Research Article

Survival and Recovery Following Wildfire in the Southern Range of the Coast Redwood Forest

Rachel Lazzeri-Aerts* and Will Russell

Department of Environmental Studies, San Jose State University,
One Washington Square, San Jose, California 95192-0115, USA

*Corresponding author: Tel.: 001-408-475-3507; e-mail: rachel.lazzeri@gmail.com

ABSTRACT

Fire plays a central role in determining structure, composition, and recruitment in many forest types. In coast redwood forests, the role of fire is not well understood and scant literature exists on post-fire response, particularly in the southern part of the range. In order to better understand patterns of survival and recruitment following fire for coast redwood (*Sequoia sempervirens* [lamb. ex D. Don] Endl.) and associated tree species, three sites in the Santa Cruz Mountains, California, USA, were sampled following wildfire. Randomly selected 10 m diameter plots were used to collect data on survivorship and post fire regeneration in order to analyze short-term responses including mortality, crown retention, basal sprouting, canopy regeneration, and seedling production. Results indicated that coast redwood had the lowest percent mortality (11.98 %) and highest mean canopy retention (43.10 %) of all species sampled, followed by Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) (25.54 %), tanoak (*Notholithocarpus densiflorus* [Hook. & Arn.] Manos) (23.27 %), combined oak species (*Quercus* sp.) (6.67 %), and Pacific madrone (*Arbutus menziesii* Pursh) (4.13 %). In addition, associated species experienced higher survival rates when proximate to coast

RESUMEN

El fuego desempeña un papel central en la determinación de la estructura, composición y reclutamiento en diversos tipos de bosque. En los bosques costeros de secoyas, el papel del fuego no se entiende bien y existe escasa literatura sobre las respuestas post-incendios, particularmente en la parte sur de la cordillera. Para entender mejor los patrones de sobrevivencia y reclutamiento de la secoya costera (*Sequoia sempervirens* [lamb. ex D. Don] Endl.) y especies arbóreas asociadas después del fuego, se muestrearon tres sitios en las Montañas de Santa Cruz, California, EUA después de un incendio. Se establecieron parcelas de 10 m de diámetro, seleccionadas aleatoriamente, para colectar datos de sobrevivencia y regeneración post-incendio con el fin de analizar las respuestas a corto plazo incluyendo mortalidad, retención de copa, rebrotes basales, regeneración de dosel y producción de plántulas. Los resultados indicaron que la secoya costera presentó el porcentaje más bajo de mortalidad (11.98 %) y la más alta retención de copa (43.10 %) de todas las especies muestreadas, seguida por el abeto Douglas (*Pseudotsuga menziesii* [Mirb.] Franco) (25.54 %), tanoak (*Notholithocarpus densiflorus* [Hook. & Arn.] Manos) (23.27 %), encinos (*Quercus* sp.) (6.67 %) y madroño del Pacífico (*Arbutus menziesii* Pursh) (4.13 %). Además, las especies asociadas experimentaron tasas de sobrevivencia más altas cuando estaban cercanas a las secoyas. Los árboles redwoods. Coast redwood trees also exhibited the highest canopy regeneration (53 %), the highest average density of basal sprouts (3.54×10^4 ha), and the greatest average number of seedlings, ranging from zero to 2.09×10^5 seedlings ha^{-1}. Overall, coast redwood appeared to have a balance of fire adaptive features, exceeding all associated species, which allow individual trees to withstand fire, while at the same time promoting recruitment following fire.

de secoya costera también presentaron la regeneración de dosel más alta (53 %), la densidad de rebrotes basales promedio más alta (3.54×10^4 ha) y el mayor promedio de número de plántulas, desde cero hasta 2.09×10^5 plántulas ha^{-1}. En general, la secoya costera presentó un equilibrio de características de adaptación al fuego, superior al de las especies asociadas, lo que permite a los árboles individuales tolerar el fuego, promoviendo al mismo tiempo el reclutamiento después del fuego.

Keywords: canopy retention, regeneration, Santa Cruz Mountains, *Sequoia sempervirens*, sprouting

Citation: Lazzeri-Aerts, R., and W. Russell. 2014. Survival and recovery following wildfire in the southern range of the coast redwood forest. Fire Ecology 10(1): 43–55. doi: 10.4996/fireecology.1001043

INTRODUCTION

Disturbance events are important in determining the composition and structure of biotic communities. Coast redwood (coast redwood [Lamb. ex D. Don] Endl.) forests are generally considered not to be disturbance dependent (Olson Jr. *et al.* 1990, Arno and Allison-Bunnell 2002). Gap phase succession, as a result of individual tree mortality, is considered the primary successional driver, rather than large-scale disturbance caused by fire or flood (Busing and Fujimori 2002). Large stand-replacing events are exceedingly rare in this forest type due to a suite of adaptive features that allow coast redwood to survive and regenerate prolifically following fire events. Fire does, however, play an important role in shaping the coast redwood community by increasing the relative dominance of coast redwood over other less fire-adapted species.

