Influence of Compounding Fires on Coast Redwood Regeneration and Stand Structure

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Abstract
Disturbance is fundamental to forest ecosystem function, but climate change will continue to increase both disturbance frequency and intensity in the future. Forests subject to increasingly frequent and intense disturbances are more likely to experience overlapping (compounding) disturbance effects. Compounding disturbances may exert unpredicted, non-additive stresses on ecosystems, leading to novel conditions that may exceed the capacity for local species to survive and regenerate. We further hypothesize that compounding disturbances could alter physical and chemical growing conditions in forest soils in ways that disadvantage tree species poorly adapted to the impacts of novel disturbance regimes. Forest composition, structure, and function could shift following increased pressure on one or more species. A better understanding of these remnant effects will be essential to managing and conserving coast redwood (Sequoia sempervirens (D. Don) Endl.) forests, which are projected to see increased frequency of fire under future climate scenarios. Our objectives in this study were to quantify the effects of time-since-fire and single vs. compounding disturbances on coast redwood forest structure, composition, and regeneration dynamics, and to evaluate the effects of abiotic soil qualities on post-fire regeneration. We stem mapped and field sampled coast redwood forests burned in 1985, both 1985 and 1999, 2008, and 2013 and modeled observed regeneration counts as a function of single vs. compounding fires, understory light, and post-fire nutrient levels. Forest structure, composition, and regeneration following compounding disturbance were most similar to the redwood-dominated forest of the recent 2013 burn. There were no unique effects of compounding disturbance on soil nutrient levels, although calcium peaked following the most recent fire. None of the predictors in our hypothesized model were significant, showing that soil legacies and nutrients may not be highly influential in regeneration processes following fire and that the number of fires in an area may have a complex influence on regeneration dynamics. However, this study underlines the need for further research into additional compounding fire disturbances in coast redwood forests to confirm whether the observed homogenized forest conditions were the result of compounding fire disturbance. Such outcomes would have negative implications for ecosystem services and overall function if compounding disturbances are more frequent in the future.

Keywords: climate change, coast redwood, compounding disturbance, disturbance interactions, fire, Sequoia sempervirens

Introduction
Forests provide invaluable ecosystem services and sociocultural resources, and are adapted to specific historical disturbance regimes. Disturbances are important to forest ecosystem function, but climate change will continue increasing the frequency and intensity of forest disturbances in the future (Dale et al. 2001, Millar and Stephenson 2015). Although ecosystems are often able to maintain function following a disturbance to which they are adapted, altered disturbance conditions can lead to lowered ecosystem tolerance to change (Johnstone et al. 2016). Therefore, increased frequency and intensity in disturbance regimes may exert non-additive impacts on ecosystems, leading to novel conditions that exceed an ecosystem’s capacity to survive and regenerate (Buma and Wessman 2011, Metz et al. 2013). Understanding the effects of novel disturbance conditions requires an emphasis on forest resilience, the ability to absorb and adapt to ongoing change (Walker et al. 2004), and the

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mechanisms that confer resilience (Johnstone et al. 2016). However, long-term ecosystem function is at increased risk when the mechanisms that confer ecological resilience have not yet recovered from previous disturbances before a subsequent event occurs (Buma 2015). Such compounding disturbances occur when multiple ecosystem perturbations are either concurrent (e.g., disease and fire) or occur closely enough in time that recovery from the first disturbance is not complete before additional disturbances occur (e.g., two fires in rapid succession; Paine et al. 1998). For example, coast redwood (Sequoia sempervirens (D. Don) Endl.) forests can experience unexpectedly high mortality following compounding disturbances (Metz et al. 2013). Research into resilience over a sequence of time since disturbance can inform management decisions under regimes of increasingly frequent disturbance and higher mortality.

