The role of fire in the competitive dynamics of coast redwood forests

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Abstract. Fire is a major component of the disturbance regime and a critical determinant of competitive outcomes in many ecosystems. In forests dominated by coast redwood (Sequoia sempervirens), fire was frequent and ubiquitous prior to European settlement, but fires have been exceedingly small and rare over the last 70-80 years because of aggressive fire prevention and suppression policies. As a result, many aspects of redwood fire ecology remain poorly understood. However, in 2008 a single storm ignited numerous fires throughout the redwood region, providing a rare opportunity to conduct replicated fire effects research. One year post-fire, we investigated competitive dynamics by quantifying bole survival and basal sprouting, for redwood and associated species, at four field sites that spanned much of the latitudinal range of redwood and encompassed (1) second-growth and old-growth stands, (2) burned and unburned areas, and (3) a wide range of fire severities. We employed a mixed effects analytical framework and found that: (1) the probability of bole survival was greater for redwood than for its primary competitor (tanoak; Notholithocarpus densiflorus), (2) this divergence was much more pronounced at higher fire severities, and (3) tanoak exhibited a slight advantage in terms of post-fire basal sprouting, but the dominance of tanoak basal sprouts in burned areas was reduced relative to unburned areas. For many disturbance types in many ecosystems, the empirical data necessary for effective management decisions are lacking, and studies incorporating vegetative tree regeneration are especially scarce. Our work demonstrates the importance of utilizing unique field research opportunities to test current theories, while unequivocally documenting that fires of all severities increased the abundance of redwood relative to tanoak, and that higher severity fires more strongly favored redwood.

Key words: basal sprouting; bole survival; competition; disturbance; fire effects; forest dynamics; *Lithocarpus densiflorus*; *Notholithocarpus densiflorus*; redwood; *Sequoia sempervirens*; tanoak; wildfire.

Received 19 October 2010; revised 29 November 2010; accepted 30 November 2010; published 20 December 2010. Corresponding Editor: D. P. C. Peters.

Citation: Ramage, B. S., K. L. O'Hara, and B. T. Caldwell. 2010. The role of fire in the competitive dynamics of coast redwood forests. Ecosphere 1(6):art20. doi:10.1890/ES10-00134.1

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INTRODUCTION

Variation in a range of factors can explain the coexistence of multiple tree species in temperate forests, including the ability to endure and/or respond to disturbance (Petraitis et al. 1989, Loehle 2000, Nakashizuka 2001, White and Jentsch 2001). Similarly, disturbances often have profound effects on competitive dynamics; for instance, species that are competitively inferior in

undisturbed environments may become competitively equivalent or superior following disturbance (Frelich and Reich 1999, Suding 2001). Shifts in relative abundance can result from differential responses to the post-disturbance environment (e.g., better utilization of increased light levels) as well as direct disturbance effects (e.g., divergent survival rates, disturbance-activated regeneration; Frelich and Reich 1999, White and Jentsch 2001).

In order to persist in any environment, sedentary species must exhibit successful strategies of *resistance* (the ability to avoid or prevent disturbance impacts) and/or *resilience* (the ability to restore pre-disturbance conditions; sensu Millar et al. 2007). For trees, bole survival is analogous to resistance, while post-disturbance basal sprouting and seedling recruitment are forms of resilience (i.e., positive neighborhood effects; sensu Frelich and Reich 1999). Survival and regeneration in disturbed environments are not necessarily correlated, and both may be highly dependent upon disturbance type and severity, as well as tree species, bole diameter, and other factors (Frelich and Reich 1999, White and Jentsch 2001). Species-specific knowledge of both survival rates and regeneration patterns, across a range of other relevant variables, is thus required for accurate prediction of post-disturbance communities and long-term forest dynamics.

Post-disturbance seedling recruitment has long been studied, but vegetative sprouting from surviving root systems, which dominates the regeneration stratum in some forest types, has received much less research attention (Loehle 2000, Bond and Midgley 2001, Dietze and Clark 2008, Caplat and Anand 2009). Basal and root sprouts typically grow faster and are often more abundant than conspecific seedlings (Bond and Midgley 2001, Dietze and Clark 2008), and thus seedling recruitment may be of negligible importance for population persistence; root systems of some woody species have survived for thousands of years through numerous episodes of above-ground mortality (Bond and Midgley 2001). The ability to sprout from the root system is primarily a broadleaf trait, but coast redwood (Sequoia sempervirens), which possesses the ability to rapidly initiate vigorous sprout growth from lignotubers (i.e., underground burls), is a notable exception. This characteristic has contributed substantially to redwood's resilience to both natural and anthropogenic disturbances (Del Tredici 1998).

Fire is a critical component of the disturbance regime in many ecosystems, including coast redwood forests. Fires were frequent and ubiquitous in redwood forests prior to European settlement (mean return intervals of 6–25 years have been estimated throughout the entire redwood range; Lorimer et al. 2009), but fires have been relatively rare and small over the last 70–80 years because of fire suppression efforts (Oneal et al. 2006, Donovan and Brown 2007). Due to the scarcity of opportunities to study fire in recent decades, many aspects of redwood fire ecology remain poorly understood (including the role of fire in the regeneration dynamics and long-term persistence of redwood and associated species; Lorimer et al. 2009), thereby forcing land managers to make important decisions without sufficient data.

During the late spring and early summer of 2008, following two years of drought, more than 2,000 fires were ignited in central and northern California, the majority of which were caused by a dry lightning storm on 20 June. Numerous fires occurred in redwood forest, burning primarily as low-severity surface fires with occasional small pockets of crown torching, and encompassing both young and old stands on protected public lands that spanned much of the redwood range. These fires have presented a valuable opportunity to examine post-fire survival and regeneration, especially considering that (1) fire effects studies in all vegetation types are notoriously plagued by pseudoreplicaton (van Mantgem et al. 2001), and (2) the fire season of 2008 could prove to be a harbinger of changing climatic conditions; recent models have predicted increases in the annual area burned for much of northern California, including parts of the redwood region (Fried et al. 2004, Lenihan et al. 2007).