A variety of species interface with coast redwood within the coastal mixed evergreen forest mosaic in the Santa Cruz Mountains, located in coastal central California, USA. Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) is a common co-dominant and exhibits similar fire resistant properties as coast redwood, including thick insulating bark and high crown (Hermann and Lavender 1990). However, Douglas-fir has no ability for basal or epicormic sprouting, so that complete loss of foliage for an individual results in mortality without exception. The same is true for ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and knobcone pine (*Pinus attenuata* Lemmon). However, both pine species seed prolifically following fire, particularly knobcone pine—a true fire-dependent species with serotinous cones (Lanner 1999, Barbour 2007). Several hardwood species are associated with coast redwood forests in the southern range, including Pacific madrone (*Arbutus menziesii* Pursh); a variety of oak species, including California live oak (*Quercus* agrifolia Née), canyon live oak (*Q. chrysolepis* Liebm.), and interior live oak (*Q. wislizeni* A. DC.); tanoak (*Notholithocarpus densiflorus* Hook.); and California bay (*Umbellularia californica* [Hook & Arn.] Nutt.). These species present little above-ground fire resistance with relatively thin bark, but exhibit substantial post-fire sprouting ability. Other than coast redwood, California nutmeg (*Torreya californica*

Torr.) is the only other sprouting conifer associated with the southern range of coast redwood forests. California nutmeg is a minor component of the forest mix, however, and has only modest sprouting ability.

Naturally ignited fires are rare in the coastal forests where coast redwood thrives due to high atmospheric moisture content along the coast (summer fog) and the rarity of lightning strikes in the dry season (Brown *et al*. 1999, Brown and Baxter 2003). When fire does occur, intensity tends to be relatively low, resulting in low mortality, although flame lengths can vary significantly. Bark thickness and height to live crown both increase with age and maturity, increasing the ability of older coast redwood trees to survive fires (Olson Jr. *et al.* 1990). Agee (1993) and Scanlon (2007) observed that size and age of trees, as well as fire intensity, play a role in coast redwood's ability to survive fire. Their observations, in addition to quantitative data from Finney and Martin (1993) and Ramage *et al.* (2010), suggest that larger, mature coast redwoods are able to survive moderate to high intensity fire events, while smaller immature trees can be killed by relatively low intensity fire events.

Following fire, coast redwood trees regenerate vigorously from both basal sprouts and seed (Agee 1993, Scanlon 2007), although seeds often have a short viability period and are typically less numerous than sprouts (Olson Jr. *et al.* 1990). As a result, 40% to 81% of coast redwood trees originate as sprouts (Douhovnikoff *et al.* 2004). Additionally, epicormic sprouts can regenerate quickly from stem and branch tissue to replace the crowns of damaged trees (Olson Jr. *et al.* 1990). Finney and Martin (1993) found that only a few trees smaller than 15 cm diameter at breast height (dbh) did not regenerate either through epicormic or basal sprouts following prescribed fire, suggesting that larger mature trees also resprout better than smaller immature trees.

Much of the previous research in the coast redwood region has focused on fire history and fire frequency, and a majority of this research has focused on the periods of Native American and Spanish occupation. During these time periods, fire return intervals were estimated to be between 6 years and 135 years (Finney and Martin 1989, Greenlee and Langenheim 1990, Finney and Martin 1992, Brown and Swetnam 1994, Brown *et al*. 1999, Brown and Baxter 2003, Stephens and Fry 2005). Due to the loss of Native American ignitions and the beginning of active fire suppression in the early twentieth century, fire frequency was markedly reduced (Brown and Baxter 2003, Stephens and Fry 2005).

Lorimer *et al.* (2009) state that there is a lack of research on the response of coast redwoods and associated species to fire, with specific regard to sprouting and seedling establishment. Additionally, the bulk of previous research has been conducted in the northern and central regions, which differ from the southern coast redwood region in terms of climate, growing conditions, and forest composition. Compared to coast redwood forests in the northern part of the range, stands in the southern extent are smaller and less continuous, receive less annual precipitation, and vary from northern coast redwoods in genetics, forest composition, and forest ecology (Noss 2000). Limited understanding of how coast redwoods and their forest associates respond to fire can limit fire management, conservation, and restoration efforts. The objectives of this research were to: 1) quantify post-fire mortality and crown retention for coast redwoods and associated species following fire; and 2) quantify post-fire regeneration and recruitment of coast redwoods and associated species. Based on previous research, we predicted that coast redwood would exhibit the lowest levels of mortality, and the highest levels of canopy retention, regeneration, and recruitment.

METHODS

Study Sites

We collected data at three sites that experienced wildfire within two years prior to sampling. Fire severity varied within and between sites, with pockets of crown fire present on all sites. Study sites were located in Santa Clara and Santa Cruz counties of California, USA, in the southern range of the coast redwood (Figure 1, Table 1). Elevation within the Santa Cruz Mountains ranges from sea level to about 1000 m, and climate is considered temperate to hot, with a heavy marine influence in the form of summer fog. Winter precipitation ranges from 40 cm to 152 cm, and falls predominately as rain. Past land management in-