Regeneration is a key mechanism of post-disturbance forest resilience, but can decrease markedly following changes in disturbance characteristics (Buma and Wessman 2011). Soil legacies, the functional modifications to soil that linger after disturbances, can exert a strong influence over regeneration density (Vacchiano et al. 2014). The frequency and severity of disturbances influences the production of soil legacies (Certini 2005), including both surface and belowground properties like mineral soil exposure, aggregate stability, reductions in exchangeable K and Mg, cation exchange capacity (CEC), total N and long-term increases in organic carbon (Johnson and Curtis 2001, Vacchiano et al. 2014). A better understanding of soil legacies and their influences is especially relevant in coast redwood forests, which are experiencing increased pressure from multiple types of disturbance, including fire (Metz et al. 2013, Ramage et al. 2010). It follows that novel disturbance regimes could alter physical and chemical growing conditions in forest soils and affect regeneration patterns for years after disturbance events, leading to changes in forest composition and structure.

The objectives of this research were to better understand how single and repeated fires exert controls on coast redwood regeneration, stand structure, and composition by: 1) assessing differences in stand structure and composition over varying times since fire disturbance and between single and repeat burns, 2) quantifying the effect of time since fire and single vs. compounding disturbance on nutrient levels in coast redwood forests and 3) by modeling coast redwood seedling and sprout regeneration as a function of soil nutrient levels, single vs. repeated fires, and understory light.

Materials and Methods

Site Descriptions

Our primary goal in site selection was to identify locations with varying, but evenly spaced amounts of time since last fire disturbance in the Big Sur ecoregion of California. Additionally, we selected sites with north or northeast aspect, 45 to 300 m in elevation, and similar soil types (described below). Our final site selections included two surface fire events at Landels-Hill Big Creek Reserve (“Big Creek”) and two surface fire events at Pfeiffer Big Sur State Park (“Pfeiffer”). Big Creek provided our two oldest burn locations: one area burned in 1985 and a second burned both in 1985 and 1999 (Department of Forestry and Fire Protection 2015; Mark Readdie, personal communication). Burned areas in Pfeiffer comprised our two most burn events: one burned in 2008 and a second burned in 2013 (Department of Forestry and Fire Protection 2015). The 1985 Gorda-Rat fire consumed 22,662 ha (U.S. Department of Agriculture Forest Service 1986), burning the majority of the Big Creek property. We used this fire as the earliest fire event in order to create a timeline from 1985 to present. The second burn site at Big Creek was located in an area last burned in the 1999 Kirk fire but also burned in the 1985 Gorda-Rat fire, making this a compounding burn site. The Kirk fire consumed 35,086 ha and burned more than half of the Big Creek property (National Interagency Fire Center, n.d.). Burned areas in Pfeiffer comprised our two most recent burn events: one area burned in 2008 and a second burned in 2013 (Department of Forestry and Fire Protection 2015). The 2008 Basin-Complex fire burned 65,890 ha, including much of the northwestern portion of Pfeiffer (Department of Forestry and Fire Protection 2015, InciWeb 2008), whereas the 2013 Pfeiffer fire burned 371 ha in
a small portion of the park’s southwestern edge (InciWeb 2013). Fire perimeter data (Department of Forestry and Fire Protection 2015) for both properties show that our study sites experienced fire infrequently, with a gap of 68 years prior to the 1985 Gorda-Rat fire at Big Creek and no previous fire recorded at Pfeiffer since perimeter records began in the late 1800s. The 1985, 2008, and 2013 burn histories corresponded to one soil type in the NRCS Web Soil Survey (Soil Survey Staff 2014): Gamboa-Sur complex (Gamboa: Haploxerolls, Sur: Haploxerolls; Soil Survey Staff 2003). The 1985/1999 burn histories were from the McCoy series and rock outcrop-Xerorthent association. Like Gamboa and Sur, the McCoy series is a moderately deep and well-drained Mollisol (Argixerolls) but with a higher clay content (Ludington et al. 2005, Soil Survey Staff 2003). Soil pits at each burn site confirmed that underlying soils were very similar across burn histories.

