

Prolific Post-fire Persistence: Resilience and Resprouting in the Iconic Coast Redwood

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Abstract

Background

Historically frequent-fire forest ecosystems are now facing increased size, frequency, and severity of fires attributed to climate change, intensive forest management, and fire exclusion. Understanding post-fire resilience in forest ecosystems is critical amidst escalating challenges posed by recent increases in fire activity. Coast redwood (*Sequoia sempervirens*) provides a model system for examining post-fire persistence via resprouting in a highly fire resilient ecosystem. Here, we identify the most informative fire-damage metrics for post-fire basal resprouting, quantify the relative influence of tree-, stand-, and climate-level drivers of post-fire basal resprouting, and examine the relationship between epicormic and basal resprouting following fire for redwood.

Results

Post-fire redwood basal resprout responses (presence and abundance) were most strongly associated with bole char ratio, a relativized measure of fire damage (ratio of bole char height to total tree height). Both the presence and abundance of basal resprouting did not detectably decline with increasing fire damage but rather increased continuously. In addition to fire damage, the probability of basal resprouting, total resprout biomass, and other responses decreased with higher climatic water deficit. Epicormic resprouting of the tree bole was positively related to basal resprout probability.

Conclusions

As climate change drives increased fire activity and severity in many forest ecosystems, prolific post-fire resprouting can facilitate rapid recovery and the long-term persistence of redwoods. These positive post-fire outcomes are slightly tempered by observations of reduced resprouting abundance (both basal and epicormic) in warmer and drier locations, suggesting there may be climatic limitations in the post-fire resprouting ability of redwoods. While further study is needed to examine the long-term trajectory of redwood forests following high-severity fire, our study provides forest managers with sound expectations that resprouting will promote redwood persistence, though may be hindered in the future by extreme drought events.

INTRODUCTION

Many forest ecosystems historically associated with low- to moderate-severity fire are now experiencing increased frequency and patch sizes of high-severity fire across the world (Jones et al. 2022; Parks and Abatzoglou 2020; Westerling 2016). Alteration of historic fire regimes in recent decades has been attributed to climate change, intensive forest management, and fire exclusion (Abatzoglou and Williams 2016; Buma and Wessman 2011; Moritz et al. 2012). Fire exclusion policies enacted since the early 20th century include the removal of fire through disruption and outlawing of cultural burning practices by Indigenous Peoples and aggressive fire suppression (Roos et al. 2020; Stephens et al. 2016; Swetnam et al. 2016). Given these abrupt changes to fire regimes of many forest ecosystems, there is increased interest and concern about the potential effects of modern wildfire on forest resilience (Beisner et al., 2003; Davis et al., 2019; Keeley et al., 2019; Landesmann et al., 2021).

Forest resilience following disturbance is characterized by both persistence and recovery (Falk 2017; Holling 1973). Persistence is defined as the ability to survive and continue to grow or reproduce following environmental stressors or disturbances at both the individual and community level (Falk et al. 2022). Persistence through resprouting is a

common resilience strategy in fire-prone ecosystems (Bates et al., 2022; Clarke et al., 2013; Keeley & Pausas, 2022; Waters et al., 2010). Resprouting often stems from meristematic tissue, and is hormonally controlled through reduction of auxin flow from actively-growing shoots toward dormant buds, triggering a resprouting response (Finney 1993; Meier et al. 2012). However, species across fire regimes vary widely in their ability to resprout following fire (Del Tredici 2001; Pausas et al. 2004). Basal resprouting (i.e. trunk reiteration) refers to the development of new shoots that originate from dormant buds near stem bases or lignotubers at or below the ground surface, while epicormic resprouting refers to branch initiation from dormant buds beneath the bark along the bole and branches (Pausas et al. 2016). Both epicormic and basal resprouting are traits of persistence, enabling the individual (or genet) to survive following fire and other disturbances (Clarke et al. 2013; Falk et al. 2022; Noble and Slatyer 1980).

Basal resprouting response is characterized by both resprout presence and abundance. Resprout presence denotes that fire damage was sufficient to stimulate resprouting while not surpassing the damage threshold to kill bud bank reserves (Clarke et al. 2013; Vesik and Westoby 2004). Many previous studies and vegetation modeling programs (e.g., FVS; Reinhardt and Crookston 2003) consider post-fire basal resprouting in fire prone environments as a simple binary factor (presence/absence). Resprout abundance is the magnitude with which trees resprout following fire, and has rarely been quantified (Pausas et al. 2004; Teixeira et al. 2020; Vesik and Westoby 2004), despite the potential importance of abundance measures to provide insights on post-fire plant recovery responses and future ecosystem trajectories.

