# STAND AND TREE GROWTH CHARACTERISTICS OF *QUERCUS GARRYANA* AND *QUERCUS KELLOGGI* WOODLANDS IN NORTHWESTERN CALIFORNIA

By

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A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Masters of Science in Natural Resources: Forest, Watershed, and Wildland Sciences

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May 2015

#### ABSTRACT

# STAND AND TREE GROWTH CHARACTERISTICS OF QUERCUS GARRYANA AND QUERCUS KELLOGGI WOODLANDS IN NORTHWESTERN CALIFORNIA

#### Madelinn Schriver

Oregon white oak (Quercus garryana) and California black oak (Q. kelloggii) woodlands are unique ecosystems in the Pacific West that support high levels of biodiversity, yet little is known about their current and historic stand establishment patterns, nor the variability of stand structure and its effect on oak-tree growth. With concerns of local extirpation due to native Douglas-fir (*Pseudotsuga menziesii*) encroachment, my research objectives were to characterize the variability of age and stand structure, current tree regeneration, and oak growth in 10 mixed oak-conifer woodlands from xeric to mesic site conditions in the North Coast region of California. Each site varied from open canopy oak-dominant woodland to closed canopy coniferdominant forest. Most white and black oak trees established from 1850 to 1910 with minimal (< 0.05%) establishment after 1950. Conversely, most Douglas-fir trees established after ~ 1950. All sites exhibited high proportions of oak seedling mortality in open stands while closed stands supported lower densities of oak seedlings and greater proportions of shade tolerant tree species. White oak had slower growth (p-value < 0.001) and higher proportions of mortality in conifer-dominant stands in comparison to oak-dominant stands. White oak growth was more sensitive to overstory Douglas-fir than black oak, whose shade tolerance and mortality appeared to be influenced by

environmental gradients and potentially past conifer harvests. The high proportion of Douglas-fir establishment, and the lack of successful oak recruitment, suggests the effects of altered disturbance regimes enabling these ecosystems to transition into coniferdominant stands.

#### ACKNOWLEDGEMENTS

Funding for this project was provided by a Division of Agriculture and Natural Resources Grant through the University of California. Special thanks to the Primary and Co- Investigators for their collaborative efforts at creating and facilitating this research which allowed us to begin this research at a running pace from the start: Yana Valachovic, Lenya Quinn-Davidson, J. Morgan Varner, Rosemary Sherriff, Maggie Kelly, Rick Standiford, and Matt Potts. I specifically want to thank my mentor Dr. Rosemary Sherriff who has been ever supportive and shared her time willingly with me over the years. Dr. Sherriff's countless hours of advice, feedback, and review helped craft this project into reality and gave me a new perspective of looking at the natural world critically through a biogeographic lens. I would also like to thank Dr. Jeffrey Kane for serving on my committee, providing useful advice and novel suggestions. Lastly, I am ever grateful to my field assistants Radoslaw Glebocki, Brian Hodge, Amy Livingston, and Brendan Twieg for their strong arms, and to my lab assistants Crystal Neuenschwander, Allison Potts, and Olivia Zotter for their keen eyes.

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#### CHAPTER 1: LITERATURE REVIEW

1.1 Oregon White Oak (Quercus garryana) Ecology

#### 1.1.1 Natural range

Oregon white oak (*Quercus garryana* Dougl. ex Hook.) is a broad-leaved deciduous tree that grows along the Pacific Coast. White oak occupies a range of diverse climates, with average monthly temperatures ranging between 8° to 18°C and average annual precipitation between 170 mm to 2630 mm (Stein, 1990). The natural range of Oregon white oak extends from southern British Columbia to central California, occupying the cool and humid coastal regions of British Columbia, Canada, and northern California, as well as the hot, dry interior foothills of the Sierra Nevada (see Figure 1.1.1). The elevation range of this species is between sea level and 2290 m (Stein, 1990).



Figure 1. The natural range of Quercus garryana (Little, 1984).

Oregon white oak grows on soils of at least four orders: Alfisols, Inceptisols, Mollisols, and Ultisols. Specific soil series include Hugo and McMahon, soils derived from alluvial deposits (poorly drained Amity and Dayton series), sedimentary parent material (deep, well-drained Steiwer, Cartlon, Peavine, Bellpine, Melbourne, and Willakenzie series), and basic igneous rocks (moderately deep, well-drained Nekia, Dixonville, and Olympic series) (Stein, 1990). A subsurface clay layer that restricts water penetration is characteristic of soils in most of these series (Stein, 1990). In the North Coast region of California, Oregon white oak occurs on well-drained, slightly acidic loams (Jackson et al., 1998). Soils associated with Oregon white oak stands are generally acidic, ranging in pH from 4.8 to 5.9 (Stein, 1990).

#### 1.1.2 Oregon white oak plant communities

Oregon white oak is found in a variety of plant communities ranging from pure closed-canopy stands, as a component of mixed hardwood stands or mixed hardwoodconifer forests, and as scattered trees in savannas and woodlands (Stein, 1990). Pure stands usually indicate sites that are exposed or drought-sensitive for other tree species during at least part of the year or that have frequent disturbances (e.g., fire or logging). Common hardwood associates include tanoak (*Notholithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), California black oak (*Quercus kelloggii*), and blue oak (*Quercus douglasii*). Common conifer associates include ponderosa pine (*Pinus*) *ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), Port Orford-cedar (*Chamaecyparis lawsoniana*), coast redwood (*Sequoia sempervirens*), and knobcone pine (*P. attenuata*) (Stein, 1990). In the North Coast region of California, hardwood associates include tanoak and Pacific madrone, while Douglas-fir is the primary conifer associate. The understory plant community of Oregon white oak woodlands varies greatly based on soil, topography, climate, and disturbance histories, but is primarily composed of exotic annual grasses and forbs and occasional native perennial grasses (Stein, 1990; Tveten & Fonda 1999; Engber et al., 2011).

#### <u>1.1.3 Tree regeneration</u>

Oregon white oak reproduces by two means: vegetatively from epicormic sprouts and sexually through acorn production and germination. Sprouting commonly occurs when a disturbance triggers dormant buds to become active along the bole, root collar or stump (Stein, 1990). Types of disturbance associated with basal and epicormic sprouting include high severity fire (Regan & Agee, 2004), crown dieback (Tveten & Fonda, 1999), and removal of neighboring overstory conifers (Devine & Harrington, 2006). Even when repeated fires top-kill seedlings and small diameter (0.1 to 10.0 cm dbh) stems, Oregon white oak can resprout from the root collar (Regan & Agee, 2004). Larger diameter white oaks with thicker bark are more resistant to fire injury (Regan & Agee, 2004). Based on these characteristics, Oregon white oak is considered a disturbance-adapted tree species (Stein, 1990). While sprouting is a successful mode of regeneration at local spatial scales, acorn germination is a more successful mode of regeneration at broader spatial scales.

Acorns are an important mode of regeneration for Oregon white oak. They are an important food source for many animal species, especially native grey squirrels (Sciurus griseus) and acorn woodpeckers (Melanerpes formicivorus) who commonly cache acorns in the soil. Rodents and birds, which can act as vectors for acorn dispersal, facilitate oak regeneration at broader spatial scales. If left unburied, the acorns are readily consumed by rodents and mule deer (Odocoileus hemionus) (Fuchs et al., 2000). Once germinated, Oregon white oak seedlings can experience high rates of mortality due to herbivory and desiccation from insufficient soil moisture caused by competing grasses (Regan & Agee, 2004; Devine et al., 2007a). In Washington and British Columbia, the presence of Oregon white oak seedlings appears to be unaffected by overstory shading (Fuchs et al., 2000; Devine et al., 2007a). Fuchs et al. (2000) found regeneration of Oregon white oak seedlings below Douglas-fir overstories, indicating that additional factors (e.g., moisture limitations and herbivory) influence seedling survival. Yet, low rates of Oregon white oak regeneration in Oregon and Washington are also associated with the presence of overstory Douglas-fir and a lack of disturbance (i.e., fire). Oregon white oak's ability to tolerate shading by overstory Douglas-fir appears to be related to their developmental stage, as tolerance decreases with age (Fuchs et al., 2000). The lack of agreement on the effects of overstory Douglas-fir on oak regeneration warrants further investigation.

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#### 1.1.4 Shade tolerance and growth response to overstory conifers

Mature Oregon white oaks are shade intolerant (Sugihara & Reed, 1987). In mixed oak-conifer stands where Douglas-fir occupies dominant canopy positions, the shorter stature oaks are shaded, leading to crown dieback and eventual oak mortality (Devine & Harrington, 2006; Franks, 2007; Devine & Harrington, 2013). When overstory Douglas-fir trees are removed, radial growth of larger-diameter ( $\geq$  19 cm dbh) Oregon white oaks increases as does acorn production, indicating the capacity of longsuppressed trees to rapidly recover (Devine & Harrington, 2013). Little is known about the time it takes Oregon white oak growth to respond to initial Douglas-fir co-dominance and subsequent overstory dominance.

#### 1.2 California Black Oak (Quercus kelloggii) Ecology

#### 1.2.1 Natural range

California black oak (*Quercus kelloggii* Newb.) is a broad-leaved deciduous tree that grows along the inland foothills and mid-slopes of the Pacific West (southern Oregon-northern California). California black oak occupies a range of diverse climates, where the average daily mean temperature ranges from -1° to 8°C in January and 19° to 28°C in July, and the average annual precipitation ranges between 300 mm to 2540 mm (McDonald, 1990). The natural range of California black oak includes the northern distribution from 44.5°N latitude in Oregon and extends southward where the species grows abundantly in California's North Coast Range and the western side of the Sierra Nevada, and eventually ends in Baja California (Figure 2) (McDonald, 1990).



Figure 2. The natural range of *Quercus kelloggii* (Little, 1984).

The elevation range of California black oak is more variable than Oregon white oak. In the Willamette Valley of west-central Oregon, California black oak ranges between 135 to 305 m in elevation (McDonald, 1990). In south-central Oregon and the Klamath mountains, California black oak only grows at higher elevations of 610 to 915 m (McDonald, 1990). California black oak elevation range widens to ca. 150 to 1830 m in elevation in California's North Coast Range (McDonald, 1990). In the Sierra Nevada, California black oak is most abundant and attains its largest stature with an elevation range between 460 to 2380 m in the northern Sierra; both upper and lower elevation limits increase from north to south (McDonald, 1990).

California black oak grows primarily on two soil orders: Alfisols and Inceptisols, with occasional occurrence on Mollisols (McDonald, 1990). About 75 soils series in California support California black oak. Important soil series in northwestern California include Boomer, Cohasset, Josephine, Sites, and Sheridan (McDonald, 1990). The soil variable most limiting to California black oak is internal drainage (McDonald, 1990). Unlike Oregon white oak, increasing clay content in the surface soil coincides with decreasing incidence of California black oak (McDonald, 1990). California black oak grows best on medium- to coarse textured, deep, and well-drained soils but is usually found on rocky slopes with thin soils derived from diverse parent materials (McDonald, 1990). Soils in the North Coast region of California that support productive California black oak stands are deep, slightly acid loams and gravelly clay-loams derived from sandstone and shale (McDonald, 1990). The co-occurrence of both Oregon white oak

and California black oak indicates soils with low clay content and enough drainage for black oak to persist.

#### 1.2.2 California black oak plant communities

California black oak is usually found as a component of hardwood stands or of mixed hardwood conifer forests. Commonly associated hardwood species include tanoak and Pacific madrone. At lower elevations, other hardwood species include Oregon white oak, interior live oak (*Quercus wislizenii*), coast live oak (*Q. agrifolia*), Engelmann oak (Q. engelmannii), and blue oak (McDonald, 1969). At higher elevations, Pacific dogwood (*Cornus nuttallii*), bigleaf maple (*Acer macrophyllum*), California bay laurel (Umbellularia californica), and canyon live oak (Q. chrysolepis) intermix with black oak (McDonald, 1969; McDonald, 1990). Common conifer species include ponderosa pine, Douglas-fir, grand fir (Abies grandis), white fir (A. concolor), and Incense cedar (*Calocedrus decurrens*) (McDonald, 1969; McDonald, 1990; Cocking et al. 2012; Cocking et al. 2014). Associated hardwood trees in northwestern California stands are California bay laurel, Pacific madrone, and tanoak, with coast live oak at the most southern extent. Similar to Oregon white oak, Douglas-fir is the primary conifer species associated in northwestern California stands. The understory plant community includes at least 30 species of shrubs, the most common being poison-oak (Toxicodendron diversilobum) (McDonald, 1990).

#### 1.2.3 Tree regeneration

Similar to Oregon white oak, California black oak can reproduce vegetatively through sprouts and sexually through acorn germination. Sprouting commonly occurs when a disturbance triggers dormant buds to become active at the root collar, bole, or crown. Disturbances associated with sprouting include oak pruning (McDonald, 1990), stems top-killed from high severity fires (Skinner et al., 2006; Cocking et al., 2012; Cocking et al., 2014), and fire-related mortality of neighboring overstory conifers (Cocking et al., 2014). Similar to Oregon white oak, sprouting appears to be a highly successful mode of natural regeneration for California black oak (McDonald, 1990). Based on California black oak's ability to avoid stem mortality in low-severity, high frequency fires (Skinner et al., 2006; Taylor, 2010) and to regenerate from sprouts following higher severity fires (Cocking et al., 2012), this species is considered to be adapted to a broad range of fire severities (McDonald, 1990). While California black oak readily sprouts after fire, the sprouting response and overall survival rates of black oak varies among fire severities and stand structure characteristics. In northern California, Cocking et al. (2014) found faster sprout development in areas of higher-severity fire than in areas of lower-severity fire. Additionally, the probability of no sprouting due to complete California black oak mortality (top killed stems that did not re-sprout) following a fire increased with greater overstory conifer dominance (Cocking et al., 2012).

