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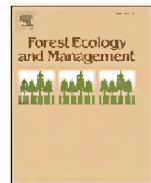
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California black oak responses to fire severity and native conifer encroachment in the Klamath Mountains

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ABSTRACT

Fire exclusion in forests across the western United States has resulted in widespread vegetation change, often with notable increases in density and cover of fire-sensitive species. In California oak woodlands, encroachment by the more shade-tolerant native Douglas-fir (*Pseudotsuga menziesii*) is particularly common, and results in the piercing and eventual overtopping of crowns of shade-intolerant trees. We investigated canopy competition, paired tree ages, and post-fire effects in a recently burned, encroached California black oak (*Quercus kelloggii*) woodland. Pre-fire woodland overstory was heavily dominated by Douglas-fir, which commonly pierced and overtopped California black oak crowns. Trees that pierced overstory oak crowns were younger (mean difference = 43.6 years, $p < 0.001$) than their paired oaks. Fire effects were variable, leaving some areas unchanged and others with complete above-ground stem mortality. Although above-ground stem-kill was often high for California black oak, the majority (82%) resprouted from the root collar. Logistic modeling revealed a significant relationship between California black oak mortality and neighboring Douglas-fir height and plot heat load index. The probability of California black oak mortality increased as neighboring Douglas-fir height increased and decreased with increasing heat load index. Probability of mortality for Douglas-fir decreased with increasing tree size, while the probability of California black oak top-kill was much higher than that for 20–30 cm dbh Douglas-fir across a continuous measure of char height. Results indicate that competitive pressure from encroaching trees may compromise California black oak's ability to survive fire while resilience of encroaching Douglas-fir improves with greater size. Caution should be taken when planning and implementing restoration activities in California black oak woodlands to minimize loss of compromised, remnant oaks while still achieving adequate removal of encroaching conifers.

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1. Introduction

In western North America, fire is believed to have played a crucial role in the formation and maintenance of many ecosystems (Agee, 1993). The effects of periodic fire are especially important in the development and maintenance of oak savannas and woodlands (Abrams, 1992; Scholes and Archer, 1997; Tveten and Fonda, 1999; Peterson et al., 2007; Engber et al., 2011). In California, historically frequent natural and cultural ignitions enabled persistence of these disturbance-prone ecosystems, harboring species with strong resilience to and dependence on recurrent fire (Holmes et al., 2008). In the past century, fire exclusion has led to or enabled alteration of oak woodland composition by allowing increased

establishment of fire-susceptible native conifers that compete for resources with pre-existing oaks.

California black oak (*Quercus kelloggii* Newb.) is one of the most widespread of the western oaks, inhabiting mid- to high elevations from southern Oregon to Baja California, Mexico (McDonald, 1990). California black oak often associates with other fire-prone species, notably ponderosa pine (*Pinus ponderosa* Laws.) (McDonald, 1969) and other fire-tolerant hardwoods in northern California (Sugihara et al., 1987; Fry, 2008). California black oak endures in fire-prone environments by avoiding stem mortality in low-intensity fire (Skinner et al., 2006; Fry, 2008; Taylor, 2010) and sprouting vigorously from the root collar, bole, or crown when more severe fire occurs (McDonald, 1969; Plumb, 1980; McDonald and Tappeiner, 1996; Skinner et al., 2006). Among western USA oaks, leaf litter from California black oak ranks as the most flammable (Engber and Varner, 2009). Skinner et al. (2006) suggest that the more rapid decomposition of California black oak litter, historically greater presence of herbaceous understory plants, and insufficient crown

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mass to support canopy fires indicate historically frequent low-intensity fire as the agent for maintaining large, overstory black oaks with much lower densities of conifers than currently seen in much of the Klamath region. Thus, understory fuel conducive to frequent low-intensity fire, re-sprouting capacity, and association with fire-prone species suggest the integral role fire historically played in California black oak-dominated woodlands prior to fire exclusion. During the recent regime of fire suppression (post – 1910), increases in native conifer establishment in California black oak ecosystems were noted by the mid-20th century in the southern Cascades (Barr, 1946) and later in the Sierra Nevada (Vankat and Major, 1978). Recent research by Stewman (2001) and observations from others (McDonald and Tappeiner, 1996; Garrison et al., 2002; Skinner et al., 2006) suggest that California black oak ecosystems are highly susceptible to encroachment by conifers, particularly Douglas-fir, white fir (*Abies concolor* (Gordon & Glend) Hildebr.), and incense-cedar (*Calocedrus decurrens* (Torr.) Florin).

Encroachment by native conifers in California oak woodlands is of increasing conservation concern. Among coniferous invaders, native Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is the predominant encroaching species in formerly open, fire-adapted oak woodlands of Northwestern California. Douglas-fir encroachment has been documented in several native oak ecosystems including Oregon white oak (*Quercus garryana* Hook.) (Reed and Sugihara, 1987; Engber et al., 2011), coast live oak (*Quercus agrifolia* Née) (Barnhart et al., 1996; Hunter and Barbour, 2001), as well as California black oak (Stewman, 2001; Skinner et al., 2006). At the seedling and sapling stage, Douglas-fir is highly susceptible to fire (Ryan and Reinhardt, 1988; Engber, 2010), but becomes increasingly resistant with the development of thicker bark as trees age, a so-called negative bark allometry (Jackson et al., 1999). Once established, Douglas-fir recruitment to the overstory is achievable by canopy through-growth (Hunter and Barbour, 2001) or via

existing canopy gaps. This presents the possibility for two divergent temporal pathways: one in which frequent fire promotes persistence of oak woodland structure by limiting conifer establishment, and another in which long fire-free intervals facilitate conifer establishment and subsequent oak decline (Fig. 1).

Low vigor and elevated tree stress have been linked to greater susceptibility to fire for many species in different regions (Waring, 1987; Van Mantgem et al., 2003; Varner et al., 2009; O'Brien et al., 2010) and can be brought on by increasing competition from neighboring vegetation (Asbjørnsen and Brudvig, 2007; Marcos et al., 2007; Oheimb et al., 2010). Increased resource competition from encroaching conifers on individual California black oaks may reduce overall oak health and impair their resilience to subsequent stress and injury caused by fire. Post-fire effects studies in California have reported highly variable mortality for California black oak and indicate a consistent re-sprouting response (often referred to as “top-kill”) that appears to vary with fire intensity. In low-intensity prescribed fires in the Sierra Nevada, Kobziar et al. (2006) observed mortality of California black oak ranging from 10% to 60% (excluding top-kill). At a similar Sierra Nevada site Stephens and Finney (2002) reported 100% stem mortality of California black oak but noted that 90% of top-killed oaks re-sprouted from the root collar following low to moderate intensity prescribed burns. In contrast, Fry (2008) observed only one dead California black oak 4 years after a low-intensity prescribed burn in central California and did not note any re-sprouting. In a wildfire, Regelbrugge and Conard (1993) reported similar results (74% above-ground kill, 89% re-sprouting) to those found for California black oak in prescribed fire by Stephens and Finney (2002).

