

Article

Initial Floristic Response to High Severity Wildfire in an Old-Growth Coast Redwood (*Sequoia sempervirens* (D. Don) Endl.) Forest

Mojgan Mahdizadeh and Will Russell * 

Department of Environmental Studies, San Jose State University, San Jose, CA 95192, USA; mojgan.mahdizadeh@sjsu.edu

* Correspondence: will.russell@sjsu.edu; Tel.: +1-415-505-5800

Abstract: Climate driven increases in fire frequency and severity are predicted for Mediterranean climatic zones, including the Pacific coast of California. A recent high severity wildfire that burned in the Santa Cruz Mountains affected a variety of vegetation types, including ancient coast redwood (*Sequoia sempervirens* (D. Don) Endl.) stands. The purpose of this study was to characterize the survival and initial recovery of vegetation approximately six months after the fire. We sampled thirty randomly selected points in an old-growth coast redwood forest to examine and compare survival, crown retention, and post fire regeneration of trees by species, and the recovery of associated understory plant species. *Sequoia sempervirens* exhibited the highest post-fire survival (95%), with lower survival rates for subcanopy hardwood associates including tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos) (88%), coast live oak (*Quercus agrifolia* Nee.) (93%), Pacific wax myrtle (*Myrica californica* (Cham. & Schltld.) Wilbur) (75%), Pacific madrone (*Arbutus menziesii* Pursh) (71%), and the lowest survival recorded for the canopy codominant Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (15%). Canopy retention and post fire regeneration were also highest for *S. sempervirens* and lowest for *P. menziesii*, indicating that *S. sempervirens* had a competitive advantage over *P. menziesii* following high severity crown fire. Both canopy survival and regeneration were greater for larger height and diameter trees; and basal sprouting was positively associated with tree height and diameter for *S. sempervirens* and *N. densiflorus*. Observed recovery of understory species was modest but included the reemergence of coast redwood associated herbaceous species. **The robust nature of survival and recovery of *S. sempervirens* following this extreme fire event suggest that the removal of scorched, and the seeding or planting of trees, following this type of fire is contraindicated.** The decline of *P. menziesii* is of concern, however, and suggests that repeated high severity fires driven by climate change could eventually lead to vegetation type conversion.



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1. Introduction

Forests in Mediterranean systems are at risk due to the effects of climate driven weather patterns and a history of resource exploitation [1,2]. Fire frequency and severity are projected to increase as a result [3,4], leading to shifts in forest composition and structure [5]. In California, a century of systematic fire suppression coupled with prolonged drought conditions have led to extensive tree mortality and record fires in recent years [6,7]. The coast redwood forest, dominated by the iconic tree species *Sequoia sempervirens* (D. Don) Endl., is of particular interest due to its inherent resilience to fire coupled with a dependence on a cool and moist marine layer originating from the Pacific Ocean [8].

The history of natural fire in the coast redwood forest has been one of predominantly infrequent and low severity disturbance [9,10]. Natural ignitions occur from lightning strikes, and storms generally occur during the rainy season when fuels have high relative humidity. The occurrence of lightning storms in the dry season, as those that preceded the

CZU Lightning Complex Fire, are historically rare but can have a significant impact when they occur.

Indigenous burning was initiated approximately 13,000 years ago in California [11,12], generally increasing fire frequencies in coast redwood forests. Intentional burning continued into the early European-settlement period as a result of grazing practices and post-logging slash burning. Systematic fire suppression beginning in the early part of the 20th century led to a significant fire regime shift and increased overall fuel load in the region [13,14]. Widespread timber harvesting in the coast redwood forest over the past centuries has also altered forest structure resulting in an increase in the abundance of fine fuels, fuel continuity, and the potential for high severity crown fires. In addition, fire frequency and severity are increasing throughout the western United States as a result of land use changes and climate driven drought severity [15,16], which could lead to undesirable ecosystem changes [5].

