

AN ABSTRACT OF THE THESIS OF

Laurie A. Gilligan for the degree of Master of Science in Botany and Plant Pathology presented on February 11, 2010.

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Abstract approved:

Patricia S. Muir

Large areas of non-coniferous communities in southwestern Oregon are thinned to reduce fire hazard and accomplish ecosystem restoration, under the assumption that current fuel loads are unnaturally high. Although Oregon white oak (*Quercus garryana*) woodlands are a characteristic landscape component in this region, little is known about their current or historical stand structures. Managers lack information on which to base restoration-focused fuel reduction prescriptions. I inventoried 40 Oregon white oak dominated woodlands across 2 study areas in southwestern Oregon, and describe here their stand characteristics and age structures. I 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, and fire history also appeared related to several stand structures. Peak establishment of living Oregon white oaks generally occurred during 1850-1890, sometimes occurred in the early 1900's, and recruitment rates were low post-fire suppression.

Recruitment of sapling-sized oak trees (< 10 cm dbh, ≥ 1.3 m tall) was generally low and their ages ranged from 5 to 164 yr; they were not necessarily recent recruits. The range of stand and age structures, and the variation in their apparent relations to site factors and history, suggests that site-by-site management prescriptions may more effectively accomplish restoration goals than do current treatments. Prescriptions should include follow-up monitoring with attention to effects on oak recruitment.

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Stand Structures of Oregon White Oak (*Quercus garryana*) Woodlands and their
Relationships to the Environment in Southwestern Oregon

by
Laurie A. Gilligan

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

Laurie A. Gilligan, Author

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TABLE OF CONTENTS

	<u>Page</u>
Introduction	1
Study Area.....	4
Methods.....	7
Study site selection and plot layout.....	7
Stand structure data.....	8
Increment core and cross section preparation	10
Statistical analysis	11
Patterns in stand structure	11
Tree age predictions	12
Results	17
Tree and shrub species composition	17
Patterns in stand structure and relationships to environment.....	18
Stand Age Structures and Changes over Time.....	27
Tree ages	27
Regeneration	28
Tree age predictions from stand structural variables	30
Age structures.....	30
Discussion	34
Overview	34
Tree and shrub species composition and density.....	35
Patterns in stand structure and relationships to environment.....	37
Oregon white oak diameter and age structure.....	41
Regeneration	42

TABLE OF CONTENTS (Continued)

	<u>Page</u>
Changes in stand structures over time.....	46
Management implications	48
Conclusions	51
Bibliography.....	53
Appendices	61

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Study area in Jackson County, southwestern Oregon.....	5
2. NMS ordination of all plots (triangles) in stand structural space (2 of 3 dimensions shown)..	20
3. Age class distribution of small (10.0-10.9 cm dbh) cored Oregon white oak trees ($n=58$).....	28
4. Representative Oregon white oak age (year of origin in 20-yr bins) and sapling height distributions (Sap = sapling height) paired with diameter distributions across species for the same stands.	32
5. Distribution of Oregon white oak tree and sapling (Sap) year of origin across all stands.	34

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Correlation (Pearson's r) of stand structural and environmental variables with NMS ordination axes.....	22
2. Correlation (Pearson's r) of stand structural and environmental variables with NMS ordination axes for each study area.....	24
3. Oregon white oak regeneration levels indicated by sapling to tree (S:T) ratios (after Muick and Bartolome 1987), broken down by study area.	29
4. Nonparametric multiplicative regression age prediction models for each study area	31

LIST OF APPENDICES

<u>Appendix</u>	<u>Page</u>
A. Oak woodland sampled site and stand characteristics	62
B. Sapling dynamics	68
C. Relationships of Oregon white oak sapling;tree ratios to heat load	69
D. Woody species stand composition and cover by stand	70
E. Relationship of Oregon white oak dbh to age	73
F. Oregon white oak sapling age distribution of sampled sites	74
G. Stand structures	75
H. Relationships between age structure and the environment.....	84

LIST OF APPENDIX FIGURES

<u>Figure</u>	<u>Page</u>
1. Relationships of sapling:tree (S:T) ratios to heat load.	69
2. Relationship between sampled Oregon white oak tree dbhs and age counts.....	73
3. Distributions of Oregon white oak sapling year of origin across 12 sites, which spanned a range of sapling to tree ratios (n=85; aging based on increment cores taken at 0.8 m or on discs cut at ground level).....	74
4. Distributions of Oregon white oak tree year of origin and sapling height paired with diameter distributions for all tree species by stand.....	76
5. NMS ordination of 40 stands in age structural space.....	84

LIST OF APPENDIX TABLES

<u>Table</u>	<u>Page</u>
1. Environmental characteristics for sampled oak woodlands by stand.....	62
2. NMS stand structural matrix variables, and range across sites.....	66
3. NMS environmental matrix variables, and range across sites.	67
4. Sapling age predictions for Oregon white oak.....	68
5. Years for Oregon white oak trees to reach sapling height (0.8 m) from base (0.05 m).	68
6. Environmental variables evaluated for relationship to Oregon white oak sapling:tree (S:T) ratios using NPMR	69
7. Best NPMR model for predicting sapling:tree ratios.....	69
8. Tree species composition and percent cover.....	71
9. Shrub species composition and percent cover..	72

Stand Structures of Oregon White Oak (*Quercus garryana*) Woodlands and their Relationships to the Environment in Southwestern Oregon

Introduction

Oregon white oak (*Quercus garryana*, also known as Garry oak)-dominated woodlands 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). Alternatively, dense oak woodlands in particular may be the product of decades of fire suppression that permitted atypically dense tree ingrowth into historic 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. 2007). 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).

Case studies of Oregon white oak communities across the species' range from British Columbia to northern California have found that many 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). 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). 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 caused by a frequent low-severity fire regime that left widely-spaced trees (USDI 1998).

On southwestern Oregon public lands, fuels reduction treatments alter the current structure of oak woodlands, creating a more open oak landscape by targeting shrubs and smaller diameter trees for removal. For example, over 74,000 ha of the ~347,000 ha of public lands (across all vegetation types) managed by the Medford Bureau of Land Management (BLM) district have been treated for fuels reduction since 1996 (USDI 2007). Treatments are often driven by the dual-directive to reduce the threat of severe wildfire in the wildland-urban interface and accomplish restoration, using the guidelines of national and local mandates (Healthy Forest Restoration Act 2003, USDI 2007). To evaluate whether the fuels treatments are likely to restore historic oak woodland stand structures, however, more information is

needed on their historic and current structures and the factors that influence them. Investigations on the role of fire or other factors that influence non-coniferous stand structures have largely been concentrated in regions other than southwestern Oregon (e.g., Tveten and Fonda 1999, Erickson 2002), or 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). Generalizations that assume uniform fire regimes throughout one vegetation type in different regions can render restoration efforts ineffective or detrimental; such efforts should be based on understanding of the spatial complexity inherent in local natural disturbance processes (Veblen 2003, Duren 2009). To help identify whether restoration of Oregon white oak woodlands in southwestern Oregon is needed, and to inform restoration objectives and approaches, baseline data on current stand structures and regeneration status are needed.

The primary objectives of this study were to characterize current 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. The specific study questions were: (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 or fire history? (3) Are stand structures and age structures related and, if so, how? (4) What is the regeneration status of Oregon white oak 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? I provide new information on the condition, environmental associations, and history of Oregon white oak populations in an understudied portion of their range. This information can inform the development of regionally-specific models for restoration of oak woodlands on the public lands of southwestern Oregon where fuels reduction is also a priority.

Study Area

This 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 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 climate is temperate Mediterranean with cool, wet winters and warm, dry summers. Both study areas have been subject to anthropogenic disturbances such as mining, grazing, farming, settlement, land conversion, introduced exotic species, and fire use. Native Americans inhabited land in this region for thousands of years prior to European settlement, leaving behind a complex footprint of human influence on the landscape. In 1846, the Applegate Trail was completed, which created a passage for steady European settlement (Lawrence 1971). After the discovery of gold in Jacksonville, OR in 1851 (LaLande 1995), ensuing conflicts displaced Native Americans, settlement populations boomed and land uses shifted. Fire suppression policies began in the early 1900's, 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 Jackson County until fire-fighting technology advanced in the mid-1900's, and specifically when airplanes began dropping fire retardant in 1956 (Pyne 1982, Frost and Sweeney 2000).

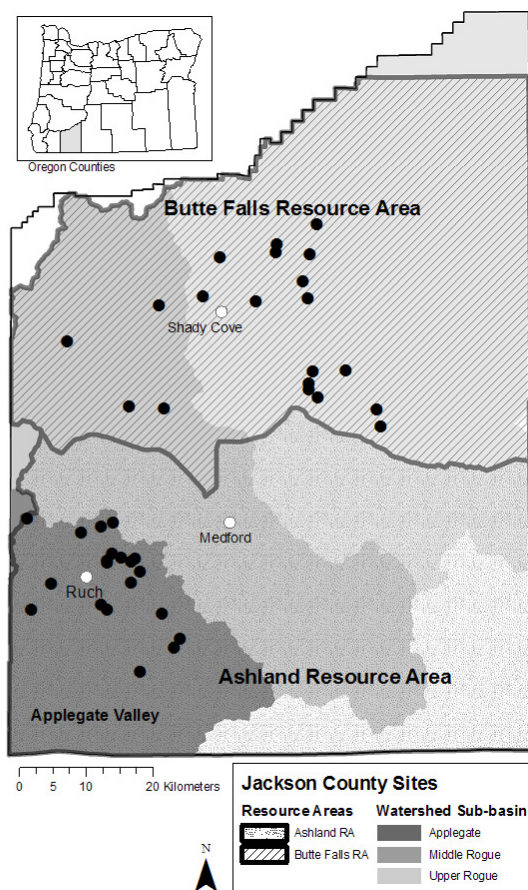


Figure 1. Study area in Jackson County, southwestern Oregon. Study sites are represented by circles and were located in Applegate Valley of the Ashland Resource Area and in the Butte Falls Resource Area, on USDI BLM land.

The regional vegetation zone is classified as Interior Valley pine-oak-Douglas-fir (*Pinus-Quercus-Pseudotsuga*) (Franklin and Dyrness 1973). Tree cover ranges from entirely Oregon white oak, to codominance with California black oak (*Quercus kelloggii*), madrone (*Arbutus menziesii*), ponderosa pine (*Pinus ponderosa*), incense

cedar (*Calocedrus decurrens*), and occasional Douglas-fir (*Pseudotsuga menziesii*). Common shrubs are poison oak (*Toxicodendron diversilobum*), whiteleaf manzanita (*Arctostaphylos viscida*), buckbrush ceanothus (*Ceanothus cuneatus*), and mountain mahogany (*Cercocarpus betuloides*). The understory is occupied by a variable mixture of native and exotic grasses and forbs intermixed with rock outcrops, leaf litter, exposed soil, and small mammal mounds.

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 in review). Study sites were spread over a 68 x 53 km area. Butte Falls land ownership is divided into a 1-km² checkerboard of public/private ownership, whereas the Applegate has larger contiguous ownership patches.

The Applegate Valley study sites are located in and around the unincorporated community of Ruch (42°14' N, 123°2' W) within the Applegate watershed sub-basin. Long-term mean annual temperature is 11.5°C and mean annual precipitation is 646 mm (Western Regional Climate Center [WRCC] 2009). Butte Falls is less topographically dissected than the Applegate, and its sites are within the Middle and Upper Rogue watershed sub-basins, in and around 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 higher than in the Applegate (853 mm; WRCC 2009). Soil types overlap between the 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

In the summer of 2008 I sampled oak woodlands on 20 sites in each resource area (Figure 1). Site locations were randomly selected with the GIS extension Hawth's Analysis Tools (Beyer 2004) using GIS layers that identified Oregon white oak-dominated vegetation (Ecoshare 2008, Pfaff 2007a), stratified to represent the range of soil types on which these oak communities occur and to avoid known disturbances such as fuels treatments or logging. Evidence of recent cattle presence (dung) was, however, observed on two site revisits, and it is possible that grazing occurred in other sites as well. 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 treatment. Data from these sites were excluded from most analyses but were retained for Oregon white oak tree age predictions; these sites are noted separately in results on stand-level diameter and age distributions. If randomly pre-selected GPS coordinates did not match the oak woodland community type (with Oregon white oak cover $\geq 25\%$) and sampling constraints in the field, the site was relocated to the nearest oak woodland, and sampling was centered on a randomly chosen point (compass direction and number of paces from woodland edge to plot center were selected with computer-generated random numbers), within the woodland patch. 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 (Appendix A). There were recorded wildfires (back to 1910) for many sites, with the most recent occurring in 1963.

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 tree seedling-sized regeneration were recorded. Relict trees were defined as having structures 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

I visually estimated percent cover of trees and shrubs at life form and species levels from plot center. When the plot had relatively uniform cover, visual estimates of cover were calibrated against the average of estimates in four cardinal directions from plot center made with a convex spherical densiometer (held at ~1 m height). I 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). I also recorded relict tree frequency (0-4; number of large plot quadrants in which relicts occurred) and a constrained count of relicts (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). Sapling data

included number of stems, species, and height for all live tree species ≥ 1.3 m tall and <10 cm dbh. In the seedling-sized regeneration subplots, I recorded the species and number of stems for regeneration (all living tree species < 1.3 m tall), and tallied the number of Oregon white oak regeneration stems that occurred under Oregon white oak tree driplines. Because the distinction between seedlings and sprouts was often not clear, they were lumped as seedling-sized regeneration. Sprouts visibly attached to a living parent tree base were treated as part of the adult tree rather than as seedling-sized regeneration. Shrub data included number of stems and stem basal diameter for all live shrub species > 1.3 m tall (excluding poison oak).

Additional data were recorded on Oregon white oaks only. Relict tree crown width measurements were taken on tree upslope, downslope, and parallel-to-sideslope radii in the 0.1 ha plot. 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 approximately 0.8 m with an increment borer to determine tree age. The largest stem of multiple-stemmed trees was cored. I cored all stems from five multiple-stemmed trees across three sites to estimate the age range encompassed by multiple-stems of the same tree. The smallest and largest living trees (≥ 10 cm dbh) of each conifer species were also cored when present. Six stands from each study area (totaling 12), selected to span the range of Oregon white oak sapling densities observed across all stands, were revisited in the summer of 2009. At that time, up to 10 Oregon white oak saplings (≥ 1.3 m tall and <10 cm dbh) per stand were cored at 0.8 m or cut at ground-level for aging, and their heights and dbhs were measured. The smallest diameter

sapling was selected for sampling, and the remaining sampled saplings were selected randomly.

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 2007*a*).

Increment Core and Cross Section Preparation

Cores were mounted with glue on grooved wood and belt-sanded from a coarse to fine surface, finishing with 400 grit paper and a 600 grit paper hand-sand if annual rings were unclear. I 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 ages were 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. Tree age resolution to the exact year of establishment was not needed for my purposes, so I did not cross-date.

Statistical Analysis

Patterns in Stand Structure

To examine patterns in oak woodland stand structure across all sites and within each study area, and their relationships to environmental attributes or disturbance history, I used nonmetric multidimensional scaling ordinations (NMS; Mather 1976, Kruskal 1964). Attributes measured at the individual tree or shrub level were converted to plot means to characterize overall stand structures in a 26-variable matrix (Appendix A). Variables were square root or log transformed if their skew was > 1 and if transforming decreased the skew (McCune and Grace 2002). Values for these variables were on different scales, thus, each was relativized by its standard deviate.