Variability in fire damage and intensity has been associated with basal resprouting response across numerous species. Absolute measures of fire damage (e.g. bole char height, crown scorch height) that also represent proxy measures of fire intensity are often positively correlated with resprouting (Bates et al., 2022; Simler et al., 2018; Woodward et al., 2020) though it is unclear which metrics are most informative. Relativized metrics (i.e. crown volume scorch) of fire damage have been shown to be the best predictor of post-fire mortality in many conifers, (Cansler et al. 2020; Hood et al. 2018) and may also be informative of post-fire resprouting presence and abundance.

Basal resprouting responses following fire are also influenced by tree, stand, and climate characteristics. Tree characteristics including diameter (Bates et al., 2022; Pausas, 1997; Woodward et al., 2020), height (Gurvich et al. 2005), and leaf area (Malanson and Trabaud 1988) tend to be positively associated with resprouting response following fire. Stand density and resulting light availability are inversely proportional to resprouting response following fire and other disturbances for some hardwood and conifer species (Barrett, 1988; Bates et al., 2022). Climate characteristics, such as drought occurrence and intensity, are widely known to effect growth and regeneration of coniferous seedlings and saplings, but their influence on resprouting are not well understood. Given the wide range of observed resprouting responses following fire among species, additional studies examining species-specific resprouting responses across a wide range of tree, stand, and climate characteristics are warranted.

Variation in interpretations regarding post-fire resprouting dynamics across species may be due, in part, to the variables measured. Resprout abundance is commonly sampled using relatively simple approaches such as stem counts or cover estimates (Mahdizadeh and Russell 2021; Ramage et al. 2010; Woodward et al. 2020). It is possible that sampling approaches that use metrics that better reflect important plant processes (e.g. productivity, photosynthetic capacity), such as resprout biomass and leaf area may provide better insights into resprouting response following fire.

The relationship between post-fire epicormic and basal resprouting remains largely unexplored. Given that both types of resprouting are triggered by similar mechanisms following damage from heat (e.g. Finney 1993), it is possible that they could show positively linked responses following fire. However, this outcome presumes that carbohydrates are not limited and that epicormic and basal resprouts do not compete internally for stored carbohydrates. Since both epicormic and basal resprouting are reliant on carbohydrate storage and mobilization (Morisset et al. 2012; Peltier et al.

2023; Clarke et al. 2013), allocation of carbon to epicormic sprouts may result in reduced presence or abundance of basal resprouts or vice versa. Other research indicates that non-structural carbohydrates are reduced for conifer species following fire and influence non-structural carbohydrate mobilization (e.g. Reed and Hood 2024). Thus, it is plausible that the allocation of carbohydrates to epicormic and basal resprouting may be altered following fire.

Coast redwood (*Sequoia sempervirens*) provides a model system for examining post-fire resprouting in a highly resilient ecosystem. Redwoods exhibit various traits that enable them to survive relatively low-intensity fire (Lorimer et al. 2009; Stephens and Fry 2005), including fire resistance via thick, fibrous bark (Varner and Jules 2016), high crown bases with efficient self-pruning of lower branches (Stephens et al. 2018), and persistence through basal and epicormic resprouting (e.g. Lazzeri-Aerts and Russell 2014).

The 2020 CZU Lightning Complex burned across one of the largest contiguous redwood forests in the central portion of its range, which extends from southwest coastal Oregon to Big Sur, California, USA. The 34,000-ha wildfire burned across redwood forests with a diverse management history, and more than half of the burned area was classified as high severity (Miller and Thode 2007), which provides an ideal opportunity to study resprouting in secondary redwood forests across a gradient of fire severity. The main objective of this study was to examine the relationship of fire, tree, stand, and climate characteristics and resprouting response (presence and abundance) in a secondary redwood forest two-years after the 2020 CZU Lightning Complex. Specific questions of this study were:

1. Are absolute or relativized measures of fire damage more informative to post-fire basal resprouting responses?
2. How do basal resprouting responses vary with increasing levels of fire damage?
3. What are the relative influences of tree, stand, and climate drivers on basal resprout responses?
4. What is the relationship between basal and epicormic resprouting responses?