Coast redwood is adapted to withstand fire, with a high crown, thick fibrous insulative bark, and vigorous clonal sprouting ability [17]. Trees that appear severely damaged following crown fire, and have lost all foliar tissue, can begin to replace canopy within a few months through epicormic sprouting [18]. However, the loss of the structural components of crown may limit the ability of the canopy to provide habitat for rare and endangered species such as the marbled murrelet and the northern spotted owl, though some have argued that this risk has been overestimated [19]. The loss of canopy can also affect the diversity and abundance of understory plant species, particularly those coast redwood associates that are adapted to a moist, shady environment. In addition, invasive species can take advantage of gaps created by high severity crown fire further impacting redwood forest endemics [18]. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is often a co-dominant canopy species with *S. sempervirens*. Mature *P. menziesii* have relatively thick insulating bark which enables them to withstand fire [20]; however, they lack the ability for post-fire sprouting and rely on regeneration from seed. *Pseudotsuga menziesii* seedlings have the potential for rapid initial growth post fire, but this potential may be limited following high severity fire. Tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos) is the most abundant subcanopy species in the central and southern range of the coast redwood forest [21]. This shade-tolerant evergreen tree can sprout vigorously post fire even when top killed [22]. However, some research suggests that its relative response to fire is under-studied [23]. Other common associate redwood species are California bay (*Umbellularia California* (Hook. & Arn.) Nutt.), Pacific madrone (*Arbutus menziesii* Pursh), and a variety of hybridizing oak species (*Quercus*, sp.), which have little fire resistance but do have the ability to sprout following fire [18].

Fire behavior in the coast redwood forest is unpredictable and tends to result in a patchwork of mixed intensities on the landscape [24,25]. Historically, high intensity crown fires have been rare in this forest type but may be increasing in frequency as a result of human induced climate change [26]. It is imperative, therefore, to examine the influence of such crown fires on mature coast redwood communities. The goal of this study was to estimate survival and recovery of *S. sempervirens* and its associated tree and understory species following a high severity fire, and to determine if severe fire gives a successional advantage to particular species.

2. Materials and Methods

2.1. Site Description

Big Basin Redwoods State Park is located in the heart of the Santa Cruz Mountains (37.42° N/122.05° W), and is the oldest State Park in California, having been established in 1902. The Park is 10 km from the ocean with elevations ranging from sea level to over 600 m. Average daily temperatures range between 12.7 °C to 23.3 °C, and the site receives an average of 549 mm of precipitation annually mostly during the wet winter months. During the summer, the forest receives most of its moisture from marine fog, which is absorbed by the foliar tissue of *S. sempervirens* and some of its understory associates [27]. Big Basin is home to the largest continuous stand of old-growth coast redwoods south of San Francisco.

S. sempervirens and *P. menziesii* dominate the upper canopy while *N. densiflorus*, *Quercus* sp., *Umbellularia californica* and *A. menziesii* dominate the subcanopy. In 2020, a massive wildfire caused by dry lightning and exacerbated by drought conditions and windstorms swept through the Santa Cruz Mountains. The CZU Lightning Complex Fire burned 350 km² in Santa Cruz and San Mateo Counties between 16 August 2020 to 22 September 2020, affecting 97% of the acreage in Big Basin State Park.

2.2. Sampling Design and Measurements

We randomly selected thirty sample points within an approximately 20 ha area in the central old-growth section of Big Basin State Park with a minimum of 20 m between plots. Data collected at each point included, aspect measured with a handheld compass, slope collected with a clinometer, and percent canopy cover estimated with a spherical densiometer. We recorded all trees > 4 cm in diameter within a 10 m radius of the sample point and designated them as living or dead based on the existence of live crown or sprouts emerging from the bole. Trees of < 4 cm in diameter were recorded as saplings. We noted the following metrics for each individual tree: species; height measured with a laser rangefinder; diameter at breast height; ocular assessment of live canopy; ocular estimates of epicormic sprouting; the number of saplings, and seedlings by species; and the number of basal sprouts. In addition, basal sprouts were divided by height classes, defined as small (0.0–0.5 m), medium (>0.5–1 m), and large (>1 m). Species and percent cover were recorded for all understory plants occurring on plots, and observations were made regarding understory vegetation occurring within the study area.