Table 1—Description of soil type, soil series, lithology, and climate factors for the four burn histories used in this study

<table>
<thead>
<tr>
<th>Site</th>
<th>Burn year</th>
<th>Soil type⁴</th>
<th>Soil series⁴</th>
<th>1st and 2nd most common lithology</th>
<th>Mean annual temperature</th>
<th>Mean annual precipitation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Creek Reserve</td>
<td>1985</td>
<td>Very gravelly very fine sandy loam; Stony sandy loam</td>
<td>Gamboa; Sur</td>
<td>Sandstone, mudstone</td>
<td>13.54 °C⁵</td>
<td>67.61 cm⁶</td>
</tr>
<tr>
<td></td>
<td>1985 &amp; 1999</td>
<td>Loam</td>
<td>McCoy</td>
<td>Sandstone, mudstone</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>Very gravelly very fine sandy loam; Stony sandy loam</td>
<td>Gamboa; Sur</td>
<td>Sandstone, mudstone</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pfeiffer Big Sur State Park</td>
<td>2013</td>
<td>Very gravelly very fine sandy loam; Stony sandy loam</td>
<td>Gamboa; Sur</td>
<td>Sandstone, mudstone</td>
<td>14.28 °C⁴</td>
<td>99.29 cm⁸</td>
</tr>
</tbody>
</table>

⁴ Soil Survey Staff 2003.
⁵ Ludington et al. 2005.
⁶ 12/2005 – 2/2016 (Whale Point Station, Western Regional Climate Center 2016a).
⁷ 7/2001 – 2/2016 (Big Sur Station, Western Regional Climate Center 2016b).

**Design of the Long-Term Plot System**

Beginning in June 2015, we installed plots at Big Creek using randomly selected sampling locations in ArcMap (version 10.2.2, Esri, Redlands, CA, 2014). We selected two locations from each fire with comparable aspect, elevation, slope, and coarse soil designations. In each location per burn, we randomly placed ten 0.01 ha square sampling plots (10 plots x 2 locations x 2 burn years = 40 plots). In the summer of 2016, we continued this sampling in the two additional burn histories at Pfeiffer Big Sur State Park following the same protocol. The purpose of these plots was to allow sampling for soils and coast redwood regeneration and for long-term monitoring of forest community and composition as a result of altered disturbance regimes.

**Sampling Overview**

Within each 0.01 ha plot we counted, mapped, and measured the diameter of all overstory trees and saplings at 1.37 m (diameter at breast height, DBH) above the ground. All overstory trees were tagged, along with a subset (10 percent) of clumped sprouts and seedlings. We defined sprouts and
seedlings as individuals < 1.37 m in height and < 2.5 cm diameter at base. Of individuals meeting these criteria, individuals that were also > 1 m away from a mature tree were categorized as seedlings.

We also quantified abiotic variables relevant to tree regeneration, including understory light availability and soil nutrient levels. At the center of each 0.01 ha subplot, we took a hemispherical photograph using a Nikon Coolpix 5000 35 mm digital camera and Nikon FC-E8 0.21x lens (Nikon, Tokyo, Japan) mounted 1 m above the ground and positioned with the top side of the camera facing north (Pastur et al. 2012). A tripod with bubble level was used to correct for uneven terrain below the camera. We used Gap Light Analyzer (version 2.0, Frazer et al. 1999) to process the hemispherical photos and calculate percent total light at each subplot center. Soil sampling for chemical analysis and detection of soil legacies from fire occurred on all 80 plots in May 2016. Soil samples were collected from the A horizon (0 to 10 cm depth) of each site. Litter and duff layers were first discarded from the soil surface. Twelve equally sized soil subsamples were then collected in a stratified sampling design across each subplot and mixed for a composite sample. We air dried soil samples to a constant weight prior to chemical analysis, sieved them (using a 2 mm screen), and sent them to A&L Western Agricultural Labs (Modesto, CA, USA) for processing for macronutrient content. Nutrients of interest (NO$_3^-$, NH$_4^+$, PO$_4^{3-}$, and Ca$^{2+}$) for analysis were selected based on previous studies indicating their importance in the Cupressaceae family (of which coast redwood is a member) and in other forest ecosystems (Hawkins and Robbins 2014, Rao and Rains 1976, Trant et al. 2016).