Attempts to model the probability of California black oak mortality from fire have been problematic (Stephens and Finney, 2002) or lacked adequate data to model complete mortality as opposed to top-kill (Regelbrugge and Conard, 1993). Kobziar et al. (2006) found that California black oak deviated from a consistent pattern

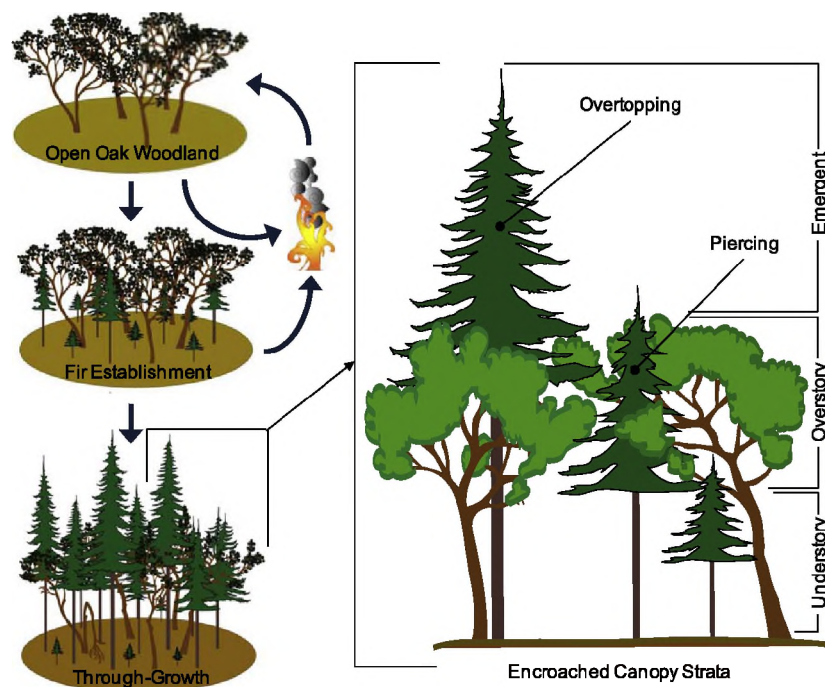


Fig. 1. Conceptual pathway illustrating the pattern of Douglas-fir encroachment in oak woodlands. Frequent fire limits establishment by killing young conifers and maintaining open oak woodland. Without fire, conifers establish and subsequent through-growth results in increased competition with distinct canopy stratification. Canopy strata depictions adapted from Oliver and Larson (1996) and Hunter and Barbour (2001).

of dbh significance in predicting tree mortality of other species. None of these studies incorporated neighborhood effects such as competition by other trees, nor analyzed in greater detail the distinction between complete mortality and top-kill and its role in California black oak fire resilience and post-fire response.

The inconsistencies in California black oak post-fire mortality research call for further investigation. The scope of this study encompasses the need to understand the process of encroachment in California black oak woodlands and how encroachment may present challenges to persistence, maintenance and restoration of oak ecosystems in the broader region. This research addressed the combined effects of conifer encroachment and fire in California black oak woodlands at a site in the Klamath Mountains of northern California. We specifically tested the following hypotheses:

H₁: Douglas-fir emerging into California black oak crowns are younger than paired oaks.

H₂: Canopy occupation by encroaching Douglas-fir impairs the ability of overstory California black oaks to survive fire.

To test the first hypothesis we evaluated species composition and relative crown position within overstory California black oak crowns and surrounding canopy, and determined the age difference between overstory oaks and trees emerging into (piercing) their crowns. To test the second hypothesis we modeled the probability of oak mortality in relation to structural and compositional characteristics of competing vegetation in the vicinity of overstory oaks. The results will inform management decisions regarding the use of fire and other restoration techniques in California black oak ecosystems.

2. Methods

2.1. Site description

The study site was located in the Klamath Mountains near Somes Bar, California (N 41° 31' 07" W 123° 33' 23"; Fig. 2). The climate of the region is Mediterranean, with cool, wet winters and hot, dry summers. Most of the precipitation occurs between November and April, with highest average precipitation during December and January (Western Regional Climate Center, 2011). Low fuel moisture and warm, strong regional winds can create fire weather conditions (Skinner et al., 2006), which may occur during the fire season throughout most of the summer and fall months. Lightning and human ignitions are historically common in the Klamath region, and estimates of pre-suppression era (ca. pre-1900) fire return intervals range from 5 to 22 years (Wills and Stuart, 1994; Taylor and Skinner, 1998, 2003; Skinner et al., 2006) for low elevation forests where California black oak grows. Fire frequencies decreased dramatically early in the 20th century following the success of wildland fire suppression (Taylor and Skinner, 2003). Examination of California fire history records indicate that no fires occurred at the study site after 1900 until the site burned in 2008 (California Fire and Resource Assessment Program, 2011).

Vegetation in the Klamath region exhibits substantial diversity and complexity (Whittaker, 1960, 1961; Odion et al., 2010). Skinner et al. (2006) provide broad elevation distinction into lower montane, mid-upper montane, and subalpine ecologic zones. The lower and mid-montane zones, in which California black oak is commonly found, are characterized by patterns of mixed evergreen forests, woodlands, and shrublands. Mixed evergreen forests are typically dominated by Douglas-fir, tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, C.H. Cannon, & S. Oh), Pacific madrone (*Arbutus menziesii* Pursh), and canyon live oak (*Quercus chrysolepis* Liebm.), with scattered, large ponderosa pine and sugar

pine (*Pinus lambertiana* Douglas). Deciduous oaks and pine become more important on exposed upper slopes, poor soils, and dry southerly and westerly aspects. These areas take on a more open canopied woodland structure often including Oregon white oak, blue oak (*Quercus douglasii* Hook. & Arn.), and California black oak with ponderosa, sugar, and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) assuming greater dominance alongside Douglas-fir (Skinner et al., 2006). Many woodlands, including those with a substantial California black oak component, are prone to encroachment by Douglas-fir (Stewman, 2001).

2.2. Field sampling

Plots were located between 610 and 750 m above sea level on the southeastern flank of Dillon Mountain (1400 m). The area burned in the summer of 2008 in the Siskiyou Complex, a group of several large, lightning-ignited fires. The site burned between 11 and 13 July and was selected for its wide range in fire severity (0–100% overstory tree mortality), presence of California black oak, and accessibility. Species composition and forest structure were representative of mixed evergreen forests occurring on southerly aspects at low to mid elevations in the region (e.g., Stewman, 2001; Skinner et al., 2006).

Tree sampling was conducted at 23 months post-fire and focused in the immediate vicinity of individual focal oaks rather than at a stand-level within the study site. Plots (314 m²) were centered on overstory California black oak trees (≥ 25 cm dbh) and data were collected on trees within the immediate vicinity (10 m radius) of these overstory oaks (e.g., Stewman, 2001; Spector and Putz, 2006). Twenty-five plots were located at focal oaks, which were selected if they were the first oak (≥ 25 cm dbh) encountered along a transect (with a random azimuth between 0° and 360°) originating at the edge of the site or at a previously selected oak. To minimize the potential for neighboring plot effects, plots were established at oaks at least 50 m apart. In each plot all trees ≥ 10 cm dbh were tagged, and their dbh, height, canopy position, condition (live, dead, or top-killed), and maximum bole char height measured. Heights for trees with broken tops or severely leaning stems were excluded as these were not considered representative of true stem length. Slope and aspect were recorded for each plot on the downhill side of the focal oak.

Canopy position was visually estimated for all trees. Individual trees were categorized into emergent, overstory, or understory canopy strata, a classification system modified from systems used in oak woodlands and tree competition studies (Oliver and Larson, 1996; Hunter and Barbour, 2001; Bechtold, 2003). Trees were considered emergent if two-thirds or more of their crown length was above the main canopy, in the overstory if at least one third of their crown length was within the main canopy, and in the understory if two thirds or more of their crown length was below the main canopy. The main canopy volume was defined as the space occupied by the majority of proximal dominant and co-dominant tree crowns in the plot (Fig. 1).