Results of this study provide insight into the factors and conditions that contribute to variation in persistence and recovery through basal resprouting following fire in a highly resilient and fire adaptive tree species. Given the projected increases in fire activity over the coming decades, results from this study will help advance our understanding of post-fire resprouting dynamics with implications toward better prediction of post-fire vegetation dynamics and future forest trajectories necessary to inform and improve management.

MATERIALS AND METHODS

Study Area

We evaluated basal resprouting of redwood dominant forests within the 2020 CZU Lightning Complex along the central coast of California. Beginning on August 16th, 2020, the CZU burned 34,000 ha over 37 days in the Santa Cruz Mountains (*CZU Lightning Complex (Including Warnella Fire) Incident Report* 2020). Fifty-two percent of the CZU burn area was classified as high-severity fire (> 572 RdNBR; Miller and Thode 2007). All sampling occurred across six California state and county parks, including Año Nuevo State Park (SP), Big Basin SP, Butano SP, Henry Cowell SP, Wilder Ranch SP, and Pescadero Creek County Park (*Appendix 1*). Sampled stands were dominated by redwood and often contained tanoak (*Notholithocarpus densiflorus*), Douglas-fir (*Pseudotsuga menziesii*), and coast live oak (*Quercus agrifolia*). Study sites ranged in elevation from 10 and 800 m with slopes between 3 and 65%. The dominant soil type for the study site was generally classified as coarse loamy mixed (*Ben Lomond Series Soil Survey* 2009). The 30-yr mean annual temperature for the region was 14.6°C and the mean annual precipitation was 108 cm, falling primarily as rain in the winter months. The year before the CZU complex was warmer and drier than average, with only 48 cm of precipitation and an average temperature of 15.8°C. In the two years following the fire, prior to our data collection,

conditions were slightly warmer and wetter, with an average of 115 cm and an average temperature of 15.0°C (PRISM Climate Group 2022).

The Santa Cruz Mountains have an extensive logging history representative of most of the range of coast redwood, including the removal of primary forests and subsequent development of secondary forests with high stand uniformity. Big Basin SP was established in 1902, setting aside 3110 ha and later receiving another 1532 ha donation in 1916 (Cowman and Russell 2021). Butano SP was established in 1951, Henry Cowell SP in 1954, and Año Nuevo SP in 1968. Prior to preservation, much of forest area within these parks was clear-cut, and converted to secondary forests. The early protection of these forests allowed for the development of mature secondary redwood stands across much of our study site, though evidence of multiple harvests was present at some sites (Burns et al. 2018; Jensen 1939).

Data Collection

Focal Tree Characteristics

For our tree-level sampling, 77 redwoods within the CZU perimeter were selected using a stratified random sampling approach. Trees were selected across five fire damage strata, based on the ratio of bole char height to total tree height (Table 1). Tree selection was constrained by site accessibility and primarily occurred along established trails and roads within state or county parks. Sampled trees were separated by a minimum of 200 m from other sampled trees to avoid potential spatial autocorrelation and located at least 100 m from trails, roads, or structures to reduce any edge effects or other undesired influences. Selected trees were limited to dominant or codominant crown positions within their respective stands and a diameter at breast height (DBH) greater than 30 cm. Sampling was conducted within secondary forests that included trees 21–67 m tall and 31–170 cm DBH. A minimum of 10 sampled trees within each severity strata were sampled but the sample size varied based on availability (Table 1).

Table 1
Post-fire redwood selection damage classifications. Bole damage was calculated as a percent of bole char height to total tree height.

<i>Damage Classification</i>	<i>Bole Damage</i>	<i>Sample Size</i>
Extreme	> 90%	10
High	50–90%	16
Moderate	30–50%	16
Low	10–30%	19
Very Low	< 10%	15

A suite of tree size, fire damage, and growth measurements were taken two years post-fire for each focal tree. DBH was measured at 1.37 m above the average ground level of the tree. Total tree height, crown base height (CBH), bole char height (BCH), and crown damage height (CDH) were recorded to the nearest 0.1 m using a laser rangefinder. We could not determine foliar scorching and consumption heights for trees in our study site, as scorched foliage had fallen prior to sampling, so CDH was used to represent the maximum height of crown scorch and consumption. BCH and CDH were then relativized to total tree height and noted as bole char ratio (BCR) and crown damage ratio (CDR), respectively. Post-fire epicormic resprouting response was quantified by visually estimating total sprouting cover in two categories: percent cover of total bole and percent cover of total tree crown branches rounded to the nearest 5%. A cambium kill rating was assessed using a cambium punch in the four cardinal directions at 0.5 m above average ground level,

partitioning the bole of the tree into quadrants. Dead cambium was denoted by the presence of a dry and dark phloem layer. Live cambium was denoted by a moist, red-pink phloem layer. A rating was given from 0 to 100% in increments of 25%, with 100% denoting dead cambium from all four cardinal directions.