Data Analysis
We tested for changes in soil nutrient status following burn events and then modeled coast redwood regeneration as a function of soil qualities and abiotic site variables. We used ANOVA to compare soil nutrient levels between burn histories and employed Tukey’s HSD test to distinguish nutrient levels between burn years for instances where an ANOVA global $F$ test was significant. We then used a generalized linear model (GLM) with a negative binomial distribution and log link function to model counts of coast redwood seedlings in each random subplot as a function of burn year, levels of soil nutrients, and percent available light (Bolker et al. 2009). We tested a full model including burn event, understory light, NO$_3^-$, NH$_4^+$, P, and Ca$^{2+}$ to determine whether nutrient levels across burn years were drivers of redwood regeneration. Statistical analyses were run in $R$ (R Core Team 2015), with the MASS package employed for GLM analysis (Venables and Ripley 2002).

Results and Discussion
Diameter distribution among the four burn histories showed distinct differences (figs. 1 and 2). In all burn histories, the average stand density (trees per hectare) was highest in small sizes classes (0 to 2.5 cm and 2.6 to 10.0 cm DBH). However, in the two oldest single fire areas (1985 and 2008), the diameter distributions show patterns typical of uneven-aged stands, compared with more even-aged stand characteristics in the diameter distributions of the compounding fire disturbance (1985/1999) and in the most recent single fire disturbance (2013). The compounding fire disturbance was also most similar to the 2013 single fire disturbance event in the amount of regeneration (0 to 2.5 cm DBH stems). These results indicate that the compounding fire disturbance in these coast redwood forests may have resulted in an environment that remains similar to more recently burned areas, even 16 years following disturbance. Moreover, the compounding disturbance plot is noticeably more homogenous, with coast redwood overwhelmingly dominant, than either the 1985 or 2008 single disturbances, though it is comparable to the makeup of the 2013 burn. This may indicate that the compounding disturbance drove a shift to a forest environment dominated by a more fire-adapted species. These results would be consistent with the hypothesis that fire reduces tanoak ($Notholithocarpus densiflorus$ (Hook. & Arn.) P.S. Manos, C.H. Cannon, & S.H. Oh) dominance compared with coast redwood in recently burned areas due to higher coast redwood survival in the overstory (Lazzeri-Aerts and Russell 2014, Ramage et al. 2010), higher basal sprout density (Lazzeri-Aerts and Russell 2014), and reduced tanoak sprout dominance in burned compared with unburned
areas (Ramage et al. 2010). Additionally, fire perimeter records beginning in the late 1800s show that these areas of forest have re-burned at longer intervals than the 16 years between fires on our sites (Department of Forestry and Fire Protection 2015). However, data are not available on the pre-fire composition of these stands, so a component of these differences may also be related to site-specific variables.

Figure 1—Distribution of stem diameter classes across four burn histories. Distribution of overstory (> 5 cm diameter at 1.37 m height) tree diameter size classes across four burn histories by average trees per hectare (TPH). The 1985/1999 burn was burned twice and is considered a compounding disturbance. UMCA = *Umbellularia californica*, SESE = *Sequoia sempervirens*, QUWI = *Quercus wislizeni*, LIDE = *Lithocarpus densiflorus*.