To further assess crown competition for individual California black oaks, trees that were piercing or overtopping California black oak crowns (Fig. 1, *sensu* Barnhart et al., 1996; Hunter and Barbour, 2001) were tallied, and pairs of piercing tree with pierced oak were cored to determine tree ages (e.g., Hunter and Barbour, 2001). All trees were cored at 20 cm above the root-shoot interface parallel to the slope contour using standard tree-age sampling techniques. Consecutive cores were taken higher than 20 cm (<6% of cored trees), but not higher than dbh, if the wood at 20 cm was rotten or fire scars prevented analysis. Cores were mounted, sanded and annual rings were counted using standard methods (Fritz, 1976) under a 4.5× binocular microscope. We did not cross-date sampled cores because our focus was on the relative age difference between

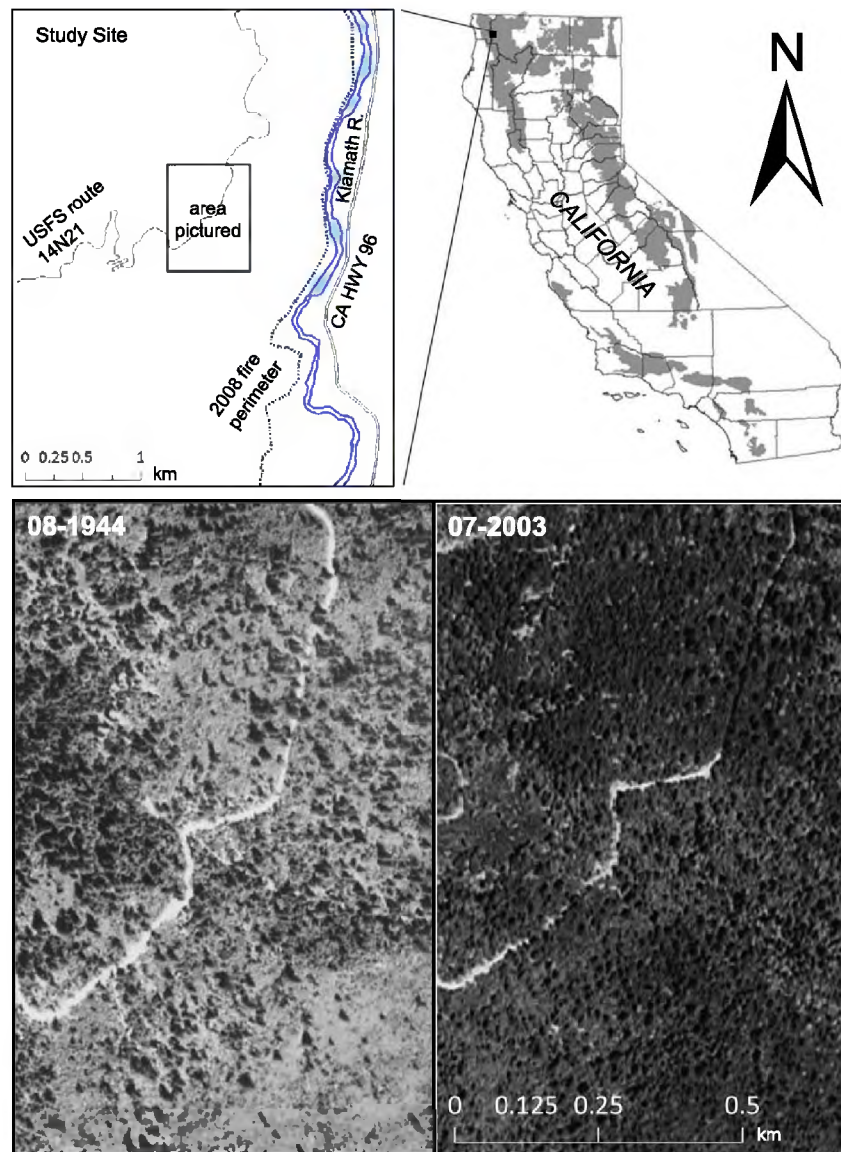


Fig. 2. Site location (top) with aerial imagery from August, 1944 (bottom-left) and July, 2003 (bottom-right). Shaded areas represent National Forest lands in California.

paired trees. Douglas-fir and oaks typically have exceptional circuit uniformity (e.g., Douglass, 1922; Estes, 1970), and other recent studies (Garrison et al., 2002; Taylor, 2010) in nearby study areas found no evidence for missing or false rings. For those cores missing the inner-ring date (pith), the number of years to pith was estimated using a method developed by Duncan (1989). Estimates to pith year were consistently low for both piercing trees (3 ± 2.5 years) and pierced oaks (4 ± 3.1 years). All visual assessments of canopy position and crown competition were made by the same observer throughout the study.

Fire effects were measured on all tagged trees within the 25 plots. Maximum bole char height (measured as the highest point of continuous charring along the tree's bole), a coarse predictor of fire intensity (Cain, 1984), was measured on all trees with a laser rangefinder except those that had snapped or had epiphytic moss that clearly carried fire beyond the flaming zone (common on

several *Quercus* sp.). In 2010 (25–27 months post-fire), tree mortality was tallied in two categories for conifers (dead or living). A third category, "top-kill", was used to describe hardwood stems killed above dbh but sprouting basally (e.g., Barton, 2002). Dead and top-killed trees were inventoried for those affected by recent fire and excluded when death appeared to occur prior to the fire. Persistent bark, marcescent foliage, and lack of prolonged decay on recent fire-killed stems were used to distinguish recent fire-caused mortality from trees that died before the 2008 fire.

2.3. Data analysis

The majority of analyses focused on relationships between Douglas-fir and California black oak because other species existed in low numbers, and previous research on California black oak (Stewman, 2001) and other California oak woodland encroachment

consistently identifies Douglas-fir as the predominant encroaching species (Reed and Sugihara, 1987; Barnhart et al., 1996; Hunter and Barbour, 2001; Engber et al., 2011).

To test for differences in size and height among species, an unbalanced analysis of variance (ANOVA) nested by plot was used on data from all trees. Post-hoc pair-wise comparisons were made using the Tukey–Kramer HSD multiple comparisons test. ANOVA was also used to test for differences among species for plot-level estimates of percent mortality and reduction in plot basal area due to fire ($N = 25$ for Douglas-fir and California black oak; $N = 23$ for all other species combined).

Proportions of emergent, overstory, and understory trees were analyzed using a chi-square test to determine whether the observed distribution of Douglas-fir, California black oak, and an aggregated grouping of the remaining species in the three canopy strata was proportional to that observed for all species combined. Observed counts of emergent, overstory, and understory trees for each species category were tested against expected counts. Expected counts were calculated for the three species groups (Douglas-fir, California black oak, and 'other' species) using the actual proportions of emergent, overstory, and understory trees observed across all species in plots at the study site.

Difference in tree age between piercing trees and associated oaks was tested using a paired *t*-test. In all, 72 pairs (144 trees) were analyzed. As a conservative measure, when an oak was pierced more than once, it was paired for analysis with the oldest of all trees that pierced its crown. Of the 144 cored trees, 16 oak and 2 piercer cores lacked sufficient inner-ring curvature to estimate number of rings to pith. Analysis of age difference between oaks and paired piercers was performed including all pairs, and also separately for piercing trees in categories relating to evidence and estimation of the piercer pith.

A set of logistic models for predicting post-fire complete mortality (top-killed stems included as "live" rather than dead) of California black oak across all plots ($N = 25$) were weighed against each-other using Akaike's Information Criterion, corrected for small sample size (AIC_c; i.e. Burnham and Anderson, 2002). An initial screening revealed plot-level California black oak attributes (mean dbh, height, BA, and density) to be poor predictors of California black oak complete mortality when compared to Douglas-fir plot-level attributes (Table 1). Since Douglas-fir is a known encroacher and initial screening of variables showed California black oak estimates to be poor predictors of complete mortality, candidate predictive models were formed using primarily plot-level attributes for Douglas-fir. These included Douglas-fir basal area ($\text{m}^2 \text{ha}^{-1}$), tree density (stems ha^{-1}), and average total height (m). Slope and aspect were condensed into a single attribute – heat load index (HLI) as defined by McCune and Keon (2002):

$$\text{HLI} = 0.339 + 0.808 * \cos(L) * \cos(S) - 0.196 * \sin(L) \sin(S) - 0.482 * \cos(A) \sin(S) \quad (1)$$

where HLI is the heat load index, L is the site latitude, S is the plot slope, and A is the plot aspect (angle values in radians). In addition, average maximum bole char height (calculated as one value for each plot) was included as a predictor. In all, 10 candidate models were tested to determine the best model for predicting probability of plot-level complete mortality for California black oak. For all tests significance was determined using $\alpha = 0.05$. Data were transformed (natural log) prior to analysis where appropriate and reported as such in the results.