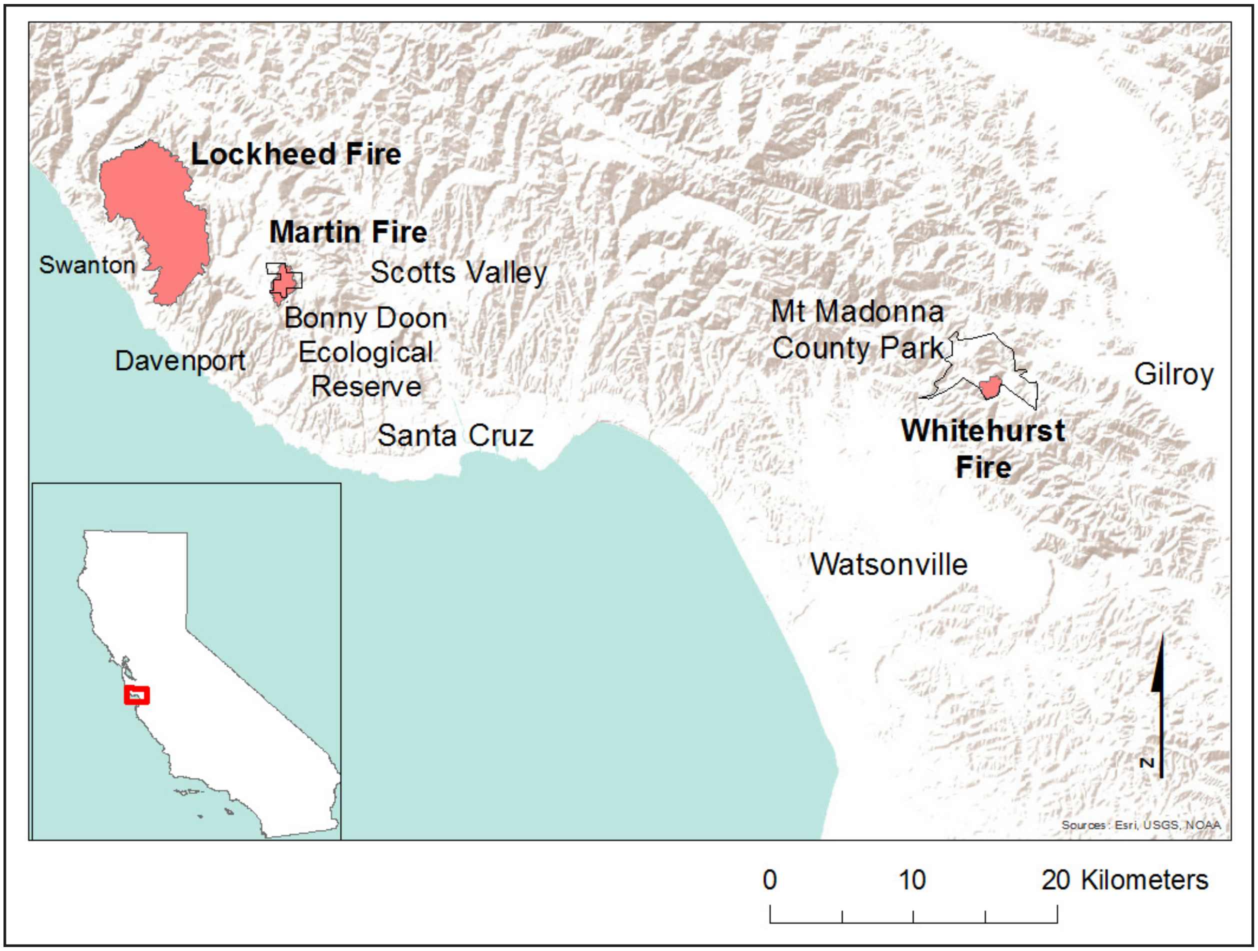

Figure 1. Site locations of three fires in the Santa Cruz Mountains, California, USA.

Table 1. Site descriptions and locations of three fires in the Santa Cruz Mountains, California, USA.

Fire	Location (latitude; longitude)	Distance from coast (km)	Elevation (m)	Fire dates	Area burned
Martin	N 37° 3’ 24.4”; W 122° 8’ 17.6”	5.75	365 to 518	11 to 15 Jun 2008	210 ha
Whitehurst	N 36° 59’ 51.8”; W 121° 41’ 34.2”	16.25	195 to 490	21 to 26 Jun 2008	103 ha
Lockheed	N 37° 4’ 1.4”; W 122° 12’ 22.9”	2.53	61 to 335	12 to 23 Aug 2009	3163 ha

cludes pre-European burning, extensive logging, and ranching (Noss 2000, Barbour *et al.* 2001, Anderson 2005, Diekmann *et al.* 2007). Prior to the institution of fire suppression in the early part of the twentieth century, there were frequent fires from mills, railroads, and other human activity (Stephens and Fry 2005, Stephens *et al.* 2007). Today, large human populations create a growing wildland-urban interface necessitating greater fire control (Alexander and Sawyer 1997), and while there have been several large wildfires in the two counties over the past century, none of the study sites had burned within the past 50 years.

The Martin Fire Site

The Martin Fire occurred 11 to 15 June 2008 in the Bonny Doon Ecological Reserve (Figure 1). It burned 210 ha, 17.4 ha of which consisted of coast redwood forest, ranging in elevation from 365 m to 518 m. Sample plots ranged from 418 m to 514 m. National Oceanic and Atmospheric Administration (NOAA) stations in Felton and Santa Cruz, California, provided temperature and precipitation data. Temperatures on the day the fire started were 33.9 °C in Felton and 32.8 °C in Santa Cruz. Over the next four days, daytime temperatures ranged from 25 °C to 33.3 °C in Felton and 18.3 °C to 20.6 °C in Santa Cruz. There was no recorded precipitation at either weather station for the month of June, and the area had experienced drought conditions for the previous two years. While unconfirmed, the fire was suspected to be human caused. Once started, a northerly wind quickly pushed the fire south through much of the reserve (CAL FIRE 2008). The reserve, which lies 5.75 km from the ocean, is the largest unfragmented area of Santa Cruz sandhills (McGraw and Levin 1998). Due to this geological diversity, the Martin Fire site was the most diverse in terms of vegetation types and included coast redwood, closed cone pine, ponderosa pine, oak, and Santa Cruz cypress communities. The impact of the fire varied dramatically across the site, with the highest severity stand-replacing fire occurring in the closed cone pine community, and the lowest severity fire occurring in the coast redwood-dominated stands.