If the bole of any tree is killed by fire, the ability to sprout from surviving belowground tissue is clearly beneficial in terms of maintaining site occupancy. Many second-growth redwood stands, some of which were harvested more than 100 years ago, are stocked in large part by stems that originated as basal sprouts from cut stumps, and Daubenmire & Daubenmire (1975) have also argued that many massive old-growth trees originated as basal sprouts around ancient snags. Post-fire basal sprouting may also be advantageous in the absence of bole death. Fire-induced death of neighboring trees may dramatically reduce canopy cover, and fires that do not kill canopy trees, but cause crown scorch and/or death of subcanopy trees or shrubs, may increase understory light levels enough to facilitate

regeneration of shade intolerant species (Veirs 1982). Post-fire sprouting at the base of surviving stems will (1) increase the amount of understory light that is captured (potentially providing additional photosynthates to the parent root system and/or excluding competitors), and (2) position young stems for rapid release if firedamaged boles subsequently break or die. Abbott (1987) and Stuart (1987) have documented that basal sprouts originating at the base of living old-growth redwood trees can persist for at least 78 years and attain considerable size (at least 26 meters in height and 58 cm in diameter). Genets and/or species with more vigorous basal sprout growth will achieve greater relative dominance (at least in the short term), and thus post-fire basal sprouting patterns should be key determinants of future stand structure and composition.

Several anecdotal reports (e.g., Fritz 1931) and retrospective studies (Abbott 1987, Stuart 1987, Brown et al. 1999) have provided evidence that wildfire induces basal sprouting by redwood trees, and one publication has documented sprouting following prescribed fire (Finney and Martin 1993). In addition, fire likely stimulates basal sprouting by some species co-occurring with redwood. Of particular importance to competitive dynamics in redwood forests is the post-fire sprouting response of tanoak (Notholithocarpus densiflorus syn. Lithocarpus densiflorus). This highly shade tolerant broadleaf evergreen, which produces acorns that serve as a valuable food source to a wide variety of wildlife species (Tappeiner et al. 1990), is the most abundant associate of redwood in the central and southern regions (sensu Sawyer et al. 2000a), and the most abundant broadleaf tree species throughout the entire redwood range (Tappeiner et al. 1990, Sawyer et al. 2000a). Tanoak trees can sprout

vigorously following fire (Donato et al. 2009), even in the absence of bole death (Kauffman and Martin 1990), but no relevant studies have been conducted within the redwood region, and thus the relative responses of these two species have not been investigated.

We examine the role of fire in the competitive dynamics of forests dominated by coast redwood. Our specific objectives were to: (1) compare post-fire survival and basal sprouting responses of redwood and tanoak; (2) compare basal sprouting in burned and unburned areas, and in second-growth and old-growth stands; (3) integrate these findings with existing literature to examine the role of fire in the long-term competitive dynamics of redwood forests; (4) assess whether fire facilitates the coexistence of redwood and tanoak; and (5) improve the capacity for effective management of redwood forests by addressing a major deficiency in empirical data.

Methods

Site, transect, and plot selection

Field sites were selected to span the latitudinal range of redwood forest that was burned in the late spring and early summer of 2008, to cover a wide range of slope positions, aspects, and associated variation, and to represent old-growth and second-growth stands. We intentionally avoided areas that had undergone partial cutting so that all sites could be clearly categorized as second-growth or old-growth. Field sites are outlined in Table 1. All second-growth stands were approximately 60–80 years old in 2008: the areas we sampled at Jackson Demonstration State Forest were logged in the 1920s and 1940s; Eureka Canyon Forest was initially harvested around 1930 and has also undergone occasional individual tree selection harvesting

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Site	County	Approx. Latitude	Stand Age Status
Jackson Demonstration State Forest	Mendocino	39.4 N	Second-growth
Montgomery Woods State Park	Mendocino	39.2 N	Old-growth
Eureka Canvon Forest	Santa Cruz	37.0 N	Second-growth
Pfeiffer Big Sur State Park, Julia Pfeiffer	Monterev	36.1 N	Old-growth
Burns State Park, Big Creek Reserve,			8
and Los Padres National Forest			

Notes: All counties are in the state of California. All Monterey County ownerships are proximate and treated as one site. Stand age status applies to all sampled areas, but not necessarily to the entirety of each site.

since then (most recently in 1997). At both second-growth sites, to the best of our knowledge, none of the areas we sampled burned in the period between the initiation of the secondgrowth stand and the fires of 2008. At our Monterey County sites, several fires occurred during the past few decades, but perimeters are not precisely known. Depending upon the specific location, the most recent fires to affect our Monterey County plots probably occurred in 1985, 1977, or 1972 (i.e., 23-36 years prior to the fires of 2008), although it is possible that some small pockets had not burned since 1924. At Montgomery Woods State Park, state fire records (which extend back to 1950) document no fire activity prior to 2008.

At each field site, we selected several representative stands that spanned a broad range of slopes, slope positions, aspects, and fire severities (at this stage, fire severity was assessed via visual examination of crown scorch and litter/duff consumption, as well as reports from firefighters and land managers). Within each stand, we installed a linear group of plots (i.e., transect). The first plot of each transect was located at a random location at the bottom of a drainage or the top of a ridge, and subsequent plots were installed at regular intervals (50 m or 100 m) up or down the slope, following an azimuth that was predetermined with the aid of a topographic map; precise locations of plot centers were randomized (a random distance between zero and 10 m in a random direction). If less than three redwoods (living or dead, ≥ 10 cm diameter at breast height; DBH) were present within a 20 meter radius, plot center was randomly relocated (and this was repeated if necessary). At every site, transects were installed in stands that had burned in 2008 (i.e., *burned*), as well as in areas that had not burned in at least 20 years (i.e., unburned); within each site, the majority of plots (57–82%) were installed in burned areas.

Data collection

Circular plots of variable sizes were installed to ensure that at least three redwoods ≥ 10 cm DBH, hereafter referred to as *mature*, were captured within each plot. All individuals of all tree species ≥ 10 cm DBH were sampled in a 1/100 ha area (5.64 m radius); if less than three mature redwoods (living or dead) were present within this radius, the radius (for redwood only, not any other tree species) was extended to 7.98 m (1/50 ha), and then again to 11.28 m (1/25 ha) if necessary. If an 11.28 m radius failed to capture 3 redwoods, additional redwoods were sampled (up to 20 m) to achieve the minimum. All other tree species were sampled within a 5.64 m radius only (redwood sampling was emphasized to satisfy the objectives of a concurrent study).