Logistic regression was also used to evaluate the effects of fire on the probability of mortality for Douglas-fir. This analysis is similar to methodologies used in several tree mortality studies (e.g., Ryan and Reinhardt, 1988; Regelbrugge and Conard, 1993; Kobziar et al., 2006). Douglas-fir measurements of dbh across all plots were separated into three diameter class categories (10–20 cm, 20–30 cm, and >30 cm) and each was analyzed in logistic regression with maximum bole char height as the predictor variable. To enable meaningful comparison, probability of California black oak above-ground mortality (completely killed stems and top-killed stems treated both as "dead") was also tested using logistic regression against maximum bole char height. Inability to accurately measure char height on many oak stems (bark sloughing and presence of flammable moss) resulted in a smaller sample size for California black oak and prevented the ability to create separate size class groups (as for Douglas-fir). Probability of California black oak above-ground mortality was, therefore, analyzed in one group including all trees with recorded maximum bole char heights. Maximum bole char height was transformed (natural log) prior to analysis.

3. Results

3.1. Neighboring competition

The canopy surrounding focal oaks was dominated by Douglas-fir, the most abundant species, accounting for 56.6% of all tagged trees (Table 2). California black oak ranked second in abundance (23.9%, including focal oaks) while tanoak, Pacific madrone, canyon live oak, ponderosa pine, and sugar pine were much less common (<9% for each). Bigleaf maple (*Acer macrophyllum* Pursh) and Pacific dogwood (*Cornus nuttallii* Audubon) were each found in only one plot (four trees and one tree, respectively). Douglas-fir had the highest average tree density within each focal oak's proximity (577 ± 232 trees ha^{-1}), and in 24 of 25 plots it had the highest density of all tree species, ranging from 191 to 1050 trees ha^{-1} . California black oak was present at much lower density averaging 243 ± 164 trees ha^{-1} including focal oaks. Douglas-fir and California black oak exceeded all other species in basal area, averaging $38.0 (\pm 18.3)$ and $11.8 (\pm 5.3)$ $\text{m}^2 \text{ha}^{-1}$, respectively (Table 2).

Analysis of variance across all trees revealed significant species differences in dbh ($p < 0.001$, $F = 6.17$, $\text{df} = 98$) and tree height ($p < 0.001$, $F = 16.86$, $\text{df} = 98$). In general, the two pines had larger average diameters and heights relative to others, although only ponderosa pine was significantly larger than the rest (48.9 ± 22.3 cm dbh and 25.8 ± 9.9 m tall, respectively). Canyon live oak had the smallest average dbh (13.9 ± 3.5 cm) and was significantly shorter than other species (8.7 ± 2.8 m; Table 2). Douglas-fir and California black oak did not differ significantly in dbh or height after accounting for plot effects.

Proportions of Douglas-fir, California black oak, and 'other' species in emergent, overstory, and understory categories were not equivalent ($p < 0.001$, $\chi^2 = 22.2$, $\text{df} = 4$). Emergent Douglas-fir

Table 1

Results from initial screening of single variables with logistic regression to predict probability of California black oak complete mortality. Plot-level estimates were used for all predicting variables. Prior to analysis all height (ht), basal area (BA), and density (dens) values were transformed with natural log or square root. Note the lack of significance for California black oak predictors.

Predicting variable	G-stat	p-Value
Heat load index	3.061	0.080
Ave max char ht	2.141	0.143
Douglas-fir plot BA	3.555	0.059
Douglas-fir plot dens	0.000	0.998
Douglas-fir ave ht	4.588	0.032*
California black oak plot BA	0.003	0.960
California black oak plot dens	0.118	0.731
California black oak ave ht	0.031	0.860

* Indicates a significant statistic.

Table 2

Mean and standard error (SE) for density, basal area (BA), dbh, and height of trees within 10 m of focal California black oaks at Dillon Mountain, California. *N* is the total number of trees tagged for each species, and the frequency (freq) is the proportion of plots in which each species occurred.

Species	<i>N</i>	Freq	Density (stems ha ⁻¹)		BA (m ² ha ⁻¹)		dbh (cm)		Height (m)	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
<i>Pseudotsuga menziesii</i>	453	1.00	577	46.50	38.01	3.26	24.11	0.76	19.56	0.38
<i>Quercus kelloggii</i>	191	1.00	243	32.90	11.78	1.05	22.40	0.78	13.65	0.42
<i>Notholithocarpus densiflorus</i>	62	0.72	79	13.90	3.81	0.78	22.32	1.38	15.83	0.81
<i>Arbutus menziesii</i>	29	0.44	37	11.30	2.56	0.83	27.63	2.07	15.74	1.38
<i>Quercus chrysolepis</i>	17	0.44	22	5.73	0.35	0.10	13.92	0.85	8.71	0.68
<i>Pinus ponderosa</i>	14	0.36	18	6.39	3.99	1.53	48.88	5.97	25.76	2.66
<i>Pinus lambertiana</i>	9	0.24	11	4.82	0.71	0.32	25.82	3.91	20.56	2.37
<i>Acer macrophyllum</i>	4	0.04	5	5.09	0.32	0.32	28.33	1.26	21.13	1.03
<i>Cornus nuttallii</i>	1	0.04	1	–	0.01	–	10.30	–	5.00	–

occurred more often than expected and contrasted sharply with California black oak which was absent from the emergent stratum. Approximately 10% of all Douglas-fir were emergent, accounting for 80% of all emergent trees. Ninety-two percent of trees that were piercing or overtopping California black oak were Douglas-fir. Tan-oak, sugar pine and ponderosa pine were rarely observed in either category (only 5, 3, and 2 trees, respectively).

3.2. Age differences

Annual ring counts confirmed that oaks were substantially older than piercing trees (Fig. 3). Across all pairs, oaks were on average 44 years older than trees piercing their crowns ($p < 0.001$, $t = 10.56$, $df = 71$), and age was significantly different regardless of whether the pith was recorded for the piercing tree or not (Table 3). Piercing trees averaged 67 ± 9 years old and ranged from 35 to 104 years in

Table 3

Results of one-sided, paired *t*-tests for aggregations of tree pairs based on oak and piercing tree core pith presence. "N pairs" indicates the number of pairs (of a piercer and pierced oak constituting a pair) analyzed in each category.

	<i>N</i> pairs	Age difference (years) [CI]	<i>t</i>	<i>p</i> -Value
Piercer and oak pith	4	19 [8,29]	5.48	<0.05
Piercer pith only	26	51 [34,67]	6.41	<0.001
Piercer pith estimated	40	43 [32,53]	8.25	<0.001
Piercer pith estimation not possible	2	22 [6,38]	17.49	<0.05

[CI] = 95% confidence interval for the mean age difference.

age, while pierced oaks were consistently older (110 ± 36 years) with a wider age range (48–210 years). Piercing tree cores that had a pith year (i.e. did not need to be estimated) were 68 ± 7 years old while those with estimated pith years were only slightly younger averaging 65 ± 10 years old. Pith years were recorded for only seven oaks with an average of 90 ± 22 and a range of 76–139 years old. Oaks with estimated pith years ($n = 45$) were 108 ± 35 years old, and oaks that could not be estimated due to rot and fire scars in their centers ($n = 20$) were at least 122 ± 41 years old.

3.3. Fire effects

Fire effects varied tremendously across plots at Dillon Mountain. The range of maximum char height across all measured stems was 0–33.2 m, while plot averages for maximum char height ranged from 0.5 to 21.5 m. Above-ground stem mortality ranged from 0% to 100% for all species (Table 4). Although above-ground stem mortality was generally high (71%) for California black oak, complete mortality (dead stems that failed to re-sprout) was much lower (13%). The vast majority (82%) of all killed California black oak stems re-sprouted after the fire. Even though oaks frequently re-sprouted, basal area was still substantially reduced by fire and percent losses in basal area ranged from 0% to 100% for all species. Although not statistically different from other species ($p = 0.51$), California black oak had the greatest average reduction in basal area (65%), while Douglas-fir had the lowest (52%) among tree species (Table 4).