#### 1.2.4 Shade tolerance and growth response to overstory conifers

Similar to Oregon white oak, California black oak's tolerance of shade varies with age (McDonald, 1969). California black oak seedlings grow well in full sunlight and are also able to persist beneath dense shade (Roy, 1962). In mesic environments of the Pacific West where Douglas-fir occupies dominant canopy positions, short-statured mature California black oaks are shaded, leading to a decline in oak growth and eventual oak mortality (Barnhart et al., 1996; Stewman, 2001). In drier, fire-prone environments (e.g., Klamath Mountains), edaphic factors and topography are the primary controls on the distribution of tree species (Taylor & Skinner, 1998). On drier southwest-facing slopes, the mosaic of soil types and heterogeneous topography allow California black oak trees to persist beneath mixed-conifer canopies (Taylor & Skinner, 1998). Due to the environmental heterogeneity in the North Coast region of California, the growth response of California black oak to overstory conifer may be highly variable within this region. Similar to Oregon white oak, little is known about the interaction of California black oak growth and Douglas-fir overstory dominance, nor the regional variability of growth responses.

1.3 Altered Disturbance Regimes and Ecosystem Response in the Pacific West

In the Pacific West, fire-related studies show substantial declines in the frequency of fire in savannas, woodlands, and forest ecosystems (Agee, 1993; Skinner et al., 2009; Taylor, 2010). Historically, oak communities of the Pacific West were thought to have been maintained by natural and anthropogenic fires (Thilenius, 1968; Boyd, 1986; Tveten & Fonda, 1999; Thysell & Carey, 2001). Altered spatial patterns of fire have been associated with changes in land-use during the 19<sup>th</sup> and 20<sup>th</sup> centuries (Skinner et al., 2009) with active suppression of fire beginning in the early to mid-20<sup>th</sup> century, which reduced the fire return intervals in many areas (Agee, 1991; Agee, 1993; Taylor, 2010). In the Pacific West, important landscape changes have been altered by Euro-American settlement, timber harvesting, livestock grazing, ex-urban development, and active fire suppression policies. The response of plant species to altered fire regimes and other land use changes vary substantially by ecosystem and geographic location.

From British Columbia to California, substantial changes in oak community structure and species composition have occurred during the last 100 to 150 years (Thilenius, 1968; Reed & Sugihara 1987; Gedalof et al., 2006; Gilligan & Muir, 2011). Peak establishment of living Oregon white oaks typically occurred during the mid-1800s to early 1900s, with limited to no oak recruitment and subsequent invasion by conifers in many environments (Gedalof et al., 2006; Gilligan and Muir, 2011). These changes have been largely attributed to the sensitivity of oak and co-dominant species to fire exclusion (Tveten & Fonda, 1999; Engber & Varner, 2012). Yet, livestock grazing and the introduction of non-native grasses and annuals have been a substantial disturbances but the effect of these disturbances on stand structure is less clear (Jimerson & Carothers, 2002).

Euro-American settlers introduced domestic livestock (cattle and sheep), and 30yrs ago livestock grazing was the most widespread land use in the western U.S. (Crumpacker, 1984). Twenty years ago, two-thirds of all oak woodlands in California were grazed (Huntsinger, 1997). The effects of grazing on plant communities is difficult to study due to the rarity of ungrazed land for comparison, and the inability to distinguish between current and historic range management practices (Fleischner, 1994). Available research has shown both positive and negative effects of grazing on oak woodland regeneration. Positive grazing effects include reduced moisture competition between oaks and understory vegetation (Hall et al, 1992) and reduced habitat for acornconsuming rodents. Negative effects of grazing include livestock consuming oak seedlings and acorns (Hall et al., 1992; Sweicki et al, 1997) and soil compaction limiting root growth of developing oak seedlings (Gordon et al., 1989). Available research from the Rocky Mountains and the Great Plains indicate that livestock grazing alters forest dynamics through grass-tree interactions and grass-fire interactions (Belsky & Blumenthal, 1997). Heavy grazing reduces the presence of understory grasses as well as the abundance of fine-fuels in the understory (Painter& Belsky, 1993) thereby reducing fuel mass and continuity that sustaines surface fires. Given the strong competitive influence grasses have on oak seedling establishment and survival, and the importance of fine-fuels for maintaining a frequent fire regime, livestock grazing has potentially had a

substantial influence on stand dynamics of oak woodlands during the 19<sup>th</sup> and 20<sup>th</sup> centuries.

#### 1.4 Vegetation Change in Oak Woodlands in the Pacific West

Increases in native conifer establishment were noted in Oregon white oak woodlands by the 1980s in the North Coast region of California (Reed & Sugihara, 1987) and in California black oak ecosystems by the mid-20<sup>th</sup> century in the southern Cascades (Barr, 1946). Douglas-fir, a native species that co-exists in many stands, abundance has reportedly increased in many oak ecosystems including coast live oak (Hunter & Barbour, 2011), Oregon white oak (Reed & Sugihara, 1987; Engber et al., 2011), as well as California black oak (Stewman, 2001; Skinner et al., 2006). In stands without periodic fire (and often with continued grazing), Douglas-fir overtops oaks and becomes the dominant canopy species, and understory plant composition shifts towards shade tolerant species (Thysell & Carey, 2001; Devine et al., 2007b; Livingston, 2014). The replacement of oak-dominant stands by conifer-dominant stands can represent a loss of endemic biodiversity (Thysell & Carey, 2001; Livingston, 2014). However, the temporal and spatial patterns of tree establishment in mixed oak-conifer stands is not well understood in northwestern California.

# CHAPTER 2: ESTABLISHMENT AND GROWTH PATTERNS OF MIXED OREGON WHITE OAK AND CALIFORNIA BLACK OAK WOODLANDS IN NORTHWESTERN CALIFORNIA

#### 2.1 Introduction

Over the last century, the cover and dominance of native trees has increased dramatically in many North American grasslands, savannas, woodlands, and forests (Copenheaver et al., 2004; Moore & Huffman, 2004; Gedalof et al., 2006; Stam et al., 2008; Gilligan & Muir, 2011) – a phenomenon referred to as tree encroachment or densification. Potential causes of tree encroachment include changes in land use and settlement patterns, extirpation of native peoples and livelihood, fire-exclusion (Thilenius, 1968; Skinner 1995), shifts in grazing regimes (Scholes & Archer 1997), increasing atmospheric CO<sub>2</sub> (Bond & Midgley, 2000), and climate changes (D'Odorico et al., 2010). Consequences of tree encroachment and forest densification can include: reduced herbaceous cover (Stam et al., 2008; Engber et al., 2011; Livingston, 2014), loss of biodiversity (Thysell & Carey, 2001); altered fuel structure through the loss of herbaceous fuels and more fuel ladders (Engber et al., 2011). In many cases, these changes have led to the loss of structural heterogeneity and spatial complexity on the landscape and altered disturbance regimes (e.g., Skinner 1995, Skinner et al., 2006).

In the Pacific West, recent studies suggest that Oregon white oak (Gedalof et al., 2006; Gilligan & Muir, 2011) and California black oak (Skinner et al., 2006) ecosystems

have undergone substantial change to stand structure. Studies in Oregon white oak stands in Oregon report a period of mass oak establishment following the timing of Euro-American settlement (Gilligan & Muir, 2011; Thilenius, 1968). Additionally, in Washington where former Oregon white oak savannas and woodlands have been colonized by Douglas-fir during the early to mid-20<sup>th</sup> century, Douglas-fir has grown above the shade intolerant oaks, suppressing oak growth and leading to oak mortality (Devine & Harrington, 2013). Yet where mixed oak-conifer ecosystems occur in the North Coast region of California, there is a paucity of information on the variability of past and current patterns of stand establishment and stand dynamics, as well as a lack of consensus on the factors influencing oak regeneration. In northwestern California diverse soils and heterogeneous topography can be the primary controls on the distribution of tree species (Taylor & Skinner, 1998), and the patterns of stand structure (and oak growth) may be more variable than Oregon white oak stands found in Oregon and Washington. Understanding the variability in stand structure and growth trends in context of the environmental setting is important to better predict and manage oak-conifer dynamics in a heterogeneous landscape with altered disturbance regimes.

The primary objective of this study was to characterize the variability of current and past patterns of tree establishment and growth in Oregon white oak and California black oak woodlands interspersed within conifer-dominated stands along a regional gradient in the North Coast region of California. The specific research questions were: (1) What are the temporal and spatial patterns of oak and conifer establishment in mixed oak-conifer woodlands throughout the North Coast region of California? (2) What is the influence of stand structure and composition on oak growth trends, and how do they vary across a regional gradient of mixed oak-conifer stands? and (3) What are the current tree regeneration patterns across stands throughout the study region?

#### 2.2 Methods

#### 2.2.1 Study area

The study area was located in the North Coast Range of California in Humboldt and Mendocino counties, spanning 2° of latitude from 41.17° to 39.02° (Figure 3). The North Coast Range has a Mediterranean climate with cool-wet winters and warm-dry summers. The influence of the ocean generally moderates temperature extremes on the coast where temperatures rarely drop below freezing and fog can occur throughout most of the year. While the inland regions of both Humboldt and Mendocino County experience slightly cooler winters than the coastal regions, the summer climate varies greatly with highs from 27° to 37° C depending on the elevation and distance from the ocean.

The North Coast region of California hosts a mosaic of plant community types ranging from conifer-dominated, mixed-evergreen forests to oak woodlands and savannas (Stein, 1990). I focused on the mixed-Oregon white oak and California black oak woodlands that transition from oak dominant to conifer dominant stands, which are characteristic of mixed-Oregon white oak and California black oak stands in the North Coast region of California. Additional evergreen conifer-hardwood tree species in this region include white fir (*Abies concolor*), Incense cedar (*Calocedrus decurrens*), California bay laurel (*Umbellularia californica*), canyon live oak (*Quercus chrysolepis*), Pacific madrone (*Arbutus menziesii*), tanoak (*Notholithocarpus densiflorus*), coast live oak (*Q. agrifolia*), and California buckeye (*Aesculus californica*).



Figure 3. Study area located in Humboldt and Mendocino county in the North Coast region of California (map credit: M. Eitzel). Ten study sites are indicated by dots and site codes.

#### 2.2.2 Site selection and field sampling

Within the region, ten sites were sampled during the summers of 2013 and 2014 in contiguous woodlands dominated by Oregon white oak and California black oak with Douglas-fir as the primary co-dominant species (Figure 3). Sites ranged in elevation from 375 m to 1180 m (Table 1) and occupied rolling and dissected terrain. Mean July-August temperature (warmest months) varied across sites from 11.5 °C to 14.4°C and most sites had less than 2000 mm of annual precipitation (Figure 4; PRISM Climate Group, 2015). In order to examine whether stand structure varies among local climate gradients, sites were ranked from xeric to mesic based on site-specific climate averages using the mean temperature during the two hottest months (July and August) and mean annual precipitation with extrapolated climate data from PRISM (Table 1 & Figure 4). At each site, nine 0.1-ha circular plots were selected from randomly generated locations and stratified by open-oak woodland (3 plots), transitional woodland-forest (3 plots), and closed mixed hardwood-conifer forest (3 plots) stand types based on visual assessment in the field. Open (i.e. open oak woodlands) stands were characterized as pure oak canopy stands with understory Douglas-fir. Transitional (i.e. transitional woodland forests) stands were characterized as stands with oaks and Douglas-firs at the same canopy level with none or only a few Douglas-fir crowns above the oak crowns. Closed (i.e. closed mixed hardwood-conifer forests) stands were characterized as stands with the majority of Douglas-fir trees overtopping oak trees, where oak canopies exist within or below conifer canopies. Four sites showed no visible signs of past harvesting or other major land use
disturbances (e.g., mining), while the other six sites had evidence of past conifer harvests or thinning (conifer stumps) more than 50 yrs ago in open, transitional, and/or closedforest plots (Table 1). At sites with past conifer harvests, only half of the plots had stumps (28 plots without stumps and 26 plots with stumps). In each 0.1-ha plot, species, diameter at breast height (1.37 m; "dbh"), single or multi-stem and status (live/dead) were recorded for all trees ( $\geq$  5 cm dbh). Canopy position was visually estimated for all trees and categorized into dominant, co-dominant, intermediate, and overtopped canopy classes, using a classification system modified from other oak woodland and tree competition studies (Hunter & Barbour, 2001; Cocking et al., 2012). The 10 closest Oregon white oak and California black oak trees from plot center were mapped and cored at 30-cm height above the root-shoot interface to estimate tree ages (Stokes & Smiley, 1996). Multi-stem trees were tallied, and when cored, the largest stem was selected to determine tree age. Additionally, the 10 closest evergreen conifer/ other hardwood tree species from plot center were mapped and cored. Up to five of the largest and closest living trees outside of the plot were also cored in order to best estimate the oldest establishment dates within the sampling area. To characterize current tree regeneration, seedlings (< 30 cm tall) and saplings (< 5 cm dbh and > 30 cm tall) were tallied by species using six randomly-located nested 1x2 m plots and one randomly located nested 0.025-ha plot, respectively, within each 0.1-ha plot. The physical environment (slope (0 to 90 degrees), aspect (0 to  $360^{\circ}$ ), slope position (ridgetop, saddle, valley bottom, and upper, middle, or lower third), slope type (concave, convex, undulating and flat, or planar), elevation (m), GPS coordinates, and signs of disturbance (e.g., windthrow, fire,

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grazing) were also recorded at each 0.1-ha plot. Aspect values (°) at the plot-scale were transformed into a solar radiation index (0 to 1) to characterize plot locations from warmer/drier (1) to cooler/wetter (0) topographic positions (Roberts & Cooper, 1989) (see equation below).