One stand was identified as an outlier (mean plot distance > 2 standard deviations from the grand mean) in the full 36-stand analysis, two in the Applegate, and one in the Butte Falls ordination. Deleting the outliers from the analysis had little effect on the relative positions of stands in stand structural space; rather, the overall breadth of stand structural space decreased. There was high heterogeneity among stands such that deletion of initial outliers produced new outliers in the following analyses. Because of this and because no biological case could be made for excluding the outliers (their stand characteristics were not anomalous), they were all retained in analyses.

A secondary matrix included environmental and disturbance history variables for each site (Appendix A). Variables included resource area, mean spring precipitation, elevation, heat load (McCune 2007), topographic position, shrub cover, mean shrub basal diameter, fire occurrence history (=0/1, recorded back to 1910, sites

with no recorded fire but with externally visible fire scars or charcoal on >1 tree also =1), years since wildfire (back to 1910), and distance from the nearest road. Topographic positions were ranked by hillside location and degree of protection, with the gradient ranging from bottomlands (=1) to draws, slopes, and exposed ridgetops (=8).

NMS ordinations were carried out using PC-ORD v. 6.93 beta (McCune and Mefford 2009) with random starting configurations in the conservative “slow and thorough” autopilot option with 250 real data iterations. I used Euclidean distances because there were negative numbers in the data set. The ordination solutions were orthogonally rotated to maximize correlations between stand structural axes and the environmental and disturbance variables, and the number of dimensions chosen for the final ordination was based on the result providing the lowest stress with statistical significance. I investigated relationships between gradients in stand structure and environmental and disturbance variables using correlation coefficients and visual overlays. The large number of comparisons examined between environmental variables and structural gradients, relative to the number of sampled stands (particularly in separate ordinations of resource areas), suggest that caution should be used in interpreting correlation coefficients (Pearson’s r) between environmental variables and stand structures.

Tree age predictions

To describe current 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. The purpose of these regressions was to estimate the age of uncored trees. I 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 logging 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 $\leq 10\%$; *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 $\geq 20\%$; 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.

I developed age prediction models for each resource area separately because separate models 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), excluding those with extensive rot, very small rings, or multiple centers. 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.

Efforts to predict ages for the subsample of aged saplings ($n=69$ across 12 sites) based on height were unsuccessful. Sapling ages were predictable based on dbh, but sapling dbh was not recorded at the sites where saplings were not aged (Appendix B). Thus, analysis of age structure patterns did not include predicted ages for sapling-sized individuals.

I 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, predicted ages for trees > 200 yr are less certain than those for younger trees, and are probably disproportionately underestimated. Nevertheless, it is likely that they established prior to 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

Oregon white oak tree ages (actual and predicted) were summarized graphically to describe and evaluate stand age structures. Six yr were added to each tree's or sapling's counted or predicted age (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 (Appendix B). When predicted ages were less than counted ages for trees with partial cores, the counted age was used in age structure analyses. I grouped trees in 20-yr age bins; this resolution was appropriate given error rates associated with age predictions. Two sapling height groups (≤ 4 m and > 4 m) were also included in age structure analyses, to facilitate a coarse assessment of their contribution to age structures and dynamics.

I 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). I evaluated major gradients in age structures (characterized using tree age minimum and maximum, range, skew, and kurtosis; and the median of combined tree and sapling ages) and their relationships to environmental and disturbance variables using NMS ordination.

Age structures were categorized as follows to evaluate trends in apparent Oregon white oak regeneration: (1) relatively continuous regeneration throughout, (2) relatively continuous regeneration until recently (zero to few saplings), (3) pulsed regeneration and zero to few saplings, (4) relatively low but continuous regeneration marked by one major pulse, (5) recent tree invasion or disturbance, with no trees $> \sim 100$ yr. While ages for most saplings were not available, it was important to include sapling-sized individuals in these categorizations. I did this by assessing the continuity of sapling heights and dbhs (when recorded) and by incorporating available sapling ages.

I used sapling to tree ratios (S:T) to examine apparent levels of Oregon white oak regeneration and regeneration across tree species 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). While 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.

I assessed whether apparent Oregon white oak regeneration success, as indicated by S:T ratios, could be predicted based on site environmental attributes (Appendix C). I used NPMR models to investigate the predictive power of variables including shrub data (cover and basal diameter); tree stem density, basal area, and canopy cover; soils (depth and texture; potential moisture status (spring precipitation, heat load); topography and disturbance (wildfire occurrence, years since wildfire, and site distance from nearest road). Variables were log transformed if their skew was > 1 and if transforming decreased the skew.

Results

Tree and Shrub Species Composition

The 36 sampled oak woodlands had a mean tree cover of 54% and mean Oregon white oak cover of 41% (Appendix D). 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 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 some stands, cover by other hardwoods was similar to that of Oregon white oak. California black oak occurred in 47%, madrone in 36%, and incense-cedar in 17% of stands. The entire tree inventory included 2547 tree- and 969 sapling-sized individuals.

All stands supported shrubs, with shrub cover ranging from 2–75% (Appendix D). Poison oak 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, buckbrush ceanothus, birchleaf mountain mahogany, deerbrush (*Ceanothus integerrimus*), Saskatoon serviceberry (*Amelanchier alnifolia*), and hollyleaved barberry (*Mahonia aquifolium*). The largest individuals included a 60.3 cm (basal diameter) whiteleaf manzanita, a 32.5 cm buckbrush ceanothus, and a 29.0 cm birchleaf mountain mahogany.

Patterns in Stand Structure and Relationships to Environment

Patterns across all stands - Tree densities, sizes, and stand structures ranged widely across sampled stands (Appendix A). Stand densities (tree + sapling stems) ranged from 150-1810 stems per ha, with a range of 90-1100 trees \geq 10 cm dbh per ha and 0-850 saplings per ha. Tree basal areas ranged from 4.5-42.4 m²/ha. Stands included variable proportions of single and multiple-stemmed Oregon white oaks, with a range of 0-66% of trees multiple-stemmed. Twenty eight percent of Oregon white oak trees across all size classes were multiple-stemmed, 10% \geq 30 cm dbh were multiple-

stemmed, and none ≥ 50 cm dbh were multiple-stemmed. Mean heights of Oregon white oak trees ranged from 5.1-9.1 m. 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. Oak tree mortality was generally low, and ranged from 0-18%. Ten stands had no relict trees within the 0.1 ha plot, and four of those had no relicts in sight. The average relict density (counted in the 0.1 ha plot) in stands that supported them was 21 relicts per ha.

Non-metric multidimensional scaling extracted two strong and interpretable gradients in stand structure across all stands, along with a third but weaker gradient. This ordination, and those within each study area, 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 full 36-stand 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 1).

Stands with relatively high proportions of Oregon white oaks in smaller dbh classes and higher sapling densities, stand densities (# of tree + sapling stems) and cover were towards the low end of the axis; 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 represented a gradient in proportions of multiple-stemmed trees; tree height, basal area and health values; and Oregon white oak seedling-sized regeneration densities, and accounted for 41.4% of the variance in the data. Stands with lower proportions of multiple-stemmed but relatively tall trees,

lower tree health values, and higher Oregon white oak seedling-sized regeneration densities were positioned 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. 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.

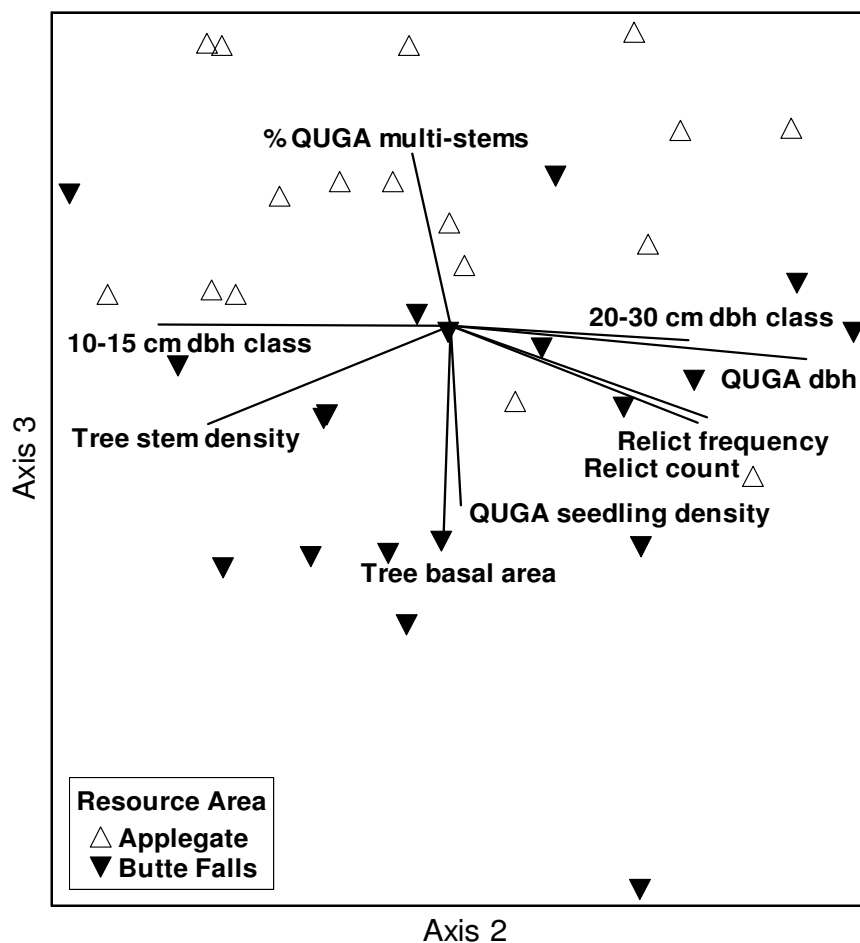


Figure 2. NMS ordination of all plots (triangles) in stand structural space (2 of 3 dimensions shown). Vectors represent the strongest gradients ($r^2 \geq 0.4$) in stand structure along Axes 2 and 3. QUGA = *Quercus garryana*. See Table 1 for variable definitions and units.

Table 1. 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)	0.18	-0.73	-0.47
Tree cover (across species, %)	0.16	-0.51	-0.53
Tree basal area (m ² /ha)	-0.15	-0.12	-0.67
Tree height (mean, m)	0.56	-0.02	-0.59
QUGA tree density (trees/ha)	-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)	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.

Percent soil silt was the only environmental variable strongly correlated with patterns in stand structure across the study area ($r = 0.59$ with Axis 3; Table 1, maximum $|r|$ for other variables = 0.40). Although the two study areas were intermixed, many plots from the Applegate fell higher on Axis 2 than those from Butte Falls (Figure 2), so it was not surprising that influential stand structural and environmental variables differed by resource area, as indicated by ordinations within

study areas. Other correlations of environmental variables with Axis 3 were weaker, but collectively appeared to reflect drier 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.

Patterns within study areas

In the Applegate Valley NMS ordination ($R^2 = 88.6\%$, final stress = 8.9, 61 iterations; Table 2), spring precipitation and percent silt were the environmental variables most strongly associated with the two strongest gradients in stand structure (Axes 2 and 3, respectively). The range of soil silt values among stands was, however, generally small, thus of uncertain biological significance (range across all but two stands = 37.8% - 39.9%; two stands had lower values of 32.3% and 24.7%). Mean shrub diameter was also positively correlated with Axis 3. Taller trees and Oregon white oak saplings, higher Oregon white oak sapling densities and proportions of small diameter (10-15 cm) trees, and stands with higher S:T ratios were all positively correlated with the gradient in precipitation; while Oregon white oak percent cover, dbh, proportions of larger dbh classes, and relict abundances were all negatively correlated with this gradient (Axis 2). Stands with higher percentages of soil silt and larger shrub diameters tended to support higher Oregon white oak tree, sapling, and stand densities (of all tree species); higher Oregon white oak percent cover and percentages of multiple-stemmed Oregon white oak trees and higher proportions of the smallest-diameter Oregon white oak trees (Axis 3, Table 2).

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

	Axis 1	Axis 2	Axis 3
Applegate Valley			
% variance explained by axes	13.9%	20.3%	54.3%
Environmental or structural attribute			
Spring precipitation (mm)	0.06	0.53	0.04
Soil silt (%)	0.03	-0.03	0.69
Shrub basal diameter (mean)	-0.04	-0.30	0.47
Topographic position	-0.46	-0.05	0.16
Stand stem density (tree+sapling stems/ha)	0.74	0.20	0.70
Tree cover (across species, %)	0.69	-0.06	0.40
Tree basal area (m ² /ha)	0.50	-0.35	0.28
Tree height (mean, m)	0.40	0.51	-0.43
QUGA tree density (trees/ha)	0.33	-0.33	0.64
QUGA cover (trees+saplings+regeneration, %)	0.23	-0.57	0.48
QUGA tree height (mean, m)	0.27	0.30	-0.46
QUGA tree mortality (% dead)	-0.11	-0.44	-0.62
QUGA % multi-stemmed trees	-0.15	0.20	0.48
QUGA crown ratio (mean, %)	-0.27	-0.06	-0.56
QUGA sapling height (mean, m)	0.50	0.51	0.19
QUGA sapling density (saplings/ha)	0.58	0.59	0.45
Sapling:Tree	0.22	0.70	-0.11
PSME saplings (%)	0.56	0.35	-0.45
PSME tree mortality (% dead)	0.64	0.02	-0.36
QUGA % in 10-15 cm dbh size class	0.44	0.82	0.47
QUGA % in 15-20 cm dbh size class	-0.16	-0.85	-0.18
QUGA % in 20-30 cm dbh size class	-0.27	-0.66	-0.49
QUGA % in 40+ cm dbh size class	-0.20	-0.25	-0.67
QUGA tree dbh (mean, cm)	-0.47	-0.69	-0.64
Relict tree frequency	-0.13	-0.45	-0.83
Relict tree constrained count	-0.13	-0.47	-0.84

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. Topographic positions range from (=1) most protected and lowest slopes/valleys to (=8) most exposed and highest slopes/ridgetops (Appendix A).

Table 2. Correlation (Pearson's r) of stand structural and environmental variables with NMS ordination axes for each study area (Continued).

	Axis 1	Axis 2	Axis 3
Butte Falls			
% variance explained by axes	48.1%	16.1%	23.8%
Environmental or structural attribute			
Soil depth to restrictive layer (cm)	0.61	-0.22	-0.17
Years since wildfire	-0.61	0.19	0.37
Wildfire occurrence (binary)	0.45	-0.01	-0.17
Distance to nearest road (m)	-0.17	0.50	-0.34
Shrub basal diameter (mean, cm)	-0.38	0.48	0.00
Stand stem density (tree+sapling stems/ha)	0.58	-0.84	0.23
Tree cover (across species, %)	0.59	-0.55	0.37
Tree basal area (m ² /ha)	-0.01	-0.45	0.79
Tree height (mean, m)	0.29	-0.30	0.62
QUGA cover (trees+saplings+regeneration, %)	-0.05	-0.56	0.59
QUGA tree height (mean, m)	0.11	-0.03	0.65
QUGA tree mortality (% dead)	-0.46	-0.40	0.18
QUGA sapling height (mean, m)	0.45	0.00	-0.35
QUGA sapling density (saplings/ha)	0.48	-0.68	-0.08
Sapling:Tree	0.29	-0.48	-0.24
PSME saplings (%)	0.45	-0.41	-0.28
PSME tree mortality (% dead)	0.23	-0.66	-0.14
QUGA regeneration density (stems/0.01 ha)	-0.46	-0.26	0.27
Tree health score (mean)	-0.10	0.68	-0.10
QUGA % in 10-15 cm dbh size class	0.83	-0.51	-0.14
QUGA % in 15-20 cm dbh size class	-0.57	0.36	0.17
QUGA % in 20-30 cm dbh size class	-0.82	0.22	0.23
QUGA % in 30-40 cm dbh size class	-0.53	0.51	0.00
QUGA % in 40+ cm dbh size class	-0.51	-0.14	0.71
QUGA tree dbh (mean, cm)	-0.88	0.34	0.46
Relict tree frequency	-0.72	0.29	0.49
Relict tree constrained count	-0.72	0.16	-0.60

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. Topographic positions range from (=1) most protected and lowest slopes/valleys to (=8) most exposed and highest slopes/ridgetops (Appendix A).