Results from AIC_c model selection showed that probability of complete mortality of California black oak increased with increasing Douglas-fir height and decreased with increasing HLI (Fig. 4 – left). The logistic equation for the best-fit model of California black oak mortality took the form:

$$P_m = \frac{ht^{3.97}}{ht^{3.97} + e^{(10.06+4.454*HLI)}} \quad (2)$$

where P_m is the probability of oak mortality, ht is the mean Douglas-fir height (m), and HLI is the heat index value for a given plot

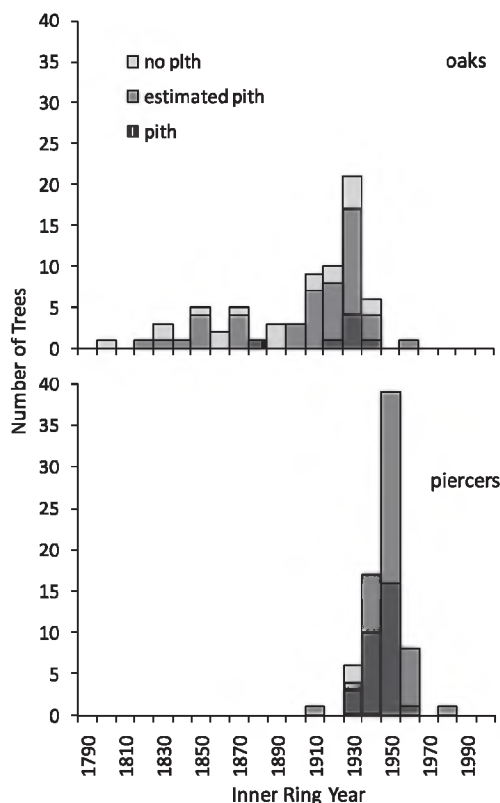


Fig. 3. Inner ring years for piercing trees and pierced oaks.

Table 4

Post-fire tree mortality and basal area change in plots 2 years after fire at Dillon Mountain, California. "Above-ground" refers to all stems killed above ground-level while "complete" refers only to those that failed to re-sprout. Conifers other than Douglas-fir and hardwoods other than California black oak are reported separately. Frequency (freq) refers to the proportion of plots in which each species category was found.

Species	Freq	% Mortality				% BA reduction	
		Above-ground		Complete			
		Mean	Range	Mean	Range	Mean	Range
<i>Pseudotsuga menziesii</i>	1.00	65	0–100	65	0–100	52	0–100
Other conifers	0.48	44	0–100	44	0–100	57	0–100
<i>Quercus kelloggii</i>	1.00	71	0–100	13	0–40	65	0–100
Other hardwoods	0.84	47	0–67	3	0–33	69	0–100

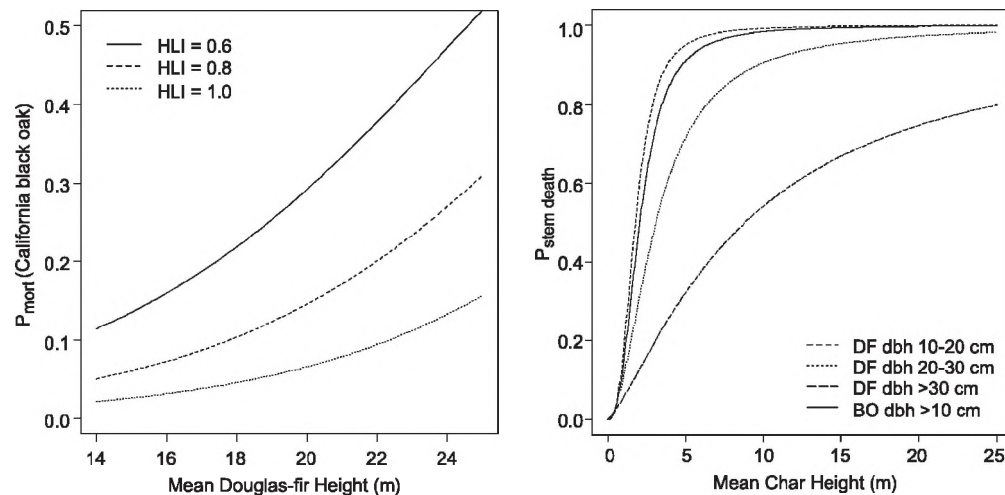


Fig. 4. Logistic Models showing the probability of complete mortality of California black oak (excluding top-kill) as related to Douglas-fir average height and heat index (HLI) (left), and the probability of above-ground stem death (including top-kill) for Douglas-fir and California black oak as related to maximum char height (right). DF and BO indicate lines for Douglas-fir (in the given size groups) and California black oak, respectively. Axes were abbreviated to keep the graph on the left within the observed data range for both x and y variables.

($G = 9.005$, $df = 1$, $p = 0.011$). The second-best model was also significant ($p = 0.012$) and included HLI and Douglas-fir plot basal area (Table 5). Since Douglas-fir height and basal area were highly correlated ($R = 0.58$, data not shown), we used only the best of the two predictors in the final model.

The probability of Douglas-fir mortality increased with increasing maximum char height for all class sizes ($p < 0.001$ for all dbh classes). Maximum char height was also a significant predictor of the probability of California black oak above-ground mortality ($p < 0.001$). The probability of mortality was lower for larger

Table 5

Results of AIC_c model selection using binary logistic regression analysis to predict the probability of California black oak complete mortality. The model with the lowest AIC_c value is the best descriptive model for predicting the probability of California black oak complete mortality relative to the other models. The change in AIC_c value (ΔAIC_c) reflects the magnitude of relative loss in descriptive ability. Three additional models at the bottom of the table show a loss in descriptive ability and higher p -value when similar plot variables for California black oak are added to the model with the lowest AIC_c . Note that the model with the lowest AIC_c is also the model with the most significant p -value (top row in table). Plot-level estimates were used for all predicting variables. Prior to analysis all height, basal area (BA), and density (dens) values were transformed with natural log or square root.

	Log-likelihood	AIC_c	ΔAIC_c	G-stat	p -Value
HLI + DF ht	−69.74	146.61	0.00	8.78	0.012
HLI + DF plot BA	−69.96	147.07	0.46	8.32	0.016
DF ht	−71.83	148.20	1.59	4.59	0.032
HLI + DF plot BA + DF ht	−69.11	148.22	1.61	10.03	0.018
DF plot BA	−72.35	149.24	2.62	3.56	0.059
HLI	−72.59	149.73	3.12	3.06	0.080
HLI + DF plot BA + DF plot dens + DF ht	−68.83	150.81	4.20	10.60	0.032
HLI + DF plot dens	−72.48	152.10	5.49	3.28	0.194
DF plot dens	−74.12	152.79	6.18	0.00	0.998
HLI + ave max char ht + DF plot BA + DF plot dens + DF ht	−68.72	154.10	7.48	10.81	0.055
HLI + DF ht + CBO plot BA	−69.62	149.24	2.62	9.01	0.029
HLI + DF ht + CBO plot dens	−69.01	148.02	1.41	10.23	0.017
HLI + DF ht + CBO ht	−69.63	149.26	2.64	8.99	0.029

Definitions of acronyms: HLI = heat load index, DF = Douglas-fir, BA = basal area, CBO = California black oak.

Douglas-fir dbh classes. Probability of California black oak above-ground mortality was more similar to the probability of mortality for the smallest Douglas-fir size class than for larger size classes (Fig. 4 – right).