The Whitehurst Fire Site

The Whitehurst Fire burned in Mt. Madonna County Park (Figure 1) from 21 to 26 June 2008. The park is 14 km from the ocean, and burned within an elevation range from 195 m to about 490 m above sea level. Sample plots ranged from 424 m to 487 m. The two closest NOAA weather stations are in Gilroy and Watsonville, California, which recorded temperatures of 41.7 °C and 40 °C, respectively, on the first day of the fire. Daytime temperatures ranged from 22.2 °C to 39.4 °C in Gilroy and 16.7 °C to 35.6 °C in Watsonville for the duration of the fire. Gilroy received trace amounts of precipitation on 22 June and Watsonville received none for the month of June. This area had also been experiencing drought conditions. The lightning-ignited fire burned 103 ha, nearly all of which were coast redwood or mixed evergreen forests. While large-scale stand replacement did not occur on the Whithurst Fire site, occasional crowning activity did occur in areas along the western flank where CAL FIRE personnel performed a back burn. There was little wind, so the heat from the back burn went up into the canopy (personal communication, Battalion Chief D. McLean, CAL FIRE, Santa Clara, California, USA, 2010).

The Lockheed Fire Site

From 12 to 23 August 2009, the Lockheed Fire burned 3163 ha in the Swanton area north of Santa Cruz, California. An unattended campfire was determined to be the source of the fire. NOAA recorded a temperature of 22.2 °C in Santa Cruz the day the fire started and ranged from 20 °C to 27.2 °C for the duration of the fire. Drought conditions continued from 2007 and 2008, and the only precipitation recorded was 0.051 cm on 2 August 2009. Additionally, the marine fog layer was absent during the first two days of the fire and there were northerly winds present, which allowed the fire to spread quickly (CAL FIRE 2009*a*). Elevations ranged from 61 m to 335 m above sea level, and sampling occurred between the elevations of 115 m and 276 m . Data collection took place in the Little Creek Management Unit of Swanton Pacific Ranch (Figure 1), which is actively managed for timber and is dominated by young second growth forests, including some recently harvested stands (Swanton Pacific Ranch Nonindustrial Timber Management Plan, http://www.spranch.org/forest_management.ldml). Coast redwood dominated much of the fire area, with associated Douglas-fir, tanoak, and Pacific madrone common on ridge tops. Fire behavior was highly variable across the site, ranging from small areas of low severity surface fire to large areas of moderate intensity fire, and pockets of higher intensity crown fire. CAL FIRE (2009*b*) estimated the burn severities for the entire Lockheed Fire at: 14 % very high severity, 37 % high severity, 43 % moderate severity, and 6 % low severity.

Plot Design and Measurements

We collected data between January 2009 and September 2010. At each site, we used 30 randomly selected circular plots with a 10 m diameter for a total of 90 plots. At the center of each plot, we measured aspect and slope with a handheld clinometer to determine if post-fire conditions were correlated to physical parameters. Canopy retention (foliage retained through fire) and regenerated canopy (new foliage produced after fire from epicormic sprouts) for each species were also measured at plot center using a convex spherical densiometer and ocular assessment based on foliage color. In most cases, the distinction between retained and regenerated canopy was quite apparent, as new foliage was noticeably lighter in hue.

The following assessments were made for each individual tree:

- tree species (*Quercus* species were combined as those without foliage were difficult to distinguish);
- dbh (diameter at breast height);
- tree height, measured with a hand held clinometer;
- mortality (defined as the lack of residual or sprouted green tissue on base, bole, or branch);
- bole char height, measured with a clinometer;
- presence or absence of retained canopy (defined as foliage retained through fire);
- and presence or absence of regenerated canopy (defined as epicormic sprouting that occurred following the fire event).

Post-fire regeneration was assessed on each 10 m diameter plot by counting the number of seedlings of each species and the number of basal sprouts for all sprouting trees (coast redwood, tanoak, oak, and Pacific madrone) in three height classes (small: 0.0 m to 0.5 m; medium: 0.5 m to 1.0 m; large: >1.0 m).

Analysis

One-way ANOVAs (analysis of variance), two sample *t*-tests, and linear regression analyses were conducted on a Systat 13 platform (Systat Software Inc., Chicago, Illinois, USA) with an alpha level of 0.05. The ANOVA was used to conduct comparisons between species for several independent variables, including mortality, canopy retention, and the number of basal sprouts. Data were tested for homogeneity using the Bartlett's chi-square statistic, and post-hoc analyses were conducted using the Bonferroni test for pair-wise differences between groups. Two sample *t*-tests were used to compare differences in tree size (dbh and height) between trees that exhibited canopy retention versus those that did not, and for trees that exhibited canopy regeneration versus those that did not. Linear regression analysis was used to analyze correlations between bole char height versus canopy retention, and overall mortality versus the density of coast redwood stems.

RESULTS

Fire severity varied from plot to plot, with bole char heights ranging from 0 m to >50 m. The highest average bole char heights occurred on Pacific madrone, Douglas-fir, and combined oak species (10.92 m ± 1.53 m SE; 10.32 ± 1.72 m SE; 9.24 m ± 1.32 m SE), followed by coast redwood and tanoak (7.95 m ± 0.49 m SE and 2.00 m ± 0.25 m SE, respectively). However, seven of the eight highest bole char heights occurred on coast redwood, with the maximum height at 52.78 m. The next highest maximum bole char heights were found for Douglas-fir (38.58 m) and ponderosa pine (32.41 m). Bole char height varied substantially from site to site, with the highest levels found on the Lockheed Fire site and the lowest on the Whithurst Fire site (Figure 2).