2.3. Data Analysis

We employed the Shapiro-Wilk test of normality for each variable prior to the following analysis. Pearson's correlation coefficient analysis was used to examine plot data for the following variables: residual live canopy, regenerated canopy, tree density, mean height and diameter, mean basal sprouting, and the percent cover of all understory species. Survival of trees with regard to size (height and diameter) was compared between species using two sample *t*-tests for unequal variance. The relationship between the number of basal sprouts and tree size (height and diameter) was explored with linear regression analysis for all species combined, and for those species with a sufficient sample size and that exhibited normal data distributions. The number of basal sprouts was compared between species using one-way ANOVA with subsequent Tukey post-hoc analysis. We used R package version 2.7-1 (R Foundation for Statistical Computing, Vienna, Austria.) and Microsoft Excel version 16.49 (Microsoft Corporation, Minneapolis, NM, USA) for analysis and graphing.

3. Results

3.1. Post Fire Survival

A total of 487 individual trees of six species were recorded within the sample plots including two coniferous canopy species (*S. sempervirens* and *P. menziesii*), and four hardwood subcanopy species (*N. densiflorus*, *Quercus agrifolia* Nee., *Myrica californica* (Cham. & Schltdl.) Wilbur, and *A. menziesii*). Eighty-five percent of the trees sampled survived the fire based on the presence of live canopy or basal sprouting. *Sequoia sempervirens* exhibited the highest overall survival and *P. menziesii* the lowest (Figure 1). *Quercus agrifolia* and *N. densiflorus* exhibited the highest survival rate among the hardwood species, with *M. californica* and *A. menziesii* lower. Coniferous trees that survived had significantly higher measures of diameter and height than those that did not survive: *S. sempervirens* ($t = 4.150, p < 0.001$; $t = 2.632, p = 0.022$), and *P. menziesii* ($t = 2.843, p < 0.013$; $t = 4.890, p < 0.001$).