All data were collected in the summer of 2009 (one year after the fires). Data collection consisted of plot-level as well as individual tree-based variables. If a bole was split below breast height, each fork ≥ 10 cm DBH was treated as a separate tree. For all trees, we recorded DBH and assigned a bole health status of living or dead; a bole was considered dead if no green foliage was present in the original canopy or as epicormic sprouts on the bole or branches (basal sprouts were excluded). For dead boles in burned areas, we recorded our best estimates of whether tree death occurred prior to the 2008 fires or during/after the fires. Evidence of recent death included the presence of fine twigs and dead foliage, as well as vigorous basal sprouting (for applicable species).

In burned areas, bole char height was measured for each tree. For all species, we recorded the height of the highest point at which any bole char was visible (with a hypsometer when necessary), and for redwood trees (which tend to have highly flammable outer bark layers), we also recorded the height of the highest point at which all bark and fissures were completely blackened (on at least one side of the tree). The latter bole char height metric (i.e., contiguous bole char), is equivalent to the "category 2" bole char of Kobziar et al. (2006). Contiguous bole char height was not recorded for hardwoods because preliminary data collection efforts suggested that hardwood fissures were very rarely blackened and that the degree of charring in bark fissures was more closely related to fissure patterns of individual trees than to fire intensity or severity. In addition, crown scorch height was measured on all trees that accurately recorded this variable (i.e., trees with greater than 0% but less than 100% crown scorch).

Basal sprouts were quantified with two separate metrics: sprout area (two-dimensional projected areal coverage) and sprout height (the greatest height achieved by any sprout). Basal

sprouts were defined as all vegetative sprouts <3cm DBH arising from litter/duff/soil that were within 30 cm of exposed wood (e.g., bole or root flare), as well as all sprouts arising from exposed wood that were within 30 cm from the litter/duff/ soil interface. We focused exclusively on basal sprouts, as opposed to seedlings, because seedlings of all species were scarce and small (typically <10 cm tall) in burned areas, whereas basal sprouts were ubiquitous and vigorous (frequently >100 cm tall) and clearly dominated the post-fire regeneration stratum. We also recorded tallies of juvenile basal stems (≥ 3 cm and <10 cm DBH), living and dead, for each tree. However, in burned areas, our dataset contained only seven living juvenile basal stems (one redwood, six tanoak), compared to a total of 526 mature trees. The extremely low number of living juvenile basal stems in burned areas, and the uncertainty about how many were present prior to burning, impeded meaningful analysis, and thus juvenile basal stems were not considered further.

Data analysis

Prior to data analysis, we calculated a plotlevel measure of fire severity: the mean contiguous bole char height for all redwood trees within each plot. We required a standardized plot-level measure so that we could more easily examine the effects of wildfire across species, and we chose to focus on redwood because, due to our experimental design, at least three redwoods occurred in every plot (other species were often absent). We focused on contiguous bole char because redwood bark retains char for a very long time, and managers at both of our oldgrowth sites confirmed that non-contiguous charring (i.e., char interspersed with newly exposed bark) was visible on redwood boles prior to the 2008 fires. We also approximated plot-level crown scorch height in order to facilitate easier comparison with other studies. In Appendix A, we explain why crown scorch height was not used as the primary measure of severity, and describe the relationship between crown scorch and contiguous bole char.

All tree species other than redwood and tanoak were omitted from all analyses. Redwood and tanoak respectively accounted for 66% and 26% of total sampled stems in burned areas (and

percentages were very similar in unburned areas), limiting the potential for inferences about other species. The total number of occurrences of non-redwood conifers and non-tanoak broadleaved trees, in burned areas, was 24 and 16, respectively; in comparison, comparable numbers for redwood and tanoak were 348 and 138, respectively. In burned areas, trees that were deemed to have experienced bole death prior to the fires of 2008 were excluded from all analyses, and in unburned areas, all trees with dead boles were excluded.

For all analyses, we used the function *glmmPQL* from the *MASS* package in the R statistical software (R Development Core Team 2009). This function uses a penalized quasilikelihood procedure to adjust for any overdispersion in the response variable (our sprout area and sprout height data were highly nonnormal and over-dispersed), while accounting for nested random effects (our sampling scheme consisted of plots within transects within sites; Zuur et al. 2009). A binomial distribution (with a logit link function) was specified for the bole survival analysis, and gamma distributions (with logarithmic link functions) were specified for both basal sprout variables.

Bole survival was examined in burned areas only, but sprout area and sprout height were analyzed in both burned and unburned areas (in separate models). Throughout the process of model development for our three primary variables of interest (bole survival, sprout area, and sprout height), nested random effects (site/ transect/plot) were consistently included while potential fixed effect predictors were evaluated. Species, DBH, and stand age status were considered as fixed effect predictors in all models. In models for burned areas (bole survival as well as basal sprouting), plot-level fire severity was also considered. In addition, squared terms and interactions between each of these variables were tested. Because of the relatively small and manageable number of candidate predictors, we were able to avoid automated model development algorithms (which many statisticians have criticized as inconsistent and blind to underlying biological processes; Quinn and Keough 2002), and instead relied upon an iterative process informed by prior ecological knowledge and graphical examination of predicted values and residuals. We did not retain any terms with pvalues greater than 0.10 (except for single-term predictors that were components of significant interactions). Other researchers using the function *glmmPQL* (which does not provide deviance, AIC, or qAIC values) have also relied upon pvalues of model terms to determine whether such terms should be included in the final model (e.g., Laucht et al. 2008, Le Cadre et al. 2008, Chapman et al. 2009).