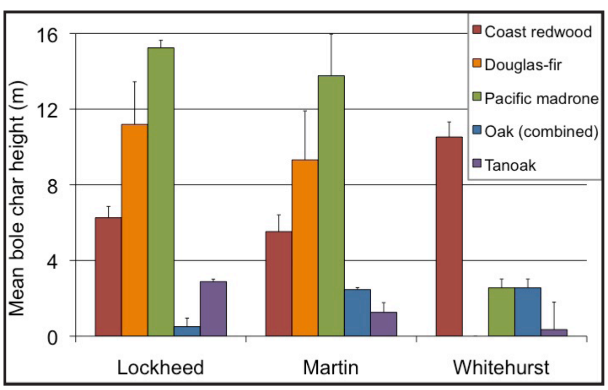

Figure 2. Bole char height (mean ± SE) of five most common species across three wildfire sites in the Santa Cruz Mountains, California, USA.

Post-Fire Survival

Coast redwood trees exhibited the lowest mortality across all sites (F_4 = 13.889, P < 0.001), followed by Pacific madrone, oak, tanoak, and Douglas-fir (Table 2). Variation occurred between sites, with the highest mortality for all species found on the Lockheed Fire site and the lowest found on the Whitehurst Fire site (Figure 3). Coast redwood trees also had the highest mean canopy retention across all three sites (43.10 %) (F_4 = 7.234, P < 0.001), followed by Douglas-fir (25.54 %), tanoak (23.27 %), combined oak species (6.67 %), and Pacific madrone (4.13 %).

Table 2. Average mortality of five most common tree species across three sites in the Santa Cruz Mountains, California, USA.

Species	% mortality ± SE
Coast redwood	11.98 ± 3.29
Pacific madrone	24.67 ± 10.64
Oak species	27.02 ±7.3
Tanoak	29.90 ± 5.5
Douglas-fir	74.46 ± 8.77

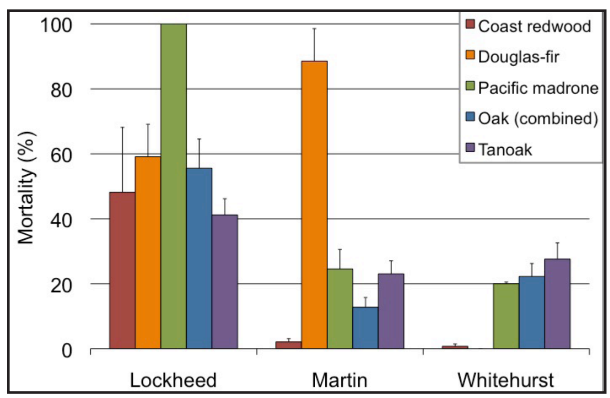

Figure 3. Post-fire mortality (mean % ± SE) of five most common tree species across three sites in the Santa Cruz Mountains, California, USA.

The size of individual trees (height and diameter) was associated with post-fire tree survival, with coast redwood exhibiting 100 %

survival for all individual trees greater than 7.5 cm dbh. Coast redwood, tanoak, and combined oak species each exhibited significantly larger mean dbh for trees that retained residual canopy than for trees that did not (Table 3). Trees that retained canopy following fire were significantly taller than those that did not. In addition, regression analysis indicated a significant negative correlation between residual canopy retention and bole char height for all species combined (P < 0.001, R^2 = 0.466). This relationship was not as clear for coast redwood, which experienced the highest maximum bole char heights, as well as the greatest survivorship. The bark of coast redwood is less compact than associated species such as Douglas-fir, however, and may facilitate greater flame lengths up the bole of the tree.

In an unexpected result, the presence of coast redwood appeared to afford associated trees a better chance of survival. Linear regression indicated a significant negative correlation between mortality across all species and the density (stems ha^{-1}) of coast redwood trees on individual plots (P = 0.036, R^2 = 0.206).

Table 3. Paired *t*-test comparisons of height and diameter of trees with and without canopy retention, and height and diameter of trees with and without regenerated canopy, following three wildfires in the Santa Cruz Mountains, California, USA.

Species	Mean height with canopy retention ± SE (m)	Mean height without canopy retention ± SE (m)	*t*-statistic	*P*-value
Coast redwood	33.3 ± 1.3	9.1 ± 0.8	15.658	<0.001
Tanoak	21.3 ± 1.4	6.0 ± 0.6	9.951	<0.001
Douglas-fir	26.1 ± 5.2	16.7 ± 3.6	1.470	0.158
Pacific madrone	11.9 ± 1.1	7.6 ± 1.2	2.657	0.027
Oak	17.8 ± 3.0	3.9 ± 0.6	4.524	0.017
Species	**Mean dbh with canopy retention ± SE (cm)**	**Mean dbh without canopy retention ± SE (cm)**	***t*-statistic**	***P*-value**
Coast redwood	66.5 ± 3.1	16.8 ± 1.6	14.235	<0.001
Tanoak	42.7 ± 3.3	10.9 ± 1.3	8.989	<0.001
Douglas-fir	50.3 ± 12.0	46.1 ± 8.5	0.267	0.791
Pacific madrone	26.8 ± 5.6	21.3 ± 3.4	0.491	0.627
Oak	52.0 ± 15.2	12.7 ± 1.7	4.848	<0.001
Species	**Mean height with regenerated canopy ± SE (m)**	**Mean height without regenerated canopy ± SE (m)**	***t*-statistic**	***P*-value**
Coast redwood	30.6 ± 1.3	6.7 ± 0.6	17.035	<0.001
Tanoak	15.9 ± 1.4	6.0 ± 0.7	6.188	<0.001
Douglas-fir	24.3 ± 5.4	17.8 ± 3.6	0.982	0.340
Pacific madrone	8.8 ± 2.0	8.1 ± 1.3	0.299	0.772
Oak	13.2 ± 1.9	3.1 ± 0.6	4.990	0.001
Species	**Mean dbh with regenerated canopy ± SE (cm)**	**Mean dbh without regenerated canopy ± SE (cm)**	***t*-statistic**	***P*-value**
Coast redwood	31.0 ± 2.9	6.7 ± 1.2	17.981	<0.001
Tanoak	17.3 ± 3.1	6.5 ± 1.4	6.504	<0.001
Douglas-fir	24.3 ± 12.4	21.2 ± 8.3	0.491	0.626
Pacific madrone	27.4 ± 5.9	11.8 ± 2.9	3.419	0.003
Oak	28.8 ± 3.1	7.1 ± 2.4	6.833	<0.001