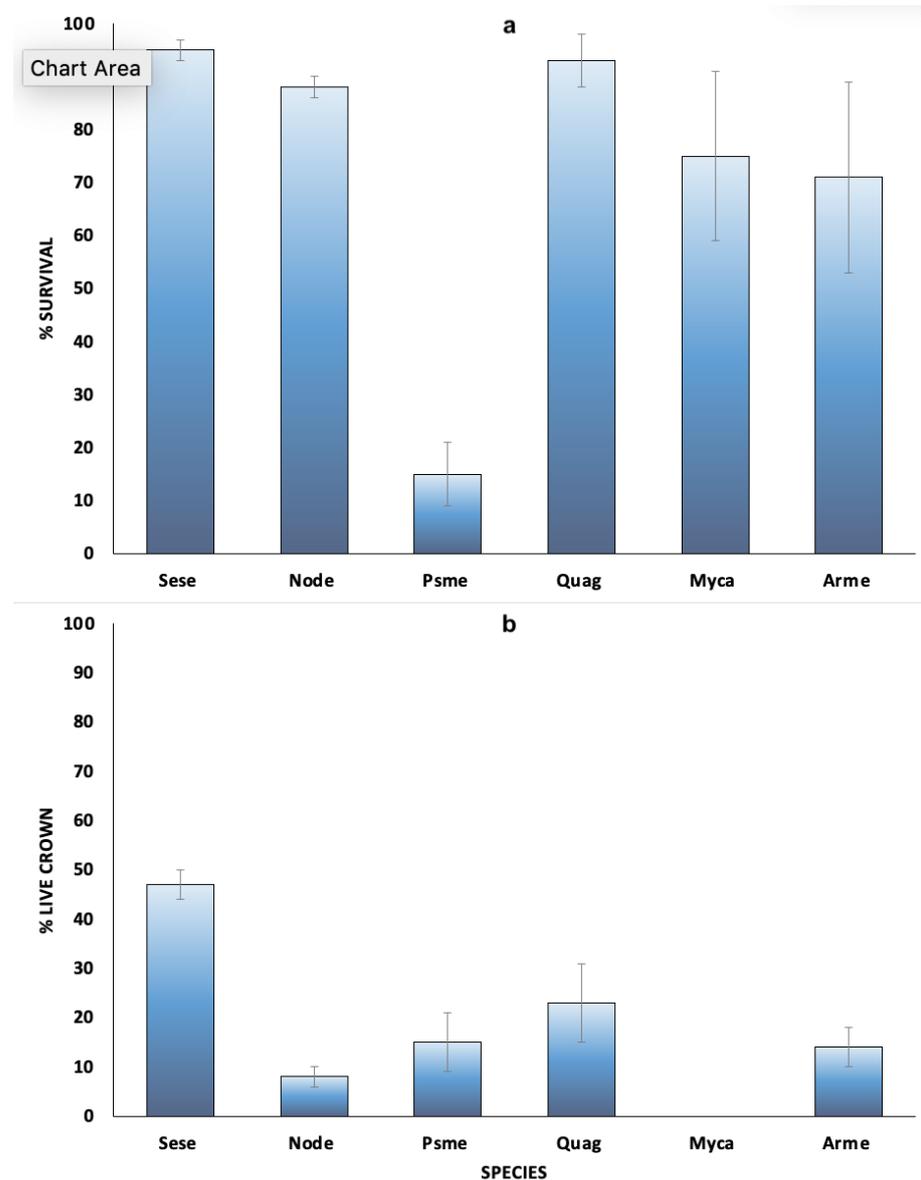


Figure 1. Percent survival (a); and percent trees exhibiting crown retention (b); following a high severity crown fire in Big Basin Redwoods State Park, California. Sese = *Sequoia sempervirens* (D. Don) Endl.; Node = *Notholithocarpus densiflorus* (Hook. & Arn.) Manos; Psme = *Pseudsuga menziesii* (Mirb.) Franco; Quag = *Quercus agrifolia* Nee.; Myca = *Myrica californica* (Cham. & Schltld.) Wilbur; Arme = *Arbutus menziesii* Pursh. Error bars indicate standard error.

Live crown retention was generally low following the fire, but significant variation was evident among species with *S. sempervirens* exhibiting the highest percent of trees with crown retention, and *P. menziesii* the lowest (Figure 1). *Quercus agrifolia* had the next highest measure of trees with retained live crown after *S. sempervirens*, while no live crown was observed for *M. californica*. Percent cover of residual live canopy was positively associated with tree height and diameter for all tree species combined ($r = 0.648$; $r = 0.565$), and crown retention was positively correlated with the density of *S. sempervirens* ($r = 0.575$).

3.2. Post Fire Recovery of Trees

Vigorous sprouting in response to fire was observed for all tree species, with the exception of *P. menziesii* which does not have the ability to produce clonal sprouts (Figure 2). The highest average number of basal sprouts per individual tree was found for *S. sempervirens* ($F = 5.05$; p

< 0.01), (31.9, SE = 3.6), followed by *N. densiflorus* (16.6, SE = 1.2), *Q. agrifolia* (15.5, SE = 2.9), *A. menziesii* (9.6, SE = 5.0), and *M. californica* (3.6, SE = 1.8).