Structural attributes negatively correlated with Axis 3 included Oregon white oak tree height, crown ratio, mortality, proportions of large diameter trees and abundance of relict trees. Stands with higher stand densities, basal areas, and percent cover; more dense and taller Oregon white oak saplings, higher proportions of Douglas-fir saplings and tree mortality, and smaller mean dbhs of Oregon white oaks were associated with more protected and lower slope topographic positions (Axis 1),

whereas higher and more exposed topographic positions were associated with more open and less densely stocked stands with larger mean Oregon white oak tree dbhs and fewer saplings.

In Butte Falls, the environmental variables most strongly associated with patterns in stand structure were years since wildfire and soil depth, with more time since wildfire and shallower soils positioned lower on the strongest axis (Axis 1; NMS ordination overall $R^2 = 88.0\%$, final stress = 10.2, 103 iterations; Table 2). Stands with higher Oregon white oak mortality, seedling-sized regeneration density, proportions of larger dbh classes and more abundant relicts tended to be positioned towards the low end of the axis, while those with higher stand and sapling densities and cover, larger proportions of small diameter trees, and taller oak saplings were positioned towards the high end of the axis. Stands positioned high on Axis 2, which represented 16% of the variance in stand structure, tended to be farther from the nearest road and had relatively large mean shrub basal diameters and higher tree health scores, but lower stand densities, cover, and basal areas. Stands towards the top of Axis 2 also tended to have relatively low Oregon white oak cover, sapling densities, sapling to tree ratios, and proportions of the smallest dbh class stems, and lower Douglas-fir mortality (Table 2). Stand structure patterns on Axis 3 were not strongly associated with any environmental attributes, but the axis tended to separate stands with relatively tall trees, high basal areas, Oregon white oak cover, and proportions of large diameter oaks with widely spaced relict trees from those with shorter trees, lower basal areas, and lower Oregon white oak cover, but with more clustered and numerous relict trees.

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 (which include 6 yr added to compensate for growth to core height) if seedlings or sprouts were browsed or did not have a single dominant stem dating to establishment (Hibbs and Yoder 1993). Cores from 221 trees yielded nearly complete counts to pith. Using transparencies, I 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 from a single tree ($n = \text{five two- to four-stemmed trees across three stands}$) was 3-50 yr.

The mean age count for Oregon white oaks in the smallest tree dbh class (10.0- < 11.0 cm) was 113 yr. This class, however, included trees that ranged from 59 to 162 yr old (Figure 3). Thus, the presence of saplings (<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 Oregon white oak trees encountered had stems between 10-20 cm dbh. The median 1-cm dbh class encountered across all sites (15- < 16 cm) had a similar counted age range (84-150 yr) to that of 10 cm dbh trees (Appendix E). 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).



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

Sapling ages

Ages of cored Oregon white oak saplings ($n=85$; ≥ 1.3 m tall, <10 cm dbh) spanned from 8-164 yr (Appendix F). The mean sapling age was 83 yr, although the mean was 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 were aged, at least one sapling was younger than the sampled Oregon white oak trees, but only half had saplings with establishment dates after 1951. 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 36 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), and nearly two-thirds of stands also had low or very low sapling to tree ratios across all tree species. S:T 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; $xR^2 = 0.80$, $P = 0.001$; Appendix B).

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.

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

The range of Oregon white oak S:T ratios across study areas was not strongly predicted by environmental variables. The strongest predictor variable identified by NPMR was heat load, but the relationship was weak ($xR^2 = 0.16$, $P = 0.08$ from 100 Monte Carlo runs; NPMR; Appendix C). In this model, higher Oregon white oak S:T ratios were generally positively associated with relatively moderate heat loads, and S:T ratios were lowest on sites with the highest heat loads (Appendix C). S:T ratios were, however, also low in sites across the entire range of heat loads.

Tree age predictions from stand structural variables

NPMR successfully predicted ages for non-cored and 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 age structures of surviving Oregon white oak trees suggest a tendency towards pulsed regeneration (Figure 4; Appendix G), with limited recruitment since the 1930's 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. Ordination of stand age structures did not reveal strong correlations of gradients in age structure with environmental variables (Appendix H).

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)	-	18.5
Sensitivities		
Dbh (log, cm)	0.44	0.38
Mean # of stems/tree	0.43	0.18
Heat load	0.73	-
Spring precipitation	-	0.36
Tree cover (%)	0.58	-
Stand stem density (stems/ha)	-	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.

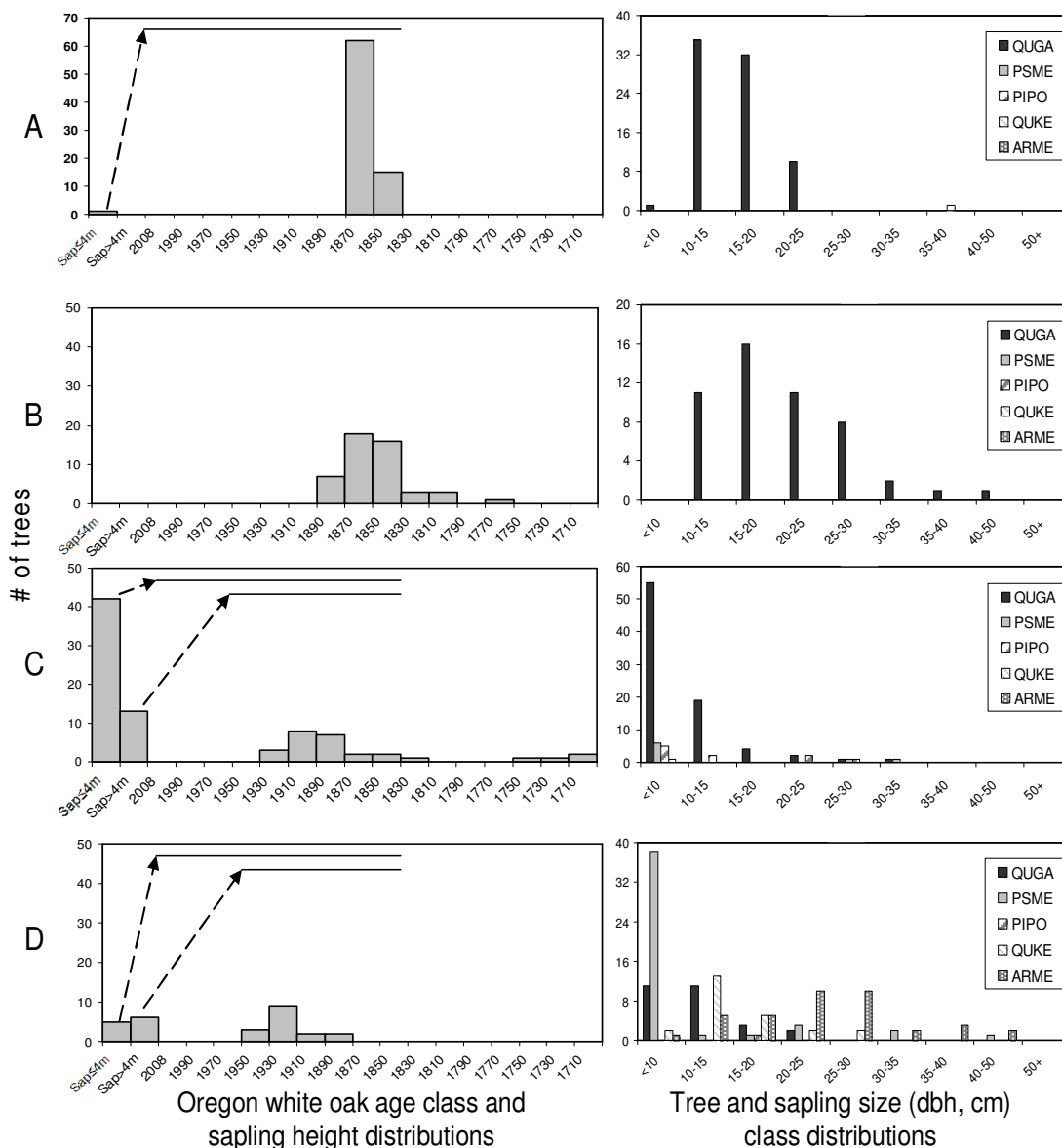


Figure 4. Representative Oregon white oak age (year of origin in 20-yr bins) and sapling height distributions (Sap = sapling height) paired with diameter distributions across species for the same stands. Arrows show observed age range of sapling height classes across all stands in which saplings were aged. Tree age structures are based on both counted and predicted ages. Stand A illustrates single pulse recruitment. Stand B illustrates historic 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*.

In many stands, the highest rates of establishment for currently surviving Oregon white oak trees occurred after European 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 this time, 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 half of 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 established post-settlement, and recruitment increased after estimated effective fire suppression. Ponderosa pines established both post- and pre-European 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.

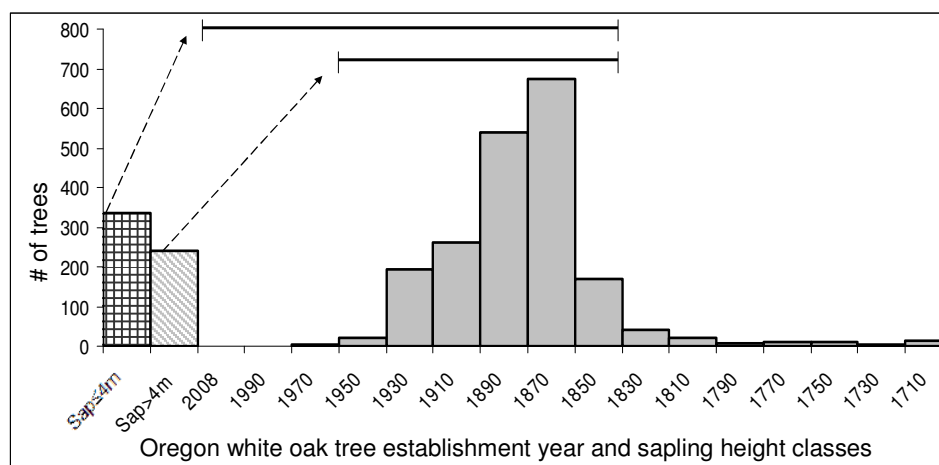


Figure 5. Distribution of Oregon white oak tree and sapling (Sap) year of origin across all stands. Data include both actual (cored) and estimated (using non-parametric multiplicative regression) tree ages. Sapling abundances are reported by height classes. Horizontal bars associated with sapling height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

Two of the four stands that probably experienced prescribed burning within the last 9 yr had little to no Oregon white oak regeneration; one of these two did support considerable Douglas-fir regeneration. The other two of these four stands had low Oregon white oak regeneration, with some (~1/3) to most of it probably originating post-1956 (saplings < 4m); one also supported considerable Douglas-fir regeneration.

Discussion

Overview

Tree and sapling age and size distributions in sampled woodlands suggest that age structure and recruitment dynamics may have shifted shortly after European settlement and again after fire suppression became more effective. For example, stands often had low current rates of regeneration success (based on sapling to tree ratios of surviving individuals), few sites showed evidence of continuous recruitment, and many experienced an unusually large oak regeneration flush between ~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). Although saplings established both pre- and post- fire suppression, most of those sampled established pre-1956 (Appendix G). The following discussion examines how the surveyed southwestern Oregon stand structures compare to Oregon white oak communities in other regions, interprets their apparent relationships to the environment, and explores implications of apparently major shifts in stand structures over time (using inferences from surviving tree size and age structures).

Individual environmental variables were weakly correlated with gradients in stand structure; the strongest correlations related to edaphic characteristics, potential site moisture status or fire history, depending on the study area. Collectively these represented a gradient from the harshest, driest sites in the Applegate study area to higher quality 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 after 1936. Stand structures on sites that experienced the most recent recorded fires (in 1955 or 1963) did appear to be fire-influenced.

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 further 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). While continuous patches of Oregon white oak woodlands identified with GIS varied from < 50 m to ~1600 m in extent, communities were patchier in the field; typically < ~300 m of continuous woodland occurred before transitioning to patches of prairie, chaparral, or conifer forest. This small spatial scale variation in communities suggests that these woodland patch-types may be more similar to ecotonal woodlands from other regions, than to the large contiguous expanses of former savanna which often serve as a restoration reference model. Consequently, the woodlands I sampled may be greatly influenced by adjacent patch-types.

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. Forested stands of Douglas-firs that dominated and overtopped large oaks were observed in both study areas, but were excluded from this study. I incidentally aged cross-sections of two intact large (54 and 65 cm diameter) Oregon white oak stumps from a heavily Douglas-fir overtopped oak woodland in the Applegate study area (cross-sections courtesy of BLM). These trees were 442 and 450 yrs old when they were cut during a wildfire, and showed a pronounced decrease in ring widths in the ~50-60 yr before death.

Relict tree densities were only about one-tenth of those observed in the northernmost part of Oregon white oak's historic savanna range in British Columbia,

and appear to be higher than relict densities reported from the Willamette Valley, although the latter comparison is uncertain owing to inconsistencies on relict definitions (Thilenius 1968, Gedalof et al. 2006). In general, ranges in tree densities in the stands I sampled overlapped with those documented for Oregon white oak-dominated communities both to the north and south (Thilenius 1968, Sugihara and Reed 1987, Thysell and Carey 2001, Gedalof et al. 2006). However, the highest stand densities that I encountered far exceeded the highest stand densities documented further north in Vancouver Island, British Columbia, where oak communities were formerly savanna (Gedalof et al. 2006), and also exceeded those reported for the narrow ecotonal 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 1940's in the Bald Hills of northern California (Sugihara and Reed 1987). Oregon white oak tree basal areas were often similar to those documented in other Oregon white oak communities (e.g., Riegel et al. 1992, Thysell and Carey 2001). In general, the Oregon white oaks that I inventoried in southwestern Oregon were shorter in stature than those reported for more northerly regions (e.g. Thysell and Carey 2001, Devine and Harrington 2007).

Patterns in Stand Structure and Relationships to Environment

Stand structures tended to diverge between the two study areas across a gradient from relatively high tree stocking (in terms of basal area, percent cover, and density) and low percentages of multiple-stems in the Butte Falls Resource Area to lower stocking and higher percentages of multiple-stems in the Applegate. This

gradient suggests that lower precipitation in an already seasonally droughty and relatively harsh environment may affect stand structures in the Applegate by reducing productivity (shorter Oregon white oak trees and less abundant seedling-sized regeneration than in the slightly more mesic Butte Falls). In contrast, Butte Falls study sites appeared better able to support stands with relatively high percentages of non-Oregon white oaks and taller Oregon white oaks. The tendency for tree health scores to be lower in Butte Falls than in the Applegate may be related to higher stocking in Butte Falls, which may lead to more competition for light, space, or other resources there. The correlation of soil silt percentages with this overall gradient in stand structure may suggest that more silty (and less clayey) soil textures contribute to the relative harshness of sites in the Applegate. The tendency for Applegate sites to support higher proportions of multiple-stemmed Oregon white oaks might suggest a more sensitive, oak top-killing response to fire or disturbance in many Applegate sites. The shrubby Oregon white oak subspecies, Brewer's oak (*Quercus garryana* var. *Breweri*), was not observed in surveyed sites, but it is possible that some of the oaks I sampled were influenced by hybridization with Brewer's oak (present in higher elevation woodlands [Pfaff 2007a]), in which case they might exhibit a multiple-stem morphology without disturbance. The gradient separating stand structures between study areas, however, accounted for less than half of the variation in overall stand structures; many factors undoubtedly interact to influence these stand structures, including individual site history, and differences in sites' successional stages and trajectories. Extensive variability among Oregon white oak stands and associated

complex relationships to the environment were also observed in the northernmost part of the species' range (Erickson 2002).