Post-Fire Regeneration

Coast redwood had the highest average percentage of regenerated canopy of surviving trees (52.91% ± 3.8% SE), followed by Pacific madrone (44.12% ± 2.3% SE), combined oak species (46.05% ± 2.7% SE), and tanoak (41.79% ± 4.2% SE). In addition, coast redwood, tanoak, and combined oak species trees with regenerated canopy tended to be taller and have greater diameters than those that did not (Table 3).

Overall, coast redwood trees had higher (F_3 = 5.774, P = 0.001) basal sprout density than any other species, with the exception of Pacific madrone, which was statistically equivalent (P = 0.145). In the smallest height class (0.0 m to 0.5 m), there was no difference in sprout production among the four species capable of basal sprouting. In both the medium (0.5 m to 1.0 m) and large (>1.0 m) size classes, coast redwood had higher mean numbers of basal sprouts per tree than other species (Figure 4).

Coast redwood also exhibited the highest overall regeneration through seed (Table 4), although seedling density was highly variable and site specific. At the Lockheed Fire site, a mean of 450 ± 175 SE coast redwood seedlings ha^{-1} were found, with a mean of 4.18 × 10^4 ± 748.7 SE coast redwood seedlings ha^{-1} at the Whitehurst Fire site. In contrast, no coast redwood seedlings were found at the Martin Fire site. Seedling density was variable between plots as well, with a maximum of 2.09 × 10^5 seedlings ha^{-1} found on a single plot at the Whitehurst Fire site, while many plots contained no coast redwood seedlings at all. There was no correlation found between seedling numbers and slope, aspect, or canopy cover, and the seasonality of the fires was nearly equivalent for the site with the greatest number of seedlings and the site with the least number of seedlings.

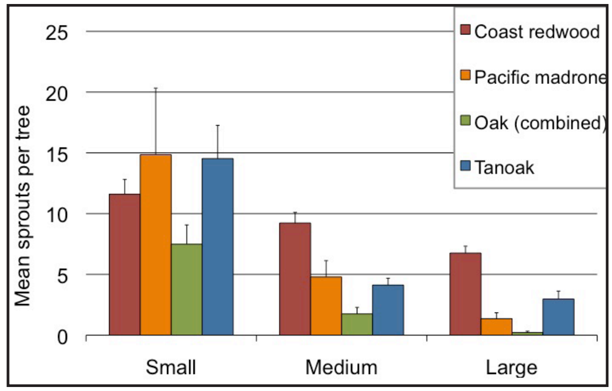

Figure 4. Number of basal sprouts per tree (mean ± SE) in three height classes (small: 0 to 0.5 m; medium: 0.5 m to 1.0 m; large: >1.0 m) on three wildfire sites in the Santa Cruz Mountains, California, USA.

DISCUSSION

As predicted, the results of this study indicated that coast redwood in the southern range was unusually well adapted to fire both in terms of survival and recovery. Coast redwood exhibited the lowest levels of post-fire mortality and canopy loss, in addition to the highest levels of post-fire regeneration and recruitment of all tree species sampled. In addition, larger trees appeared to be better able to withstand fire than smaller trees. These results are consistent with the findings of research in the

Table 4. Mean number of seedlings per ha ± SE on three sites following wildfire in the Santa Cruz Mountains, California, USA.

Fire	Coast redwood	Tanoak	Douglas-fir	Pacific madrone	Oak
Martin	0	302 ± 149	125 ± 75	25 ± 11	198 ± 95
Whitehurst	4.12 x 10^5 ± 1.87 x 10^5	97 ± 25	0	275 ± 275	495 ± 251
Lockheed	450 ± 175	25 ± 25	150 ± 75	0	50 ± 25

northern range (Agee 1993, Scanlon 2007, Ramage *et al.* 2010).

Coast redwood, as well as all associated species, experienced the highest average mortality on the Lockheed Fire site, as compared to the other two fire sites. The Lockheed Fire site also exhibited the highest average bole char height, suggesting that fire severity may have been higher on that site compared to the other two. However, the Martin Fire site had very similar bole char heights with much lower mortality, suggesting that bole char height was not a very good predictor of mortality. These results may have been confounded to some degree by differences in management history between sites. While all sites had been logged in the late 1800s and early 1900s, the Lockheed Fire site had experienced more recent logging activity, with the evidence of selective harvest apparent on some of the plots.

Interestingly, Pacific madrone had the second lowest average level of mortality after coast redwood, even though the majority (86 %) of plots containing madrone experienced no crown retention. Thin bark and relatively low crown heights make madrone susceptible to above-ground damage (McDonald and Tappeiner 1990); however, its ability to regenerate vigorously through basal sprouting lowered the rate of mortality even for trees with complete canopy loss.