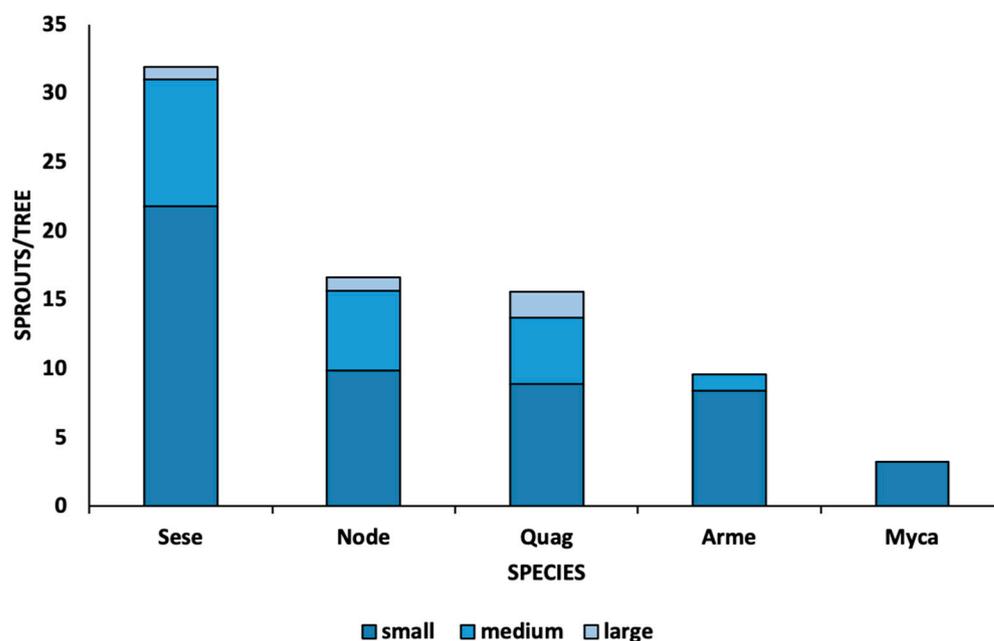


Figure 2. Post fire sprouting by size-class following a high severity crown fire in Big Basin Redwoods State Park, California. Sese = *Sequoia sempervirens* (D. Don) Endl.; Node = *Notholithocarpus densiflorus* (Hook. & Arn.) Manos; Psme = *Pseuotsuga menziesii* (Mirb.) Franco; Quag = *Quercus agrifolia* Nee.; Myca = *Myrica californica* (Cham. & Schltdl.) Wilbur; Arme = *Arbutus menziesii* Pursh. Height classes were defined as small (0.0–0.5 m), medium (>0.5–1 m), and large (>1 m).

We observed positive associations between mean percent post fire canopy regeneration and both tree diameter and tree height ($r = 0.278$; $r = 0.355$). Very little regeneration through seedlings was observed for any species with only fourteen *S. sempervirens* and seven *N. densiflorus* seedlings observed within plots. The lack of *P. menziesii* seedlings was a particularly critical finding, as conal regeneration is not possible for this species. However, though there were no *P. menziesii* seedlings recorded within the plots, there were patches of seedlings observed in other areas in the Park that appeared not to have burned as intensely and some *P. menziesii* canopy had been maintained.

The number of basal sprouts, for all species sprouting combined as a dependent variable, exhibited a positive linear relationship with both tree height and tree diameter as independent variables ($R^2 = 0.373$; $p < 0.001$; $R^2 = 0.199$; $p < 0.001$) (Figure 3). Linear relationships were also observed for *Sequoia sempervirens* ($R^2 = 0.287$, $p < 0.001$; $R^2 = 0.142$; $p < 0.001$) and *N. densiflorus* ($R^2 = 0.293$, $p < 0.001$; $R^2 = 0.261$; $p < 0.001$) between basal sprouting and tree height and tree diameter; while no relationship was observed for *Q. agrifolia*, *M. californica*, and *A. menziesii*. In addition to basal regeneration, the scorched boles of many redwood trees survived the fire and responded by sprouting epicormically (Figure 4).