4. Discussion

4.1. Encroachment and oak resilience

Reduced fire frequency has led to densification in many forests throughout western North America (Vankat and Major, 1978; Parsons and DeBenedetti, 1979; Covington and Moore, 1994). Aerial photos of the Dillon Mountain study site in northern California reveal substantial canopy recruitment of conifers from at least 1944 until the site burned in the 2008 Siskiyou Complex (Fig. 2). Tree age comparisons confirmed later establishment of trees within oak crowns, particularly young Douglas-fir. Douglas-fir's propensity to pierce and overtop overstory oaks at this and other locations (Barnhart et al., 1996; Hunter and Barbour, 2001) illustrates the change in structure and composition occurring in California black oak ecosystems. The difference in growth between these two species is exemplified by the observed dominance of Douglas-fir in the emergent canopy stratum. Douglas-fir is capable of heights >70 m with substantial yearly height growth maintained for 200 years or more (Hermann and Lavender, 1990). California black oak is slower-growing, and rarely exceeds heights of 40 m (McDonald, 1990; Garrison et al., 2002). Considering height-growth ability alone, California black oak appears to be at a severe disadvantage in the presence of many fast-growing, taller trees.

At Dillon Mountain the probability of complete mortality (killed stems that did not re-sprout) of California black oak was not closely related to fire intensity (as estimated by bole char heights), but was instead better explained by encroaching tree characteristics; in particular the height of neighboring Douglas-fir (Fig. 4 – left, Table 4). One possible explanation for this pattern may be that competitive effects of taller encroaching trees induced lower vigor of shade intolerant California black oaks (McDonald, 1969, 1978). Lower tree vigor due to neighboring competition has been widely reported (Asbjørnsen and Brudvig, 2007; Marcos et al., 2007; Oheimb et al., 2010) and associated tree stress impairs fire resilience for many tree species (Waring, 1987; Swezy and Agee, 1991; Ryan, 2000; Van Mantgem et al., 2003; O'Brien et al., 2010). Although not quantified, crown dieback was commonly seen for oaks at Dillon Mountain and has been observed in other encroached oak woodlands (Barnhart et al., 1996; Spector and Putz, 2006). Oak vigor is likely to deteriorate proportionally to any amount of crown loss, and could affect California black oak resilience to fire. Although speculative, this explanation for the pattern seen between Douglas-fir height and California black oak mortality is plausible and warrants further study.

Significant shifts in forest fuel structure due to a period of fire absence at Dillon Mountain could also contribute significantly to observed mortality patterns and hinder California black oak fire resilience. The relationship with HLI observed across plots at Dillon Mountain suggests an effect of the interaction between localized plot exposure and fuel condition on post-fire complete mortality of California black oak. Many studies have linked increases in forest fuel load to greater fire-related tree mortality. Of particular concern in some ecosystems is the effect of duff smoldering on tree mortality (Swezy and Agee, 1991). In some pine ecosystems, even low-intensity fires can cause substantial tree mortality through smoldering of increased duff material after many years of fire absence (Varner et al., 2009; O'Brien et al., 2010). This illustrates that fuel structure does not need to produce high fire intensity to play a significant role in fire effects. It highlights the need to discover less

apparent mechanisms for California black oak post-fire mortality that may explain significance of HLI when fire-intensity surrogates like char height are not.

4.2. Fire severities promote divergent forest structures

High variation in fire effects was evident in plots at Dillon Mountain. While some plots in this study had 100% above-ground mortality, others had no mortality. The high incidence of top-killed re-sprouting oaks supports the possibility of a stand-replacing endurance mechanism (McDonald, 1990; McDonald and Tappeiner, 1996). In addition to this mode of persistence, the broad range in ages of California black oaks in plots at Dillon Mountain (Fig. 3) and other areas in northern California (Taylor, 2010) provides clear evidence that uneven-aged stands exist. This evokes questions regarding age structure and spatial relationships in California black oak stands and whether recruitment from seed within sprout stands might muddle interpretation of observed age distributions. Taylor (2010) observed stronger California black oak recruitment from seed than from re-sprouts and also saw substantial stem survival in stands that burned following a long fire-free period. Some California black oaks at Dillon Mountain were old enough to have survived the equivalent of 10+ fires even for conservative estimates of historic fire return intervals in the region (Taylor and Skinner, 1998, 2003; Skinner et al., 2006), and California black oak commonly exceeds 250 years old in other fire-prone locations (McDonald, 1990; Garrison et al., 2002; Taylor, 2010). The occurrence of fire scars on mature oaks (McDonald, 1969; Fry, 2008) is also strong evidence that California black oak can survive fire and persist in stands containing younger re-sprouted trees.

The alternative between formation of even-aged California black oak stands (from re-sprouts) and survival of uneven-aged, conifer-encroached stands sets up the potential for divergent forest structures resulting from fire. In this study, oak stem survival often coincided with patterns of Douglas-fir survival (Fig. 4 – right). Because Douglas-fir cannot re-sprout following fire, alternative structural outcomes are produced where areas of high fire severity paradoxically allow recovery of California black oak through post-fire re-sprouting, and survival of Douglas-fir in low-severity areas allows continuance of the encroached condition and the possible replacement of California black oak (Fig. 5). Variation in climate and vegetation composition across the range of California black oak may influence observed differences in this pattern for different regions. The suite of potential encroaching species is likely to change with changes in regional tree species composition.

4.3. Restoration and the future of California black oak

The ecological and cultural values of California black oak are well-documented (Wolf, 1945; McDonald, 1978; Bowyer and Bleich, 1980; McDonald and Huber, 1994; Koenig et al., 2008), and although infrequently used, its value as commercial timber is also high (McDonald, 1969, 1978, 1990; McDonald and Tappeiner, 1996). Despite these strong incentives for management and restoration, recent observations reveal that many California black oak stands in the region are in a similar condition to stands at Dillon Mountain (McDonald and Tappeiner, 1996; Stewman, 2001; Garrison et al., 2002; Skinner et al., 2006). The alternative post-fire effects observed in this study shed new light on management considerations for encroached California black oak and reflect a life history strategy described for other re-sprouting species globally (Vesk and Westoby, 2004). Skinner et al. (2006) allude to these alternative outcomes and their relationship with high- and low-intensity fire. They specifically highlight the ability of California black oak to develop strong root reserves and persist underneath conifers as shrubs with continual growth and dieback. Given

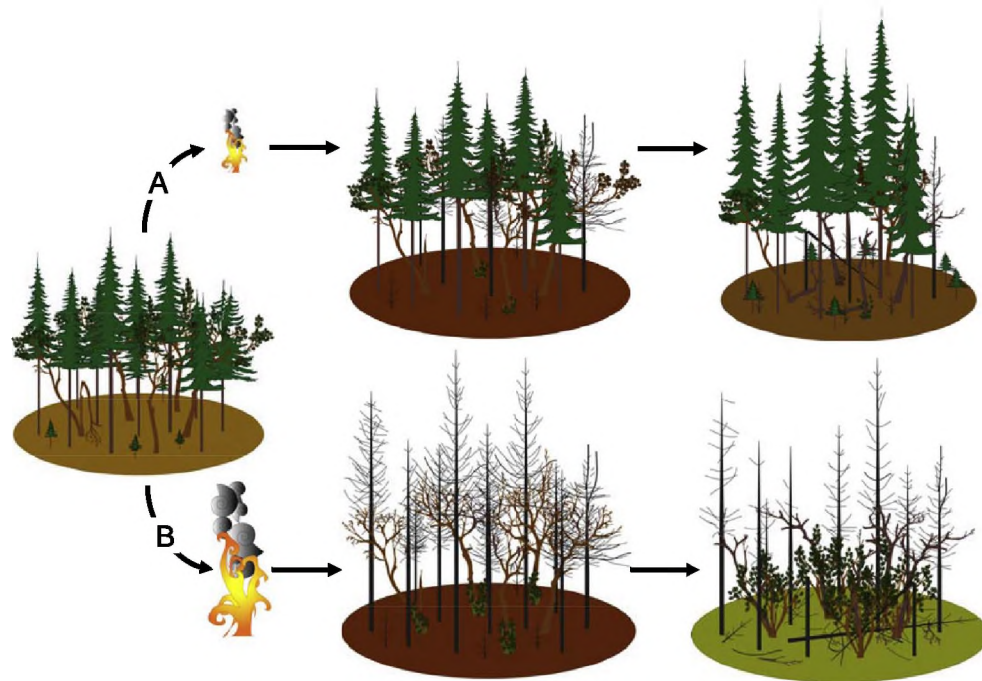


Fig. 5. Conceptual diagram of divergent pathways for high and low-severity fire in conifer-encroached California black oak woodlands. Low-severity is characterized by low overstory mortality and continued competition with encroaching conifers (A), and high-severity by an abundance of re-sprouting California black oaks and lack of surviving overstory tree crowns (B).

adequate light, these persistent shrubs can re-emerge as a dominant overstory (McDonald and Tappeiner, 2002), analogous to the reproductive strategy of re-sprouting plants in many other regions (Bellingham and Sparrow, 2000). However, the lifespan of such seedlings and their minimum light requirements for survival are unclear. This information is crucial, especially where density and average size of invading conifers is high. Application of low-intensity prescribed fire in such stands may not have a restorative effect since larger conifers have greater ability to survive (Ryan and Reinhardt, 1988) and continue to inhibit light to understory oaks. Low-intensity fires may, in fact, be counterproductive in encroached stands with tall Douglas-fir since the probability of existing overstory oak mortality may be higher than in stands with shorter firs or those in which encroachment has not occurred.