Some soil nutrients examined (Ca$^{2+}$, PO$_4^{3-}$, NO$_3^-$, and NH$_4^+$) showed differences among burn histories. Comparisons between burn years for Ca$^{2+}$ showed significantly higher levels in the 2013 burn ($F = 6.2395; P = 0.0014$; fig. 3). Phosphorus levels were significantly higher in the 2008 burn, and lowest in the twice-burned 1985/1999 burn ($F = 8.6996; P = 0.0002$; fig. 4). For nitrogen, NO$_3^-$ levels did not significantly differ between burn years ($F = 2.0433; P = 0.1235$) but NH$_4^+$ levels were significantly higher in the area burned once in 1985 ($F = 4.2612; P = 0.0106$; Figures 5 and 6). Our results support the findings of previous work, in which Ca$^{2+}$ concentrations increased following slash burning in eucalyptus forest and remained high for 2 years (Tomkins et al. 1991). Other studies have noted similar patterns with some variation: for example, increased Ca$^{2+}$ following fire in a jack pine (*Pinus banksiana* Lamb.) barren for 1 year (Smith 1970), or up to 21 years following wildfire in a boreal forest in Quebec (Simard et al. 2001). However, our work contrasts with other studies documenting pulses in Ca$^{2+}$ lasting shorter (< 2 years, Khanna and Raison 1986) periods of time. Compounding fire disturbances did not result in significantly higher long-term Ca$^{2+}$ levels in our study. Phosphorus availability often increases within the first year following a fire (Romanyà et al. 1994), but it can be followed by a quicker, though more variable decline than that of Ca$^{2+}$ (Macadam 1987). In our study, phosphorus was highest eight years post-fire and lowest in the compounding 1985/1999 burn, but the 2013 burn and 1985 single burn were indistinguishable from one another.
This is contrary to what previous work suggests about post-fire phosphorus dynamics. Our sampling may have missed an early peak for the most recently burned sites and additional variation could reflect site-specific characteristics. Nitrogen fluctuations in our burned areas generally followed the pattern of past research. Previous studies have documented pulses in NH$_4^+$ for a year or more following fire with a lagged increase in NO$_3$, but increases in one or both forms of inorganic nitrogen may be gone within one to five years (Covington et al. 1991, Covington and Sackett 1992, Grogan et al. 2000). In this study, NH$_4^+$ concentrations were significantly higher in the single 1985 burn compared with any other burn, but there were no other significant differences between nitrogen levels and burn year. This could be an indication that initial pulses in one or both of these nutrients did occur but dissipated by the time of our sampling, though.

Figure 2—Species makeup for regeneration in the 0 to 2.5 cm diameter class (diameter at 1.37 m height) across four burn histories by average trees per hectare (TPH). The 1985/1999 burn was burned twice and is considered a compounding disturbance. UMCA = *Umbellularia californica*, SESE = *Sequoia sempervirens*, QUWI = *Quercus wislizeni*, LIDE = *Lithocarpus densiflorus*.
Figure 3—Ca$^{2+}$ levels across four burn histories. Bars not connected by the same letter are statistically different from one another ($p < 0.05$).

Figure 4—PO$_4^{3-}$ levels across four burn histories. Bars not connected by the same letter are statistically different from one another ($p < 0.05$).
Figure 5—NO$_3^-$ levels across four burn histories. Bars not connected by the same letter are statistically different from one another ($p < 0.05$).

Figure 6—NH$_4^+$ levels across four burn histories. Bars not connected by the same letter are statistically different from one another ($p < 0.05$).

We used a generalized linear model to test the hypothesis that Ca$^{2+}$, PO$_4^{3-}$, NO$_3^-$, and NH$_4^+$ levels would be important predictors of coast redwood regeneration in addition to burn year and percent total understory light in our study sites. However, none of the variables was significant in predicting the amount of coast redwood regeneration (table 2). These results contrast findings from Vacchiano et al. (2014), which showed that decreases in nutrient levels from fire were associated with increased Scots pine (*Pinus sylvestris* L.) regeneration. Our findings do not indicate preference for post-fire establishment conditions in coast redwood forests both in terms of belowground soil conditions and aboveground light availability.
Table 2—Output of generalized linear model (GLM) analysis for selected predictor variables modeling observed numbers of coast redwood regeneration at the subplot level