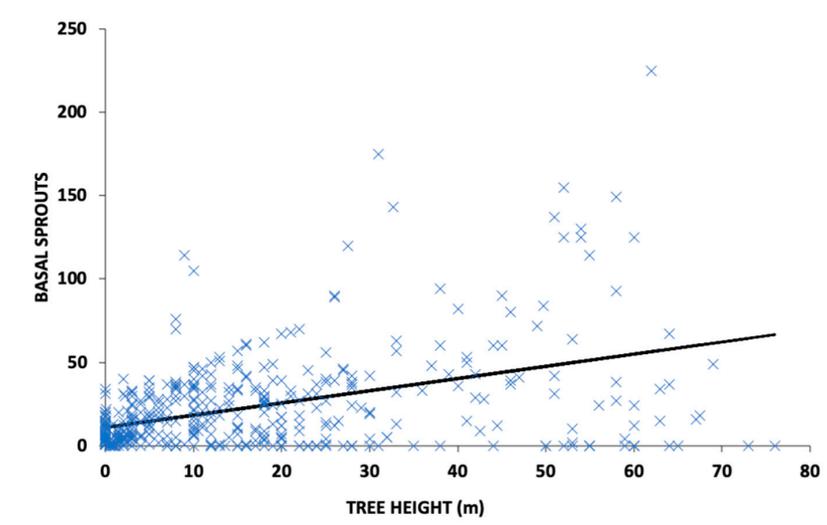


Figure 3. Scatter plot of the number of post-fire basal sprouts combined for *Sequoia sempervirens* (D. Don) Endl.; *Notholithocarpus densiflorus* (Hook. & Arn.) Manos; *Quercus agrifolia* Nee.; *Myrica californica* (Cham. & Schltld.) Wilbur; and *Arbutus menziesii* Pursh), in relation to tree height produced in response to a high severity crown fire in Big Basin Redwoods State Park, California.



Figure 4. Epicormic sprouting in response to high severity crown fire on a group of *Sequoia. Sempervirens* (D. Don) Endl. in Big Basin Redwoods State Park, California.

3.3. Reestablishment of Understory Species

Recovery of understory species following the fire, from both sprouts and seeds, was modest with an average of slightly less than 4% total cover across the samples; however,

sixteen species were recorded on the burned plots, with the sprouting shrub, *Vaccinium ovatum* Pursh., being the most prevalent (Table 1). Understory recovery appears to be related to overstory conditions, as understory cover was associated with canopy retention ($r = 0.402$), especially for *V. ovatum* ($r = 0.354$). *Trillium ovatum* Pursh was also found to be associated with canopy regeneration and was the only understory species found to be associated with *S. sempervirens* density ($r = 0.491$; $r = 0.563$) (Figure 5). All of the species observed on the sample plots were native coast redwood forest associates, however *Genista monspessulana* (L.) L. A. S. Johnson a highly invasive non-native species was observed in the area.

Table 1. Percent cover of sixteen recovering understory species recorded following a high severity wildfire in Big Basin Redwood State Park in the Santa Cruz Mountains, California.

Species	Mean% Cover (\pm SE)
All species combined	3.97 (\pm 1.6)
<i>Vaccinium ovatum</i> Pursh.	2.79 (\pm 1.4)
<i>Equisetum arvense</i> L.	0.67 (\pm 0.67)
<i>Polystichum munitum</i> (Kaulf.) C. Presl.	0.31 (\pm 0.30)
<i>Viola sempervirens</i> Greene	0.31 (\pm 0.30)
<i>Stachys bullata</i> Benth.	0.30 (\pm 0.30)
<i>Oxalis oregana</i> Nutt.	0.20 (\pm 0.17)
<i>Galium</i> spp.	0.17 (\pm 0.17)
<i>Cardamine californica</i> (Nutt.) Greene	0.04 (\pm 0.33)
<i>Trillium ovatum</i> Pursh	0.02 (\pm 0.01)
<i>Pteridium aquilinum</i> (L.) Kuhn	0.01 (\pm 0.01)
<i>Lysimachia latifolia</i> (Hook.) Cholewa	0.01 (\pm 0.01)
<i>Toxicoscordion fremontii</i> (Torr.) Rydb.	0.01 (\pm 0.01)
<i>Rubus ursinus</i> Cham. & Schlttdl.	0.01 (\pm 0.01)
<i>Adenocaulon bicolor</i> Hook.	0.01 (\pm 0.01)
<i>Viola cuneate</i> S. Watson	0.01 (\pm 0.01)
<i>Prosartes hookeri</i> Torr.	0.01 (\pm 0.01)



Figure 5. Perennial herb *Trillium ovatum* Pursh sprouting through charred fuel following a high severity crown fire.