As was true for gradients in stand structure across study areas, those within each study area were also associated only weakly with measured environmental variables. Percent soil silt was most strongly correlated with stand structures in the Applegate Valley, however, the small range in soil silt across most sites seemed unlikely to cause a strong biological response. Two sites, however, had much lower silt percentages than the others; these may have influenced the strength of this correlation with stand structures. The low silt sites each supported unique soils (Manita loam and Tallowbox gravelly sandy loam) that were not present in other sites, although some soil characteristics were overlapping.

Spring precipitation also had a weak correlation with Applegate Valley stand structures. Relatively abundant sapling regeneration and taller trees in stands with higher precipitation suggest a positive effect of growing season precipitation on young tree growth, and also may suggest that lower precipitation might slow the transition from seedlings/sprouts to saplings. Although there was a modest range in precipitation across sites (104 to 130 mm), differences in plant associations in the Applegate have been associated with this range of variation in precipitation (Riegel et al. 1992, Pfaff 2007a). This suggests that differences in stand structures may also reflect, in part, differences in precipitation. Oregon white oak tree diameters might be expected to be larger for a given age where there is higher precipitation (Maertins 2008); however, that was not the case here. Clearly, the relationships of sapling

success and tree growth to the environment of Applegate sites are more complex than can be explained by a simple effect of precipitation.

Butte Falls stand structures were not correlated with precipitation levels, but were correlated with fire occurrence and time since fire. Sites that had recorded fire occurrences since 1910 and more recent fires often had deeper soils, relatively high stem and sapling densities, and higher proportions of trees in the smallest Oregon white oak diameter size classes. The apparent positive association of deeper soils with fire occurrence may suggest that sites with deeper soils are more likely to support sufficient fuels to carry fire relatively well. In turn, the positive association of small tree and sapling densities with sites that burned relatively recently may result from fire-initiated regeneration from sprout or seed (Regan and Agee 2004), enhanced by increased soil moisture in deeper soils (Murphy 2008). Stand structures in the Applegate might also have been correlated with fire history if they had experienced more recent fire (the most recent recorded fire there was in 1936).

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, Maertins 2008), soil limitations (Erickson 2002, Murphy 2008) and oak resilience to (prescribed) fire effects (Regan and Agee 2004, Fry 2008). The inconsistencies between my study areas in the apparent importance of these relationships suggest, however, that other factors are also influential.

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 my study area (e.g., Thilenius 1968, Sugihara and Reed 1987). Sapling-sized Oregon white oaks were often older than expected. Sapling 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 sometime done (e.g., Thilenius 1968, Muick and Bartolome 1987, Jackson et al. 1998); 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 both even- and uneven-aged stands, whereas age-growth dynamics might differ across stand types. While the stand-level mean number of stems per tree was an age predictor in models for both study areas, with trees of a given dbh tending to be younger in stands with higher mean numbers of stems per tree, the number of stems per individual tree was not included in models. The lack of correlation between stem number and age on an individual tree basis suggests that the predictive power of mean number of stems per tree may reflect the influences of disturbances that affect the occurrence of multiple stems rather than physiological differences between single- and multiple-stemmed trees. Variables that may indicate resource limitations were also important predictors, including those that may reflect availability of light or moisture (tree density or cover and heatload or spring precipitation). 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. The contribution of putative moisture stress variables to age-prediction models was variable, and suggested that there may be little tree growth response to moisture limitation until the stress reaches a threshold (Erickson 2002).

Regeneration

Oak regeneration problems have been noted and investigated in oak communities in the western United States for approximately 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 information on Oregon white oak regeneration rates in southwestern Oregon, and the one published report of low regeneration attributed it, at least in part, to unnaturally high stand densities caused by fire suppression (Riegel et al. 1992). I did find low Oregon white oak sapling to tree ratios in many stands, which coupled with the old ages of many saplings, may suggest that regeneration difficulties are common in southwestern Oregon as well. Causes for slowed or halted regeneration are, however, uncertain.

Seedling-sized oak regeneration was present in all stands, and often abundant, so 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 also, potentially, by particularly favorable site quality. Relatively benign site quality may also explain the positive association of seedling-sized regeneration with Oregon white oak driplines as well; adult tree presence indicates site or microsite suitability, and the trees may ameliorate the harshness of microsite conditions (Carvell and Tryon 1961).

Conifer encroachment consequent to fire exclusion reduces Oregon white oak growth and regeneration, (e.g., Reed and Sugihara 1987, Gedalof et al. 2006, Devine and Harrington 2006) and is considered the largest threat to persistence of Oregon white oak ecosystems, aside from land conversion (Fuchs 2001). However, this is unlikely to be a primary factor limiting sapling recruitment in the stands that I sampled, given that I selected stands that were not heavily encroached by conifers.

Other mechanisms that may inhibit sapling recruitment in southwestern Oregon are more difficult to document but are probably more applicable to most of the woodlands I surveyed. The seedling-to-sapling transition period can be lengthy, and browsing can defer that transition (Hibbs and Yoder 1993, Bartolome et al. 2002). Deer and deer signs were commonly observed in my study sites, hence browsing might limit sapling recruitment. Livestock grazing and trampling can also have negative effects on the transition from oak seedlings to saplings but do not necessarily lower seedling densities, perhaps in part because grazing can increase the duration of higher soil moisture levels during the dry season, favoring seedling survival (Hedrick and Keniston 1966, Jackson et al. 1998). It is likely that cattle grazed during recent times on at least some of the sites I sampled and they may have influenced sapling recruitment.

Additional factors that may contribute to the generally low (but variable) sapling densities that I observed include competition from exotic grasses (Barnhart et al. 1996, Thysell and Carey 2001); historic clearcutting (Brooks and Merenlender 2001); predator extirpation that increased herbivore densities (MacDougall 2008, Ripple and Beschta 2008), hydraulic mining (LaLande 1995), competition for soil water, particularly in the presence of conifers or low precipitation during the growing season (Devine and Harrington 2007, Devine et al. 2007), and high tree stocking levels. Lack of disturbance may also limit the transition between the seedling and sapling layer if, for example, fire reduces competition and thereby stimulates growth of surviving regeneration. Sprouting may be the primary regeneration mechanism (compared to in seeding), and if so, prolonged periods without fire (> 100 yr) in many sites may be detrimental to regeneration levels (Sugihara and Reed 1987). The correspondence between the onset of effective fire suppression and an apparent lack of sapling and tree recruitment suggests that absence of fire may be a contributing factor.

Levels of oak recruitment are often assessed by comparing densities of oaks in small versus large size classes, and low or declining sapling recruitment has been considered problematic in other regions for similar species (Muick and Bartolome 1987, Thomas 1987). Further, the existence of a reverse-J shaped recruitment curve in an uneven-aged stand is commonly taken to suggest that recruitment is sufficient to replace mortality and that the stand is likely to persist (Larsen et al. 1999). This tenet, however, assumes that recruitment must either be continuous or characterized by frequent episodic pulses. We do not know whether this concept applies to Oregon white oak. Until more information is available about pre-settlement stand conditions

or long-term oak population dynamics, there is uncertainty in interpreting low or diminishing sapling recruitment (Lorimer 1993).

Low regeneration may be normal if stands are fully stocked, due to 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 considering 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 vegetative recruitment by sprouting (Agee 1996) and increasing resource availability. The generally low tree mortality rates that I observed suggest that most stands were not overstocked, but may also suggest that oak communities in this region are slow to change, and may not need an abundance of regeneration (indicated by a reverse-J shaped recruitment curve) for stand perpetuation.

Higher Oregon white oak S:T ratios in mixed-oak stands (mixed-oak and oak-madrone) than in stands with higher proportions of Oregon white oak cover (open oak and oak woodland) may suggest that stands with higher soil moisture levels, and perhaps deeper soils capable of supporting conifers, better support oak regeneration (although may risk conifer encroachment in the absence of fire) than do drier sites. Saplings in dense stands may not indicate recent regeneration, however, if competition suppresses tree diameter growth. In addition, the temporal dynamics of regeneration may be different in oak woodlands with higher heat loads than in those with relatively low heat loads, as suggested by generally lower sapling to tree ratios on sites with the highest heat loads.

Changes in stand structures over time

Most surviving Oregon white oaks in my study areas established in the mid-late 1800's, after European settlement, although their ages 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), associated with the period of European settlement.

If fire set by settlers was frequent and widespread (LaLande 1995), human-set fire that topkilled and resprouted oaks may be responsible at least in part, for the apparent post-European settlement origins of many surviving trees (Regan and Agee 2004). Oak recruitment also coincided with high livestock stocking levels in southwestern Oregon, which began in the 1850's and continued through the 1890 – 1920's (LaLande 1995, Hosten et al. 2007). Overgrazing following peak use and the poor market of the Great Depression resulted in a large drop in sheep and cattle grazing levels post-1920's (LaLande 1995). Heavy livestock grazing may have decreased oak competition with grasses, but mechanisms by which grazing would facilitate such a marked flush of oak regeneration are not obvious. Other changes in land use associated with European settlers may have had positive effects on sapling recruitment (e.g., increased hunting reduced ungulate herbivory, until predator eradication [MacDougall 2008], and resprouting stimulated by woodcutting). The oak recruitment flush also occurred after a climatic transition from extended drought during ~ 1815 - 1850 (and likely more wildfire) to wetter and cooler conditions (indicated by the Palmer Drought Severity Index, smoothed to reduce inter-annual variability; Cook et al. 2004, Messier 2008). This recruitment flush corresponded with

increased tree growth rates and recruitment in nearby mixed conifer riparian areas, which may have been related to increased light availability in fire-thinned stands, followed by conditions amenable to successful tree recruitment (Messier 2008).

It remains unknown whether tree densities in oak woodlands increased after Euro-American settlement. It is commonly assumed that Oregon white oak tree densities were lower before than after European settlement (e.g., Stein 1990, Riegel et al. 1992, Fuchs 2001), and the structures of stands dominated by < 150 year old trees, with low densities of open-grown trees, that I surveyed are consistent with this conception. Historical records (e.g., General Land Office [GLO] surveys) document that dense oak woodlands occupied substantial portions of the landscape in southwestern Oregon during the 1850's (Hickman 2005, Hosten et al. 2007). However, our mechanistic knowledge of oaks' environmental limitations and response to fire does not preclude the possibility that there was a great deal of landscape patchiness in the past, which included both historic woodlands (perhaps with higher densities of post-burn small diameter sapling resprouts than of old, slow growing saplings) and environmentally-limited open-oak patches. I observed high patchiness in community types and a diversity of stand structures - some with multiple open-grown relicts (which may indicate historically more open conditions), but others with few to no relicts. Increased frequency of human-set fires during the European settlement period from the mid-1800's through the early 1900's, relative to pre-settlement (Frost and Sweeney 2000), may have caused tree mortality and partially erased stand histories in denser stands. Thus, inferences about historic stand structures based on current relict densities are only speculative.

Management Implications

Fuels treatments can be useful in the wildland-urban interface to reduce the threat of uncontrollable wildfire, particularly in close proximity to human habitation or other developments. Challenges arise, however, when fuels treatments are also intended to restore ecosystems that are presumably altered by fire suppression. In such cases, we need to understand whether fuels treatments foster or are detrimental to restoration goals. This understanding is enhanced by knowledge about current stand structures and histories, both of which were quite variable in my southwestern Oregon study sites. Some stands appeared to regenerate in pulses, possibly in response to disturbance such as high intensity fire. Others had truncated bell-curve shaped age structures, which suggested abundant and continuous recruitment followed by a fairly abrupt decline in regeneration, possibly in response to high stand densities or other factors, such as lack of disturbance by fire. Even though it is not clear that low regeneration rates in southwestern Oregon threaten the persistence of Oregon white oak communities in the region, managing these communities to increase Oregon white oak regeneration would diversify their stand and age structures and advance knowledge about ways to foster regeneration should the species begin to die without replacement. It is not clear that current fuels treatments that use hand-cut pile burn or mechanical mastication and leave widely spaced trees and shrubs favor oak regeneration, and they may inadvertently increase cover by exotic annual grasses (Perchemlides et al. 2008). In a comparison of treated and untreated chaparral-Oregon white oak communities in the Applegate Valley 4–7 yr post-treatment, oak regeneration was suggestively lower in treated sites ($P = 0.07$; Perchemlides et al.

2008). Further, treatments that cut shrubs may also reduce low-to-the-ground shrub cover beneficial to small mammals that disperse mycorrhizae necessary for successful transitions from Oregon white oak seedlings to saplings (Frank et al. 2006).

In contrast, prescribed fire may be useful and possibly preferable to treatments that rely exclusively on mechanical thinning for achieving restoration or perpetuation of oak-dominated communities. Oaks are fire adapted, and unlike many conifers that are prone to overtopping oaks, they can survive fire (or resprout after topkill) and thus, gain a competitive advantage post-burn (Sugihara and Reed 1987). However, fire also poses risks of changing understory composition, particularly by inadvertently increasing cover by exotic annual grasses (D'Antonio and Vitousek 1992) or causing unexpected vegetation successional trajectories if fires are uncharacteristically severe owing to unnaturally dense pre-fire conditions. Further, prescribed burning may not be implementable in the wildland-urban interface, given the current densities of many Oregon white oak woodlands. If restoration is needed, but stands are too dense to safely prescribe fire, those with encroaching Douglas-fir could benefit from prioritizing cutting treatments that selectively remove Douglas-fir. For example, in the Bald Hills oak communities of northern California, the Redwoods National and State Parks implemented a locally-adapted restoration plan that includes removal of conifers and exotic species, coupled with prescribed burning at intervals ≥ 3 yr (Hosten et al. 2006); these intervals are intended to minimize encroachment of Douglas-fir (Sugihara and Reed 1987). Fuels treatments such as low intensity underburning or broadcast burning may mimic natural disturbances and stimulate oak regeneration via sprouting and by creating canopy gaps in which recruitment can occur. We do not know what

structures characterized historic Oregon white oak communities in southwest Oregon, but the varied age structures and complex relationships of stand structures to site conditions and histories that we observed indicate that uniform fuels treatments may not benefit all types. Application of various treatments in monitored adaptive management areas would help identify those that support long-term oak community persistence. Tree size or age structures and the presence/absence of young saplings should be considered before applying prescribed burns, because fires can kill young oak trees. Such mortality may be particularly important in sites where recruitment is present but limited, particularly if fires are repeated at frequent intervals (< 10-14 yr; Fry 2008). In sites where burning would be likely to help achieve regeneration objectives, it should be infrequent enough to allow regeneration to transition to sapling and fire-safe sizes. In sites with encroaching Douglas-fir, however, fires frequent enough to prevent it from overtopping and outcompeting oaks (~3-5 yr) may be recommended (Sugihara and Reed 1987).

More research is needed to better understand how variables that appear to reflect site moisture status, which were related to patterns in stand structure, affect oak recruitment. Information derived from such research will help discern whether site-to-site variation in regeneration levels is due to unique (and very slow to change) site characteristics, such as soil or microclimate position, or to attributes that can be manipulated by management. If regeneration is substantially affected by site moisture status, future climate change-induced alterations in moisture regimes might increasingly restrict Oregon white oak's distribution, particularly given that

southwestern Oregon is the driest part of the species' range (Franklin and Dyrness 1973).