Fire intensity thresholds that must be met to ensure high mortality of encroaching fir trees can be defined by the size of Douglas-fir in encroached stands (Fig. 4 – right). Where this threshold cannot be met by typical prescribed fires, occurrence of high-severity wildfire may promote re-establishment of oaks through re-sprouting. Managers must consider more feasible means of initial restoration to open adequate growing space. Some programs have adopted restoration practices that initially remove Douglas-fir by girdling or harvesting, and thereafter, maintain oak woodlands by limiting the re-establishment of Douglas-fir seedlings with prescribed fire (Devine and Harrington, 2006; Engber, 2010). Preservation of old, remnant California black oaks presents additional concerns if lowered vigor and altered fuel structure have the potential to reduce their resilience even to prescribed fire. Until mechanisms for California black oak fire-related mortality are fully understood, managers should attempt to mitigate any potential loss of old oaks in fire-prone landscapes.

This research supplements the growing body of work on oak woodland encroachment (Reed and Sugihara, 1987; Barnhart et al., 1996; Stewman, 2001; Hunter and Barbour, 2001; Garrison et al., 2002) that clearly depicts the dramatic changes that have oc-

curred in woodland ecosystems of northern California and the uncertain fate of California black oak and similar tree species. Restoration of encroached California black oak woodlands will require multiple stages with continual maintenance that may prove operationally difficult. Studies and discussion of mortality and fire effects are often over-simplified by focusing too heavily on fire-intensity, while complicating effects of competition and vegetation shifts remain overlooked. The results in this study highlight the need to broaden investigative approaches to studying post-fire tree mortality and improve our understanding of mechanisms that promote fire-resilience so that effective restoration and management can be achieved.

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References

- Abrams, M.D., 1992. Fire and the development of oak forests. *BioSciences* 42, 346–353.
- Agee, J.K., 1993. *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington, DC.
- Asbjørnsen, H., Brudvig, L.A., 2007. Ecohydrological implications of removing encroaching woody vegetation from a bur oak savanna (Iowa). *Ecol. Restor.* 25, 58–60.
- Barnhart, S.J., McBride, J.R., Warner, P., 1996. Invasion of northern oak woodlands by *Pseudotsuga menziesii* (Mirb.) Franco in the Sonoma Mountains of California. *Madroño* 43, 28–45.
- Barr, P.M., 1946. The research program of Blodgett Forest of the University of California. *J. For.* 44, 738–741.
- Barton, A.M., 2002. Intense wildfire in southeastern Arizona: transformation of a Madrean oak-pine forest to oak woodland. *For. Ecol. Manag.* 165, 205–212.