Presentation of results

Throughout the results section of this paper, model output tables display slope estimates and standard errors on the transformed scale (logit for survival analyses, log(y + 1) for sprout area and height), while all figures display predicted values on the original scale of the response variable. DBH was significant in all models and thus effective visual representation of our findings is dependent upon appropriate illustration of the effects of this predictor. Given the overall objective of understanding the effects of fire on stand-level competitive relationships between redwood and tanoak, we have opted to display DBH with curves that represent percentiles, calculated separately for each species and stand age status (hereafter referred to as "percentile curves"). For instance, we have used an equivalent line thickness (the graphical parameter we have used to indicate DBH) for second-growth redwood trees of 33.8 cm DBH and secondgrowth tanoak trees of 20.7 cm DBH, because these values represent the respective medians for each of these species on second-growth sites (Table 2). Examining differences in species performance at equivalent DBH values is an interesting tree-level physiological question (and we present bole survival data in this manner in Appendix B), but given that we have focused

Table 2. Distribution statistics for DBH (in burned areas) by species and stand age status.

	Second-growth		Old-growth		
DBH (cm)	Redwood	Tanoak	Redwood	Tanoak	
Maximum	133.2	54.7	351.7	65.6	
90th percentile	69.9	36.7	139.6	34.3	
Median (50th)	33.8	20.7	52.1	15.4	
10th percentile	13.5	11.9	12.2	10.5	
Minimum	10.0	10.0	10.0	10.0	

Note: Distributions for unburned areas were very similar.

primarily on the relationship between fire and stand-level competitive dynamics, we believe DBH percentiles are more informative. We do not provide any absolute abundance data because (1) this study focuses on fire-induced *changes* in *relative* abundance and (2) abundance estimates would be biased by the requirement that at least three redwoods per plot be sampled.

Results

Bole survival

Post-fire bole survival was affected by species, DBH, fire severity, and stand age status (Table 3); a squared term for DBH was found to be significant, as well as the following interactions: species imes fire severity, and stand age status imesDBH. Across all DBH values in young and old stands, increasing fire severity reduced bole survival much more steeply for tanoak than for redwood; the ability to endure fire was comparable for these two species at low fire severity, but redwood exhibited a strong survival advantage at higher fire severity. Due to the presence of significant interaction terms, many of the other differences between redwood and tanoak were conditional upon the values of the predictor variables.

At low fire severity (i.e., the 10th percentile: a mean plot-level contiguous bole char height on redwood of 0.6 m, and an approximate crown scorch height of 9.2 m), there was little difference between second-growth redwood and tanoak trees of median DBH or larger; both had predicted bole survival probabilities approximating or equaling one (Fig. 1). Old-growth redwoods were similarly resistant to low severity fire, but old-growth tanoaks of median DBH had slightly lower survival probabilities (approx. 0.9),

Table 3. Predictors of post-fire bole survival.

Predictor	Est.	SE	P-value
(Intercept) Tanoak – DBH – DBH ² – Fire severity – Second-growth – Tanoak × fire severity – Second-growth × DBH	3.4351 -1.6216 0.1183 -0.0004 -0.1867 4.3580 -0.9186 0.1636	0.8403 0.4753 0.0299 0.0002 0.0791 1.3808 0.1871 0.0532	$\begin{array}{c} 0.0001\\ 0.0007\\ 0.0001\\ 0.0194\\ 0.0231\\ 0.0874\\ < 0.0001\\ 0.0023 \end{array}$

Note: Redwood was the baseline species and old-growth was the baseline stand age status.



Fig. 1. Probability of bole survival as a function of species, DBH, fire severity, and stand age status. Redwood is displayed with solid gray lines and tanoak is displayed with broken black lines. Fire severity is quantified as the mean contiguous bole char height (m) for all redwood trees within each plot. Limits of the x-axis represent the minimum and maximum fire severities within our dataset, and vertical gray dashed lines mark the 10th percentile ("low"), median ("moderate"), and 90th percentile ("high") of fire severity. Line thickness indicates tree DBH; lines represent (from the thinnest to the thickest) the minimum, the 10th percentile, the median, the 90th percentile, and the maximum, *calculated separately for each species and stand age status*. For instance, in the second-growth cell, the thickest redwood line represents a DBH of 133.2 cm, while the thickest tanoak line represents a DBH of 54.7 cm (see Table 2); note that several redwood curves overlap at the top of the plotting area. Triangles (for redwood) and circles (for tanoak) mark the points at which median DBH curves intersect the 10th percentile, median, and 90th percentile of fire severity.

reflecting the fact that the median DBH of tanoak was lower in old-growth stands (15.4 cm) than in second-growth stands (20.7 cm; Table 2), and that survival probability was greater in secondgrowth stands (after accounting for all other model predictors). In young and old stands, bole survival probability declined with decreasing DBH (from median to minimum DBH) more steeply for redwood (not because of an interaction between species and DBH, but because of a larger spread in DBH values for redwood). This resulted in higher survival probabilities for small tanoaks than for small redwoods; for instance, in second-growth stands, bole survival was estimated at approximately 0.7 for the smallest tanoaks and approximately 0.35 for the smallest redwoods.

At moderate fire severity (i.e., the 50th percentile: a mean plot-level contiguous bole char height on redwood of 2.7 m, and an approximate crown scorch height of 11.7 m),

bole survival probabilities for redwood and tanoak trees of median DBH diverged in both second-growth and old-growth stands (Fig. 1). Redwood trees of median DBH (or larger) had survival probabilities approaching or equaling 1 (in second-growth and old-growth stands), but estimates were lower for tanoaks of median DBH in second-growth (approx. 0.85) and old-growth (approx. 0.55) stands. In young and old stands, survival probabilities for the smallest and largest trees were very similar for redwood and tanoak; species differences were most pronounced for intermediate DBH values. Survival probabilities for trees of equivalent DBH were nearly identical at moderate fire severity (approx. 1.0 for 30 and 50 cm DBH trees, and approx. 0.25 for 10 cm DBH trees).

At high fire severity (i.e., the 90th percentile: a mean plot-level contiguous bole char height on redwood of 9.0 m, and an approximate crown scorch height of 19.2 m), redwood exhibited a

superior ability to survive wildfire across all DBH percentiles, but this difference was most apparent for trees of median DBH; in both young and old stands, survival probabilities were nearly 1 for redwood and close to 0 for tanoak. Patterns were similar for trees of equivalent DBH. Redwood consistently exhibited superior survival probabilities, but these differences ranged from minor (e.g., 10 and 50 cm DBH trees) to very pronounced (e.g., 30 cm DBH trees); the approximate probability of bole survival for 30 cm DBH trees was 0.95 for redwood, but only 0.10 for tanoak.