Solar radiation index = 
$$\frac{1 - \cos(\left(\frac{\pi}{180}\right)(\alpha - 30))}{2}$$

Table 1. Site information for 10 mixed oak-conifer woodlands (xeric to mesic climate from top to bottom) containing openoak woodland (Open), transitional woodland-forest (Transitional), and closed mixed hardwood-forest stands (Closed) in northwestern California. Site latitude, longitude, and elevation are averaged across nine plots per site. Climate characterizations are based on mean July-August temperature and total annual precipitation (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu).

Site				Open		Transition	nal	Closed		
	Latitude	Longitude	Elevation	Slope (°)	Aspect <sup>a</sup>	Slope (°)	Aspect	Slope (°)	Aspect	Solar radiation
	(°N)	(°W)	(m)	Mean (Range)		Mean (Range)		Mean (Range)		difference <sup>b</sup>
	(11)	()	(III)	Medil (Runge)		Medil (Runge)		Medin (Runge)		(open - closed)
WC	40.95	123.66	375	24 (14-34)	S	27 (15-35)	SE	23 (19-26)	SE	0.18
BV*	39.02	123.54	564	30 (24-34)	Ν	23 (14-32)	W	30 (28-34)	Ν	0.21
BM	40.51	123.53	1180	22 (14-27)	SW	16 (14-22	S	17 (9-22)	S	0.12
CP*	39.75	123.29	503	14 (7-21)	NE	9 (0-16)	Ν	18 (15-23)	Ν	0.06
LE*	40.90	123.79	595	18 (12-25)	NW	18 (16-19)	W	23 (16-29)	SW	- 0.46
HS*	40.04	123.63	645	18 (15-22)	Ν	18 (14-23)	NE	17 (6-24)	NE	0.26
YJ*	40.55	123.81	914	24 (19-31)	SW	22 (18-27)	SE	24 (8-42)	SW	0.24
IB	40.71	123.90	775	23 (18-31)	S	28 (24-34)	S	22 (14-29)	SE	0.21
EB*	40.24	123.92	384	16 (14-18)	Е	19 (10-37)	W	16 (11-26)	SW	- 0.47
BH	41.17	123.89	585	12 (11-14)	NW	16 (13-22)	Ν	16 (12-22)	Ν	0.25

\* Sites with past conifer harvesting in open, transitional, and/or closed plots.

<sup>a</sup> Aspect: N north, NW northwest, W west, SW southwest, S south, SE southeast, E east, NE northeast.

<sup>b</sup> Difference between average solar radiation index in open woodland plots and closed forest plots. Positive differences indicates higher values (warmer) in open plots and lower values (cooler) in closed plots and vice versa for negative differences.



Figure 4. Annual precipitation and mean July-August temperature (warmest months) across 10 mixed oak-conifer woodland sites in northwestern California.

## 2.2.3 Data analysis

#### 2.2.3.1 Tree age.

Tree cores were mounted, sanded, and counted following standard dendrochronology techniques (Fritts, 1976). Cores were measured under a binocular microscope and subsequently measured with a tree-ring scanning system (WinDendro software, Regent Instruments, version 2009b). Annual ring widths were visually crossdated and statistically verified using the computer program COFECHA (Holmes, 1983). When core samples did not include the pith, a geometric model of annual tree growth was used to estimate the number of years to pith (Duncan, 1989). Cores missing the pith by more than 15 years or those with rotten centers were considered minimum age counts and excluded from further tree establishment analyses. Tree ages could be older than reported if seedlings or sprouts were browsed or lacked a single dominant stem dating to establishment (Hibbs & Yoder, 1993), and the lack of a coring height correction for tree age. Thus, we summarized tree establishment dates into 20-yr age bins. To evaluate whether the exclusion of minimum-aged cores from age analyses omitted earlier tree establishment, tree dbh ranges were assessed for Oregon white oak, California black oak, and Douglas-fir differentiating complete cores from minimum ages cores at each site (Appendix C). If the dbh of a tree with a minimum age count was within the size range of trees with complete ages, age figures were assumed to be representative of the minimum aged tree. Additionally, linear regression models were created for tree dbh and age for these same species at each site as well as across sites (see Table 3).

#### 2.2.3.2 Temporal and spatial patterns of tree establishment.

To examine temporal patterns of tree establishment between oaks and conifers, species were grouped into two categories (Oregon white oaks and California black oaks in comparison to evergreen conifer/other hardwoods). I inspected the proportion of tree establishment for two equal time periods: 1805 to 1904 and 1905 to 2006. The youngest tree established in 2006, therefore this was the cutoff year for analyses. Additionally time periods were analyzed to assess if altered fire regimes in this region could have influenced tree-establishment dynamics. Fire is thought to have maintained many oak ecosystems, and a significant decline in fire frequency occurred around 1900 in nearby locations (Taylor & Skinner, 1998). The proportion of each tree type between time periods was assessed using a chi-squared test ( $\alpha = 0.05$ ) with Yates correction for continuity using SigmaPlot (Systat Software, San Jose, CA). To examine spatial patterns of tree establishment between oaks and conifers within sites, plot scale tree establishment was graphed and visually evaluated for simultaneous timing among plots. Additionally, the proportion of multi-stemmed Oregon white oak and California black oak trees was calculated for each plot in order to assess trends between the duration of plot-scale tree establishment and stem structure. If fewer than three cores were sampled per non-oak species across plots for each site, cores from multiple tree species were grouped together and reported as "other".

#### 2.2.3.3 Variability of stand structure and tree regeneration.

Sites and stand types (i.e. open, transitional, and closed) were compared using stand information (density and basal area of live stems, density of dead stems, and conifer stump density) and tree regeneration (density of seedlings and saplings) (n = 90 plots). Other evergreen conifer/hardwood tree species (other than Douglas-fir) were grouped as "other". Trees were partitioned into five cm dbh classes for all tree species to examine tree diameter distributions and species composition across sites (Appendix E). For Oregon white oak, California black oak, and Douglas-fir, means and ranges of stem density and basal area (per hectare, derived from each 0.1-ha plot) are summarized for each site per stand type, as well as across sites, and across stand types (Appendix A). Due to the non-normal distribution of the data, Kruskal-Wallis non-parametric test with a post-hoc Kruskal-Nemenyi multiple-comparison was used to assess differences in stand structure and regeneration among sites and stand types.

Regional variability of basal areas, stem densities, and regeneration densities were assessed for each stand type among sites using a Kruskal-Wallis test ( $\alpha = 0.05$ ). When sites differed, a post-hoc Kruskal-Nemenyi multiple-comparison test was used to isolate pair-wise differences ( $\alpha = 0.05$ ). Due to low sample sizes (three plots per stand type per site) and the reduced power of non-parametric tests, type II errors could be possible. Across sites, variability of stand information and tree regeneration among stand types was assessed using a Kruskal-Wallis test ( $\alpha = 0.05$ ). When stand structure (e.g., Douglasfir basal area) or regeneration (e.g., Douglas-fir seedling density) significantly differed among stand types, a post-hoc Kruskal-Nemenyi multiple-comparison test was used to isolate pair-wise differences ( $\alpha = 0.05$ ) (Pohlert, 2014).

#### 2.2.3.4 Timing and effects of overstory Douglas-fir on oak growth.

I compared growth trends of Oregon white oak and California black oak in closed and open stands to examine the potential effect of Douglas-fir canopy position on oak growth. Growth measurements of each cross- dated core were standardized by dividing the growth of each year by the average growth of the entire record (horizontal line) in order to conserve growth trends yet enable comparisons among individual trees (Schweingruber, 1989; Cook & Kariukstis, 1990). Fitted lines tend to be biased by measurements close to the pith, therefore if the pith was present, or the estimated number of years to pith was equal to or less than five, the 10 inner-most ring measurements were removed prior to fitting mean lines (Fang et al., 2010). Due to the temporal variability of Douglas-fir establishment in closed stands (described below; Table 7) oak growth was analyzed at the plot scale then averaged across closed stands (n = 3 closed plots per site). Closed canopy ring-width indices (RWI) for each plot were evaluated from the initial timing of Douglas-fir establishment (a minimum of 2 trees during a 10-yr period at plotlevel) (i.e. plot-level date). No overstory Douglas-fir occurred in open stands, thus open canopy RWI were evaluated from the earliest timing of Douglas-fir establishment across the entire site (i.e. site-level date). Species-specific average RWI were developed at individual plots and averaged across open and closed stands at each site (Appendix F).

The removal of overstory Douglas-fir can increase Oregon white oak growth (Devine & Harrington, 2013), thus the potential effect of past conifer harvests on oak growth trends was evaluated for sites with large diameter (> 50 cm) conifer stumps in closed stands. Stump diameters at site LE were < 50 cm in closed (range: 7.6 to 23.2 cm) thus oak growth trends are less likely to be effected by conifer removal. Average oak growth chronologies from closed canopy stands were visually assessed for changes in growth uncharacteristic of age related growth trends. Growth trends related to age are frequently negative-exponential curves (see open stands in Appendix F). Abrupt increases in growth that were persistent (> 5 yrs) during the 1940s to 1960s period were interpreted at potential effects of disturbance from the removal of large diameter conifers.

To examine the effect of Douglas-fir canopy position on oak growth, I estimated the date of Douglas-fir co-dominance (DDC) and dominance (DDD) at each closedcanopy plot and used these dates as the cutoff for statistical comparisons between oak growth in closed stands versus open stands (t-test or Mann-Whitney rank sum test;  $\alpha$  = 0.05). Chronologies from open stands were used to assess oak growth unaffected by Douglas-fir canopies. To approximate the number of years it takes Douglas-fir to reach co-dominant and dominant canopy positions, I used the minimum age of Douglas-fir trees (at coring height of 30 to 80 cm) currently occupying co-dominant and dominantcanopy positions in closed stands. These site-specific ages were added to the date of initial Douglas-fir establishment (plot-level date for closed stands and site-level date for open stands) to estimate DDC and DDD in closed stand locations. Initial dates of establishment, as well as the median, minimum, and maximum age at coring height (30-50 cm) for co-dominant and dominant Douglas-fir, were reported at each site (Table 7). Regional oak-growth trends were evaluated by calculating the difference between closed and open RWI per site, and then averaged across sites per species. Positive RWI differences indicated greater oak growth in closed stands than open stands and vice versa for negative differences. In order to quantify the magnitude (proportion) of growth difference between oaks in closed versus open stands, at each site (per species), RWI values from closed stands were divided by RWI values from open stands (at the annual resolution) then subtracted by 1 (see equation below).

Growth difference = 
$$1 - \left(\frac{RWI_{closed}}{RWI_{open}}\right)$$

# 2.3 Results

# 2.3.1 Tree age structure

In total, 1747 trees and 10 species were sampled for age structure. Of the 961 cored oak trees, 86% were successfully cross-dated. Cores from 390 trees yielded counts to pith (22% of trees), and cores from 1079 trees yielded estimated counts to pith. Using a geometric model of annual tree growth, I estimated < 5 additional yrs for 69% and < 10 additional yrs for 95% of these 1079 cores. Cores from 278 trees (82% were Oregon white oak and California black oak) yielded minimum age counts due to heart rot or > 15 estimated years to pith. The youngest tree (Douglas-fir at site IB) was six yrs old and the oldest tree (Oregon white oak at site CP) was > 324 yrs old.

Across all 10 sites, Douglas-fir was the most frequently cored tree species (42% of trees cored) with a median age of 43 yrs (range: 6 to 142). Oregon white oak was the second most frequently cored species (36% of trees cored) with a median age of 136 yrs (range: 41 to > 324). California black oak was the third most frequently cored species (16% of trees cored) with a median age of 136 yrs (range: 45 to 301). Other trees species were cored relatively infrequently (6% of all trees cored) with median ages ranging between 37 to 98 yrs (Table 4).