- Bechtold, W.A., 2003. Crown position and light exposure classification – an alternative to field-assigned crown class. *North. J. Appl. For.* 20, 154–160.
- Bellingham, P.J., Sparrow, A.D., 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* 89, 409–416.
- Bowyer, T.B., Bleich, V.C., 1980. Ecological relationships between southern mule deer and California black oak. In: Plumb, T.R. (Tech. Coord.), Proceedings for the symposium of ecological management and utilization of California oaks. USDA Forest Service, Pacific Southwest Research Station, Redding, CA (PSW-GTR-44), pp. 292–296.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Cain, M.D., 1984. Height of stem-bark char underestimates flame length in prescribed burns. *Fire Manag. Notes* 45, 17–21.
- California Fire and Resource Assessment Program, 2011. <<http://frap.cdf.ca.gov/data/frapgisdata/download.asp?rec=fire>> (accessed September 2011).
- Covington, W.W., Moore, M., 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. *J. For.* 92, 39–47.
- Devine, W.D., Harrington, C.A., 2006. Changes in Oregon white oak (*Quercus garryana* Dougl. ex Hook.) following release from overtopping conifers. *Trees* 20, 747–756.
- Douglas, A.E., 1922. Some aspects of the use of the annual rings of trees in climatic studies. *J. For.* 20 (1), 888–890.
- Duncan, R.P., 1989. An evaluation of errors in tree age estimates based on increment cores in *Kahikatea* (*Dacrydium dacrydioides*). *N. Z. Nat. Sci.* 16, 31–37.
- Engber, E., 2010. Fuelbed heterogeneity, flammability, and restoration of historically fire frequent oak woodlands with fire. Master thesis, Humboldt State University, Arcata, CA.
- Engber, E., Varner, J.M., 2009. Characteristics of leaf litter flammability in the California oaks. In: 4th International Fire Ecology and Management Congress: Fire as a Global Process. Conference Proceedings, November, 2009.
- Engber, E., Varner, J.M., Arguello, L.A., Sugihara, N.G., 2011. The effects of conifer encroachment and overstory structure on fuels and fire in an oak woodland landscape. *Fire Ecol.* 7 (2), 32–50.
- Estes, E.T., 1970. Dendrochronology of Black Oak (*Quercus velutina* Lam.), White Oak (*Quercus alba* L.), and Shortleaf Pine (*Pinus echinata* Mill.) in the Central Mississippi Valley. *Ecol. Monogr.* 40 (3), 295–316.
- Fritz, H.C., 1976. *Tree-Rings and Climate*. Academic Press, London, UK.
- Fry, D.L., 2008. Prescribed fire effects on deciduous oak woodland stand structure, northern Diablo Range, California. *Rangel. Ecol. Manag.* 61, 294–301.
- Garrison, B.A., Otahal, C.D., Triggs, M.L., 2002. Age structure and growth of California black oak (*Quercus kelloggii*) in the central Sierra Nevada, California. USDA Forest Service, Pacific Southwest Research Station, Redding, CA (PSW-GTR-184), pp. 665–679.
- Hermann, R.K., Lavender, D.P., 1990. *Pseudotsuga menziesii* (Mirb.) Franco Douglas-fir, in: Burns, R.M., Honkala, B.H. (Tech. Coords.), *Silvics of North America*, volume 1 – Conifers. USFS Agriculture Handbook 654, 1080–1108.
- Holmes, K.A., Veblen, K.E., Young, T.P., Berry, A.M., 2008. California oaks and fire: a review and case study. In: Merenlender, A., McCreary, D., Purcell, K.L. (Eds.), *In: Proceedings of the sixth California oak symposium: Today's challenges, tomorrow's opportunities*. USDA Forest Service, Pacific Southwest Research Station, Redding, CA (PSW-GTR-217), pp. 551–565.
- Hunter, J.C., Barbour, M.G., 2001. Through-growth by *Pseudotsuga menziesii*: a mechanism for change in forest composition without canopy gaps. *J. Veg. Sci.* 12, 445–452.
- Jackson, J.F., Adams, D.C., Jackson, U.B., 1999. Allometry of constitutive defense: a model and a comparative test with tree bark and fire regime. *Am. Nat.* 153, 614–632.
- Kobziar, L., Moghaddas, J., Stephens, S.L., 2006. Tree mortality patterns following prescribed fires in a mixed conifer forest. *Can. J. For. Res.* 36, 3222–3238.
- Koenig, W.D., Schaefer, D.J., Mambelli, S., Dawson, T.E., 2008. Acorns, insects, and the diet of adult versus nestling acorn woodpeckers. *J. Ornithol.* 79, 280–285.
- Marcos, G.M., Obrador, J.J., Garcia, E., Cubera, E., Montero, M.J., Pulido, F., Dupraz, C., 2007. Driving competitive and facilitative interactions in oak dehesas through management practices. *Agroforest. Syst.* 70, 25–40.
- McCune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. *J. Veg. Sci.* 13, 603–606.
- McDonald, P.M., 1969. Silvicultural characteristics of California black oak (*Quercus kelloggii* Newb.). USDA Forest Service, Pacific Southwest Research Station, Redding, CA (PSW-RP-53).
- McDonald, P.M., 1978. Silviculture-ecology of three native California hardwoods on high sites in north central California. Doctoral thesis, Oregon State University, Corvallis, OR.
- McDonald, P.M., 1990. *Quercus kelloggii* Newb. California black oak, in: Burns, R.M., Honkala, B.H. (Tech. Coords.), *Silvics of North America*: volume 2 – Hardwoods. USDA Forest Service Agriculture Handbook 654, 1281–1299.
- McDonald, P.M., Huber, D.W., 1994. California's hardwood resource. Current status of the industry and an ecosystem management perspective. USDA Forest Service, Pacific Southwest Research Station, Redding, CA (PSW-GTR-153).
- McDonald, P.M., Tappeiner, J.C., 1996. Silviculture-ecology of forest-zone hardwoods in the Sierra Nevada. In: *Sierra Nevada Ecosystem Project Final report to Congress, Volume III: Assessments and Scientific Basis for Management Options*. Centers for Water and Wildland Resources, University of California, Davis.
- McDonald, P.M., Tappeiner, J.C., 2002. California's hardwood resource: Seeds, seedlings, and sprouts of three important forest-zone species. USDA Forest Service, Pacific Southwest Research Station, Redding, CA (PSW-GTR-185), 39 pp.
- O'Brien, J.J., Hiers, J.K., Mitchell, R.J., Varner, J.M., Mordecai, K., 2010. Acute physiological stress and mortality following fire in a long-unburned longleaf pine ecosystem. *Fire Ecol.* 6, 1–12.
- Odion, D.C., Moritz, M.A., DellaSala, D.A., 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. *J. Ecol.* 98, 96–105.
- Oheimb, G., von Lang, A.C., Bruehlheide, H., Forrester, D.J., Wäsche, I., Yu, M., Härdtle, W., 2010. Individual-tree radial growth in a subtropical broad-leaved forest: the role of local neighbourhood competition. *For. Ecol. Manag.* 261, 499–507.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*. Wiley, New York.
- Parsons, J.D., DeBenedetti, S.H., 1979. Impact of fire suppression on a mixed-conifer forest. *For. Ecol. Manag.* 2, 21–33.
- Peterson, D.W., Reich, P.B., Wragge, K.J., 2007. Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. *J. Veg. Sci.* 18, 3–12.
- Plumb, T.R., 1980. Response of oaks to fire, in: *Proceedings of the symposium on the ecology, management, and utilization of California oaks*. USDA Forest Service, Pacific Southwest Research Station, Redding, CA (PSW-GTR-44), pp. 202–215.
- Reed, L.J., Sugihara, N.G., 1987. Northern oak woodlands: ecosystem in jeopardy or is it already too late? USDA Forest Service, Pacific Southwest Research Station, Redding, CA (PSW-GTR-100), pp. 59–63.
- Regelbrugge, J.C., Conard, S.G., 1993. Modeling tree mortality following wildfire in *Pinus ponderosa* forests in the central Sierra Nevada of California. *Int. J. Wildland Fire* 3, 139–148.
- Ryan, K.C., 2000. Effects of fire injury on water relations of ponderosa pine. In: Moser, W.K., Moser, C.F. (Eds.), *Tall Timbers Fire Ecology Conference, 21st Proceedings – Fire and Forest Ecology: Innovative Silviculture & Vegetation Management*. Tall Timbers Research Station, Tallahassee, FL, pp. 58–66.
- Ryan, K.C., Reinhardt, E.D., 1988. Predicting post-fire mortality of seven western conifers. *Can. J. For. Res.* 18, 1291–1297.
- Scholes, R.J., Archer, S.R., 1997. Tree-grass interactions in savannas. *Annu. Rev. Ecol. Syst.* 28, 517–544.
- Skinner, C.N., Taylor, A.N., Agee, J.K., 2006. Klamath Mountains Bioregion. In: Sugihara, N.G., Van Wagtenonk, J.W., Shaffer, K.E., Fites-Kaufman, J., Thode, A.E. (Eds.), *Fire in California's Ecosystems*. University of California Press, Berkeley, CA, pp. 170–194.
- Spector, T., Putz, F.E., 2006. Crown retreat of open-grown Southern live oaks (*Quercus virginiana*) due to canopy encroachment in Florida, USA. *For. Ecol. Manag.* 228, 168–176.
- Stephens, S.L., Finney, M.A., 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. *For. Ecol. Manag.* 162, 261–271.
- Stewman, C.J., 2001. Encroachment patterns of Douglas-fir into oak woodlands in the central Klamath region. Master's thesis, Humboldt State University, Arcata, CA.
- Sugihara, N.G., Reed, L.J., Lenihan, J.M., 1987. Vegetation of the Bald Hills oak woodlands, Redwood National Park, California. *Madroño* 34, 193–208.
- Swezy, D.M., Agee, J.K., 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. *Can. J. For. Res.* 21, 626–634.
- Taylor, A.H., 2010. Fire disturbance and forest structure in an old-growth *Pinus ponderosa* forest, southern Cascades, USA. *J. Veg. Sci.* 21, 561–572.
- Taylor, A.H., Skinner, C.N., 1998. Fire history and dynamics in a late-successional reserve, Klamath Mountains, California, USA. *For. Ecol. Manag.* 111, 285–301.
- Taylor, A.H., Skinner, C.N., 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecol. Appl.* 13, 704–719.
- Tveten, R.K., Fonda, R.W., 1999. Fire effects on prairies and oak woodlands on Fort Lewis, Washington. *Northwest Sci.* 73, 145–158.
- Van Mantgem, P.J., Stephenson, N.L., Mutch, L.S., Johnson, V.G., Esperanza, A.M., Parson, D.J., 2003. Growth rate predicted mortality of *Abies concolor* in both burned and unburned stands. *Can. J. For. Res.* 33, 1029–1038.
- Vankat, J.L., Major, J., 1978. Vegetation changes in Sequoia National Park, California. *J. Biogeogr.* 5, 377–402.
- Varner, J.M., Putz, F.E., O'Brien, J.J., Hiers, J.K., Mitchell, R.J., Gordon, D.R., 2009. Post-fire tree stress and growth following smoldering duff fires. *For. Ecol. Manag.* 258, 2467–2474.
- Vesk, P.A., Westoby, M., 2004. Sprouting ability across diverse disturbances and vegetation types worldwide. *J. Ecol.* 92, 310–320.
- Waring, R.H., 1987. Characteristics of trees predisposed to die. *BioScience* 37, 569–574.
- Western Regional Climate Center, 2011. Remote Automated Weather Station (RAWS) data. <<http://www.rafts.dri.edu/>> (accessed May, 2011).
- Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30, 279–338.
- Whittaker, R.H., 1961. Vegetation history of the Pacific coast states and the “central” significance of the Klamath region. *Madroño* 16, 5–23.
- Wills, R.D., Stuart, J.D., 1994. Fire history and stand development of a Douglas-fir/hardwood forest in northern California. *Northwest Sci.* 68, 205–212.
- Wolf, C.B., 1945. *California Wild Tree Crops – Their Crop Production and Possible Utilization*. Rancho Santa Ana Botanic Garden, Rancho Santa Ana, CA.