Canada, Canadian Wildlife Service, Pacific and Yukon Region, Ladner, British Columbia.
- Gedalof, Z., M. Pellatt, and D. J. Smith. 2006. From prairie to forest: three centuries of environmental change at Rocky Point, Vancouver Island, British Columbia. *Northwest Science* 80:34-46.
- Gilligan, L. A. 2010. *Stand structures of Oregon white oak (Quercus garryana) woodlands and their relationships to the environment in southwestern Oregon*. M.S. Thesis, Oregon State University, Corvallis.
- Hedrick, D. W., and R. F. Keniston. 1966. Grazing and Douglas-fir growth in the Oregon white-oak type. *Journal of Forestry* 64:735-738.
- Hibbs, D. E., and B. J. Yoder. 1993. Development of Oregon white oak seedlings. *Northwest Science* 67:30-36.
- Hickman, O. E. 2005. *Historic vegetation as interpreted from the original 1850's land survey records in the Upper Rogue River Valley near Medford, Oregon*. Bear Creek Watershed Council, Medford, OR; expanded abstract from Proceedings of the 2005 Northwest Scientific Association Meeting, Corvallis, Oregon. Available online at <http://bearcreek-watershed.org/img/hxvegprpt2.pdf> (accessed 26 October 2009).
- Hosten, P. E., H. Whitridge, D. Schuster, and J. Alexander. 2007a. *Livestock on the Cascade-Siskiyou National Monument: a summary of stocking rates, utilization, and management*. USDI, Bureau of Land Management, Medford District. Available online at: <http://soda.sou.edu/bioregion.html>, accessed 12/30/09.
- Hosten, P. E., O. E. Hickman, F. K. Lake, F. A. Lang, and D. Vesely. 2006. Oak woodlands and savannas. In D. Apostol and M. Sinclair (editors), *Restoring the Pacific Northwest: The Art and Science of Ecological Restoration in Cascadia*. Island Press, Washington, D.C.
- Hosten, P. E., O. E. Hickman, and F. A. Lang. 2007b. Patterns of vegetation change in grasslands, shrublands, and woodlands of southwest Oregon. Southern Oregon University Digital Archives, USDI Bureau of Land Management, Medford, OR. Available online at <http://soda.sou.edu:8081/soda/main.jsp?flag=browse&smd=1&awdid=1> (accessed 26 October 2009).