Basal sprout area

In burned areas, basal sprout area was affected by species, DBH, fire severity, and stand age status (Table 4); a squared term for fire severity was found to be significant, as well as the following interactions: species \times DBH and stand age status \times DBH. In unburned areas, basal sprout area was affected by species, DBH, and stand age status (Table 4); none of these variables were significant as single-term predictors, but two interactions were significant: species \times DBH and stand age status \times DBH. Patterns for small and large trees were similar to those for median-DBH trees, but predicted sprout area decreased with increasing DBH (although only marginally for old-growth redwoods), and the effect of DBH was greater at higher fire severities (Fig. 2).

In unburned stands, both young and old, tanoak trees of median DBH exhibited greater

Table 4. Predictors of basal sprout area (dm²).

Predictor	Est.	SE	P-value
Burned model			
(Intercept)	3.5930	0.3103	< 0.0001
Tanoak	-0.2087	0.2179	0.3389
DBH	-0.0003	0.0019	0.8704
Fire severity	0.2412	0.0406	< 0.0001
Fire severity ²	-0.0166	0.0058	0.0069
Second-growth	-0.8425	0.3960	0.1672
Tanoak \times DBH	-0.0304	0.0097	0.0019
Second-growth $ imes$ DBH	-0.0090	0.0037	0.0149
Unburned model			
(Intercept)	2.9845	0.9169	0.0014
Tanoak	0.1022	0.7318	0.8891
DBH	-0.0039	0.0035	0.2717
Second-growth	-0.2883	1.2696	0.8578
Tanoak \times DBH	-0.0504	0.0249	0.0448
Second-growth \times DBH	-0.0222	0.0102	0.0310

Note: Redwood was the baseline species and old-growth was the baseline stand age status.

sprout area than redwood trees of median DBH. In burned stands, sprout area for median-DBH tanoak trees also exceeded sprout area for median-DBH redwood trees, but differences between species were greatly reduced. In both young and old stands, redwood and tanoak sprout area was nearly identical following fire of low and moderate severity, but tanoak predictions were distinctly higher than redwood predictions in areas that experienced high severity fire. For both species, in second-growth and old-growth stands, our models predicted a slight reduction in sprout area at extreme fire severities (>90th percentile).

Basal sprout height

In burned areas, basal sprout height was affected by species, DBH, fire severity, and stand age status (Table 5); a squared term for fire severity was found to be significant, as well as the following interactions: species \times DBH, species \times fire severity, and stand age status \times DBH. In unburned areas, DBH was the only significant predictor (Table 5), but species was also included so that distinct (albeit statistically indistinguishable) values could be predicted for each species. As in the section above, the following text focuses on trees of median DBH, but predictions for other DBH percentiles can be examined graphically (Fig. 3).

Although species was not a significant predictor in unburned areas (after accounting for DBH), DBH was highly significant (and negatively related to sprout height) and tanoak had a much smaller median DBH than redwood on both second-growth and old-growth sites (see Table 2). Thus, despite the lack of significance for species as a model term, tanoak generally exhibited taller basal sprouts than redwood on unburned sites. On burned sites, differences between redwood and tanoak trees of median DBH were dependent upon fire severity. In both young and old stands, median-DBH tanoak trees were predicted to exhibit greater sprout height at low and moderate fire severity, while median-DBH redwood trees had slightly higher predicted values at high fire severity. In contrast to sprout area, sprout height differences between species declined with increasing fire severity; this pattern exists because predicted tanoak sprout area peaked at a fire severity less than "high"



Fig. 2. Predicted basal sprout area as a function of species, DBH, burn status, fire severity, and stand age status. Symbology follows that of Fig. 1. In unburned second-growth stands, the predicted value for minimum-DBH tanoak trees was very high (364); the plotting area was constrained below this value in order to maximize visual interpretation of other results. Note that all curves overlap for burned old-growth redwoods.

Table 5. Predicto	rs of basal	sprout	height	(dm)
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Predictor SE Est. P-value Burned model (Intercept) 2.2071 0.1178 < 0.0001-0.2169 0.1119 0.0532 Tanoak DBH -0.0003 0.0010 0.7979 < 0.0001 Fire severity 0.1272 0.0201 -0.00940.0021 Fire severity 0.0028 Second-growth -0.44160.1438 0.0917 Tanoak \times DBH -0.0167 0.0050 0.0010 Tanoak \times fire severity -0.05350.0186 0.0042 0.0046 Second-growth \times DBH -0.00540.0019 Unburned model (Intercept) 1.6901 0.3427 < 0.0001 Tanoak 0.3165 0.2387 0.1871 DBH -0.0059 0.0021 0.0059

Notes: Redwood was the baseline species and old-growth was the baseline stand age status. In the unburned model, DBH was the only significant predictor, but species was also included so that distinct (although statistically indistinguishable) values could be predicted and plotted for each species.

(the 90th percentile of plot-level contiguous redwood bole char height), while redwood sprout area did not begin to decline until reaching an extreme level of severity.

DISCUSSION

Main findings

Redwood and tanoak both demonstrated resistance (bole survival) and resilience (basal sprouting) to fire. Redwood was far superior in terms of bole survival, especially at higher fire severities, while tanoak generally exhibited a slight advantage in terms of post-fire basal sprouting. However, tanoak basal sprouts were also more abundant than redwood basal sprouts in unburned areas, and the dominance of tanoak basal sprouts in the post-fire environment was reduced relative to unburned areas. Considered collectively, our survival and basal sprouting data suggest that fires of any severity will increase the relative abundance of redwood, and that higher severity fires will more strongly favor redwood. These findings should be highly illuminating to managers in the redwood region who are considering the use of prescribed fire and/or debating the degree to which wildfires should be suppressed.