Coast redwood also had an apparent mitigating effect on the mortality of nearby associated tree species. This result was somewhat counterintuitive as fire severity (estimated using bole char height) reached maximum heights on coast redwood trees, and although coast redwoods are adapted to withstand extreme flame lengths, many associated species are not. It may be that the elevated flame lengths associated with coast redwood were the result of highly concentrated duff (Nives 1989), or dense sprout thickets at the base of coast redwoods, and did not spread to other nearby trees. It should also be noted that, while coast redwood exhibited the highest maximum bole char height, the average bole char height for the species was modest.

The prodigious germination of coast redwood seedlings on two of the fire sites (Whitehurst and Lockheed) was also unexpected. While recruitment of coast redwoods is known to occur through both the production of seed and basal sprouts, basal sprouts are generally considered the dominant method (Douhovnikoff *et al.* 2004). And although basal sprouting was quite common, seedling populations outnumbered sprouts on many of the Whitehurst Fire and Lockheed Fire sample plots, while there was a total lack of coast redwood seedlings measured on the Martin Fire site. No correlation was found between seedling recruitment and any of the other sampled variables, leaving the question of the cause of this variation unanswered. However, at the time of sampling, many of the seedlings were lacking vigor in comparison to nearby basal sprouts, suggesting that the long-term viability of the seedlings is doubtful.

Management Implications

The ability of coast redwood to survive fire, even when all foliage has been lost, suggests that post-fire management techniques such as salvage logging are not recommended, especially if conducted to salvage fire-killed trees. While crown fires in most coniferous forests result in stand replacement (Agee 1993, Sugihara *et al.* 2006), coast redwoods rapidly produce sprouts from scorched bole and branch regenerating foliar tissue so that the original stand is retained. Additionally, residual and regenerated canopies provide interception surfaces for precipitation (Dawson 1998, Burgess and Dawson 2004), which reduces soil erosion (Biswell 1989). Presence of a canopy also provides shade to the forest floor and prevents drying of the fine surface fuels. In contrast, removing these trees through salvage logging can increase the potential for soil erosion in the short term (Kattelmann 1996; Karr *et al.*

2004), as well as increase the recruitment of ladder fuels over time. Thinning coast redwood stands as a proactive fire hazard reduction measure is counter indicated. If done, thinning should concentrate on species other than coast redwood and be followed by slash treatment. While stand thinning reduces fire hazard initially, it tends to increase the density of small stems through the production of basal sprouts over time, which can help carry a potential fire toward the crown of adjacent trees. Planting coast redwood following fire is equally unnecessary, as natural processes of regeneration from sprout and seed are more than adequate for the replacement of any lost trees.

ACKNOWLEDGEMENTS

Logistical support for this project was provided by the California Department of Fish and Game, the County of Santa Clara Parks and Recreation Department, and Swanton Pacific Ranch. Additionally, we thank the California Department of Forestry and Fire Protection for their assistance with fire maps and history.

LITERATURE CITED

Agee, J.K. 1993. Fire ecology of the Pacific Northwest forests. Island Press, Washington, D.C., USA.

Alexander, E.B., and J.O. Sawyer. 1997. Ecological subregions of California: section and subsection descriptions. USDA Forest Service Report R5-EM-TP-005, Pacific Southwest Region, San Francisco, California, USA.

Anderson, M.K. 2005. Tending the wild: Native American knowledge and the management of California's natural resources. University of California Press, Berkeley, USA.

Arno, S.F., and S. Allison-Bunnell. 2002. Flames in our forest: disaster or renewal? Island Press, Washington, D.C., USA.

Barbour, M.G. 2007. Closed-cone pine and cypress forests. Pages 296–312 in: M.G. Barbour, T. Keeler-Wolf, and A.A. Schoenherr, editors. Terrestrial vegetation of California. University of California Press, Berkeley, USA. doi: 10.1525/california/9780520249554.003.0011

Barbour, M., S. Lydon, M. Borchert, M. Popper, V. Whitworth, and J. Evarts. 2001. Coast redwood: a natural and cultural history. Cachuma Press, Los Olivos, California, USA.

Biswell, H. 1989. Prescribed burning in California wildlands vegetation management. University of California Press, Berkeley, USA.

Brown, P.M., and W.T. Baxter. 2003. Fire history in coast redwood forests of the Mendocino Coast, California. Northwest Science 77: 147–158.

Brown, P.M., M.W. Kaye, and D. Buckley. 1999. Fire history in Douglas-fir and coast redwood forests at Point Reyes National Seashore, California. Northwest Science 73: 205–216.

Brown, P.M., and T.W. Swetnam. 1994. A cross-dated fire history from coast redwood near Redwood National Park, California. Canadian Journal of Forest Research 24: 21–31. doi: 10.1139/x94-004

Burgess, S.S.O., and T.E. Dawson. 2004. The contribution of fog to the water relations of *Sequoia sempervirens* (D. Don): foliar uptake and prevention of dehydration. Plant Cell and Environment 27: 1023–1034. doi: 10.1111/j.1365-3040.2004.01207.x

Busing, R.T., and T. Fujimori. 2002. Dynamics of composition and structure in an old *Sequoia sempervirens* forest. Journal of Vegetation Science 13: 785–792.

CAL FIRE. 2008. Martin Fire damage assessment report: incident number CA-CZU-005238 Santa Clara County. California Department of Forestry and Fire Protection, Sacramento, California, USA.

CAL FIRE. 2009*a*. Lockheed Fire damage assessment report: incident number CA-CZU-007246 Santa Cruz County. California Department of Forestry and Fire Protection, Sacramento, California, USA.

CAL FIRE. 2009*b*. Lockheed Fire post fire risk assessment. California Department of Forestry and Fire Protection, Sacramento, California, USA.