Across all 10 sites, most trees with minimum age counts were within the dbh range of trees sampled with complete cores and are represented in tree establishment graphs (Appendix C). A minority of Oregon white oak, California black oak, and Douglas-fir trees with minimum age counts (18, 15, and 10 trees, respectively), representing less than 3%, 6%, and 2%, respectively, of each species age-sample size, exceeded dbh ranges of complete cores and thus, are not represented in the graphs. Exclusion of trees with minimum age counts resulted in the potential omission of earlier tree establishment dates at a few sites (see Table 2). At site WC, one minimum aged Oregon white oak tree exceeded dbh ranges of complete cores, representing 2% of the species' total tree age sample. At site BV, four minimum aged California black oak trees exceeded dbh ranges of complete cores, representing 10% of the age sample. At site BM, four Oregon white oaks and four California black oaks with minimum ages exceeded dbh ranges of complete cores, representing 6% and 13% of the age sample, respectively. At site CP, one Oregon white oak, two California black oaks, and one Douglas-fir with minimum ages exceeded dbh ranges of complete cores, representing 2%, 6%, and 2% of the age sample, respectively. At site LE, one Oregon white oak and five Douglas-fir exceeded the dbh ranges of complete cores, representing 2% and 5% of the age sample, respectively. At site HS, one minimum aged California black oak exceeded dbh ranges of complete cores, representing 5% of the age sample. At site YJ, one minimum aged Douglas-fir exceeded the dbh ranges of complete cores, representing 1% of the age sample. At site IB, one minimum aged Oregon white oak exceeded dbh ranges of complete cores, representing 2% of the age sample. At site EB, one Oregon white oak and two California black oaks with minimum ages exceeded the dbh range of complete cores, representing 2% and 9% of the age sample, respectively.

At site BH, one California black oak and one Douglas-fir with minimum ages exceeded the dbh range of complete cores, representing 9% and 1% of the age sample, respectively.

Relationships between tree age and dbh were highly consistent for Douglas-fir among sites but not for oak species (Table 3). Across sites, the linear regression between dbh and age coring height (~30-50 cm) described 50% of the variance (adjusted  $R^2$  values) and ranged from 30% to 80% among sites (Table 3). California black oak's relationship between age and size were more consistent than Oregon white oak. Across sites, the linear regression described 16% of the variance between age and size, and ranged from < 1% to 49% among sites (Table 3). Oregon white oak's relationship between age and size were the least consistent among all three tree species. Across sites, the linear regression described 12% of the variance between age and size, and ranged from < 1% to 48% among sites (Table 3). Table 2. Number of sites that include trees with minimum age counts (missing center rings) that exceeded the dbh range of trees with complete cores resulted in the potential omission of older Oregon white oak (QUGA), California black oak (QUKE), and Douglas-fir (PSME) tree establishment than represented in age structure sample (see Appendix B for data).

	QUGA	QUKE	PSME
No. of sites with no trees exceeding the size range of trees with complete cores	3	3	7
No. of sites with 1 tree exceeding the size range of trees with complete cores	6	3	2
No. of sites with $\geq 2$ trees exceeding the size range of trees with complete cores	1	4	1
No. of sites with $\geq$ 5 trees exceeding the size range of trees with complete cores	0	0	1

Table 3. Simple linear regression between tree age (y-variable) at coring height and dbh (x-variable) for Oregon white oak, California black oak, and Douglas-fir trees at 10 mixed oak-conifer woodland sites (from xeric to mesic climate conditions from top to bottom) and across all sites in northwestern California. Adjusted R<sup>2</sup> values and p-value of each linear model is reported. Significant ( $\alpha = 0.05$ ) *p*-values are bolded.

	Oregon white oak			California black oak			Douglas-fir		
Site	Equation	Adj. R <sup>2</sup>	<i>p</i> -value	Equation	Adj. R <sup>2</sup>	<i>p</i> -value	Equation	Adj. R <sup>2</sup>	<i>p</i> -value
WC	Y = 0.67x + 50.6	0.37	<0.001	Y = 0.68x + 107.9	0.35	0.004	Y = 0.67x + 50.6	0.37	<0.001
BV	Y = 0.87x + 113.3	0.23	0.001	Y = -0.22x + 135.0	-0.04	0.669	Y = 0.81x + 14.9	0.80	<0.001
BM	Y = 0.36x + 132.1	0.01	0.18	Y = 1.99x + 87.0	0.49	<0.001	Y = 0.91x + 39.5	0.56	<0.001
CP	Y = 1.99x + 87.1	0.48	<0.001	Y = 0.60x + 131.6	0.16	0.03	Y = 0.82x + 27.1	0.30	<0.001
LE	Y =29x + 141.3	-0.004	0.37	Y = 1.04x + 100.1	0.42	<0.001	Y = 0.90x + 15.0	0.45	<0.001
HS	Y = -0.09x + 142.5	-0.01	0.66	Y = 0.95x + 90.0	0.04	0.25	Y = 1.11x + 10.3	0.68	<0.001
YJ	Y = 0.27x + 127.5	-0.02	0.55	Y = 1.18x + 102.2	0.31	0.002	Y = 0.83x + 14.0	0.72	<0.001
IB	Y = 0.27x + 85.7	0.26	<0.001	Y = 0.92x + 71.7	0.35	0.03	Y = 0.61x + 19.8	0.46	<0.001
EB	Y = 0.001x + 136.2	-0.02	0.99	Y = -0.19x + 142.4	-0.05	0.60	Y = 0.79x + 28.2	0.59	<0.001
BH	Y = 0.17x + 97.0	0.01	0.22	Y = 0.17x + 97.0	0.01	0.22	Y = 0.60x + 29.6	0.61	<0.001
Across sites	Y = 0.82x + 106.7	0.12	<0.001	Y = 0.70x + 110.4	0.16	<0.001	Y = 0.82x + 24.5	0.50	<0.001

Table 4. Species-specific tree age structure (from complete tree cores) across 10 mixed oak-conifer woodlands in northwestern California. Sample size (*n* trees), median, minimum (min), and maximum (max) age (yrs) at coring height (~30 cm) are reported.

Species	Sample size	Median Age	Min Age	Max Age
Aesculus californica	24	98	50	142
Arbutus menziesii	31	75	23	129
Cedrus decurrens	3	49	29	56
Notholithocarpus densiflorus	2	41	29	53
Pseudotsuga menziesii	707	43	6	142
Quercus agrifolia	3	81	73	107
Q. chrysolepis	9	37	28	100
Q. garryana	502	136	41	324
Q. kelloggii	175	138	45	301
Umbellularia californica	15	74	35	154

## 2.3.2 Temporal and spatial patterns of tree establishment

The majority of live Oregon white oaks and California black oaks established before 1905 (80% and 85%, respectively), whereas the majority of evergreen conifer/other hardwoods established after 1905 (93%) ( $\chi^2 = 811.5$ , df = 1,  $p \le 0.001$ ). Most Oregon white oaks and California black oaks established between 1850 and 1910 (86% and 81% respectively) and often (69% of plots) within a shorter period (~20 to 40 yr) at the plot-scale for each individual site (Appendix D). However, 31% of plots exhibited a longer period (~60 to 80 yrs) of oak establishment (Appendix D). Sites that exhibited a shorter period of establishment ( $\le 40$  yrs) at the plot-scale also tended to have a higher percentage of cored multi-stemmed oak trees (e.g., 33% at site BH; Figure 5; Appendices B & D). California black oak establishment than Oregon white oak (Figure 5). Neither Oregon white oak nor California black oak trees had any tree establishment since 1973 and 1969, respectively, with less than 0.06% for either species after 1950.

Across the 10 study sites, Douglas-fir establishment occurred between 1872 and 2006 with most (73%) occurring specifically after 1950, at both sites with (BV, CP, LE, YJ) and without (WC, IB, BH) past conifer harvests (Figure 5). While past conifer harvests could have removed Douglas-fir trees that established during the 1800s, the low proportion of Douglas-fir establishment during the 1800s likely represents the low

proportion of these stumps at harvested sites (Figure 5). At the plot-scale, Douglas-fir exhibited relatively continuous establishment (within the 20-yr age bins) during a ca. 60 to 80 yr period in some of the stands (Appendix D). At most sites (8 out of 10), evergreen hardwoods established concurrently with Douglas-fir (Figures 5a, c-h, j), but the timing varied at the plot-scale (Appendix D).





Figure 5. Proportion of tree establishment by species at 10 mixed oak-conifer woodland sites from xeric (a) to mesic (j) climate. Mean proportion of cored multistemmed oak species at plot-scale are reported for each site. Sites: a) WC (n = 160 trees), b) BV (n = 141 trees), c) BM (n = 137 trees), d) CP (n = 143 trees), e) LE (n = 159 trees), f) HS (n = 149 trees), g) YJ (n = 138 trees), h) IB (n = 150 trees), i) EB (n = 145 trees), and j) BH (n = 153 trees). Only cores with a pith present or <15 yrs estimated to pith are graphed. Species codes: QUGA, *Quercus garryana*; QUKE, *Q. kelloggii*; PSME, *Pseudotsuga menziesii*; AECA, *Aesculus californica*; ARME, *Arbutus menziesii*; QUCH, *Q. chrysolepis*; UMCA, *Umbellularia californica*; OTHER,  $\leq 3$  trees cored per species grouped together (e.g., *Aesculus californica*, *Q. agrifolia*, *Q. chrysolepis*, *Umbellularia californica*.

## 2.3.3 Variability of stand structure among sites

At most sites (8 out of 10), the majority of the open-woodland plots occurred on more xeric topographic positions (i.e. southwest facing slopes, higher solar radiation index values) than the closed-forest plots (lower solar radiation index values) (see Solar radiation difference in Table 1). Oregon white oak, California black oak, and Douglasfir collectively accounted for 95% of the basal area across the 10 northwestern California sites (Appendix A). In open stands, there were no significant differences in basal area or density by species among sites (p > 0.07). In transitional stands, there were also no significant differences in basal area by species among sites (p > 0.07), but density of Oregon white oak, California black oak, "other" species (defined in Methods), and total density differed among sites (p = 0.029, p = 0.016, p = 0.027, and p)= 0.024, respectively). Multiple-site comparisons revealed greater density of California black oak in transitional stands only at BM (average: 90 stems ha<sup>-1</sup>) compared to CP (average: 23 stems ha<sup>-1</sup>) (p = 0.048). In closed stands, there were no significant differences in basal area of Oregon white oak, California black oak, or Douglas-fir among sites, but basal area of "other" species differed among sites (p = 0.021), although pair-wise site comparisons were not significant (p = 0.22). Lastly, in closed stands, there were no significant differences in density of Oregon white oak or California black oak among sites, but density of Douglas-fir and "other" species' differed among sites (p = 0.036 and p = 0.015, respectively). Multiple-site comparisons only showed greater

density of Douglas-fir at site LE (average: 940 stems ha <sup>-1</sup>) in comparison to HS (average: 250 stems ha <sup>-1</sup>) (p = 0.034).

# 2.3.4 Variability in stand structure among stand types

Oregon white oak density and basal area varied from open to closed stands (Figures 6a & e; Appendix A). Across sites, average Oregon white oak stem density in open, transitional, and closed stands was 440, 264, and 113 stems ha<sup>-1</sup>, respectively (p < 0.001). Across sites, average Oregon white oak basal area in open, transitional, and closed stands was 24.3, 15.5, and 8.3 m<sup>2</sup> ha<sup>-1</sup>, respectively (p < 0.001). Oregon white oak had higher stem densities and basal areas than California black oak across all stand types (Figures 6a,b,e,f). Across stand types, the median proportion of Oregon white oak tree mortality was 15%, and highest in closed stands (Table 6).

California black oak stem density varied by stand type; open, transitional, and closed stands had 70, 84, and 68 stems ha<sup>-1</sup>, respectively. Across sites, average California black oak basal area in open, transitional, and closed stands was 9.4, 8.0, and 8.8 m<sup>2</sup> ha<sup>-1</sup>. California black oak density and basal area were not significantly different among stand types (all p > 0.05; Figures 6b & f). Across stand types, the median proportion of California black oak tree mortality was 14%, and highest in closed stands (Table 6).

Douglas-fir density and basal area varied among all stand types (p < 0.001), and were predictively highest in closed-forest stands and lowest in open stands (Figures 6c & g). Across sites, average Douglas-fir stem density in open, transitional, and closed stands was 133, 392, and 528 stems ha<sup>-1</sup>, respectively. Average basal area of Douglas-fir in open, transitional, and closed stands was 2.3, 21.4, and 41.8 m<sup>2</sup> ha<sup>-1</sup>, respectively. Total basal area of all trees varied among all stand types (p < 0.001), and was highest in closed stands (Figure 6h). Across sites, average total basal area in open, transitional, and closed stands (P < 0.001), and was highest in closed stands was 37.3, 48.6, and 62.0 m<sup>2</sup> ha<sup>-1</sup>, respectively. However, total density of live trees was not significantly different among stand types (Figure 6d). Across sites, average total stem density in open, transitional, and closed stands was 673, 820, and 774 stems ha<sup>-1</sup>, respectively. The proportion of evergreen hardwood and conifer trees varied among stand types with greater proportions found in transitional and closed stands than in open stands (Table 5).

Across the six sites with past conifer harvests, the mean density of conifer stumps per hectare was 40 (range: 10 to 130 ha<sup>-1</sup>), representing on average 15% of the stand (range: 11 to 44 %) (Appendix A). Site CP had the greatest amount of harvesting with conifer stumps in every plot with living Douglas-fir trees (7 plots; 3 to 39% of the total density of Douglas-fir; mean diameter: 55 cm (range: 29 to 178 cm)). Site LE had the smallest diameter of stumps representing low percentages of stand structure (3 plots; 1 to 5% of the total density of Douglas-fir; mean diameter: 14 cm (range: 8 to 23 cm)). Site YJ had the largest stumps and lowest density in plots (2 plots; 1 to 2% of the total density of Douglas-fir; mean diameter: 119 cm (range: 99 to 134 cm)). Site EB had moderately sized conifer stumps representing highly variable percentages of stand structure (4 plots; 3 to 44% of the total density of Douglas-fir; mean diameter: 49 cm (range: 52 to 85 cm)). Conifer stumps at sites BV (5 plots; 5 to 17% of the total density of Douglas-fir; mean diameter: 87 cm (range: 65 to 114 cm)) and HS (5 plots; < 1 to 14% of the total density of Douglas-fir; mean diameter: 47 cm (range: 42 to 140 cm)) represented relatively low percentages of the stand structure.