Future studies to enhance understanding of the influences of disturbances on oak woodlands development would benefit from investigating stand histories in-depth. For example, sapling-sized trees are often overlooked in age structure studies, but their broad age range indicates that knowledge of their ages is important for understanding stand dynamics, in particular the extent of recent recruitment. Improved understanding of stand dynamics can enhance the management of oak woodlands in the future. In addition, management will be enhanced by knowledge gained from sustained monitoring of Oregon white oak communities after fuels treatments, whether these are intended to accomplish fire hazard reduction, restoration or both.

Conclusions

This study revealed that there are a wide range of Oregon white oak woodland stand types, encompassing even- and uneven-aged stands and variations in regeneration status. Multiple environmental and disturbance processes apparently influence the stands in ways that are difficult to generalize even within study areas. Although a large proportion of Oregon white oak-dominated communities has been lost across the species' range, large acreages of public lands in southwestern Oregon continue to support such communities, many of which are woodlands. It is important to protect and learn more about these communities, which are imperiled in much of their historic range. In particular, given the current wide scale application of fuel reduction treatments in the study area, which often have a dual objective of accomplishing hazard reduction and ecosystem restoration, it is important that we understand the

extent to which various treatment prescriptions do or do not foster perpetuation or restoration of Oregon white oak communities.

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Appendices

Appendix A Oak woodland sampled site and stand characteristics

Table 1. Environmental characteristics for sampled oak woodlands by stand. Sites 1-20 are from the Applegate Valley, and 101-120 are from the Butte Falls study area. See Table 3 for definitions of categorical and coded quantitative variables. Stand numbers followed by “x” probably received fuels treatments. Sites with recorded fire occurrence but 100 yr since recorded fire had signs of wildfire such fire scars or char on ≥ 2 trees. (Char on treated sites is assumed to be from prescribed burn, and not recorded here.)

Site	1	2	3	4	5	6x	7	8	9x	10
Elevation (m)	917	1257	909	772	905	509	609	802	1021	877
Resource Area	1	1	1	1	1	1	1	1	1	1
Shrub cover (%)	60	35	10	24	28	0.1	10	55	2	14
Topographic position code	3	5	7	6	7	5	5	7	7	4
Heatload	0.94	0.80	0.92	0.89	0.93	0.78	0.82	0.63	0.86	0.87
Soil silt (%)	24.7	37.8	38.1	39.9	37.8	39.9	39.9	39.9	37.8	37.8
Soil sand (%)	65.8	37.8	36.7	33.3	37.8	33.3	22.2	33.3	37.8	37.8
Soil clay (%)	9.5	24.4	25.2	26.8	24.4	26.8	37.9	26.8	24.4	24.4
Parent geology code	1	2	2	2	2	3	2	2	2	2
Soil type code	1	2	4	2	2	5	5	6	2	2
Spring precipitation (mm)	121	130	107	104	109	101	107	120	120	105
Depth to soil restrictive layer (cm)	61	43	82	98	43	98	98	98	43	43
Shrub basal diameter (mean, cm)	8	13.3	13.4	13.5	8	12	13	17	21	14
Cover type code	3	1	1	2	1	3	1	2	2	2
Distance to nearest road (m)	229	143	138	74	317	190	233	497	100	77
Underburn	0	0	0	0	0	1	0	0	1	0
Recorded fire occurrence	0	0	1	1	1	0	1	0	0	1
Yr since recorded fire	100	100	72	72	94	100	72	100	100	72

Table 1. Environmental characteristics for sampled oak woodlands by stand (Continued).

Site	11	12	13	14	15	16x	17	18	19	20
Elevation (m)	687	701	723	735	746	561	897	782	656	532
Resource Area	1	1	1	1	1	1	1	1	1	1
Shrub cover (%)	35	45	10	10	23	10	25	35	9	4
Topographic position code	4	3	3	8	5	7	7	3	6	4
Heatload	0.73	0.68	0.92	0.96	0.91	0.70	0.94	0.91	0.90	0.73
Silt (%)	39.9	39.9	38.1	37.8	39.9	39.9	39.9	37.8	38.1	32.3
Sand (%)	33.3	33.3	36.7	37.8	33.3	33.3	33.3	37.8	36.7	20.9
Clay (%)	26.8	26.8	25.2	24.4	26.8	26.8	26.8	24.4	25.2	46.8
Parent geology code	2	2	2	2	2	2	2	2	2	2
Soil type code	6	6	4	2	6	5	6	2	4	7
Spring precipitation (mm)	114	113	116	124	115	102	114	105	112	105
Depth to soil restrictive layer (cm)	98	98	82	43	98	98	98	43	82	147
Shrub basal diameter (mean, cm)	9	10	17	27	14	0.1	11	18	8	9
Cover type code	2	2	4	3	2	4	3	2	1	3
Distance to road (m)	30	72	875	133	323	72	30	316	53	222
Underburn	0	0	0	0	0	1	0	0	0	0
Fire occurrence	1	0	0	0	0	1	0	1	0	0
Yr since fire	72	100	100	100	100	94	100	72	100	100

Table 1. Environmental characteristics for sampled oak woodlands by stand (Continued).

Site	101	102	103	104	105	106	107	108	109	110
Elevation (m)	413	515	678	497	570	542	951	396	433	603
Resource Area	2	2	2	2	2	2	2	2	2	2
Shrub cover (%)	35	35	28	38	3	10	16	40	60	40
Topographic position code	2	1	2	3	8	1	3	3	2	3
Heatload	0.78	0.79	0.84	0.80	0.85	0.79	0.77	0.76	0.72	0.77
Silt (%)	27.9	29.8	37.8	29.8	37.8	31.5	31.5	38.8	39.9	29.8
Sand (%)	17.1	24	37.8	24	37.8	30.9	30.9	36.6	33.3	24
Clay (%)	55	46.2	24.4	46.2	24.4	37.6	37.6	24.6	26.8	46.2
Parent geology code	4	5	5	5	6	5	5	1	7	5
Soil type code	8	3	2	3	2	9	10	11	6	3
Spring precipitation (mm)	90	125	139	134	144	140	190	118	90	142
Depth to soil restrictive layer (cm)	89	76	43	76	43	84	84	142	98	76
Shrub basal diameter (mean, cm)	8	1	8	4	23	2	2	5	6	4
Cover type code	1	3	1	3	1	1	3	4	4	1
Distance to road (m)	129	30	322	34	117	45	80	38	379	281
Underburn	0	0	0	0	0	0	0	0	0	0
Fire occurrence	0	0	0	0	1	0	0	1	1	0
Yr since fire	100	100	100	100	100	100	100	53	100	100

Table 1. Environmental characteristics for sampled oak woodlands by stand (Continued).

Site	111x	112	113	114	115	116	117	118	119	120
Elevation (m)	899	644	615	842	617	629	592	568	800	622
Resource Area	2	2	2	2	2	2	2	2	2	2
Shrub cover (%)	6	5	35	40	14	2	75	58	20	15
Topographic position code	6	4	5	5	7	2	4	6	7	5
Heatload	0.85	0.76	0.88	0.89	0.90	0.93	0.65	0.90	0.90	0.63
Silt (%)	29.8	29.8	31.5	29.8	29.8	31.5	31.5	29.8	27.9	36.9
Sand (%)	24	24	30.9	24	24	30.9	30.9	24	17.1	37.2
Clay (%)	46.2	46.2	37.6	46.2	46.2	37.6	37.6	46.2	55	25.9
Parent geology code	8	9	5	8	9	5	5	5	10	11
Soil type code	3	3	10	12	12	13	14	12	15	16
Spring precipitation (mm)	185	118	143	182	139	167	126	141	169	122
Depth to soil restrictive layer (cm)	76	76	84	76	76	84	84	76	89	92
Shrub basal diameter (mean, cm)	1	3	5	15	8	12	2	4	5	11
Cover type code	4	3	2	3	3	2	3	3	3	4
Distance to road (m)	190	142	401	781	314	121	97	173	30	30
Underburn	1	0	0	0	0	0	0	0	0	0
Fire occurrence	0	0	1	0	1	0	0	1	0	0
Yr since fire	100	100	100	100	100	100	100	45	100	100

Table 2. NMS stand structural matrix variables, and range across sites.

Stand Structural Variable	Minimum	Maximum	Mean
Tree cover (trees+saps+regeneration, across species, %)	25	85	56
Stand density (stems/ha [saplings+trees] across tree species)	150	1810	990
Sapling:Tree ratio (#saps/#trees across species)	0	2.09	0.59
Tree height (mean, m, across species)	5.1	13.9	8.3
Tree health (mean score, across species)	2.0	3.0	2.7
PSME encroachment (PSME saps/PSME+QUGA saps) ¹	0	100	20
PSME tree mortality (% dead) ¹	0	100	22
QUGA cover (trees+saplings+regeneration, %)	15	75	42
QUGA tree basal area (m ² /ha)	42.4	4.5	19.5
QUGA tree density (trees/ha)	50	1080	370
QUGA sapling density (saplings/ha) ¹	0	560	150
QUGA regeneration density (stems/0.01 ha) ¹	0	344	46
QUGA relict constrained count	0	8	3.3
QUGA relict frequency	0	4	2.1
QUGA crown ratio (mean, %)	50	86	70
QUGA tree height (mean, m)	5.1	9.7	7.4
QUGA sapling height (mean, m)	6.6	0	3.3
QUGA tree dbh (mean, cm)	10.9	23.6	16.7
QUGA % multi-stemmed trees	0	66	28
QUGA # of stems/tree (mean)	1	2.4	1.4
QUGA tree mortality (% dead) ¹	3.7	18	0
QUGA % in 10-15 cm dbh size class ²	0	100	47
QUGA % in 15-20 cm dbh size class ²	0	56	31
QUGA % in 20-30 cm dbh size class ²	0	78	41
QUGA % in 30-40 cm dbh size class ²	0	18	3
QUGA % in 40+ cm dbh size class ²	0	13	3

Species codes: QUGA = *Quercus garryana*, PSME = *Pseudotsuga menziesii*. Saps = saplings. 1=log-transformed in analysis
2=square-root transformed in analysis, % in size class of all size classes per stand. Trees were defined as individuals with dbh \geq 10cm; saplings as dbh < 10 cm and \geq 1.3 m tall, and seedling-sized regeneration as < 1.3 m tall. Tree health was scored from 3-0 (3= good health, 2=poor health, 1=nearly dead, 0=dead).

Table 3. NMS environmental matrix variables, and range across sites.

Environmental Variable (Quantitative)	Minimum	Maximum	Mean
Elevation (m)	396	1257	701
Heatload (unitless; based on NPMR with input of slope, aspect, and latitude)	0.63	0.96	0.82
Spring precipitation (total mm, March+April+May)	90	190	126
Shrub cover (%)	0.1	75	25
Shrub diameter (mean, cm at ground level, poison oak not included)	0	27	10
Soil % silt	25	40	35
Soil % sand	17	66	32
Soil % clay	9	55	33
Soil restrictive layer (depth to, cm)	43	80	147
Distance to road (m)	30	875	196
Years since recorded wildfire (back to 1910, 100 = none recorded)	45	100	99
Environmental Variable (Coded Quantitative) All values listed, median (or mode) in bold.			
Topographic position: (1) valley bottom near streambed, (2) low slope table or low-midslope next to draw, (3) lower slope or mid-upper slope in draw, (4) lower-mid slope or upper-mid slope in draw, (5) mid-slope or mid-slope table , (6) upper-mid slope, or upper-slope table, (7) upper slope, (8) next to ridge or ridgetop			
Fire occurrence: (0) no fire, (1) recorded wildfire since 1910 or >2 trees with visible external fire scar or char			
Underburn: (0) = no treatment, (1) = probable underburn or broadcast burn.			
Environmental Variable (Categorical) All values listed, mode in bold.			
Parent geology material (n=11): Volcanic rocks ; sedimentary and volcanoclastic rocks, sedimentary and volcanic basaltic lava flows; sedimentary and volcanic undifferentiated tuffaceous sedimentary rocks, tuffs, and basalt; undifferentiated tuffaceous sedimentary rocks, tuffs, and basalt; sedimentary alluvial deposits; nonmarine sedimentary rocks; partially metamorphosized sedimentary rocks; metamorphic May Creek Schist; granitic intrusive rocks;			
Soil type (n=16): McMullin-Rock outcrop complex , Medco-McMullin complex, McNull-Medco complex, McNull-McMullin gravelly loam, McNull gravelly loam, Caris-offenbacher gravelly loams, Tallowbox gravelly sandy loam, McNull loam, Vannoy silt loam, Manita loam, Shefflein loam, Medco cobbly clay loam, Carney clay, Carney-Tablerock association, Vannoy-Voorhies, Speaker-Josephine complex			
Cover type (n=4): open oak, oak woodland, mixed oak , oak-madrone (see text for descriptions)			
Study area (n=2): Applegate Valley, Butte Falls			

Appendix B Sapling dynamics

Table 4. Sapling age predictions for Oregon white oak. Oregon white oak sapling age (log) prediction model (NPMR) from 12 sites where dbhs were recorded. Local linear settings were used, and P was determined from 100 Monte Carlo runs.

Predictor	Cumulative xR^2	Tolerance	Sensitivity	Average N*	Min. Model N*	P
Sapling (log) dbh	0.80	0.239	2.06	49.13	4.0	0.01

Table 5. Years for Oregon white oak trees to reach sapling height (0.8 m) from base (0.05 m). Years are differences in ages between cores taken at 0.8 m and sapling disc cut at 0.05 m ($n = 13$, collected from 8 sites). Sapling (“Sap.”) ages and diameter were measured at base (0.05 m).

Mean difference	Median difference	Min. difference	Max. difference	Sap.age range	Sap. diameter range
6	5	1	19	8-100 yr	0.9 – 7.2 cm

Appendix C Relationships of Oregon white oak sapling:tree ratios to heat load

Table 6. Environmental variables evaluated for relationship to Oregon white oak sapling:tree (S:T) ratios using NPMR. See Appendix A, Table 3 for definitions of categorical and coded quantitative variables. See Appendix D, Table 9 and Appendix A, Table 2 for variable definitions.

Elevation (m)	Heatload	Topographic position
Shrub cover (%)	CECU cover(%)	ARVI cover (%)
Soil silt (%)	Soil sand (%)	Soil clay (%)
Tree density (tree stems per ha)	Basal area (m ² per ha)	Tree cover (%)
Soil depth to restrictive layer (cm)	Parent geology	Soil type
Spring precipitation (mm, Mar.-May)	Mean shrub basal diameter (cm)	
Years since recorded wildfire	Underburn (0/1)	Cover type (tree)

Table 7. Best NPMR model for predicting sapling:tree ratios. Local mean Gaussian settings were used, and *P* was determined from 100 Monte Carlo runs. Suggestive significance of p-value probably due, in part, to low S:T ratios occurring across the entire range of heat loads.