Pre-fire focal tree biomass and leaf area were calculated from previously published allometric equations for redwood to examine the potential influence on resprouting response (Sillett et al. 2019). Predictors for total carbon and biomass include total tree height and diameter at the top of buttressing. Sapwood area at breast height was the sole predictor for leaf mass.

Stand and Climate Characteristics

Post-fire stand competition was characterized by light availability. Digital hemispherical photos were taken with a Nikon D5100 and Opeka wide-angle fisheye lens to measure canopy openness at the base of the tree at a height of approximately 0.8 m above ground. Photos were taken skyward (180°) at the opposite sides of the selected tree, approximately 2 m from the pith. Using the “OPENESS” function of the HemisphR package (Gonsamo et al. 2011), canopy openness for each image ranged from 0, delineating a fully closed canopy, to 1, delineating a completely open sky. Openness for each tree was averaged between two photos taken at opposite sides of the tree.

Climatic water deficit (CWD) for our sites was extracted from the USGS Basin Characterization Model for California. The Basin Characterization Model (BCMv8) provides fine scale (270m) modeled estimates of water balance components including recharge, runoff and evapotranspiration for the state of California using 1981–2010 30-year normals (Flint et al. 2021). CWD was averaged for 30-, 2-, 1-, and partial-year pre-fire monthly water-year averages and for 2 years post-fire.

Resprout Allometry and Biomass Estimation

A total basal resprout count was conducted for each focal tree with individual resprouts separated into three length classes ≤ 1 m (I), 1 to 2 m (II), and > 2 m (III). For each length class at each tree, ten random samples were selected using a random azimuth for a total of 30 resprouts (i.e., individual basal shoots) per tree. Stem diameter and total length of each resprout were recorded from these samples using calipers and steel tape. In cases where trees had < 10 resprouts of a given length class; all resprouts within that class were measured. One resprout from each length class present was randomly selected and extracted for further measurements and processing. From this new subset, length and stem diameter were again measured using a caliper and steel tape for later use in developing allometric equations.

Prior to lab analysis, the subset of extracted resprouts was separated into categories in the field based on the three length classes defined above. Pruners were then used to separate samples into biomass classes. Leaves were separated from the stems and placed in paper bags for later drying and weighing. Samples were separated into three biomass categories: woody stems, green stems, and leaves. Woody stems were identified as stems with an outer brown bark layer. Green stems were identified as stiff, axial shoots lacking an outer woody bark layer representative of the current year's growth. Each bag was labeled with both length and biomass classifications. All separated biomass types within each length category were dried at 101°C for 48 hours and weighed using an analytical balance to the nearest 0.01 g. Dry biomass was then calculated for each combination of length and biomass class, as well as total resprout biomass. Peripheral and green stem masses were summed into a single category of “stems”. Woody and leaf masses were grouped separately for a total of three final biomass categories – stems, woody material, and leaves.

From each extracted sample, leaf subsamples were collected representing the primary morphologies of foliage present and preserved on ice for lab analysis. For each of the subsamples collected, the leaf area was calculated utilizing a

scanner and WinFOLIA software (Regent Instruments, Quebec, Canada). Scans were uploaded onto the platform and analyzed using the leaf area meter tool. Subsamples were then dried at 101°C for 48 hours, weighed, and recorded. Leaf area was averaged between the subsamples for a given sample. Leaf area for the entire resprout was then estimated using a leaf mass (i.e., specific leaf area; Cornelissen et al. 2003) .

Data Analysis

Resprout Allometric Equations

Highly informative allometric equations were developed to calculate resprout total biomass (g), woody, stem, and leaf biomass (g), and leaf area (cm²) (*Appendix 2, Appendix 3*). All non-woody stem biomass was combined into a single category for modeling. Non-linear regression models were developed using the “nlme” package in “R” for each biomass type (leaf, woody, stem, total) and leaf area to estimate the regression coefficients and final structure of allometric equations (Pinheiro and Bates 2023). The Akaike information criterion (AIC) informed the selection of the best-fit models (Burnham & Anderson, 1998). Models with the lowest AIC values were noted as the model of best fit. If the AIC values of multiple models were within two units of difference, the simplest model was selected (Bates et al., 2015). In all, 104 individual resprouts ranging from 1.2 to 57.5 mm in stem diameter and 13.2 to 321 cm in length were used to inform the non-linear regression models and coefficients for the final equations. Separate equations were developed to predict total biomass (g), woody biomass (g), green stem biomass (g), leaf biomass (g), and leaf area (cm²) of resprouts. All biomass response variables were fit with power functions that included bivariate of stem diameter (mm) and total resprout length (cm), with four regression coefficients (*Appendix 4*). Leaf area was only a function of total resprout length with two regression coefficients (*Appendix 5*). Allometric equations were then applied to entire populations of basal resprouts for each of our focal trees utilizing a sample of 10 resprouts from each length class described above (*Appendix 6*).