In our discussion of competitive dynamics, it is useful to distinguish between three different vertical strata: the upper canopy layer, the lower



Fig. 3. Predicted basal sprout height as a function of species, DBH, burn status, fire severity, and stand age status. Symbology follows that of Figs. 1 and 2. Note that several curves overlap for burned old-growth redwoods.

canopy layer (i.e., subcanopy), and the regeneration layer (i.e., the understory). The upper canopy of redwood forests is dominated by redwood, and thus mortality of large redwoods would be required for a rapid and pronounced shift in species composition in this stratum. We have shown that large redwood trees (\geq median DBH) are extremely fire-resistant, suggesting that fire is unlikely to cause a rapid shift in upper canopy relative abundance in redwood forests; even in instances of 100% crown scorch, large redwoods typically exhibited vigorous epicormic sprouting from the bole and/or the branches. In contrast, we have found strong evidence that species composition within the subcanopy layer, which we define as the stratum occupied by mature tanoak trees (and which roughly corresponds to trees between 10 and 50 cm DBH; see Table 2), is greatly affected by fire. As fire severity increased, bole survival rates for tanoak dropped much more steeply than for redwood (even for trees of equivalent DBH), suggesting that hotter fires provide a relative advantage to redwood.

The understory layer was entirely consumed by fire in all of our burned plots, and thus we quantified relative competitive abilities in this stratum with post-fire regeneration, as opposed to differential rates of survival. In areas that had not burned, basal sprout area and height predictions were consistently higher for tanoak than for redwood, indicating that tanoak dominated the regeneration stratum after accounting for the relative abundance of mature trees. In burned areas, redwood and tanoak sprouting patterns were strongly and differentially affected by DBH and fire severity, leading to complex competitive dynamics in post-fire environments. At some combinations of predictor variables, in terms of one or both sprout metrics, fire had the effect of reversing competitive superiority in the understory; for instance, following high severity fire, redwood trees of median DBH were predicted to have slightly taller sprouts than tanoak trees of median DBH, on both secondand old-growth sites. At many other predictor combinations (in terms of both sprout metrics) tanoak maintained understory dominance, demonstrating that post-fire basal sprout growth of tanoak often exceeds that of redwood. However, differences between tanoak and redwood were consistently smaller in burned areas than in unburned areas, suggesting that fires of any severity reduce the dominance of tanoak in the understory. In Appendix C, we provide a discussion of the potential mechanisms behind our findings, as well as a more thorough examination of related redwood/tanoak research.

The role of fire in the long-term competitive dynamics of redwood and tanoak

Although our data provide only a snapshot of short-term fire effects in redwood forest, we have filled a major gap in the current body of empirical data, thereby necessitating a re-evaluation of existing theories on the longer-term role of fire. Veirs (1982) defined the current paradigm (after examining age distributions and fire scar records in redwood forests of the northern redwood region) by postulating that redwood and tanoak will continue to co-exist with or without fire. Several researchers have documented or observed the presence of redwood and tanoak regeneration (ranging from seedlings/ basal sprouts to young trees), in quantities sufficient to replace canopy trees, in the understories of redwood forests that have not burned (or been cut) for many decades (e.g., Veirs 1982, Busing and Fujimori 2002). Using a dataset collected over three decades on an alluvial oldgrowth site, Busing and Fujimori (2002) concluded that small-scale tree fall gaps alone are sufficient for the establishment of redwood regeneration (seedlings as well as sprouts), and documented that tanoak seedlings were also abundant in such gaps. However, all relevant demographic studies have been conducted at lower slope positions (e.g., alluvial flats), prompting Lorimer et al. (2009) to note that it is still unclear whether fire is necessary for redwood regeneration and persistence at upper slope positions.

Our results provide evidence that both redwood and tanoak will persist *with* wildfire, at least in the short-term, but also suggest that fire will increase the relative abundance of redwood, supporting the belief held by some foresters and ecologists that fire suppression has led to increased tanoak abundance in redwood forests over the last century. Although no quantitative historical data have been used to test this assumption, it has endured (at least in part) because of the differential regeneration requirements of these two species. Redwood sprouts will die if light levels are not adequate (O'Hara and Berrill 2010), and redwood seedlings exhibit physiological responses that are not consistent with establishment in deep shade (Peer et al. 1999). In contrast, tanoak regeneration often establishes successfully in deep shade beneath multiple canopy layers (Veirs 1982, Tappeiner et al. 1990) and young tanoak trees increase in diameter more rapidly than any co-occurring species when growing beneath a closed canopy (Veirs 1982). In addition, while tanoak readily establishes in thick litter and duff layers (Veirs 1982, Tappeiner et al. 1990), redwood seedling establishment is more successful on mineral soil (Olson et al. 1990), a substrate which is more common following fire.

All of our data were collected only one year after fire, and thus our projections cannot fully incorporate longer-term phenomena that may result from fire. Delayed fire-induced mortality will probably be minimal because neither redwood nor tanoak are known to suffer significant post-fire attack by beetles or other insects, although the long-term risk of structural failure may increase as a result of fire scars, which can serve as entry points for wood decaying fungi (Olson et al. 1990, Tappeiner et al. 1990). Vigor of surviving trees may also be affected; following fire, Abbott (1987) found that growth rates of surviving redwoods increased while growth rates of surviving Douglas-fir trees decreased (we are unaware of any such data for tanoak). Finally, understory light levels will not remain constant (as a result of, e.g., canopy expansion by surviving trees), which could lead to speciesspecific changes in basal sprout growth and mortality rates (O'Hara and Berrill 2010).

Competitive relationships may also shift after a series of fires (e.g., following a return to a higher frequency fire regime), and thus even long-term monitoring after a single fire event may fail to fully illuminate the effects of frequent fire on relative species abundances. Available data are inadequate to predict the effects of repeated fires in redwood forests, but it is possible that frequent burning may gradually reduce the abundance of tanoak. Tappeiner and McDonald (1984) noted that stumps of tanoak less than 2 cm DBH sprouted "much less vigorously" than stumps of larger tanoak, and Kauffman and Martin (1990) found that the probability of whole plant mortality decreased significantly with increasing

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pre-fire aboveground biomass of shrubby tanoaks, suggesting that if adequate recovery has not occurred between fire events, root systems may not survive. Donato et al. (2009) found a similar pattern for all hardwoods pooled (tanoak was not analyzed separately), and documented that the percent cover of tanoak, two years postfire, was lower in a "short interval" burn area than in the "long interval" burn area; however, they also noted that this difference was slight and concluded that a "short interval" (15 years) should allow for indefinite site persistence. Similarly, Ahrens and Newton (2008) inferred that tanoaks in a cut and burned Douglas-fir forest replaced 72% of pre-disturbance leaf area within 8 years.