Predictor	Cumulative xR ²	Tolerance	Sensitivity	Average N*	Min. Model N*	<i>P</i>
Heat load	0.16	0.033	1.42	9.1	1.8	0.08

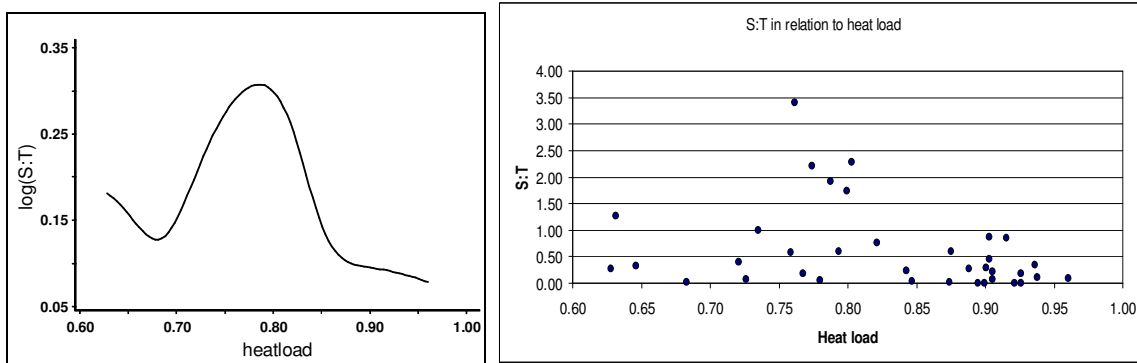


Figure 1. Relationships of sapling:tree (S:T) ratios to heat load. Modeled relationships of (log) S:Ts on left (xR² = 0.16, *P* = 0.08; NPMR); compared with raw data scatterplot of actual relationships of S:T ratios to heat load, on right. Maximum (log) S:T values (on left) corresponding to regeneration classification (after Muick and Bartolome 1987): 0.04 = very low, 0.17 = low, 0.3 = medium, > 0.3 = high.

Appendix D Woody species stand composition and cover by stand

Tree acronym definitions: QUGA = *Quercus garryana*, PSME = *Pseudotsuga menziesii*, PIPO = *Pinus ponderosa*, ARME = *Arbutus menziesii*, QUKE = *Quercus kelloggii*, PREM = *Prunus emarginata*, FRLA = *Fraxinus latifolia*, CADE = *Calocedrus decurrens*.

Shrub acronym definitions: TODI = *Toxicodendron diversiloba*, CECU = *Ceanothus cuneatus*, ARVI = *Arbutus menziesii*, CEBE = *Cercocarpus betuloides*, CEIN = *Ceanothus integerrimus*, MANE = *Mahonia nervosa* = HODI = *Holodiscus discolor*, SYAL = *Symphoricarpos albus*, AMAL = *Amelanchier alnifolia*, ROSA = *Rosa spp.*

Table 8. Tree species composition and percent cover. Stand numbers followed by “x” probably received fuels treatments.

Applegate Valley																				
Site #	1	2	3	4	5	6x	7	8	9x	10	11	12	13	14	15	16x	17	18	19	20
Total	50	25	30	60	35	70	30	55	75	55	68	55	85	35	70	60	50	70	33	35
QUGA	30	15	30	60	35	40	30	55	75	53	60	55	20	33	70	20	20	70	30	28
PSME	-	-	-	<1	-	7	-	-	-	-	-	-	25	5	-	5	15	-	3	4
PIPO	-	10	-	-	-	10	-	-	<1	5	-	<1	1	6	-	3	-	-	-	7
ARME	-	-	-	-	-	5	-	-	-	-	10	-	20	-	-	35	5	-	-	7
QUKE	20	-	-	-	-	-	-	-	-	-	-	-	50	-	-	2	20	-	-	-
PREM	-	-	-	-	-	-	-	<1	-	-	-	-	-	-	-	-	-	-	-	-
FRLA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CADE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Butte Falls																				
Site #	101	102	103	104	105	106	107	108	109	110	111x	112	113	114	115	116	117	118	119	120
Total	40	80	25	65	42	35	45	85	80	45	80	70	70	40	65	52	85	60	50	70
QUGA	40	60	22	50	40	33	35	25	27	40	55	50	65	17	30	47	70	45	40	40
PSME	-	3	-	4	-	1	3	10	-	5	6	6	2	1	25	3	15	6	6	8
PIPO	-	30	3	10	3	3	7	12	1	4	11	8	5	9	7	3	10	12	6	6
ARME	-	2	-	-	-	-	-	33	20	-	20	5	-	-	12	-	6	8	3	25
QUKE	-	15	3	8	-	<1	-	25	33	<1	<1	20	3	13	8	2	7	-	1	-
PREM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FRLA	-	5	-	-	-	3	-	-	-	-	-	-	-	<1	-	-	-	-	-	-
CADE	-	-	-	-	-	-	<1	-	-	-	<1	-	-	2	4	2	-	2	3	-

Table 9. Shrub species composition and percent cover. Stand numbers followed by “x” probably received fuels treatments.

Applegate Valley																				
Site #	1	2	3	4	5	6x	7	8	9x	10	11	12	13	14	15	16x	17	18	19	20
Total	60	35	10	24	28	<1	10	55	2	14	35	44	10	10	23	10	25	35	18	4
TODI	4	-	<1	20	3	-	5	-	<1	-	10	30	-	7	10	10	5	32	8	-
CECU	25	-	7	-	18	<1	-	-	-	4	15	12	-	-	-	<1	<1	3	7	<1
ARVI	45	-	-	-	<1	-	5	-	-	-	10	-	10	4	14	<1	5	30	-	4
CEBE	-	28	3	4	-	-	2	25	2	10	2	7	-	-	<1	-	6	-	5	-
CEIN	2	-	-	-	-	-	<1	-	-	-	-	-	-	-	1	-	2	<1	-	-
MANE	-	5	-	-	8	-	-	35	-	-	-	-	-	-	-	<1	8	-	-	-
HODI	-	-	-	-	-	-	-	-	-	-	<1	-	-	-	-	-	-	-	-	-
SYAL	-	-	-	-	-	-	-	<1	-	-	-	-	-	-	-	-	-	-	-	-
AMAL	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ROSA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Butte Falls																				
Site #	101	102	103	104	105	106	107	108	109	110	111x	112	113	114	115	116	117	118	119	120
Total	35	35	28	38	3	10	16	40	60	40	6	5	35	40	14	2	75	58	20	15
TODI	15	30	5	20	<1	2	3	25	50	6	2	4	5	10	3	2	65	20	4	-
CECU	25	2	10	5	-	4	1	1	8	25	-	-	6	-	-	<1	-	12	-	-
ARVI	-	2	18	10	3	-	-	5	4	-	-	<1	5	30	10	<1	-	12	12	14
CEBE	-	2	-	-	-	-	-	-	<1	-	-	-	8	-	-	-	-	<1	-	-
CEIN	-	-	-	<1	-	-	-	8	-	-	-	<1	2	-	<1	<1	<1	<1	<1	1
MANE	-	-	-	-	-	-	-	-	-	-	4	-	10	5	-	-	-	<1	3	-
HODI	-	5	-	-	-	-	-	<1	-	-	<1	<1	-	-	-	-	-	-	-	-
SYAL	-	3	-	-	-	-	<1	4	-	-	-	-	-	-	-	-	12	-	-	-
AMAL	-	2	-	3	-	3	15	-	-	20	-	-	<1	-	<1	-	<1	15	2	<1
ROSA	-	<1	-	<1	-	3	-	<1	-	-	-	-	-	-	-	-	<1	-	-	-

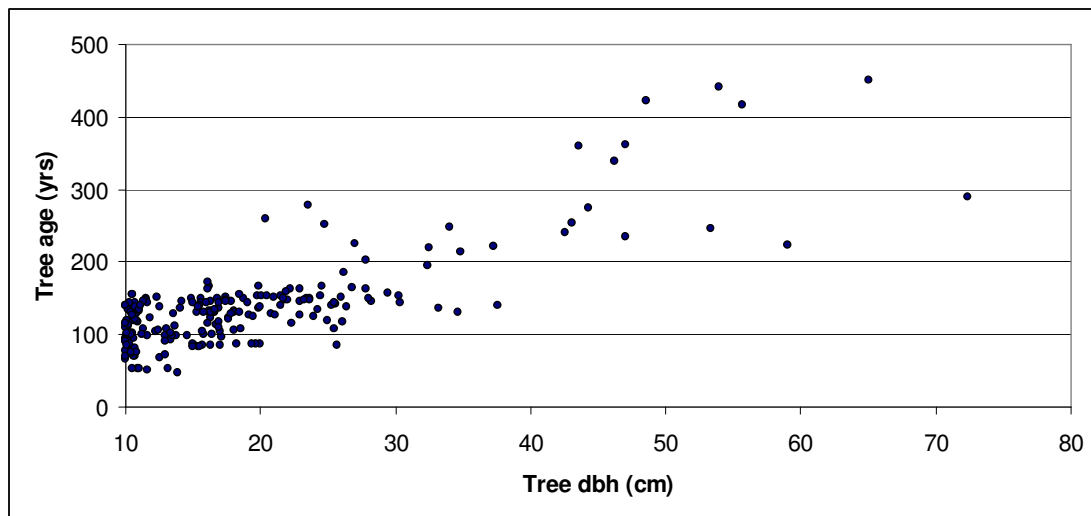
Appendix E Relationship of Oregon white oak dbh to age

Figure 2. Relationship between sampled Oregon white oak tree dbhs and age counts. Tree ages reported are from cores confidently aged to pith. Four exceptions are for several > 300 yr tree ages, from incomplete (not to pith) tree cores (=2), and from off-plot sampled tree cross sections (=2).

Appendix F Oregon white oak sapling age distribution of sampled sites

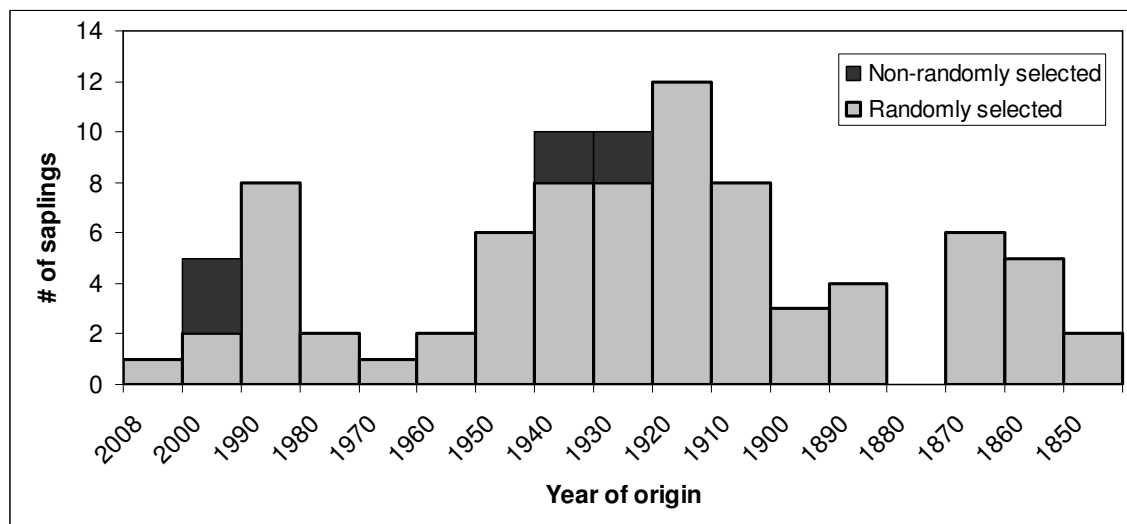


Figure 3. Distributions of Oregon white oak sapling year of origin across 12 sites, which spanned a range of sapling to tree ratios ($n=85$; aging based on increment cores taken at 0.8 m or on discs cut at ground level). In stands with ≤ 10 saplings present, all saplings were sampled. In stands with >10 saplings present, the smallest sapling was deliberately chosen for sampling (represented by dark fill). Six yr were added to counts for saplings cored at 0.8m; actual count is presented for saplings sampled at ground level.

Appendix G Stand structures

Distributions of Oregon white oak tree year of origin and sapling height paired with diameter distributions for all tree species by stand.

Stand labeling: Stands 1 – 20 were in the Applegate and 101-120 were in the Butte Falls study area. Stands 6, 9, 16, and 111 were probably treated for fuel reduction.

Acronyms definitions: QUGA = *Quercus garryana*, PSME = *Pseudotsuga menziesii*, PIPO = *Pinus ponderosa*, QUKE = *Quercus kelloggii*, ARME = *Arbutus menziesii*, CADE = *Calocedrus decurrens*, PREM = *Prunus emarginata*, FRAX = *Fraxinus latifolia*.

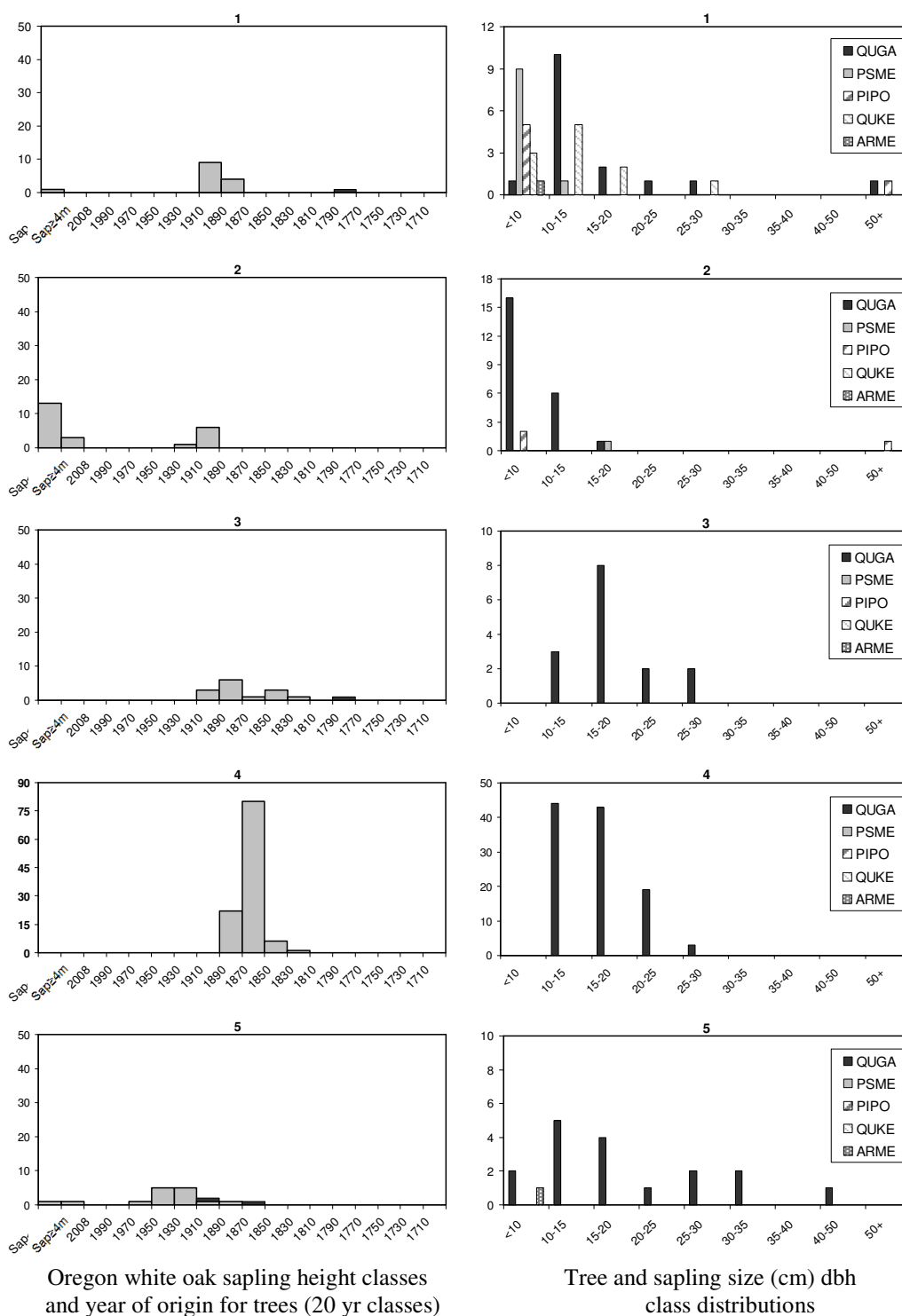


Figure 4. Distributions of Oregon white oak tree year of origin and sapling height paired with diameter distributions for all tree species by stand. Darker age bars are less confident estimates due to a smaller sample size.