Determining the Most Informative Fire-Damage Metrics for Redwood Resprouting

A two-step modeling approach was utilized to isolate the most informative fire-damage variable for both redwood resprouting probability and resprouting abundance using a Boosted Regression Trees Analysis (BRT, 10-fold Cross-Validation) in conjunction with Generalized Linear Modeling (GLMs). BRTs, a non-linear machine learning modeling method, uses the technique of boosting traditional decision trees (Breiman et al. 1984) to combine large numbers of relatively simple tree models, optimizing predictive performance (Elith et al. 2008; Friedman 2001; Gu et al. 2019). The primary BRT included all sampled damage predictors (*Appendix 8*) and were ranked by relative influence. From the primary BRT, the three most informative damage variables were fit to univariate GLMs. When partial dependence relationships in primary BRTs indicated non-linear relationships, we encoded similar form in the GLMs using polynomial terms (e.g., x^2). A cross-validated (Monte Carlo K-fold, 200 iterations) Normalized Residual Mean Squared Error (NRMSE) served as the primary evaluation metric for univariate GLMs and Akaike Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002) served as the secondary metric. When the NRMSE of two damage variables were within 0.05 standard deviations, the variable with the lower AICc was selected. Methods were repeated for selecting the most informative damage predictors of total resprout biomass, leaf biomass, and leaf area as well as resprouting probability utilizing a binomial distribution within GLMs and LogLoss (10-fold Cross Validation) as the primary evaluation metric.

Indicators of Post-Fire Resprout Presence

Data from a companion study conducted in 2021 within the fire footprint of the CZU Complex were used to examine post-fire resprouting presence in redwood (Kane and Carrasco 2025). Sample design in this study included 65 1/25th ha fixed-radius plots where mortality status and resprout presence was noted at each tree. This dataset included parallel measurements of fire damage, tree characteristics, and stand characteristics and proved to be more informative for a logistic regression model for redwood due to the higher statistical power of a larger dataset, and greater representation of non-resprouting trees due to the sample design. Pre- and post- fire CWD (mm; Flint et al., 2021) and the basal area density (m^2/ha) were calculated for each plot. Of the 718 trees in this dataset, 106 were non-basally resprouting.

We utilized BRTs for preliminary selection of variables prior to modeling. To stabilize variable importance, we performed stability selection via cross-validation (Monte Carlo K-fold, 200 iterations) of BRT models. Predictors were then ranked by median relative influence. Predictors were retained where median relative influence was $\geq 5\%$ and frequency was ≥ 0.5 for GLM modeling. When partial dependence relationships in the primary BRT signified non-linear links, we encoded the same form in the GLM using polynomial terms.

A generalized linear mixed effects model (GLMM) was developed to determine the influences of fire damage, tree, stand, and climate characteristics on the binary (presence and absence) resprouting response of redwoods following fire. Variables considered for the final analysis included the most informative fire damage predictor previously determined (BCR), DBH (cm), basal area density (m^2/ha), and pre-fire CWD (mm). Using the “lme4” package (Bates et al., 2015), a mixed effects model structure was developed with a random intercept value for each plot. A cross-validated LogLoss using a Monte-Carlo method with 200 iterations grouped by plot served as the primary evaluation metric for fixed effects and Akaike Information Criterion corrected for small sample sizes (AICc) as the secondary evaluation metric. The collinearity of covariates was checked with the “VIF” function in R (Fox and Weisberg 2021). It has been previously suggested that multicollinearity becomes severe when VIF exceeds 10 (Neter et al. 1996), though variables with a $\text{VIF} > 2$ can become problematic (Graham 2003). To be conservative, where $\text{VIF} \leq 2$, variables with higher relative influence in preliminary BRT analysis were retained to limit collinearity. When the LogLoss values of two models were within 5% relative difference, the model with the lower AICc was selected. Since a mixed effects model was utilized, we report both the marginal and conditional R^2 and calculated using the “r.squaredGLMM” function from the MuMIn package (Barton 2023) to examine the variance explained by the fixed effects alone (marginal R^2), and that explained by random and fixed effects together (conditional R^2).