All available evidence suggests that fire favors redwood, and thus fire-mediated co-existence of redwood and tanoak would require competitive exclusion by tanoak in the absence of fire. Such an outcome seems highly unlikely considering that redwood can regenerate successfully in tree fall gaps (at least on lower slope positions; Busing and Fujimori 2002); although redwood regeneration may be dependent upon disturbance, it does not appear to require fire or other large-scale disturbances. Even if tanoak could theoretically exclude redwood in the absence of disturbance, the extreme longevity of redwood (>2000 years on at least some sites; Sawyer et al. 2000b) suggests that disturbances would be required very infrequently to ensure the persistence of this species. As such, fire does not appear to be essential for redwood's persistence, and we must reject the hypothesis that fire facilitates the co-existence of redwood and tanoak (although we cannot assert this statement as definitively with regard to upper slope positions, for which relevant demographic data are lacking).

Fire undoubtedly plays a critical role in the competitive dynamics of redwood forests, but the recently introduced disease sudden oak death (SOD), which is currently causing substantial tanoak mortality in redwood stands throughout much of the redwood range (Maloney et al. 2005, Rizzo et al. 2005), may ultimately prove more consequential. In some heavily impacted areas, tanoak mortality has been documented at 90% (Ramage and O'Hara 2010) and spread risk models have predicted that the disease will

ultimately affect the entire redwood region (Meentemeyer et al. 2004). With or without fire, SOD-induced tanoak decline is directly affecting competitive relationships in redwood forests, but the compounded effects (sensu Paine et al. 1998) of SOD and fire may lead to the greatest longterm impacts. SOD has increased fuel loading (Metz et al., *in press*), and areas with high levels of recent SOD-induced tanoak mortality are at greater risk of high severity fire (Kuljian and Varner 2010; Metz et al., in press). If fires in diseased areas burn with greater intensity, such fires could act as an indirect mechanism through which SOD further reduces the abundance of tanoak relative to redwood. In addition, fires of even low severity pose a lethal threat to tanoak seedlings, any one of which could conceivably contain a gene or set of genes conferring resistance to SOD. In the past, tanoak likely persisted in frequently burned redwood forests, but the re-introduction of fire to SOD-infected redwood stands may increase the likelihood of its complete extirpation.

Scope of inference

Two important factors may limit the scope of inference for our results. First, all of our study sites were in the central and southern redwood regions, and thus we do not know the extent to which our findings apply to the northern region (defined by the contiguous range of western hemlock, *Tsuga heterophylla*; Sawyer et al. 2000*a*). Second, it is unclear whether the 2008 fires were characteristic (in terms of intensity, season, and scale) of wildfires and/or prescribed fires that occurred in the past or of those that are likely to occur in the future.

Broader implications

Post-fire basal sprouting has traditionally been viewed dichotomously (i.e., sprouters vs. nonsprouters), but a meta-analysis by Vesk and Westoby (2004) concluded that this simplistic classification does not adequately capture the full range of species responses to fire. They argue that species-level sprouting responses should be quantified by the percentage of individuals that sprout following disturbance. We have more thoroughly captured the continuous nature of competition in the regeneration stratum by analyzing basal sprout area and height. Similarly quantitative investigations of post-disturbance sprouting have been completed by other researchers, but we know of no other study that has comprehensively assessed post-wildfire competition by simultaneously considering bole survival and continuous tree-level basal sprouting responses.

Sprouting may be particularly important for understanding competitive dynamics in areas disturbed by fire and in ecosystems with species that are not easily classified along a seral gradient. In experimental canopy gaps in the southeastern United States, Dietze and Clark (2008) found that sprout height growth rates differed substantially with species, and that growth rates were higher for vegetative sprouts than for seedlings, suggesting that long-term canopy composition may be highly dependent upon early sprouting patterns. They also concluded that post-disturbance sprouts are especially important if advanced regeneration is scarce, indicating that vegetative sprouts deserve particular attention in recently burned areas. Caplat and Anand (2009) used a different approach to evaluate the importance of vegetative sprouting; they discovered that the inclusion of sprouting ability in their simulation dramatically altered predictions by allowing tree species typically considered late-successional to rapidly dominate post-disturbance environments, and concluded that a vigorous sprouting ability could enable these species to persist in areas frequently experiencing high severity disturbances. Thus, long-lived shade-tolerant trees that are capable of post-disturbance sprouting blur the traditional distinction between early- and late-successional species.

In many ecosystems, future disturbance regimes will depart from those that have been studied through the lens of modern ecological theory. Such shifts may occur for a wide range of reasons, including (1) abandonment of suppression efforts targeted at historical disturbances, (2) climate change, (3) introduction of novel disturbance agents, and (4) anthropogenic changes in landscape continuity and geomorphology. Modeling efforts, historical analyses, and controlled experiments all provide valuable information, but sound management decisions must ultimately rely on data collected in the aftermath of naturally occurring disturbances. By promptly recognizing and investigating emerging disturbances, researchers will be able to evaluate current paradigms, improve predictive ability, and facilitate more effective land management strategies.

Acknowledgments

We thank Save the Redwoods League for providing funding for this research, and two anonymous reviewers for providing useful suggestions. In addition, we thank the California State Park system, Jackson Demonstration State Forest, the town of Watsonville, the University of California Natural Reserve System, and the USDA Forest Service for allowing this study to be conducted on their lands, as well as their employees and associates for helping us to locate suitable sampling sites. Finally, we are very grateful for the excellent work of our dedicated field assistants Sarah Semmens and Lakshmi Narayan.

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APPENDIX A

QUANTIFICATION OF PLOT-LEVEL FIRE SEVERITY

We quantified plot-level fire severity as the mean *contiguous* bole char height (the height of the highest point at which all bark and fissures were completely blackened on at least one side of the tree) for all redwood trees within each plot. As explained in the main text, we focused on contiguous bole char because redwood bark retains char for a very long time, and managers at both of our old-growth sites confirmed that non-contiguous charring (i.e., char interspersed with newly exposed bark) was visible on drono 34:128-141.