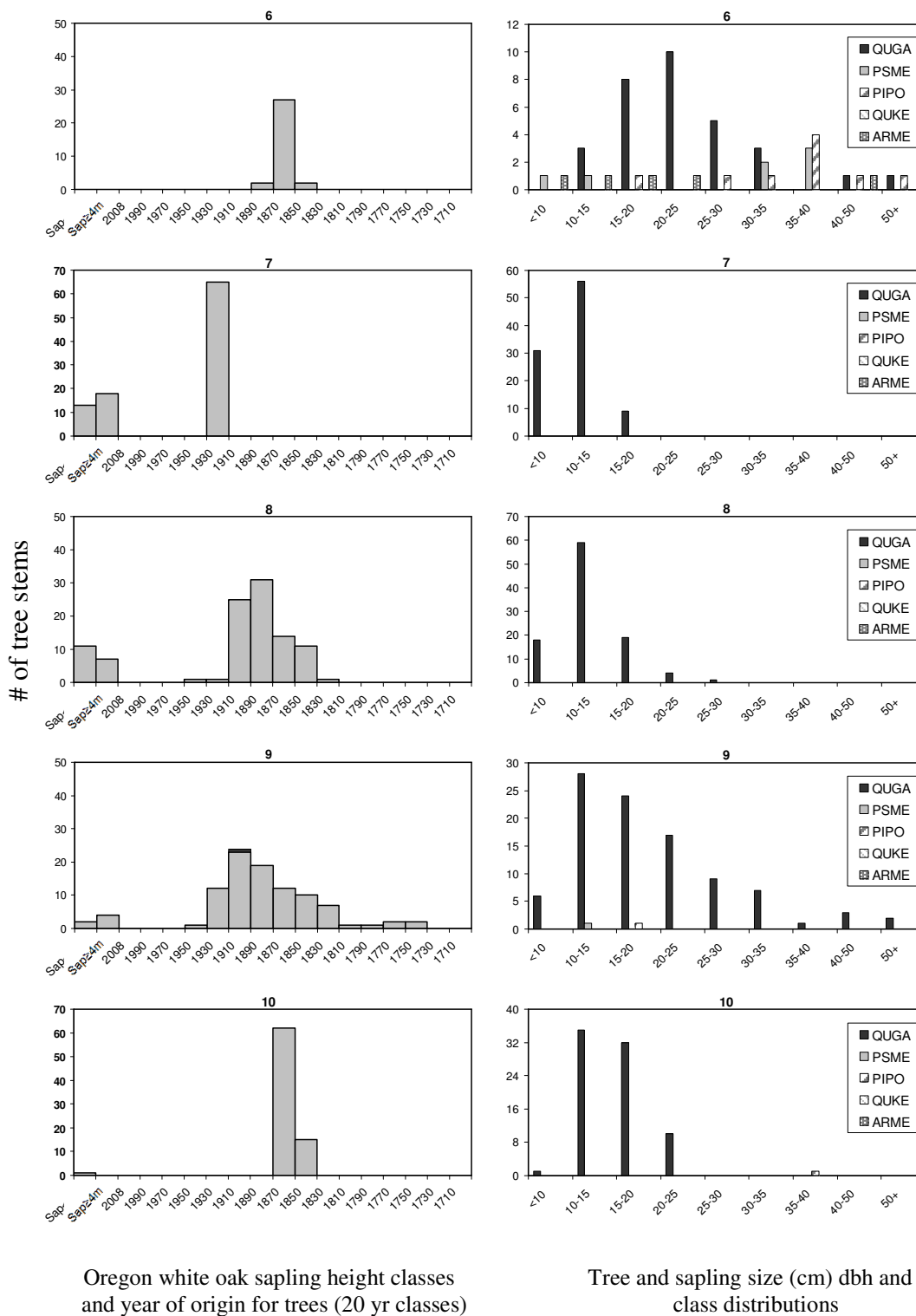
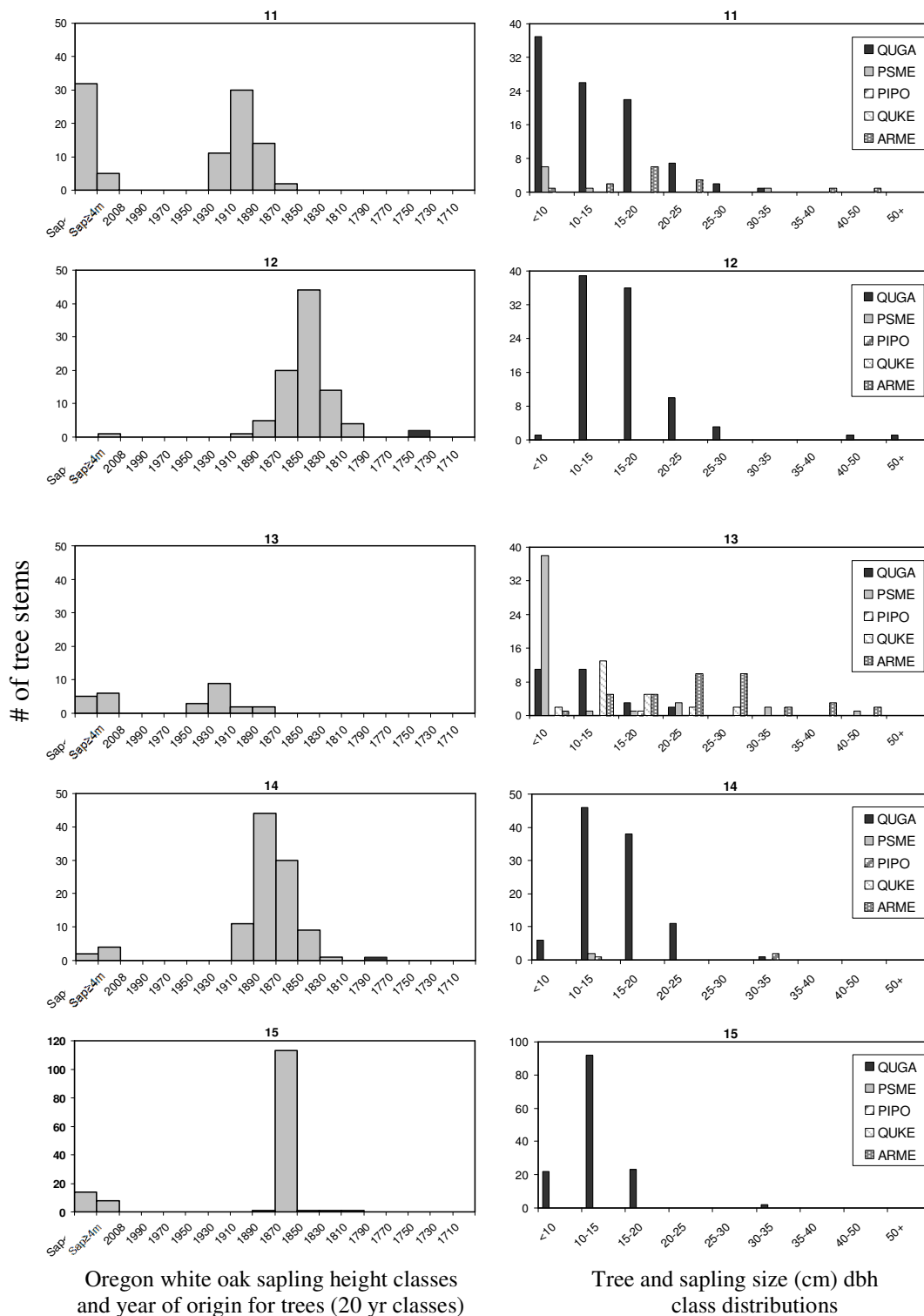


Figure 4. Distributions of Oregon white oak tree year of origin and sapling height paired with diameter distributions for all tree species by stand (Continued).



Oregon white oak sapling height classes and year of origin for trees (20 yr classes)

Tree and sapling size (cm) dbh class distributions

Figure 4. Distributions of Oregon white oak tree year of origin and sapling height paired with diameter distributions for all tree species by stand (Continued).

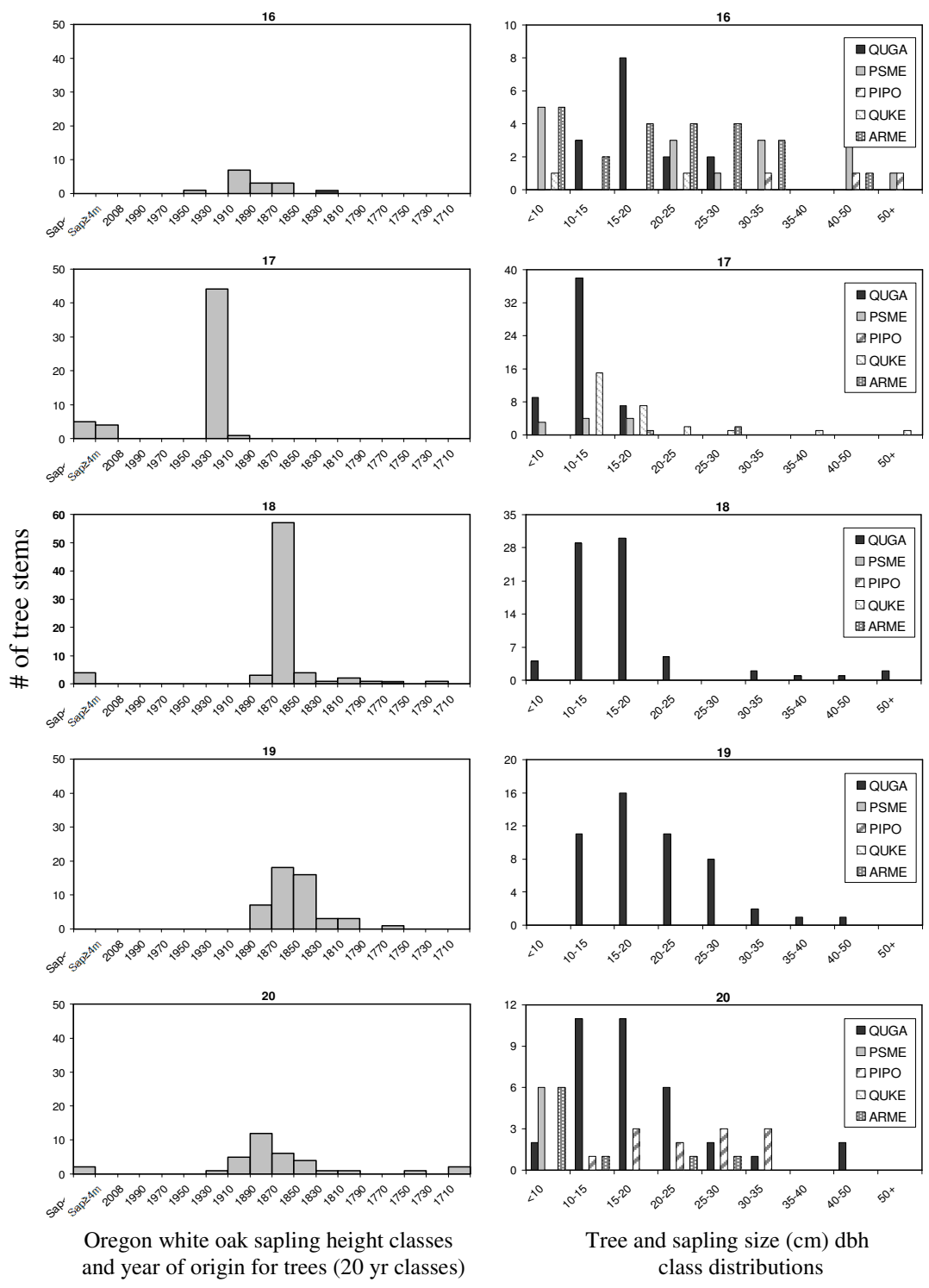


Figure 4. Distributions of Oregon white oak tree year of origin and sapling height paired with diameter distributions for all tree species by stand (Continued).

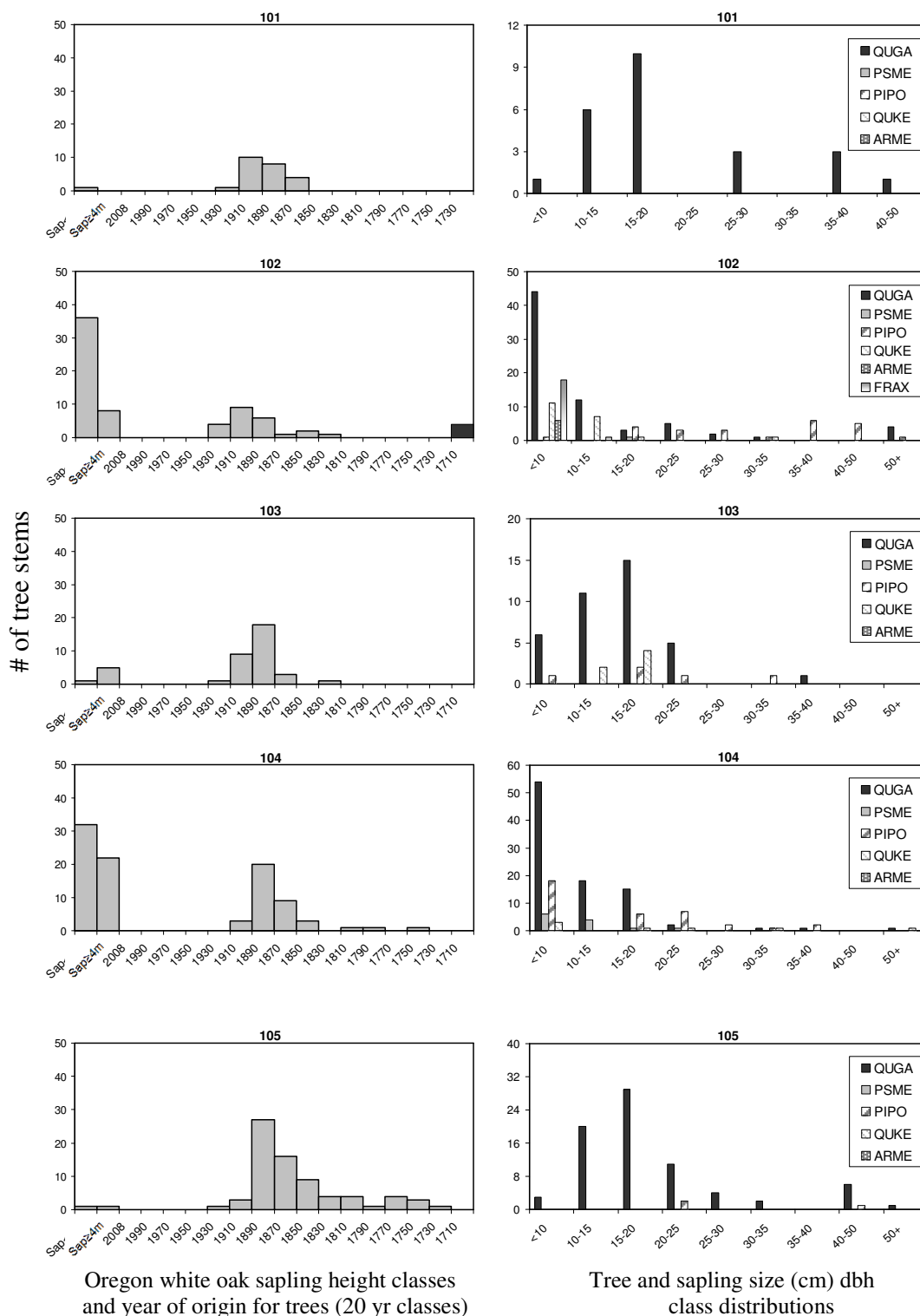


Figure 4. Distributions of Oregon white oak tree year of origin and sapling height paired with diameter distributions for all tree species by stand (Continued).