Indicators of Post-Fire Resprouting Abundance

To determine the main drivers of leaf area, leaf biomass, and total biomass of basal resprouts, we utilized the methods outlined above for variable selection using BRT and then conducted model selection using a GLM approach to determine the relationship between fire damage, stand, climate and tree characteristics on post-fire basal resprout abundance. For each GLM considered, we used a cross-validated NRMSE as the primary evaluation metric and AICc as the secondary evaluation metric. Where $\text{VIF} \leq 2$, variables with a higher relative influence in preliminary BRT analyses were retained to limit collinearity. When the NRMSE of two models were within 0.05 standard deviations, the model with the lower AICc was selected. This was repeated for each metric of resprout abundance.

Evaluating Epicormic and Basal Resprouting Relationships

To evaluate the relationship between epicormic resprouting and basal resprouting, the performance of top selected GLMs described in the abundance section above was compared to models that included predictors of post-fire epicormic sprouting including total percent cover of the tree bole and total percent cover of the crown. Interactions between epicormic variables, tree size metrics and fire damage metrics were also considered. GLM model performance was compared using the methodology described above for resprouting abundance. Epicormic and basal sprouting

relationships were validated if inclusion of epicormic variables increased model reduced error (CV-NRMSE), increased model fit (AICc), and were statistically significant ($p < 0.05$) within final models. This was repeated for each basal resprout abundance (e.g. total biomass), and presence response variable.

RESULTS

Across the CZU Lightning Complex, basal resprouts were present on 85.3% of sampled fire-damaged trees. All non-resprouting trees were classified between very low and moderate fire damage classes (Table 1) and had a bole char ratio $< 50\%$ except for a single tree that was classified within the high damage class but was not completely charred. Across focal trees, 44.2% did not resprout epicormically. These trees were observed across all fire damage classes, but none were completely charred (BCR $< 100\%$).

Determining the Most Informative Fire-Damage Metrics for Redwood Resprouting

Across all resprout response variables, the relativized measure of BCR consistently emerged as the single most informative damage predictor. In the preliminary BRT screen, BCR had the highest relative influence for every resprout variable, and its partial-dependence functions indicated a monotonic, positive relationship, with resprouting probability and abundance increasing with increased fire damage. Cross-validated GLMs corroborated the BRT rankings. For resprout presence, BCR yielded the lowest LogLoss (0.33), indicating it was the most informative measure of damage related to resprouting. Trees with fire damage close to 0 still had a resprouting probability of 0.49 (*Appendix 9*).

For resprout abundance, BCR minimized NRMSE in each case: total biomass (NRMSE = 0.69), leaf biomass (NRMSE = 0.76), and leaf area (NRMSE = 0.79; *Appendix 10*), indicating the relativized metric was the most informative of basal resprouting abundance and had a non-linear positive relationship. GLMs with a quadratic BCR term reflected the BRT partial dependence shapes, indicating sustained increases in resprout probability and abundance across the damage gradient, with no evidence of decline at higher damage (Fig. 1). Taken together, BRT influence and GLM cross-validation identify BCR as the most informative single fire-damage metric for predicting redwood resprouting probability and all measured metrics of resprouting abundance.

Resprouting Presence

Of the 718 sampled trees in the plot-based dataset (Kane and Carrasco 2025), main stem death with no basal resprouting (i.e., complete genet mortality) occurred in 7.1% of trees and 14.7% survived, but did not basally resprout. The trees that experienced main stem death and did not resprout were located in a high-erosion site that was highly exposed on a ridge. Preliminary BRT variable selection for resprouting presence converged with predictors of pre-fire CWD and plot density (m^2/ha) (*Appendix 11*) in addition to the most informative fire damage predictor of BCR.

Resprouting presence was best characterized by fire damage (BCR) and pre-fire climate (CWD) in the most parsimonious GLMM model (CV-LL = 0.33, $R^2 \text{ marginal} = 0.53$). Tree diameter was included in a model with similar predictive power, though with greater complexity (AICc = 426.8) and therefore was not selected (*Appendix 12*). With increasing fire damage, the probability of resprouting also increased. The first-degree BCR orthogonal polynomial was strongly positive and significant ($z_1 = 2.8$, $p_1 < 0.01$) and the second-degree polynomial (nonlinear component) was positive and weak ($z_2 = 1.2$, $p_2 = 0.2$). Although pre-fire CWD was not statistically significant ($z = 0.34$, $p = 0.73$), cross-validation showed small but consistent improvement in LogLoss across folds when it was included within models.