- Jackson, R. D., K. O. Fulgham, B. Allen-Diaz. 1998. *Quercus garryana* Hook. (Fagaceae) stand structure in areas with different grazing histories. *Madroño* 45:275-282.
- Johnson, D. R. 1994. Soil Survey of Jackson County Area, Oregon. USDA Soil Conservation Service, Oregon.
- Kruskal, J.B. 1964. Nonmetric multidimensional scaling, a numerical method. *Psychometrika*. 29:115-129.
- LaLande, J. 1995. An environmental history of the Little Applegate River watershed, Jackson County, Oregon. USDA Forest Service, Medford, Oregon, USA.
- Lathrop, E. W., and M. J. Arct. 1987. Age structure of Engelmann oak populations on the Santa Rosa Plateau. In T. R. Plumb and N. H. Pillsbury (editors), *Proceedings of the Symposium on Multiple-Use Management of California's Hardwood Resources*. USDA Forest Service General Technical Report PSW-100, Berkeley, CA. Pp. 47-52.
- Lawrence, M. 1971. Management Environment Analysis - History of Medford District, Bureau of Land Management. Southern Oregon University Digital Archives, Medford, OR.
- Lorimer, C. G. 1993 Causes of the oak regeneration problem. In D. L. Loftis and C. E. McGee (editors), *Proceedings of the Symposium on Oak Regeneration: Serious problems, Practical Recommendations*. USDA Forest Service General Technical Report SE-84. Southeastern Forest Experiment Station, Asheville, NC. Pp. 14-39.
- MacDougall, A. S. 2008. Herbivory, hunting, and long-term vegetation change in a degraded savanna. *Biological Conservation* 141:2174-2183.
- MacDougall, A., A. Duwyn, and N. Jones. 2010. Consumer-based limitations drive oak recruitment failure. *Ecology* 91:2092-2099.
- Maertens, T. 2008. The growth-climate relationship of Oregon white oak (*Quercus garryana*). M.S. Thesis, University of Guelph, Guelph, Ontario.
- Mather, P. M. 1976 *Computational Methods of Multivariate Analysis in Physical Geography*. John Wiley and Sons, London, UK.
- McCarthy, H. 1993. Managing oaks and the acorn crop. In T. Blackburn and K. Anderson (editors), *Before the Wilderness: Environmental Management by Native Californians*. Ballena Press, Menlo Park, CA.
- McCune, B. 2006. Non-parametric habitat models with automatic interactions. *Journal of Vegetation Science* 17:819-830.
- McCune, B. 2007. Improved estimates of incident radiation and heat load using non-parametric regression against topographic variables. *Journal of Vegetation Science* 18:751-754.
- McCune, B., and J. B. Grace. 2002. *Analysis of Ecological Communities*. MjM Software, Gleneden Beach, OR.
- McCune, B., and M. J. Mefford. 2008. HyperNiche. Nonparametric Multiplicative Habitat Modeling. Version 2.60 beta. MjM Software, Gleneden Beach, OR.
- McCune, B. and M. J. Mefford. 2009. PC-ORD. Multivariate Analysis of Ecological Data. Version 6.93 beta MjM Software, Gleneden Beach, OR.
- Messier, M. 2009. Disturbance and dynamics of riparian forests in southwestern Oregon. M.S. Thesis, Oregon State University, Corvallis.
- Muick, P. C., and J. W. Bartolome. 1987. Factors associated with oak regeneration in California. In T. R. Plumb and N. H. Pillsbury (editors), *Proceedings of the Symposium on Multiple-Use Management of California's Hardwood Resources*. USDA Forest Service General Technical Report PSW-100. Berkeley, CA. Pp. 86-91.
- Murphy, M. 2008. Edaphic controls over succession in former oak savanna, Willamette Valley, Oregon. M.S. Thesis, University of Oregon, Eugene.
- Oregon Geospatial Enterprise Office. 2009. Oregon Geospatial Data Clearinghouse. Salem, OR. Available online at <http://oregon.gov/DAS/EISPD/GEO/sdlibrary.shtml> (Accessed 8/14/2009).
- Perchemlides, K. A., P. S. Muir, and P. E. Hosten. 2008. Responses of chaparral and oak woodland plant communities to fuel-reduction thinning in southwestern Oregon. *Rangeland Ecology and Management* 61:98-109.
- Pfaff, E. 2007a. Patterns of grassland, shrubland, and woodland vegetation abundance in relation to landscape-scale environmental and disturbance variables, Applegate Watershed Southwest. MS Thesis, Southern Oregon University, Ashland.
- Pfaff, E. 2007b. Climate, topography, soils, and wildfire spatial datasets collected and processed for MS Thesis, on file, Southern Oregon University, Ashland.
- Pyne, S. J. 1982. *Fire in America: A Cultural History of Wildland and Rural Fire*. Princeton University Press, Princeton, NJ.
- Reed, L.J., and N.G. Sugihara. 1987. Northern oak woodlands-ecosystems in jeopardy or is it already too late? In T. R. Plumb and N. H. Pillsbury (editors), *Proceedings of the Symposium on Multiple-Use Management of California's Hardwood Resources*. USDA Forest Service General Technical Report PSW-100, Pacific Southwest Research Station, Berkeley, CA. Pp. 59-63.
- Regan, A. C., and J. K. Agee. 2004. Oak community and seedling response to fire at Fort Lewis, Washington. *Northwest Science* 78:1-11.
- Riegel, G. M., B. G. Smith, and J. F. Franklin. 1992. Foothill oak woodlands of the interior valleys of southwestern Oregon. *Northwest Science* 66:66-76.
- Sikes, K. G., and P. S. Muir. 2009. Influence of two fuel reduction treatments on chaparral communities of southwestern OR. *Madroño* 56:8-22.
- Sprenger, C. B., and P. W. Dunwiddie. 2011. Fire history of a Douglas-fir - Oregon white oak woodland, Waldron Island, Washington. *Northwest Science* 85:108-119.
- Stein, W. I. 1990. *Quercus garryana* Dougl. ex Hook. Oregon white oak. In R. M. Burns and B. H. Honkala (technical coordinators) *Silvics of North America: 2. Hardwoods*. USDA Forest Service Argicultural Handbook No. 654. USDA Forest Service, Washington, D.C. Pp. 650-660.
- Sugihara, N. G., and L. J. Reed. 1987. Prescribed fire for restoration and maintenance of Bald Hills oak woodlands. In T. R. Plumb and N. H. Pillsbury (editors), *Proceedings of the Symposium on Multiple-Use Management of California's Hardwood Resources*. USDA Forest Service General Technical Report PSW-100. Pacific Southwest Research Station, Berkeley, CA. Pp. 446-451.
- Thilenius, J. F. 1968. The *Quercus garryana* forests of the Willamette Valley, Oregon. *Ecology*. 49:1124-1133.
- Thysell, D. R., and A. B. Carey. 2001. *Quercus garryana* communities in the Puget Trough, Washington. *Northwest Science* 75:219-235.
- Tveten, R. K., and R. W. Fonda. 1999. Fire effects on prairies and oak woodlands on Fort Lewis, Washington. *Northwest Science* 73:145-158.
- USDA NRCS (Natural Resources Conservation Service) Soil Survey Staff. 2009. Soil Survey Geographic (SSURGO) Database for Jackson County, OR. Available online at <http://soildatamart.nrcs.usda.gov> (Accessed 8/14/2009).
- USDI. 1998. Ecosystem restoration in the Ashland Resource Area. USDI Bureau of Land Management, Medford, Oregon.
- USDI. 2007. Annual program summary and monitoring report for Fiscal Year 2007. USDI Bureau of Land Management,

- Medford, OR. Available online at http://www.blm.gov/or/districts/medford/plans/files/aps_med07.pdf (Accessed 11/2009).
- Villalba, R., and T. T. Veblen. 1997. Improving estimates of total tree ages based on increment core samples. *Ecoscience* 4:534-542.
- White, K. L. 1966. Structure and composition of foothill woodland in central coastal California. *Ecology* 47:229-237.
- Western Regional Climate Center (WRCC). 2009. Oregon climate summaries. Available online at <http://www.wrcc.dri.edu/summary/climsmor.html> (Accessed 14 August 2009).
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30:279-338.
- Wilson, S. M., and A. B. Carey. 2001. Small mammals in oak woodlands in the Puget Trough, Washington. *Northwest Science* 75:342-349.

Received 27 August 2010

Accepted for publication 2 January 2011