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redwood boles prior to the 2008 fires. We also considered expressing plot-level fire severity with crown scorch height, but reliable estimates of this metric were not available for many plots: in 25 of our 56 burned plots, all sampled trees experienced 0% crown scorch and/or 100% scorch, thereby preventing precise measurement of crown scorch height. Using this variable in our analyses would have thus necessitated the omission of many sample plots in areas of very low fire severity and very high fire severity, as well as plots of moderate fire severity in which all large trees experienced 0% crown scorch.

Although we were unable to use crown scorch height in our survival or basal sprouting analy-



Fig. A1. Relationship between mean plot-level crown scorch height (m) and mean plot-level contiguous bole char height (m), for all plots in which crown scorch height could be precisely measured on at least one redwood tree.

ses, we have approximated plot-level crown scorch heights in order to facilitate easier comparison with other studies. By regressing mean plot-level redwood crown scorch height against mean plot-level redwood contiguous bole char height (for the 31 plots in which crown scorch height could be measured), we identified a simple linear relationship between these metrics (Fig. A1). The terms "low fire severity", "moderate fire severity", and "high fire severity" (see *Results: Bole survival*) correspond, respectively, to measured mean plot-level contiguous bole char heights of 0.6, 2.7, and 9.0 m, and estimated crown scorch heights of 9.2, 11.7, and 19.2 m.

APPENDIX B

Post-fire Bole Survival of Redwood and Tanoak Trees of Equivalent DBH

In the main text, survival patterns are displayed in terms of DBH *percentiles* because of our focus on stand-level competitive dynamics. However, survival probabilities of redwood and tanoak trees of equivalent DBH may be relevant to several related ecological questions, and we therefore provide a supplementary figure with curves of equivalent DBH (Fig. B1). Note that all survival patterns are very similar to those that appear when DBH percentile curves are plotted (Fig. 1). Most notably, even when comparing redwood and tanoak trees of equivalent DBH, fires of higher severity confer a survival advantage to redwood.

APPENDIX C

Mechanistic Considerations and Connections to Previous Redwood/ Tanoak Research

No other studies have analytically compared post-fire survival probabilities of redwood and associated tree species, but some survival statistics for redwood alone are available. Finney and Martin (1993) found that redwood survival rates approached or equaled 100% for second-growth trees greater than 50 cm DBH (across all intensities of prescribed fire), and their models predicted a reduced probability of bole survival for redwoods with smaller DBH and in areas with greater fire intensity. We are unaware of any previous analyses of post-fire tanoak bole survival at the tree or plot scales.

Basal sprout area and height were predicted to increase with decreasing bole diameter and with increasing fire severity, for redwood and tanoak, in young and old stands (although the effect of diameter was minimal for old-growth redwoods). This was likely because of the increased probability of bole death for trees of smaller DBH and in areas of greater burn severity. Our preliminary sprout models included post-fire bole health status (and fire-killed boles were consistently predicted to sprout more vigorously; results not shown), but due to our focus on stand-level sprout patterns as opposed to mechanisms of sprout production, we decided the inclusion of post-fire bole status would only serve to complicate our findings. Although our final sprout models do not explicitly consider bole survival, increases in sprouting resulting from bole death are closely linked to DBH and fire severity and thus implicitly incorporated into all predicted values.

Other mechanisms are also involved in the observed relationships with diameter and fire



Fig. B1. Probability of bole survival as a function of species, DBH, fire severity, and stand age status. In contrast to Fig. 1, curves in this figure represent absolute DBH values (not DBH percentiles). Redwood is displayed with solid gray lines and tanoak is displayed with broken black lines. Fire severity is quantified as the mean contiguous bole char height (m) for all redwood trees within each plot. Limits of the x-axis represent the minimum and maximum fire severities within our dataset, and vertical gray dashed lines mark the 10th percentile ("low"), median ("moderate"), and 90th percentile ("high") of fire severity. Line thickness indicates tree DBH; lines represent (from the thinnest to the thickest) 10, 30, and 50 cm. Tanoak rarely exceeded 50 cm DBH in our dataset and thus these values span the range across which redwood and tanoak trees of equivalent DBH can be meaningfully compared.

severity; both of these predictors were highly significant in models that also included post-fire bole status (results not shown). Negative relationships with DBH might result if smaller surviving boles tend to suffer a greater degree of phloem damage than larger boles, interrupting the flow of auxin from the canopy and stimulating basal bud growth, and/or if larger (and generally older) trees retain fewer functional dormant basal buds, which has been proposed for redwood by Powers and Wiant (1970). Positive relationships between fire severity and sprouting might result if fire triggers a basal sprouting response (e.g., auxin reduction resulting from crown scorch) or if aspects of the postfire environment in more severely burned areas (e.g., higher light levels) are more conducive to vigorous sprout growth. In the understory of a thinned even-aged stand, O'Hara and Berrill (2010) found that redwood basal sprout leaf area and height increment were positively related to light availability. Negative relationships between

sprouting and fire severity, which consistently appeared at very high levels of severity, could occur as a result of dormant bud mortality. For redwood, evidence of fire-induced death of dormant basal buds has been provided by several researchers (Neal 1967, Powers and Wiant 1970, Abbott 1987, Finney 1993).

As is the case with post-fire survival, no previous studies have compared post-fire basal sprouting of redwood and tanoak, but some sprouting data are available for these two species in isolation (see Tappeiner and Mc-Donald 1984, Tappeiner et al. 1984, Kauffman and Martin 1990, Finney and Martin 1993, Ahrens and Newton 2008, Donato et al. 2009). Our extremely high sprout area predictions for small tanoak trees in unburned second-growth stands probably resulted from a unique feature of tanoak establishment: even in the absence of disturbance, tanoak seedlings repeatedly die and re-sprout, forming dense multi-stemmed clumps that eventually thin to one or several dominant sprouts (Tappeiner and McDonald 1984). Many of the smallest tanoak trees in our unburned dataset (e.g., 10 cm DBH) were still

surrounded by an expansive clump of smaller sprouts, while many larger boles had no basal sprouts remaining.