Dawson, T.E. 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117: 476–485. doi: 10.1007/s004420050683

Diekmann, L., L. Panich, and C. Striplen. 2007. Native American management and legacy of working landscapes in California: western landscapes were working long before Europeans arrived. Rangelands 29: 46–50. doi: 10.2111/1551-501X(2007)29[46:NAMATL]2.0.CO;2

Douhovnikoff, V., A.M. Cheng, and R.S. Dodd. 2004. Incidence, size, and spatial structure of clones in second-growth stands of coast redwood, *Sequoia sempervirens (*Cupressaceae). American Journal of Botany 91: 1140–1146. doi: 10.3732/ajb.91.7.1140

Finney, M.A., and R.E. Martin. 1989. Fire history in a *Sequoia-sempervirens* forest at Salt Point State Park, California. Canadian Journal of Forest Research 19: 1451–1457. doi: 10.1139/x89-221

Finney, M.A., and R.E. Martin. 1992. Short fire intervals recorded by redwoods at Annadel State Park, California. Madroño 39: 251–262.

Finney, M.A, and R.E. Martin. 1993. Modeling effects of prescribed fire on young-growth coast redwood trees. Canadian Journal of Forest Research 23: 1125–1135. doi: 10.1139/x93-143

Greenlee, J.M., and J.H. Langenheim. 1990. Historic fire regimes and their relation to vegetation patterns in the Monterey Bay area of California. American Midland Naturalist 124: 239–253. doi: 10.2307/2426173

Hermann, R.K., and D.P. Lavender. 1990. *Pseudotsuga menziesii* (Mirb.) Franco: Douglas-fir. R.M. Burns and B.H. Honkala, technical coordinators. Silvics of North America: 1. conifers. Agricultural handbook 654, US Department of Agriculture, Washington, D.C., USA. <http://www.na.fs.fed.us/spfo/pubs/silvics_manual/table_of_contents.htm>. Accessed 4 Mar 2009.

Karr, J.R., J.J. Rhodes, G.W. Minshall, F. R. Hauer, R.L. Beschta, C.A. Frissell, and D.A. Perry. 2004. The effects of postfire salvage logging on aquatic ecosystems of the American West. BioScience 54: 1029–1033. doi: 10.1641/0006-3568(2004)054[1029:TEOPSL]2.0.CO;2

Kattelmann, R. 1996. Hydrology and water resources. Sierra Nevada ecosystem project: final report to Congress, volume II, assessments and scientific basis for management options. University of California, Centers for Water and Wildland Resources, Davis, USA.

Lanner, R.M. 1999. Conifers of California. Cachuma Press, Los Olivos, California, USA.

Lorimer, C.G., D.J. Porter, M.A. Madej, J.D. Stuart, S.D.J. Veirs, S.P. Norman, K.L. O'Hara, and W.J. Libby. 2009. Presettlement and modern disturbance regimes in coast redwood forests: implications for the conservation of old-growth stands. Forest Ecology and Management 258: 1038–1054. doi: 10.1016/j.foreco.2009.07.008

McDonald, P.M., and J.C. Tappeiner. 1990. *Arbutus menziesii* Pursh: Pacific madrone. R.M. Burns and B.H. Honkala, technical coordinators. Silvics of North America: 1. conifers. Agricultural handbook 654, US Department of Agriculture, Washington, D.C., USA. <http://www.na.fs.fed.us/spfo/pubs/silvics_manual/table_of_contents.htm>. Accessed 4 Mar 2009.

McGraw, J.M., and A.L. Levin. 1998. The roles of soil type and shade intolerance in limiting the distribution of the edaphic endemic *Chorizanthe pungens* var. *hartwegiana* (Polygonaceae). Madroño 45: 119–127.

Nives, S.L. 1989. Fire behavior on the forest floor in coastal redwood forests, Redwood National Park. Thesis, Humboldt State University, Arcata, California, USA.

Noss, R.F., editor. 2000. The redwood forest: history, ecology, and conservation of the coast redwoods. Island Press, Washington, D.C., USA.

Olson Jr., D.F., D.F. Roy, and G.A. Walters. 1990. *Sequoia sempervirens* (D. Don) Endl.: redwood. R.M. Burns and B.H. Honkala, technical coordinators. Silvics of North America: 1. conifers. Agricultural handbook 654, US Department of Agriculture, Washington, D.C., USA. <http://www.na.fs.fed.us/spfo/pubs/silvics_manual/table_of_contents.htm>. Accessed 4 Mar 2009.

Ramage, B.S., K.L. O'Hara, and B.T. Caldwell. 2010. The role of fire in competitive dynamics of coast redwood forests. Ecosphere 1(6): 1–18. doi: 10.1890/ES10-00134.1

Scanlon, H. 2007. Progression and behavior of the Canoe Fire in coast redwood. USDA Forest Service General Technical Report PSW-GTR 194, Pacific Southwest Research Station, Albany, California, USA.

Stephens, S.L., and D.L. Fry. 2005. Fire history in coast redwood stands in the northeastern Santa Cruz Mountains, CA. Fire Ecology 1(1): 2–19. doi: 10.4996/fireecology.0101002

Stephens, S.L., R.E. Martin, and N.E. Clinton. 2007. Prehistoric fire area and emissions from California's forests, woodlands, shrublands, and grasslands. Forest Ecology and Management 251: 205–216. doi: 10.1016/j.foreco.2007.06.005

Sugihara, N.G., J. van Wagtendonk, K.E. Shaffer, J. Fites-Kaufman, and A.E. Thode, editors. 2006. Fire in California's ecosystems. University of California Press, Berkeley, USA. doi: 10.1525/california/9780520246058.001.0001