Plot number was used as a grouping factor to account for random effects on the intercept and was significant in all top mixed effects models as indicated by a Likelihood Ratio Test ($\sigma^2 = 0.78$, $SD = 0.88$). When tested against a null random effects model, the fixed effects of all top models without a variance parameter had a $p < 0.001$.

Effect of Tree Size, Stand Conditions, and Climate on Resprout Abundance

Across all metrics of resprout abundance (total biomass, leaf biomass & leaf area), preliminary variable selection converged on the same set of predictors and were stable under cross-validation iterations (*Appendix 13*). Total resprout biomass was best characterized by fire damage (BCR) and pre-fire climate (CWD) (CV-NRMSE = 0.72 ± 0.02 , Adj. $R^2 = 0.50$; *Appendix 14*). The relationship between BCR and total resprout biomass was non-linear and positive. With increasing fire damage, post-fire resprout productivity also increased with no indication of decreasing at higher levels of fire damage (Fig. 2). The first-degree BCR orthogonal polynomial was strongly positive and significant ($\beta_1 = 2.4E4$, $p_1 < 0.001$, $t_1 = 6.8$) and the second-degree polynomial (nonlinear component) was positive and marginally strong ($\beta_2 = 6.3E3$, $p_2 = 0.08$, $t_2 = 1.7$). Trees at sites with higher water deficit had decreased post-fire resprout productivity ($\beta = -176$, $t = -2.7$, $p = 0.009$), indicating that trees at locations with higher water stress were associated with lower resprouting abundance.

Results for resprout leaf biomass were nearly identical. The model including BCR and CWD was the most informative (CV-NRMSE 0.72 ± 0.02 ; Adj. $R^2 = 0.48$). A univariate BCR model produced equivalent error but a higher AICc (CV-NRMSE = 0.72 ± 0.02 ; AICc = 1058.7), reinforcing the effect of water deficit. Results for resprout leaf area were similar with BCR and CWD included in the most informative model (CV-NRMSE 0.72 ± 0.02 ; Adj. $R^2 = 0.49$). Similarly informative models included crown ratio (CR), which surfaced in BRT screening of tree-size predictors for this response, though did not improve error (CV-NRMSE = 0.74 ± 0.03 ; AICc = 1051.2) and increased model complexity without gains in predictive ability (*Appendix 14*, *Appendix 15*).

Across all measures, post-fire resprout abundance increased non-linearly with fire damage as the primary driver and pre-fire CWD providing a consistent additive effect. Variables such as canopy openness and CR were influential in BRT-based screening (*Appendix 13*) but contributed little unique explanatory power to GLMs once BCR and CWD were included. Predicted curves (Fig. 2, *Appendix 15*) show steeper biomass gains at higher BCR, and, at a given BCR, slightly greater resprouting under lower pre-fire moisture stress, indicating that climate moderated the dominant fire damage signal.

Epicormic and Basal Resprouting Relationship

A statistically significant relationship between epicormic and basal resprouting was only observed for resprouting presence. A polynomial term of BCR and a term of pre-fire CWD were retained from the prior established top presence model (*Appendix 12*). Inclusion of a term of epicormic resprout cover of the bole (%) ($\beta = 0.82$, $p = 0.02$) and an interaction with CWD ($\beta = 0.77$, $p = 0.04$) was the most informative model. The relationship between epicormic resprouting cover of the bole and basal resprouting presence was linear and positive, supporting the potential that epicormic and basal resprouting mechanisms may be linked. Predictive performance did not increase for any metrics of resprout abundance with higher error across all models that included epicormic sprouting terms (*Appendix 16*).

DISCUSSION

This study highlights extreme persistence through resprouting following a range of wildfire-related damage in a fire resilient ecosystem. Results from this study indicate that two years after wildfire, basal resprout presence and

abundance of secondary redwood trees were mainly driven by relativized measures of fire damage and that post-fire resprouting was most prolific with torching or crowning and the highest levels of bole char. Resprout growth rates decreased slightly with increasing pre-fire climatic water deficit. Epicormic resprouting along the bole was found to have a slight positive relationship with basal resprouting probability. The prolific persistence following high-severity fire demonstrated here displays remarkable resilience despite the potentially uncharacteristic fire activity for this fire-adaptive ecosystem.