Figure 6. Stem density and basal area of live trees in open-oak woodland (Open), transitional woodland-forest (Transitional), and closed mixed hardwood-conifer forest (Closed) stands in northwestern California (includes all 10 sites; n = 30plots per stand type). Stem density and basal area measurements include white oak (a,e), black oak (b,f), Douglas-fir (c,g), and all tree species (d,h), respectively. In each graph variables with different letters indicate significant differences (Kruskal-Nemenyi test,  $p \le 0.05$ ).

Table 5. Average proportion of tree species in open-oak woodland (Open), transitional woodland-forest (Transitional), and closed mixed hardwood-conifer forest (Closed) stands in northwestern California. Proportions are based on stem density per hectare.

Species	Open	Transitional	Closed
Abies concolor	0.000	0.001	0.000
Acer macrophyllum	0.000	0.001	0.001
Aesculus californica	0.009	0.025	0.001
Arbutus menziesii	0.010	0.037	0.036
Cedrus decurrens	0.001	0.003	0.001
Heteromeles arbutifolia	0.000	0.004	0.000
Notholithocarpus densiflorus	0.001	0.004	0.019
Pinus ponderosa	0.001	0.001	0.001
Pseudotsuga menziesii	0.197	0.477	0.682
Quercus agrifolia	0.007	0.003	0.000
Q. chrysolepis	0.003	0.013	0.001
Q. garryana	0.653	0.322	0.145
Q. kelloggii	0.104	0.102	0.087
Umbellularia californica	0.012	0.007	0.021

Table 6. Median proportion of dead compared to total California black oak, Douglas-fir, and Oregon white oak trees in open-oak woodland (Open), transitional woodland-forest (Transitional), closed mixed hardwood-conifer forest (Closed), and across all stand types (Across stands) in northwestern California.

Species	Open	Transitional	Closed	Across all stands
California black oak	0.09	0.17	0.17	0.14
Douglas-fir	0.00	0.05	0.11	0.04
Oregon white oak	0.09	0.13	0.27	0.24

#### 2.3.5 Timing and effects of overstory Douglas-fir on oak growth

By the early 1920s, Douglas-fir had established in some stands at six sites, and by the late 1960s Douglas-fir had established in some stands at all sites (see blue line in Figures 8a & b). In closed forest stands, the estimated age of co-dominant and dominant Douglas-fir trees was highly variable and ranged from 11 to 121 yrs and 25 to 141 yrs, respectively (Table 7). Although the age distributions frequently overlapped, co-dominant Douglas-fir trees were generally younger than dominant Douglas-fir trees (on average 21 yrs younger), especially at the most xeric site WC (Table 7).

Since the estimated date of Douglas-fir co-dominance (later than 1980 at all sites), Oregon white oak growth was ~ 26% slower in closed stands in comparison to open stands at seven sites (p < 0.05; see Table 7). Oregon white oak growth was greater (~ 16%) in closed stands than open stands since the estimated date of Douglas-fir co-dominance and dominance only at the HS site (p = 0.026 and p < 0.001, respectively; Appendix F). It is important to note that at sites with past conifer harvests, removal of large diameter conifers appears to have affected oak growth with increasing growth trends during the 1940s to 1970s (see sites BV, HS, EB in Appendix F). Interestingly in closed stands with and without past conifer harvests, prior to my estimated date of Douglas-fir dominance, Oregon white oak growth was greater at these locations than at locations that have continued to support open oak-dominant stands (Figure 7a).

Across sites, California black oak on average exhibited ~ 5% greater growth in closed compared to open stands since the mid-1990s, but growth differences between closed and open stands varied across sites (Figure 7b; Appendix F). At the sites with more xeric climate (site BM with no evidence of past conifer harvest and site BV with evidence of past conifer harvests in closed stands), California black oak growth was ~ 35% greater in closed stands than in open stands since my estimated date of Douglas-fir dominance (p < 0.001; Appendix F). At sites with mesic climate (site LE with no past conifer harvests, and sites EB and YJ with past conifer harvests in closed stands), California black oak growth was ~ 25% slower (p < 0.01 for all sites) in closed stands than open stands since my estimated date of Douglas-fir co-dominance and dominance (Table 7; Appendix F).

Table 7. Timing of Douglas-fir establishment, co-dominance (DDC), dominance (DDD) at the plot level, and the effects on oak growth in 10 mixed oak-conifer woodlands (xeric to mesic climate from top to bottom) in northwestern California. Sample size (*n* trees), median, minimum (min), and maximum (max) age at coring height (~30 cm) of co-dominant and dominant Douglas-fir trees in closed canopy plots are reported per site.

Site	Initial Douglas-fir	Co-	dominant Douglas-fir Age	D	ominant Douglas-fir Age	Whi	te oak	Blac	k oak
	Establishment <sup>1</sup>								
	min-max	п	Median (min-max)	n	Median (min-max)	$DDC^2$	$DDD^2$	$DDC^2$	$DDD^2$
WC	1888-1951	23	63 (34-121)	16	105 (25-125)	0.001	<0.001	5	5
BV	1922-1995	3	25 (21-103)	20	86 (40-141)	3	0.681	NA	<0.001
BM	1899-1907	8	50 (38-116)	22	88 (36-124)	<0.001	<0.001	0.001	<0.001
СР	1966-1973	15	42 (24-105)	7	78 (35-140)	<0.001	4	0.330	4
LE	1944-1959	32	54 (11-68)	13	50 (39-57)	0.158	0.318	<0.001	<0.001
HS	1899-1963	16	102 (29-105)	6	101 (90-107)	0.026	<0.001	0.951	0.407
YJ	1957-1991	28	42 (19-58)	6	65 (26-127)	<0.001	NA	<0.001	<0.001
IB	1955-1964	26	44 (36-49)	31	45 (33-89)	0.001	0.001	0.266	0.241
EB	1920-1980	10	75 (26-118)	10	83 (47-118)	<0.001	0.005	<0.001	0.018
BH	1919-1950	15	51 (43-88)	11	58 (44-134)	0.033	0.461	<0.001	0.488

<sup>1</sup> Date of Douglas-fir establishment (min. 2 trees per plot during a 10-yrs period). Three 0.1-ha closed canopy plots per site. <sup>2</sup> Significance indicated in bold font ( $p \le 0.05$ ).

<sup>3</sup> Closed plots lacked cored co-dominant Douglas-fir thus comparisons limited to DDD.

<sup>4</sup> DDD (i.e., 2031) exceeds the sample year thus comparisons limited to DDC.

<sup>5</sup> Cored black oaks were absent in open plots.



Figure 7. Mean growth difference between closed forest and open woodland Oregon white oak (a) and California black oak (b) trees across 10 sites from 1888-2013 (min. 2 Douglas-fir trees in closed stands within a 10 year period). Negative values indicate less growth in closed stands (199 and 63 trees for Oregon white oak and California black oak, respectively) than open stands (150 and 111 trees for Oregon white oak and California black oak, respectively). Gray lines correspond to min/max differences, the solid black line is the mean difference, and the blue line (right-hand axis) is the number of sites (of the 10 sampled) with Douglas-fir establishment in closed stands and species-specific oak present in closed and open stands.

## 2.3.6 Variability of current tree regeneration among sites

In open stands, there were no statistical differences in seedling density for California black oak and Douglas-fir among sites, but Oregon white oak and total seedling densities differed among sites (p = 0.038 and p = 0.022, respectively), with lower densities at sites with xeric climate compared to mesic climate (Appendix G). Multiple-site comparisons showed lower Oregon white oak and total seedling densities in open stands at the xeric site BV (average: 556 seedlings ha <sup>-1</sup> and 1,945 seedlings ha <sup>-1</sup>, respectively) than mesic site IB (average: 37,778 seedlings ha<sup>-1</sup> and 38,333 seedlings ha<sup>-1</sup> <sup>1</sup> respectively) (p = 0.048 and p = 0.045, respectively). In transitional stands, there were no statistical differences in seedling density for Oregon white oak, California black oak, or Douglas-fir among sites, but Pacific madrone and coast live oak seedling densities differed among sites (p = 0.03 and p = 0.01, respectively), although multiple-site comparisons were not significant (p = 0.93 and p = 0.44, respectively). In closed stands, there were no statistical differences in seedling density for Oregon white oak, California black oak, or Douglas-fir among sites, but canyon live oak and coast live oak seedling densities differed among sites (p = 0.027 and p = 0.028, respectively), although multiplesite comparisons were not significant (p = 0.59 and p = 0.93, respectively).

In open stands, California black oak and Douglas-fir sapling densities were not significantly different among sites, but Oregon white oak sapling densities differed among sites (p = 0.029), although multiple site comparisons were not significant (Appendix G). In transitional stands, there were no differences in sapling density for

Oregon white oak, California black oak, or Douglas-fir among sites, but Pacific madrone and canyon live oak sapling densities differed among sites (p = 0.029 and p = 0.004, respectively) although multiple-site comparisons were not significant. In closed stands, Oregon white oak, California black oak, or Douglas-fir sapling densities were not significantly different among sites, but Pacific madrone, canyon live oak, and coast live oak sapling densities differed among sites (p = 0.029, p = 0.029, and p = 0.028, respectively) although multiple-site comparisons were not significant.

## 2.3.7 Variability of current tree regeneration among stand types

Oregon white oak seedling density and total seedling density varied across all stand types (p < 0.001; Figures 8a & d). Oregon white oak seedling densities were lower in transitional and closed stands than in open stands (p < 0.001 and p = 0.003, respectively) (Figure 8a). Across sites, average Oregon white oak seedling densities in open, transitional, and closed stands were 13,528, 4,694, and 278 seedlings ha<sup>-1</sup>, respectively. Total seedling densities on average in open, transitional, and closed stands were 17,389, 7,417, and 3,000 seedlings ha<sup>-1</sup>, respectively. California black oak and Douglas-fir seedling densities were not significantly different across stand types (p > 0.08for both; Figures 10b & c). Across all sites, California black oak seedling densities on average in open, transitional, and closed stands were 2,472, 1,500, and 1,167 seedlings ha<sup>-1</sup>, respectively. Douglas-fir seedling densities in open, transitional, and closed stands evergreen hardwood and conifer seedlings varied among stand types with greater proportions found in transitional and closed stands than in open stands (Table 8).

Oregon white oak, California black oak, and Douglas-fir sapling densities were not significantly different between stand types, although total sapling density did vary among stand types (p = 0.017) with fewer saplings in open stands compared to transitional stands (p = 0.003; Figure 8h). Across all sites, average total sapling densities in open, transitional, closed were 657, 647, and 537 saplings ha<sup>-1</sup>, respectively. Oregon white oak sapling densities on average in open, transitional, and closed stands were 4, 5, and 1 sapling ha<sup>-1</sup>, respectively. Across all sites, average California black oak sapling densities in open, transitional, and closed stands were 1, 0, and 0 saplings ha<sup>-1</sup>, respectively. In contrast, Douglas-fir sapling densities on average in open, transitional, and closed stands were 945, 1,583, and 444 saplings ha<sup>-1</sup>, respectively. Oregon white and California black oak sapling densities were low among all stand types at all sites (Figures 8e & f; Appendix G). While Oregon white oak dominates the seedling stratum, Douglasfir dominated the sapling stratum (Table 8). The proportion of evergreen hardwood and conifer saplings varied between stand types with greater proportions found in transitional and closed stands than in open stands (Table 8).



Figure 8. Density of tree seedlings and saplings in open-oak woodland (Open), transitional woodland-forest (Transitional), and closed mixed hardwood-conifer forest (Closed) stand types in northwestern California (includes all 10 sites; n =30 plots per stand type). Seedling and sapling densities include Oregon white oak (a,e), California black oak (b,f), Douglas-fir (c,g), and all species (d,h), respectively. In each graph variables with different letters indicate significant differences (Kruskal-Nemenyi test,  $p \le 0.05$ ).

Table 8. Average proportion of seedling and sapling regeneration in open-oak woodland (Open), transitional woodland-forest (Transitional), and closed mixed hardwood-conifer forest (Closed) stands in northwestern California. Proportions are based on density per hectare.