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percent total light</td>
<td>0.0057</td>
<td>0.8301</td>
</tr>
<tr>
<td>Burn year 1985/1999</td>
<td>0.7070</td>
<td>0.0517</td>
</tr>
<tr>
<td>Burn year 2013</td>
<td>0.3046</td>
<td>0.4320</td>
</tr>
<tr>
<td>NO$_3$</td>
<td>0.1834</td>
<td>0.2038</td>
</tr>
<tr>
<td>NH$_4$</td>
<td>-0.0995</td>
<td>0.4160</td>
</tr>
<tr>
<td>Ca</td>
<td>0.0001</td>
<td>0.6172</td>
</tr>
<tr>
<td>P</td>
<td>-0.0100</td>
<td>0.4603</td>
</tr>
</tbody>
</table>

The results of this study must be considered alongside several limitations. Due to restraints in site access and resources we were unable to conduct research on more than one coast redwood forest area that experienced compounding fire disturbance and we did not locate an unburned (control) forest. Additionally, we did not model fire behavior as predictor of changes in stand structure and composition, and pre-fire stand composition and structure data were not available for any of our research locations. Thus, since we did not compare multiple compounding fire events, some of the observed change in stand structure and composition following compounding disturbance may be remnants of pre-disturbance forest characteristics or of variable fire behavior. Changes in soil nutrient availability may be partially related to site effects since we do not have undisturbed areas as reference, although the lack of replication of specific amounts of time since burn and numbers of burns prevents us from drawing firm conclusions.

Conclusion

In this study, a forest experiencing two fires 16 years prior to sampling showed similarities in stand structure and composition to a forest that experienced a single burn event 2½ years prior to sampling. Compounding and recently disturbed forests were similar in stand structure and increased coast redwood dominance. However, compounding fire disturbance did not leave a detectable legacy in a selection of soil nutrients that we expected to be influential for coast redwood regeneration. Despite differences in nutrient and stand structure between burn years and previously described relationships between light availability and redwood regeneration (O’Hara and Berrill 2010), these factors were not significant predictors of coast redwood regeneration. Taken together, these results may indicate that changes in coast redwood forests toward more redwood-dominated stand composition may be related to compounding fire disturbance. However, because we did not have access to multiple compounding burn sites and pre-fire stand composition and structure data, additional research is needed in order to confirm the effects of compounding disturbance in coast redwood forests. For example, current stand composition may reflect pre-fire coast redwood dominance in addition to effects of compounding fire disturbance. If future work in this ecosystem confirms the relative declines of species like tanoak that we observed following compounding disturbance, it will be important to assess what effects local declines of these species would have on ecosystem services provided by these and other associated species (Bowcutt 2014). Soil legacies specific to compounding fire disturbances do not appear to be present, and nutrient levels in our study did not seem to be limiting for coast redwood regeneration in these forests. Influences of soil conditions on stand structure and composition seen in other research (Johnstone et al. 2010, Vacchiano et al. 2014) are not confirmed in our study, showing that these feedbacks can be indirect and ecosystem specific. Our research supports previous evidence that coast redwood benefits from fire disturbance (Lazzieri-Aerts and Russell 2014), but we show that a greater understanding of compounding disturbance impacts on resilience adaptations is needed in this and other forest ecosystems. Research in other forest ecosystems shows that compounding disturbances can disrupt resilience adaptations (Buma and Wessman 2011, Gower et al. 2015). Future studies should seek to confirm whether the effects seen here can be isolated from site-specific or pre-fire...
stand conditions, as shifts in composition may be indicative of increased ecosystem vulnerability to change (Johnstone et al. 2016). Therefore, greater knowledge of the traits that confer ecological resilience and function in these forests will be important for understanding the impacts of altered disturbance regimes in the future.

Acknowledgments

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