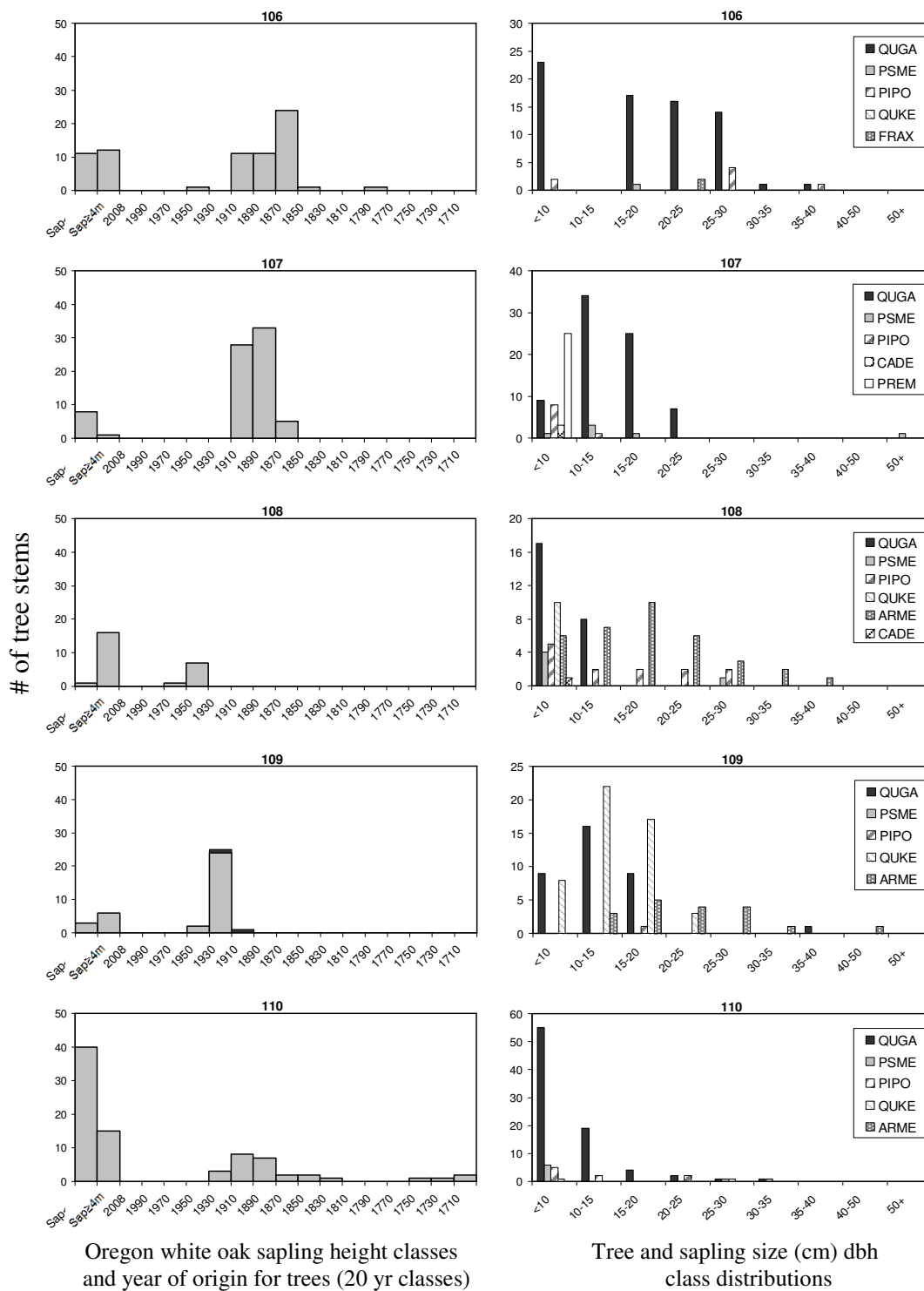


Figure 4. Distributions of Oregon white oak tree year of origin and sapling height paired with diameter distributions for all tree species by stand (Continued).

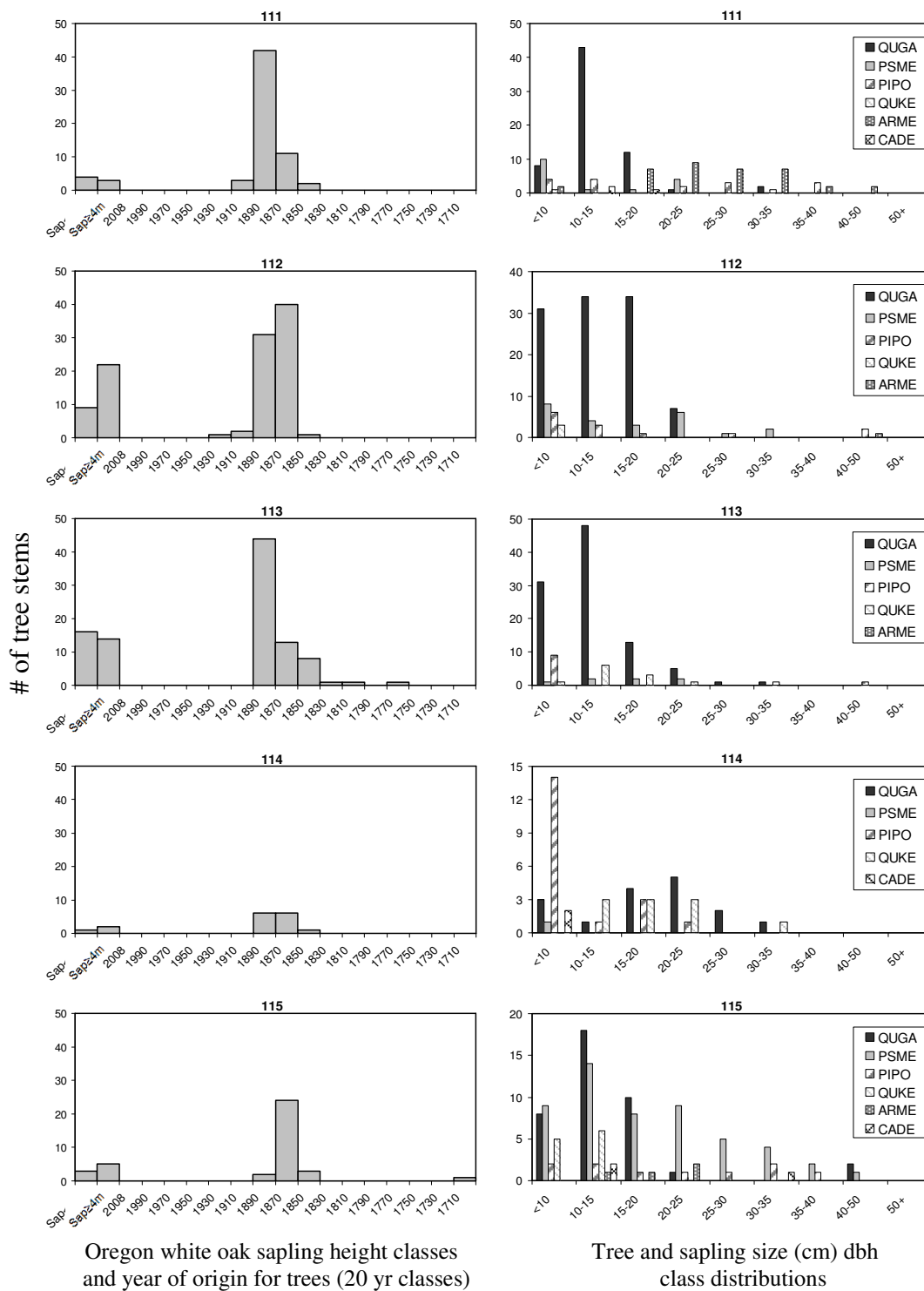
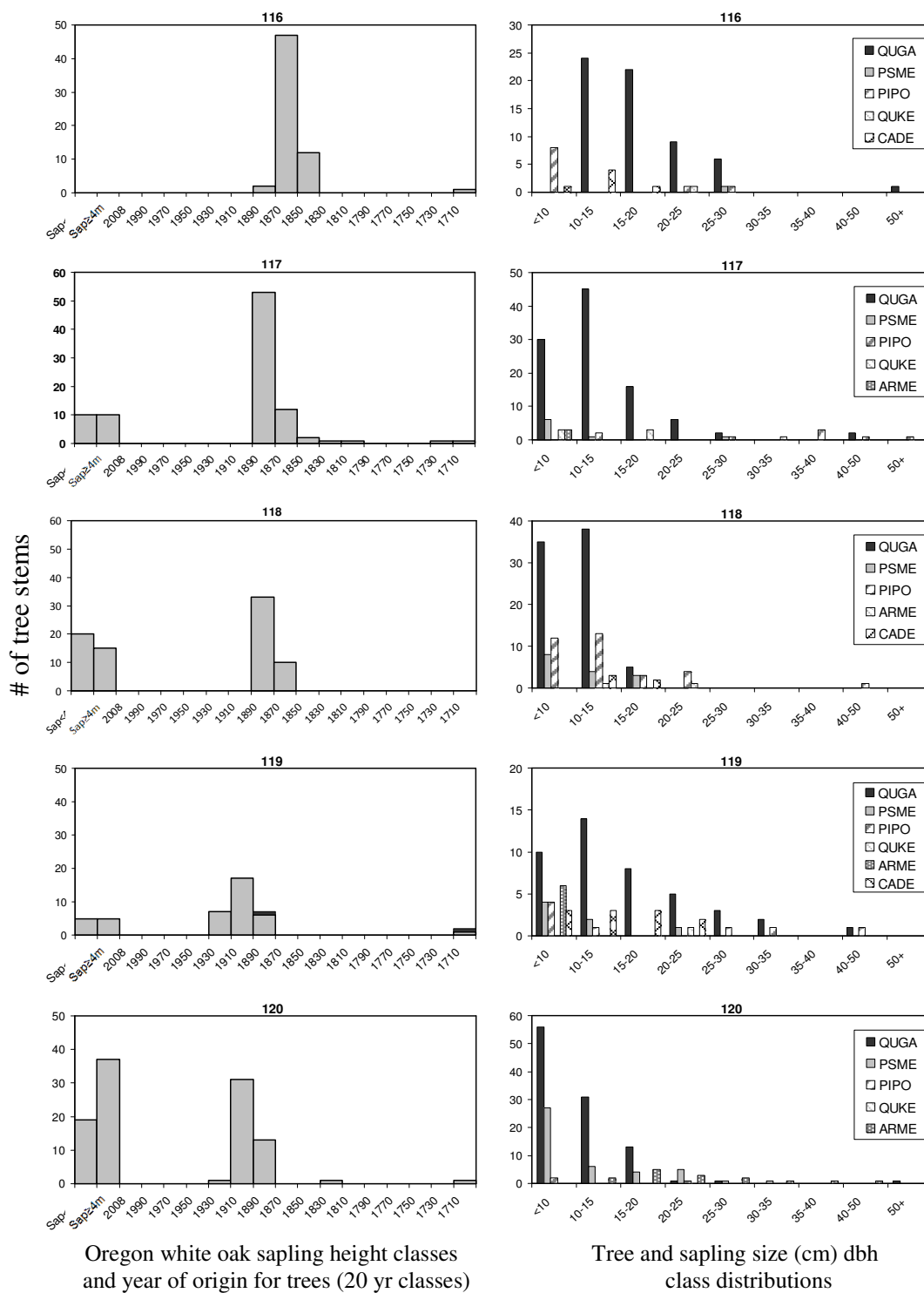


Figure 4. Distributions of Oregon white oak tree year of origin and sapling height paired with diameter distributions for all tree species by stand (Continued).



Oregon white oak sapling height classes and year of origin for trees (20 yr classes) Tree and sapling size (cm) dbh class distributions

Figure 4. Distributions of Oregon white oak tree year of origin and sapling height paired with diameter distributions for all tree species by stand (Continued).

Appendix H Relationships between age structure and the environment

NMS analysis of Oregon white oak stand age structures to detect major gradients in age structure space. Age structure variables included stand minimum and maximum Oregon white oak tree ages, age ranges, skewness, and kurtosis; median of combined tree and sapling ages (median usually fell in tree range or in estimated sapling range, except for two sites, where the median age was very close to the youngest tree age and sapling heights overlapped with heights in the tree size range, so the youngest tree age was used); and number of saplings by size classes $>$ or \leq 4m; the distance matrix used Euclidean distances. Variables in the age structure matrix were relativized by their standard deviate to weight all equally. Patterns in age structure were analyzed in relation to environmental and disturbance variables (Appendix A, Table 3).

The ordination resulted in a 2-dimensional solution and $R^2=97.3$ (Axis 1 $R^2= 33.8$, Axis 2 $R^2=63.4\%$, final instability of 0.0003, 59 iterations, and final stress=6.78). Stands with high tree age maximum, kurtosis, and skew were positioned on the high end of Axis 2, whereas plots on low end of the axis generally had high median ages. Higher minimum and median tree ages were positioned on the low end of Axis 1, and high densities of both sapling size classes were on the high end. Stand age structures were more variable in Butte Falls than in the Applegate Valley.

No environmental or disturbance variables were strongly correlated ($r \geq 0.40$) with the Oregon white oak age structure ordination. Percent silt had the strongest correlation with age structures ($r=0.39$ with Axis 2); stands located on soils with lower percentages of silt tended to have lower skew and kurtosis in tree ages, a relatively narrow range of tree ages, and a younger tree age maximum.

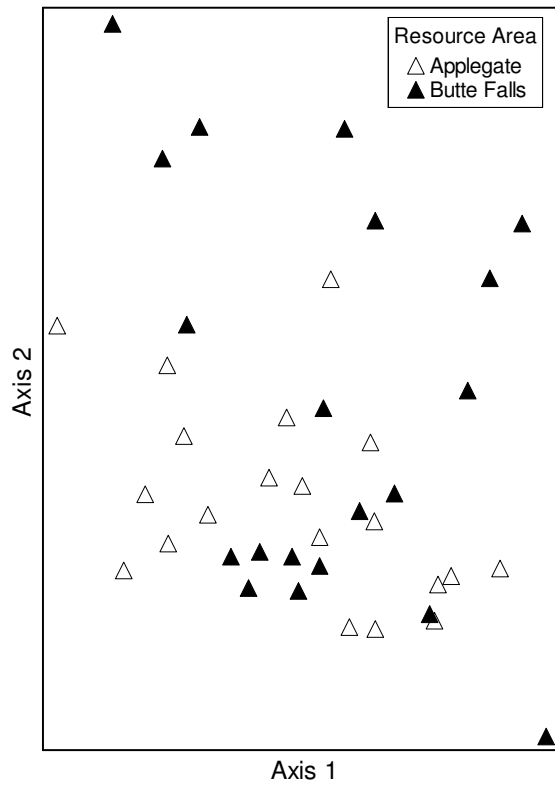


Figure 5. NMS ordination of 40 stands in age structural space.

Stands were also ordinated separately by resource area in age structural space, but no environmental or disturbance variables were strongly correlated ($r^2 \geq 0.2$) with these ordinations.