Species	Open		Transitional		Closed	
	Seedling	Sapling	Seedling	Sapling	Seedling	Sapling
Abies concolor	0.000	0.000	0.000	0.002	0.000	0.000
Aesculus californica	0.000	0.000	0.000	0.014	0.000	0.000
Arbutus menziesii	0.000	0.010	0.007	0.035	0.009	0.045
Cedrus decurrens	0.000	0.004	0.011	0.006	0.00	0.002
Heteromeles arbutifolia	0.000	0.000	0.000	0.002	0.000	0.000
Notholithocarpus densiflorus	0.000	0.004	0.034	0.019	0.157	0.092
Pinus ponderosa	0.000	0.000	0.000	0.041	0.000	0.000
Pseudotsuga menziesii	0.054	0.947	0.212	0.553	0.148	0.454
Quercus agrifolia	0.005	0.000	0.030	0.006	0.019	0.005
Q. chrysolepis	0.000	0.002	0.037	0.169	0.056	0.310
Q. garryana	0.778	0.006	0.363	0.008	0.093	0.002
Q. kelloggii	0.142	0.002	0.202	0.000	0.389	0.000
Umbellularia californica	0.021	0.024	0.101	0.144	0.130	0.089
## 2.4 Discussion

### 2.4.1 Temporal and spatial patterns of oak and conifer establishment

A regional peak in oak establishment from the 1850 to 1910 occurred across the 10 sites sampled in the North Coast region of California. The majority of oaks sampled in this study pre-date living conifers at all 10 sites, a trend that is consistent with age distributions of Douglas-fir encroached Oregon white oak ecosystems in Oregon and Washington (Thilenius, 1968; Gedalof et al., 2006; Gilligan & Muir, 2011) and California black oak ecosystems in northern California (Stewman, 2001; Cocking et al., 2012). Most oaks established during the mid-1800s to early 1900s with minimal recruitment since 1950 at all 10 sites. While the decadal timing of oak establishment varied across sites, the majority of oaks established over a relatively short period (typically  $\leq$  40 yrs) at individual sites suggesting the influence of stand-scale disturbances promoting dense oak woodlands. At a minority of plots, oak trees established more over longer periods of time indicating evidence of more localized cohort-initiating events (Appendix D).

Three principal mechanisms are often cited for stimulating oak tree establishment in grasslands: favorable climate (Duren et al., 2012); alterations in grazing regimes (Gedalof et al., 2006); and changes in fire intensity or frequency (Thilenius, 1968; Sugihara & Reed, 1987). These mechanisms may interact with factors such as acorn masting events, herbivory, and vegetation competition, resulting in complex patterns of tree establishment (MacDougall, 2008). As in much of the western U.S., in northern California these changes occurred almost simultaneously following declines in Native American populations, increases in Euro-American settlement and associated landscape effects (MacDougall, 2008). Other oak species in these stands established after Oregon white oak and California black, often simultaneously with Douglas-fir. Stand-scale disturbances leading to a peak in oak establishment during the late 1800s and early 1900s are likely due to a combination of changing disturbance and landscape-level changes such as fire, livestock grazing, reduced native ungulate populations, reduced anthropogenic burning (Thilenius, 1968; Gedalof et al., 2006; MacDougall, 2008), and favorable climate conditions for tree establishment (Duren and Muir, 2012).

A regional trend of Douglas-fir establishment following oak establishment was found throughout the North Coast region of California. While some Douglas-fir trees established prior to 1900, the majority (73%) of sampled Douglas-fir trees established since the 1950, indicating that Douglas-fir was historically present as a component of the stand structure prior to modern land-management practices but at significantly lower densities. While past conifer harvests removed a small proportion of large diameter Douglas-fir trees that likely established during the 1800s, due to the sparse density of large diameter stumps, the low proportions of Douglas-fir establishment during the 1800s is still representative Douglas-fir establishment patterns (Figure 5). Likely, active suppression of fire that began in the region before ca. 1940s and 1950s (Agee 1993; CALFIRE database) and removal of overstory conifer at harvested sites enabled a large proportion of conifers to establish since 1950. Based on age structure, the closed canopy stands I studied are better described as conifer-dominant remnant oak woodlands. The decadal timing of Douglas-fir establishment and overstory dominance varied across sites with the majority of trees established over a longer window of time (typically 60 to 80 yrs) than oak establishment, suggesting that Douglas-fir establishment has been a long-term process. For example, dominant Douglas-fir trees were older (~100 yrs) at the most xeric site WC than at the most mesic site BH (~50 yrs), suggesting that Douglas-fir tends to expand it's establishment domain slower in drier and warmer climate. The regional variability of Douglas-fir growth warrants future study into the potential influence of environmental gradients.

Stand structure in mixed-oak woodlands in the North Coast region of California appears to be related to moisture gradients similar to other studies across Oregon white oak's range (e.g., Riegel et al., 1992; Devine & Harrington, 2007). The trend of openoak woodlands persisting on warmer/drier aspects in comparison to closed forest stands suggests the influence of topography on stand structure and composition (Table 1). Warmer aspects have higher moisture stress and soil temperatures that limit conifer seed germination and seedling survival (Hermann & Lavender, 1990), favoring oak dominance (Whittaker, 1960; Ohmann & Spies, 1998). Although conifer establishment tends to occur along mesic topographies, other environmental factors clearly allow for successful establishment at more xeric aspects, as exhibited at sites LE and EB (see Solar radiation difference in Table 1). A combination of interacting disturbances (as mentioned above) and edaphic characteristics may lead to more variable patterns of stand structure (Gilligan and Muir, 2011), warranting further evaluations of the influence of environmental factors on Douglas-fir establishment.

## 2.4.2 Timing and effects of overstory Douglas-fir on oak growth

At more than half of the sites, Douglas-fir trees have long been present (ca. 100 yrs or more). Only in the last 20 to 30 yrs has oak growth declined in conifer-dominant stands compared to oak-dominant stands. It is important to note that at sites with past conifer harvests in closed stands, removal of large diameter conifers appears to have affected oak growth from the 1940s to 1970s (Appendix F). The peaked release of oak growth in closed stands (see sites BV, HS, EB in Appendix F) during this time period may reflect the temporary relief from overstory conifer shading and may have extended the time it takes Douglas-fir to substantially affect oak growth. Interestingly in closed stands, prior to my estimated date of Douglas-fir dominance, Oregon white oak growth was greater at these locations than at locations that have continued to support open oak-dominant stands (see sites in Appendix F). At sites with past conifer harvests, this pattern may be related to disturbance where oaks are released from overstory conifer harvests, this pattern may be related to more mesic conditions in these locations allowing for more favorable growth.

For Oregon white oak, the consistently higher proportion of oak mortality and slower growth in closed stands compared to open stands, suggests that expansion of

conifer establishment which leads to Douglas-fir dominance in remnant open woodlands is detrimental for Oregon white oak growth and survival. My results indicate that once Douglas-fir overtops Oregon white oak trees in formerly oak-dominant stands, it leads to greater oak mortality and reduced oak growth, which supports similar findings by Devine and Harrington (2013). The response of California black oak growth to overstory Douglas-fir appears to be more variable than Oregon white oak.

The variability of California black oak growth between closed and open stands among sites, paired with lower proportions of mortality in closed stands compared to Oregon white oak, suggests that California black oak can persist in closed-canopy conditions more than Oregon white oak in this study area. Furthermore, the ability of California black oak to grow beneath overstory Douglas-fir appears to be influenced by local climate. At two sites with more xeric climate (site CP with past conifer harvests and site BM without past harvests), California black oak growth was greater in closed stands than open stands since the estimated date of Douglas-fir dominance at both sites. The increase in growth in closed stands occurs 20 to 40 yrs after conifer harvests suggesting a growth trend rather than just a harvest effect (Appendix F). This pattern suggests that California black oak growth is potentially more limited by moisture than light resources at xeric sites (Table 7; Appendix F). Conversely, at sites with more mesic climate (both with and without past conifer harvests), California black oak growth was lower in closed stands than open stands, similar to Oregon white oak. This pattern suggests that California black oak growth is more limited by light resources than moisture at mesic sites (Table 7; Appendix F). California black oaks located on mesic

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sites may compete more intensively for light since moisture is less often limiting, and typically possess lower root to shoot ratios and fewer drought adaptations (Kaufmann 1981; Kramer 1983). Comparable findings were present in the nearby Klamath Mountains, where xeric environments enable California black oak trees to persist beneath conifers (Taylor & Skinner, 1998). Additionally, more xeric environments can support sparser conifer canopies, reducing light competition and allowing California black oak trees to remain a component in the midstory (Taylor & Skinner, 1998). The lack of a California black oak growth chronology at the most xeric site WC in open stands limits my ability to validate this relationship between California black oak growth and environmental conditions. Further tree core sampling of this species in open stands at this site could resolve this issue.

#### 2.4.3 Tree regeneration

The reduced density of Oregon white oak seedlings in transitional and closed-forests compared to open-woodlands supports findings that Oregon white oak seedling survival is strongly associated with open-canopy conditions (Thysell & Carey, 2001; Gedalof et al., 2006). The presence of Douglas-fir in the overstory likely reduces oak regeneration by limiting light resources and reducing acorns production from residual mature oaks (Devine et al., 2007a). The paucity of oak saplings in open stands (Table 8) suggests that other factors are limiting the growth of seedlings from reaching the sapling stage. Open stands had the highest density of oak seedlings at all but the most xeric sites, yet there are

few oak saplings (on average 99.9% fewer) suggesting a "bottleneck" in the transition from seedling to sapling to adult (Appendix G). These same bottlenecks have been found in savannas elsewhere (e.g., Bond & Keeley 2005; Bond 2008), and may represent a more complex dynamics in fire-prone savannas and woodlands. In dry habitats with limited soil moisture, grass competition dramatically decreases Oregon white oak seedling survival (Fuchs et al., 2000; Devine et al., 2007a). Due to their fibrous root system, grasses can outcompete oak seedlings for soil moisture, causing oak-seedling desiccation and mortality. An additional factor that could be reducing oak seedling survival is herbivory by invertebrates and vertebrates (Fuchs et al., 2000; Devine et al., 2007a). Based on the paucity of oak saplings and lack of oak tree establishment since 1950, these stands do not have adequate oak regeneration to sustain current woodlands through acorn germination alone. Single or multiple disturbance events (i.e., fire) could initiate regeneration.

### 2.4.4 Management and conservation

Where Douglas-fir trees overtop oak trees, my findings suggest that Oregon white oaks at most sites are under greater competitive stress in conifer-dominant stands than oak-dominant stands. If the goal is to promote open-oak woodlands, removal of overstory conifers through thinning has been a successful method in restoring former oak woodlands colonized by Douglas-fir during the early to mid- 20<sup>th</sup> century (Devine et al. 2007b; Devine and Harrington, 2013; Livingston, 2014). Once overstory conifers are

removed, Oregon white oak trees with severe crown dieback and decades of suppressed growth can respond vigorously with profuse epicormic sprouting and increased radial growth (Devine and Harrington, 2006; Devine and Harrington, 2013). Understory response to conifer removal includes increased cover of non-native plants (Devine et al., 2007b), therefore seeding native plants following thinning treatments may be necessary to restore native understory vegetation. Even though this study did not quantify the effects of overstory conifer removal on oak-tree growth, the observed increases in growth following past conifer harvests during the 1940 to 1960s suggests that oaks in coniferdominant stands might respond to future conifer thinning treatments in this region.

This research adds to the growing body of work on mixed oak-conifer stands (Reed and Sugihara, 1987; Barnhart et al., 1996; Hunter and Barbour, 2001; Engber et al., 2011; Cocking et al., 2012) that provides baseline information on current and historical stand dynamics in woodland ecosystems of northern California. The results of this study highlight the value of multi-site investigative approaches for stand structure studies and improves our understanding of the variability of stand dynamics within this region. The replacement of oak-dominant stands by conifer-dominant stands can represent a loss of endemic biodiversity (Thysell & Carey, 2001; Livingston, 2014) thus active management may be necessary to maintain pure oak stands in this region.

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## **APPENDICES**

## Appendix A

Oregon white oak (QUGA), California black oak (QUKE), Douglas-fir (PSME), and all species (TOTAL) stem density (stem ha<sup>-1</sup>) and basal area (m<sup>2</sup> ha<sup>-1</sup>) in open oak-woodlands (Open), transition woodland-forests (Transitional), closed mixed oak-conifer forests (Closed), and across all stand types at 10 mixed oak-conifer woodland sites (xeric to mesic climate from top to bottom) in northwestern California. Douglas-fir stump density (mean and range per hectare) in transitional and closed stands are also reported

QUGA	Open			Transitional			Closed			Across Stand Types		
Site	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
WC												
Density	657	510	840	347	100	560	110	30	200	371	30	840
BA	23.7	23.6	23.7	12.9	3.9	23.5	7.5	3.3	10.0	14.7	3.3	23.7
BV												
Density	267	0	440	150	110	200	77	40	120	164	0	440
BA	14.5	0.0	26.3	14.3	6.9	22.0	7.6	6.2	8.6	12.1	0.0	26.3
BM												
Density	497	200	670	707	590	810	83	0	220	429	0	810
BA	19.3	7.9	29.2	21.6	20.7	23.1	3.7	0.0	9.9	14.9	0.0	29.2
СР												
Density	450	290	540	80	1	200	13	0	120	191	0	540
BA	26.9	20.2	35.0	13.3	10.0	15.6	3.0	0.0	7.7	14.4	0.0	35.0
LE												
Density	427	390	470	217	120	270	63	0	120	236	0	470
BA	28.9	25.8	33.1	14.9	5.8	23.4	6.0	0.0	9.7	16.6	0.0	33.1
HS												
Density	223	90	320	157	100	260	170	60	250	183	60	320
BA	23.2	13.4	33.8	15.7	13.1	18.8	15.0	6.3	27.8	17.9	6.3	33.8
YJ												
Density	507	0	830	117	20	230	80	20	160	234	0	830
BA	21.2	0.0	31.9	6.1	2.4	11.3	5.4	1.3	11.1	10.9	0.0	31.9
IB												
Density	363	230	440	320	180	530	223	170	270	302	170	530
BA	23.2	20.0	29.7	21.9	13.7	26.3	19.7	15.2	26.5	21.6	13.7	29.7
EB												
Density	150	100	210	107	10	230	60	50	70	106	10	230
BA	28.0	14.8	43.5	9.7	0.28	16.7	5.1	3.9	7.1	14.3	0.3	43.5
BH												
Density	860	600	1310	437	350	510	217	60	360	504	60	1310
BA	33.8	27.9	37.7	24.9	24.6	25.4	10.2	3.5	17.8	22.9	3.5	37.7
Across Sites												
Density	440	0	1310	264	1	810	113	0	360	272	0	1310
BA	24.3	0.0	43.5	15.5	0.3	26.3	8.3	0.0	27.8	16.0	0.0	43.5