4. Discussion

Fire frequency and severity are projected to increase due to human induced climate change in California, and in Mediterranean systems as a whole, resulting in significant shifts in vegetation patterns [28,29]. Coast redwood forests have generally been considered to be both resistant to fire and resilient following disturbance [18], however recent fires of unprecedented magnitude have presented opportunities to study response of this forest type under extreme fire conditions.

Analysis of initial recovery suggests a successional advantage for *S. sempervirens* over its coniferous codominant *P. menziesii*. Tree size, both height and diameter, were also correlated with survival and recovery metrics including canopy retention, canopy regeneration, and basal sprouting. Recovery was variable among hardwood subcanopy and herbaceous understory species, but generally robust. These findings support previous research that suggests a post-fire advantage for *S. sempervirens* compared to co-occurring tree species, as well as a relationship between tree size and survival [18]. However, the level of mortality recorded for *P. menziesii* in this study exceeded that found in the literature. Ordinarily *P. menziesii* is considered resistant to low and moderate fire intensity and can attain canopy dominance in the presence of occasional fire. In this case, many of the largest *P. menziesii* succumbed to fire, suggesting that high burn severity could initiate a species shift in dominance toward *S. sempervirens*. Many of the trees associated with the coast redwood forest are able to regenerate clonally, but the recovery of *P. menziesii* will depend on seed availability and germination over time. Six months post fire, no *P. menziesii* seedlings were recorded in the sample plots, where fire appeared to have been intense and very little canopy had been retained. The observation of *P. menziesii* seedlings in other areas of the park was encouraging, however. A general lack of tree seedlings of any species was evident in the study area and may be linked to altered physical and chemical properties of the soil and an accumulation of a thick layer of ash on the forest floor [30]. Prolonged drought in the region may have affected, and may continue to affect, the recruitment of seedlings as well. Additional sampling will be necessary to determine if *P. menziesii* recruitment will expand in the coming seasons.

Basal sprouting, epicormic sprouting was vigorous on *S. sempervirens* trees, and was positively correlated with tree diameter and height. This supports research indicating that bud dormancy release responds to stressors such as fire [31] and drought [32] and is related to tree architecture [33] and tree vigor [34]. Subcanopy hardwood species were able to survive high severity fire primarily through basal sprouting, as the majority were top-killed. Species with more vigorous basal sprouting will likely gain greater relative dominance, and the post-fire sprouting pattern can be considered as a key determinant of future stand composition [23]. In this case, *N. densiflorus* and *Q. agrifolia* exhibited the most prolific basal sprouting suggesting that they may have a greater competitive advantage under a high severity fire regime.

The post-fire recovery of understory cover, at approximately 4%, was quite low [35]. Though cover and richness were reduced due to conditions created by the fire, it was encouraging that many of the species commonly associated with coast redwood forests, such as *Oxalis oregana*, *T. ovatum*, *Viola sempervirens*, and *Prosartes hookeri* were present [36]. The most abundant understory species observed was *V. ovatum*, which was able to regenerate vigorously from basal sprouts and underground rhizomes. While no invasive non-native species were recorded within plots, the observation of *Genista monspessulana* in the area is concerning as it can spread quickly and is adapted to post fire conditions. Further reduction of canopy through hazard tree removal could exacerbate this situation.

It will likely be many years before the influence of this fire on the forest community will be fully understood, and the specter of climate change and continuing drought may stimulate additional fires that will further influence successional patterns. *Sequoia sempervirens* is extraordinarily resilient, and even what can appear to be a lifeless blackened stump will often recover if given the chance to do so; suggesting that post-fire planting, seeding, and post-fire removal of scorched trees is counterproductive in this forest type.

Unfortunately, the post-hoc nature of this study limits the ability to assess the impact of this fire on the ecological community as a whole. For example, the loss of crown structure and the wildlife habitat that it provides is critical [19], yet quantifying this loss following a fire is challenging. In addition, long-term increases in fire intensity and frequency driven by climate change could eventually inhibit the recovery of even the most resilient species, leading to vegetation type conversion on a regional scale.

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