QUKE	Open			Transitional			Closed			Across Stand Types		
Site	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
WC												
Density	43	0	100	283	170	370	73	40	130	133	0	370
BA	1.0	0.0	2.1	8.8	2.7	15.3	9.6	1.5	17.2	6.5	0.0	17.2
BV												
Density	127	100	170	63	0	120	87	50	111	92	0	170
BA	18.5	9.2	37.2	7.4	0.0	15.5	13.4	11.3	15.2	13.1	0.0	37.2
BM												
Density	110	40	180	90	70	120	53	10	80	84	10	180
BA	13.3	7.5	18.7	9.1	4.0	15.2	8.4	0.3	19.3	10.3	0.3	19.3
CP												
Density	43	0	130	23	20	30	63	50	80	43	0	130
BA	3.9	0.0	11.8	6.8	2.8	10.9	12.5	10.1	16.3	7.8	0.0	16.3
LE												
Density	93	20	200	170	20	320	153	0	430	139	0	430
BA	11.0	1.1	26.1	14.2	2.8	31.0	12.2	0.0	33.4	12.5	0.0	33.4
HS												
Density	57	20	90	7	0	20	43	0	90	36	0	90
BA	15.9	7.7	30.8	2.4	0.0	7.1	12.4	0.0	22.6	10.2	0.0	30.8
YJ												
Density	113	0	310	107	80	130	73	10	130	98	0	310
BA	11.1	0.0	30.5	16.3	9.2	21.6	8.2	0.6	15.0	11.9	0.0	30.5
IB												
Density	37	30	40	70	30	130	43	20	70	50	20	130
BA	3.8	2.2	6.8	9.7	2.9	22.6	4.6	2.1	8.7	6.0	2.1	22.6
EB												
Density	10	0	20	13	10	20	37	20	60	20	0	60
BA	9.0	0.0	21.6	3.8	0.5	8.3	4.2	1.8	7.2	5.7	0.0	21.6
BH												
Density	70	0	210	10	0	30	50	30	80	43	0	210
BA	6.2	0.0	18.7	6.2	0.0	3.4	2.6	1.2	4.1	3.3	0.0	18.7
Across Sites												
Density	70	0	310	84	0	370	68	0	430	74	0	430
BA	9.4	0.0	37.2	8.0	0.0	31.0	8.8	0.0	33.4	8.7	0.0	37.2

PSME	Open		Transit	sitional Closed			Across Stand Types			Stumps in Trans & Closed					
Site	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
WC															
Density	110	50	190	480	390	620	610	320	940	400	50	940	0	0	0
BA	2.3	0.5	4.4	20.6	5.1	34.4	43.8	27.4	54.1	22.3	0.5	54.1			
BV															
Density	87	0	160	207	110	300	340	50	500	211	0	500	40	40	40
BA	1.0	0.0	1.9	17.2	5.2	27.0	33.1	18.1	43.2	17.1	0.0	43.2			
BM	_	_	_											_	_
Density	0	0	0	383	170	580	500	220	900	294	0	900	0	0	0
BA	0.0	0.0	0.0	28.1	17.7	42.1	57.1	38.8	79.0	28.4	0.0	79.0			
СР	20	0	00	212	110	520	100	240	510	054	0	520	00	10	120
Density	30	0	90	313	110	530	420	340	510	254	0	530	90	10	130
BA	2.1	0.0	7.8	19.4	5.2	38.5	22.4	21.2	24.4	14.8	0.0	38.5			
LE	110	20	170	620	510	720	040	820	1010	557	20	1010	22	10	00
Density	2 2	20	1/0	020	12.2	720	940 62.2	820 45 5	75 5	281	20	75 5	55	10	90
	5.5	0.2	0.5	19.5	15.2	27.1	02.5	45.5	15.5	20.4	0.2	15.5			
Density	697	10	2070	330	140	640	250	160	310	426	10	2070	23	10	30
BA	49	0.2	10.9	12.2	82	147	36.1	23.2	50.6	17 7	0.2	50.6	25	10	50
YI	1.9	0.2	10.9	12.2	0.2	11.7	50.1	23.2	50.0	17.7	0.2	50.0			
Density	100	10	280	707	340	1360	813	700	980	540	10	1360	10	10	10
BA	7.0	0.0	20.9	22.4	16.3	34.3	43.8	21.5	58.1	24.4	0.0	58.1	-		
IB															
Density	50	40	60	467	360	550	583	480	650	367	40	650	0	0	0
BA	0.4	0.2	0.5	20.0	3.5	30.3	33.0	28.5	36.3	17.8	0.2	36.3			
EB															
Density	120	0	360	130	40	300	370	320	450	207	0	450	20	10	40
BA	1.5	0.0	4.5	22.1	19.7	24.2	35.6	17.1	56.8	19.7	0.0	56.8			
BH															
Density	27	0	80	283	160	440	453	260	590	254	0	590	0	0	0
BA	0.2	0.0	0.6	32.7	11.3	54.7	51.0	38.8	66.4	28.0	0.0	66.4			
Across Sites															
Density	133	0	2070	392	40	1360	528	50	1010	351	0	2070	41	10	130
BA	2.3	0.0	20.9	21.4	3.5	54.7	41.8	17.1	79.0	21.9	0.0	79.0			

TOTAL	Open			Transitional			Closed			Across Stand Types		
Site	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
WC												
Density	903	670	1240	1270	1000	1490	957	800	1120	1043	670	1490
BA	29.2	26.0	33.3	50.2	35.6	68.7	66.0	46.1	77.6	48.4	26.0	77.6
BV												
Density	550	240	760	550	460	650	544	350	661	548	240	760
BA	40.1	37.0	45.8	52.4	35.6	67.0	59.2	38.9	70.2	50.6	35.6	70.2
BM												
Density	617	310	880	1243	1220	1270	647	470	970	836	310	1270
BA	32.9	26.6	36.6	59.7	44.2	78.6	69.2	49.1	98.3	53.9	26.6	98.3
CP												
Density	537	520	550	564	530	601	663	530	810	588	520	810
BA	33.5	25.4	40.0	42.9	32.8	62.1	42.7	40.6	44.1	39.7	25.4	62.1
LE												
Density	633	460	730	1020	790	1200	1157	890	1560	937	460	1560
BA	43.3	29.1	53.5	48.7	42.6	53.3	80.5	69.2	87.0	57.5	29.1	87.0
HS												
Density	990	290	2260	563	310	770	463	380	510	672	290	2260
BA	44.9	33.6	64.9	32.1	28.4	39.1	63.4	51.0	76.0	46.8	28.4	76.0
YJ												
Density	723	600	870	937	620	1510	970	870	1150	887	600	1510
BA	39.4	31.9	51.5	45.3	37.1	58.3	58.9	33.1	73.0	47.9	31.9	73.0
IB												
Density	453	330	530	860	570	1080	943	910	970	752	330	1080
BA	27.5	22.5	32.8	51.8	39.9	59.9	61.3	58.7	98.3	46.8	22.5	62.6
EB												
Density	370	110	780	467	80	670	680	440	950	506	80	950
BA	41.9	20.2	68.7	44.3	32.8	39.1	55.4	40.7	83.6	47.2	20.2	83.6
BH												
Density	957	670	1310	730	540	950	720	520	1030	802	520	1310
BA	40.2	27.9	55.0	58.8	36.7	79.5	63.7	58.1	72.3	54.2	27.9	79.5
Across Sites												
Density	673	110	2260	820	80	1510	774	350	1560	756	80	2260
BA	37.3	20.2	68.7	48.6	28.4	79.5	62.0	33.1	98.3	49.3	20.2	98.3

# Appendix B

The proportion of multi-stemmed Oregon white oak (QUGA) and California black oak (QUKE) trees across stand types in 10 mixed oak-conifer woodland sites (xeric to mesic climate from top to bottom) in northwestern California. Descriptive statistics are reported at the plot-scale for all trees and cored trees.

	All Trees			Cored Trees		
Site	Plot Mean	Plot Min	Plot Max	Plot Mean	Plot Min	Plot Max
WC						
QUGA	0.24	0.00	0.54	0.16	0.00	0.70
QUKE	0.27	0.00	0.67	0.18	0.00	0.66
BV						
QUGA	0.31	0.00	0.74	0.22	0.00	0.50
QUKE	0.36	0.00	0.82	0.19	0.00	0.60
BM						
QUGA	0.29	0.00	0.46	0.29	0.00	0.63
QUKE	0.21	0.00	0.58	0.07	0.00	0.40
CP						
QUGA	0.12	0.00	0.41	0.08	0.00	0.30
QUKE	0.17	0.00	1.00	0.07	0.00	0.40
LE						
QUGA	0.17	0.00	0.45	0.10	0.00	0.40
QUKE	0.08	0.00	0.43	0.07	0.00	0.33
HS						
QUGA	0.41	0.00	0.77	0.10	0.00	0.40
QUKE	0.03	0.00	0.30	0.00	0.00	0.00
YJ						
QUGA	0.33	0.00	0.83	0.22	0.00	0.70
QUKE	0.38	0.00	1.00	0.26	0.00	1.00
IB						
QUGA	0.16	0.00	0.38	0.10	0.00	0.22
QUKE	0.18	0.00	0.80	0.13	0.00	1.00
EB	0.00	0.00	0.50	0.15	0.00	0.00
QUGA	0.22	0.00	0.50	0.15	0.00	0.33
QUKE	0.06	0.00	0.57	0.07	0.00	0.60
BH	0.25	0.04	0.74	0.22	0.00	0.67
QUGA	0.35	0.04	0.74	0.33	0.00	0.67
QUKE	0.38	0.00	1.00	0.22	0.00	1.00
Across sites	0.26	0.00	0.92	0.20	0.00	0.72
QUGA	0.26	0.00	0.83	0.20	0.00	0.73
QUKE	0.21	0.00	1.00	0.22	0.00	1.00

## Appendix C

Relationship between tree size (dbh) and age (yrs) for Oregon white oak, California black oak, and Douglas-fir in 10 mixed oak-conifer woodlands (xeric to mesic climate from a-dd) in northwestern California. Solid circles represent complete tree cores, empty circles represent minimum-aged cores. Linear regression models used only age and tree sizes of complete tree cores. Sites: WC (a-c), BV (d-f), BM (g-i), CP (j-l), LE (m-o), HS (p-r), YJ (s-u), IB (v-x), EB (y-aa), and BH (bb-dd).











# Appendix D

Proportion of tree establishment by species per plot for 10 mixed oak-conifer woodland sites (xeric to mesic climate from top to bottom) in northwestern California. Only cores with a pith present or < 15 yrs estimated to pith are graphed.



Proportion of tree establishment by species per plot at site WC. Open woodland plots (ac; n = 19, 14, and 19 trees, respectively), transitional woodland forest plot (d-f; n = 17, 18, and 19 trees, respectively), closed mixed hardwood-forest plots (g-i; n = 16, 17, and 18 trees, respectively). Species code: QUGA, *Quercus garryana*; QUKE, *Q. kelloggii*; PSME, *Pseudotsuga menziesii*; ARME, *Arbutus menziesii*, CADE, *Calocedrus decurrens*; QUCH, *Q. chrysolepis*; UMCA, *Umbellularia californica*.



Proportion of tree establishment by species per plot at site BV. Open woodland plots (ac; n = 14, 20, and 20 trees, respectively), transitional woodland forest plot (d-f; n = 21, 20, and 20 trees, respectively), closed mixed hardwood-forest plots (g-i; n = 20, 20, and 21 trees, respectively). Species code: QUGA, *Quercus garryana*; QUKE, *Q. kelloggii*; PSME, *Pseudotsuga menziesii*; ARME, *Arbutus menziesii*; QUAG, *Q. agrifolia*; QUCH, *Q. chrysolepis*; UMCA, *Umbellularia californica*.



Proportion of tree establishment by species per plot at site BM. Open woodland plots (ac; n = 9, 9, and 10 trees, respectively), transitional woodland forest plot (d-f; n = 22, 21, and 17 trees, respectively), closed mixed hardwood-forest plots (g-i; n = 14, 17, and 18trees, respectively). Species code: QUGA, *Quercus garryana*; QUKE, *Q. kelloggii*; PSME, *Pseudotsuga menziesii*; QUCH, *Q. chrysolepis*.



Proportion of tree establishment by species per plot at site CP. Open woodland plots (ac; n = 10, 18, and 20 trees, respectively), transitional woodland forest plot (d-f; n = 21, 21, and 20 trees, respectively), closed mixed hardwood-forest plots (g-i; n = 21, 20, and 21 trees, respectively). Species code: QUGA, *Quercus garryana*; QUKE, *Q. kelloggii*; PSME, *Pseudotsuga menziesii*; ARME, *Arbutus menziesii*.



Proportion of tree establishment by species per plot at site LE. Open woodland plots (ac; n = 19, 15, and 18 trees, respectively), transitional woodland forest plot (d-f; n = 18, 15, and 23 trees, respectively), closed mixed hardwood-forest plots (g-i; n = 15, 18, and 18 trees, respectively). Species code: QUGA, *Quercus garryana*; QUKE, *Q. kelloggii*; PSME, *Pseudotsuga menziesii*.


Proportion of tree establishment by species per plot at site HS. Open woodland plots (ac; n = 19, 17, and 10 trees, respectively), transitional woodland forest plot (d-f; n = 19, 17, and 18 trees, respectively), closed mixed hardwood-forest plots (g-i; n = 16, 17, and 15 trees, respectively). Species code: QUGA, *Quercus garryana*; QUKE, *Q. kelloggii*; PSME, *Pseudotsuga menziesii*; AECA, *Aesculus californica*.



Proportion of tree establishment by species per plot at site YJ. Open woodland plots (a-c; n = 10, 13, and 7 trees, respectively), transitional woodland forest plot (d-f; n = 20, 19, and 16 trees, respectively), closed mixed hardwood-forest plots (g-i; n = 16, 22, and 14 trees, respectively). Species code: QUGA, *Quercus garryana*; QUKE, *Q. kelloggii*; PSME, *Pseudotsuga menziesii*; QUCH, *Q. chrysolepis*.



Proportion of tree establishment by species per plot at site IB. Open woodland plots (a-c; n = 11, 14, and 18 trees, respectively), transitional woodland forest plot (d-f; n = 18, 16, and 18 trees, respectively), closed mixed hardwood-forest plots (g-i; n = 16, 17, and 16 trees, respectively). Species code: QUGA, *Quercus garryana*; QUKE, *Q. kelloggii*; PSME, *Pseudotsuga menziesi*; UMCA, *Umbellularia californica*.



Proportion of tree establishment by species per plot at site EB. Open woodland plots (ac; n = 18, 13, and 7 trees, respectively), transitional woodland forest plot (d-f; n = 19, 15, and 18 trees, respectively), closed mixed hardwood-forest plots (g-i; n = 18, 16, and 18 trees, respectively). Species code: QUGA, *Quercus garryana*; QUKE, *Q. kelloggii*; PSME, *Pseudotsuga menziesii*; AECA, *Aesculus californica*; ARME, *Arbutus menziesi*; NODE, *Notholithocarpus densiflorus*; UMCA, *Umbellularia californica*.



Proportion of tree establishment by species per plot at site BH. Open woodland plots (ac; n = 10, 19, and 9 trees, respectively), transitional woodland forest plot (d-f; n = 20, 18, and 19 trees, respectively), closed mixed hardwood-forest plots (g-i; n = 18, 19, and 21 trees, respectively). Species code: QUGA, *Quercus garryana*; QUKE, *Q. kelloggii*; PSME, *Pseudotsuga menziesii*.

## Appendix E

Proportional distribution of diameter-class sizes of live tree stems by species across all stand types at 10 mixed oak-conifer woodland sites (xeric to mesic climate from [a] to [j]) in northwestern California. Species code: QUGA, *Quercus garryana*; QUKE, *Q. kelloggii*; PSME, *Pseudotsuga menziesii*; ABCO, *Abies concolor*; ACMA, *Acer macrophyllum*; AECA, *Aesculus californica*; ARME, *Arbutus menziesii*; CADE: *Calocedrus decurrens*; QUAG, *Q. agrifolia*; QUCH, *Q. chrysolepis*; PIPO, *Pinus ponderosa*; UMCA, *Umbellularia californica*.





## Appendix F

Oregon white oak and California black oak average growth in open oak woodlands and closed mixed oak-conifer forests stands and estimated timing of Douglas-fir codominance and dominance in closed stands at 10 sites (xeric [WC] to mesic [BH] climate from top to bottom) in northwestern California. The green dotted line represents average oak growth in open-oak woodlands, the red solid line represents average oak growth in closed mixed oak-conifer forests, and the thin blue dash is estimated timing of Douglas-fir overstory co-dominance in closed forests based on timing of Douglas-fir establishment (min. 2 trees during 10-yrs period) and minimum age of co-dominant Douglas-fir trees at the plot level, the heavy black dash is the estimated timing of Douglas-fir establishment and minimum age of dominant Douglas-fir trees at the plot scale.









## Appendix G

Oregon white oak (QUGA), California black oak (QUKE), Douglas-fir (PSME), and all species (TOTAL) seedling and sapling density (ha<sup>-1</sup>) in open oak-woodlands (Open), transition woodland-forests (Transitional), closed mixed oak-conifer forests (Closed), and across all stand types at 10 mixed oak-conifer woodland sites (xeric to mesic climate from top to bottom) in northwestern California.

OUGA	Open			Transiti	onal		Closed			Across St	Across Stand Types			
Site	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max		
WC	liteun	101111	IVIUN	liteun	101111	171u/1	liteun	101111	IVIUX	meun	1,111	111111		
Seedling	2222	833	3333	1111	0	3333	0	0	0	1111	0	3333		
Sapling	0	0	0	0	0	0	0	Ő	ů 0	0	Õ	0		
BV	-						-			-				
Seedling	556	0	1667	556	0	1667	0	0	0	370	0	1667		
Sapling	0	0	0	0	0	0	0	0	0	0	0	0		
BM														
Seedling	9444	3333	15000	1111	0	2500	0	0	0	3518	0	15000		
Sapling	0	0	0	13	0	40	0	0	0	4	0	40		
СР														
Seedling	8889	667	10833	6111	2500	9167	556	0	1667	5185	0	10833		
Sapling	0	0	0	0	0	0	0	0	0	0	0	0		
LE														
Seedling	21111	7500	35833	1389	0	333	556	0	1667	7685	0	35833		
Sapling	0	0	0	27	0	80	0	0	0	9	0	80		
HS														
Seedling	2778	0	8333	3611	1667	5833	555	0	833	2315	0	8333		
Sapling	0	0	0	0	0	0	0	0	0	0	0	0		
YJ	10070	0	10167	022	0	1667	0	0	0	2704	0	10167		
Seedling	10278	0	1916/	833	0	1667	0	0	0	3704	0	1916/		
Saping	0	0	0	0	0	0	0	0	0	0	0	0		
ID Soodling	27770	20167	12222	2611	0	5922	1111	0	2222	14167	0	12222		
Seeding	0	29107	45555	13	0	3833 40	0	0	0	14107	0	43333		
FR	0	0	0	15	0	40	0	0	0	+	0	40		
Seedling	14444	1667	34167	1389	0	2500	0	0	0	5278	0	34167		
Sanling	0	0	0	0	0	0	0	0	0	0	0	0		
BH		5	5	Ĭ	0	U		0	v	0	v	U U		
Seedling	27778	6667	49167	7222	1667	17500	0	0	0	11667	0	49167		
Sapling	40	0	80	0	0	0	13	õ	40	18	Ő	40		
Across Sites	-				-	-	-	-	-	-	-	-		
Seedling	13528	0	49167	2694	0	1750	278	0	3333	5500	0	49167		
Sapling	4	0	80	5	0	80	1	0	40	4	0	80		

QUKE	Open			Transitio	Transitional					Across Stand Types		
Site	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
WC												
Seedling	278	0	833	556	0	1667	1945	1667	2500	926	0	2500
Sapling	0	0	0	0	0	0	0	0	0	0	0	0
BV												
Seedling	0	0	0	556	0	1667	556	0	1667	370	0	1667
Sapling	0	0	0	0	0	0	0	0	0	0	0	0
BM												
Seedling	4167	1667	7500	1667	0	333	278	0	833	2037	0	7500
Sapling	13	0	40	0	0	0	0	0	0	4	0	40
CP												
Seedling	1944	0	5833	4444	3333	5833	4167	1667	7500	3518	0	7500
Sapling	0	0	0	0	0	0	0	0	0	0	0	0
LE												
Seedling	4722	0	10000	1389	0	333	278	0	833	2130	0	10000
Sapling	0	0	0	0	0	0	0	0	0	0	0	0
HS												
Seedling	2500	1667	3333	2778	833	4167	2222	833	4167	2500	833	4167
Sapling	0	0	0	0	0	0	0	0	0	0	0	0
YJ												
Seedling	556	0	1667	556	0	1667	278	0	833	463	0	1667
Sapling	0	0	0	0	0	0	0	0	0	0	0	0
IB	_	_	_		_			_			_	=
Seedling	0	0	0	278	0	833	556	0	1667	278	0	1667
Sapling	0	0	0	0	0	0	0	0	0	0	0	0
EB					_			_			_	
Seedling	5556	1667	9167	2222	0	5000	1111	0	2500	2963	0	9167
Sapling	0	0	0	0	0	0	0	0	0	0	0	0
BH												
Seedling	5000	0	15000	556	0	1667	278	0	833	1944	0	15000
Sapling	0	0	0	0	0	0	0	0	0	0	0	0
Across Sites	2.172	0	1.5000	1 500	0			0		1510	0	1
Seedling	2472	0	15000	1500	0	5833	1167	0	7500	1713	0	15000
Sapling	1	0	40	0	0	0	0	0	0	0	0	40

PSME	Open			Transiti	Transitional					Across Stand Types		
Site	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
WC												
Seedling	556	0	1667	555	0	855	0	0	0	370	0	1667
Sapling	53	0	120	320	160	640	13	0	40	129	0	640
BV												
Seedling	833	0	2500	2222	0	5833	1389	0	2500	1481	0	5833
Sapling	600	160	1200	627	200	960	387	80	920	538	80	1200
BM												
Seedling	0	0	0	4722	0	13333	0	0	0	1574	0	13333
Sapling	27	0	40	320	0	960	53	0	120	133	0	960
CP												
Seedling	0	0	0	833	0	1667	1111	0	3333	648	0	3333
Sapling	13	0	40	173	40	360	200	120	360	129	0	360
LE												
Seedling	1389	0	4167	0	0	0	278	0	833	556	0	4167
Sapling	293	0	840	120	40	240	0	0	0	138	0	840
HS												
Seedling	833	0	1667	2778	1667	3333	278	0	833	1296	0	3333
Sapling	3467	0	520	320	0	840	400	0	1040	1396	0	5200
YJ												
Seedling	2778	0	8333	1111	0	3333	278	0	833	1389	0	8333
Sapling	253	0	680	160	40	280	440	0	1320	284	0	1320
IB												
Seedling	0	0	0	1944	0	5000	278	0	833	741	0	5000
Sapling	107	0	160	760	40	2080	27	0	40	298	0	2080
EB												
Seedling	1111	0	2500	1111	0	1667	833	0	2500	1019	0	2500
Sapling	1204	0	3720	720	0	1560	906	40	2440	956	0	3720
BH												
Seedling	1945	0	4167	556	0	1667	0	0	0	833	0	4167
Sapling	173	0	520	53	0	80	13	0	40	80	0	520
Across Sites												
Seedling	945	0	8333	1583	0	13333	444	0	3333	991	0	13333
Sapling	623	0	5200	357	0	2080	225	0	2440	408	0	5200

TOTAL	Open			Transitional			Closed			Across Stand Types		
Site	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
WC												
Seedling	4166	2499	5833	7778	0	15000	3889	1667	7500	5278	0	15000
Sapling	200	0	480	1133	400	2080	440	120	1000	591	0	2080
BV												
Seedling	1945	0	4167	5000	2500	9167	2778	833	4166	3241	0	9167
Sapling	613	160	1200	653	240	960	387	80	920	551	80	1200
BM												
Seedling	13611	6666	22500	8887	0	20833	1388	833	1666	7963	0	22500
Sapling	40	0	80	960	120	1720	1747	120	3880	916	0	3880
СР												
Seedling	10833	9167	12500	11389	9166	12501	5833	1667	9167	9352	1667	12501
Sapling	80	0	240	427	40	1000	467	120	840	324	0	1000
LE												
Seedling	27222	20000	40000	3888	833	8333	2500	833	5000	11203	833	40000
Sapling	320	0	840	533	200	840	27	0	40	293	0	840
HS												
Seedling	7777	1667	14166	11111	5834	16666	3611	1667	6667	7500	1667	16666
Sapling	3467	0	5200	813	760	840	413	0	1080	1564	0	5200
YJ												
Seedling	13889	10833	19167	4167	833	6667	3889	833	7500	7315	833	19167
Sapling	267	0	680	187	40	320	493	0	1480	316	0	1480
IB												
Seedling	38333	29167	45000	6111	0	11666	1944	833	333	15463	0	45000
Sapling	107	0	160	773	40	2120	53	0	120	311	0	2120
EB	01200	5000	10500	7500	5000	10024	2611	0	0000	10022	0	42500
Seedling	21389	5000	42500	/500	5000	10834	3611	0	8333	10833	0	42500
Sapling	1267	0	3800	933	600	1600	1213	40	3280	1138	0	3800
BH	24702	((7	50024	0224	2500	10167	<i></i>	0	1000	14527	0	50924
Securing	54725 212	00/	JU834 600	0334 52	2300	1910/	122	40	220	1433/	0	30834 600
Sapling	213	U	000	33	U	80	133	40	320	1333	0	000
Across Siles	17290	0	50924	7417	0	20822	2000	0	0167	0268	0	50924
Seeding	1/389	0	50054 5200	(41)	0	20833	5000	0	2000	9200	0	50054 5200
Sapting	037	U	5200	04/	0	2120	331	U	3880	014	U	5200