Informative Damage Metrics for Resprouting Response

Both resprout presence and abundance were strongly associated with relativized fire damage (BCR) (*Appendix 9*). Fire-related tree damage has been shown to influence post-fire resprouting response in other species (G. Bates et al. 2022; Simler et al. 2018), as well as in redwood (Ramage et al. 2010; Woodward et al. 2020), though no known studies have utilized a relativized fire damage metric to characterize this relationship. Relativized crown scorch (e.g., crown scorch volume) has been frequently used in post-fire tree mortality studies across species (e.g., Cansler et al. 2020; Hood et al. 2018) and relativized bole char height has been used occasionally to predict mortality (Fowler and Sieg 2004; Kennedy and Johnson 2014). Our study represents the first known application of relativized fire damage measures to post-fire resprouting. Higher bole char ratios are indicative of greater potential relative damage to the cambium (Hood et al. 2008) and fire presence in the upper crown of mature trees, implying either partial or full crown consumption resulting from intense thermal environments and direct flame contact, as well as greater fire intensity (Varner et al. 2021). The stronger and consistent influence of BCR in estimating post-fire redwood resprouting response suggests that relativized measures of fire damage that incorporate the influence of cambial damage and crown consumption is likely more informative than previously used measures of absolute fire damage. This relativized measure provides a more comprehensive assessment of fire-related damage that is relevant to resprouting response in the secondary forests we sampled; but would benefit from further validation in future studies of redwood and other species.

High Severity Fire Rarely Limits Redwood Basal Resprouting

Both resprouting presence and abundance were not diminished with increased fire damage. Trees with the highest levels of fire damage (BCR = 100%) had the highest probability and abundance of resprouting (*Fig. 2, Appendix 10, Appendix 15*). The presence of an upper threshold at which trees did not resprout or had diminishing abundance of resprouting was not observed, save for one highly exposed ridgeline site with high erosion that had exposed roots and lignotubers. The lack of an observed fire damage threshold is consistent with findings in the northernmost portion of the redwood range (Woodward et al. 2020) though observed at the stand-level (e.g., resprout cover and height). Results were also consistent with previous observations of low observed redwood mortality (1% for trees > 30 cm) resulting in limited reduction or complete cessation of basal resprouting following high-severity fire (Kane and Carrasco 2025). Thus, the weight of evidence suggests that a threshold at which resprouting response is reduced may not exist within the range of our observed intensity, possibly due to substantial basal bud bank insulation provided by mineral soil and bark (Choczynska and Johnson 2009; Clarke et al. 2013). It is also possible that basal resprouting in redwood may be impacted by frequent fire return that has been previously observed in other highly resilient systems (Fairman et al. 2019). If damage to the belowground bud bank is minimal under conditions of high fire intensity, resprouting presence and abundance following fire would be constrained only by active bud bank size, carbohydrate availability, and carbohydrate mobilization.

Our findings contradict prior studies that have observed declining resprouting response with increasing fire damage in other species (e.g. Masaka et al. 2000; Vesik and Westoby 2004), as well as in redwood (Ramage et al. 2010). The contradictions between our observations and resprouting response previously observed by Ramage et al. (2010) likely reflect differences in fire intensity between fires and methods of characterizing fire damage between studies. It is likely

that the use of relative bole char height (i.e., bole char ratio) was better at characterizing fire damage that is relevant to resprout response than absolute bole char measures (e.g., bole char height; Ramage et al. 2010).

Tree Size Does Not Limit Resprouting

Interestingly, we did not find tree size to be related to post-fire resprout response in our study. Decreased resprout abundance with increasing tree size has been previously observed in redwood though at a larger range of stem sizes: 2.5 to 290 cm (Woodward et al. 2020); 10 to 352 cm (Ramage et al. 2010), than our sample range (31 to 171 cm). The fires in these studies were generally less intense than the CZU Lightning Complex. The inclusion of sites with larger trees with greater resistance to fire damage (e.g., bark thickness) as well as lower fire intensity may have resulted in decreased fire damage and decreased resprouting compared to our study.

The lack of a link between tree size and resprout presence and abundance suggest carbohydrate storage and mobilization is similar across the range of tree sizes we examined (31 cm to 171 cm DBH). Carbohydrate storage and mobilization drives resprout response (Bowen and Pate 1993; Pate et al. 1990). Following fire, substantial carbohydrate mobilization occurs in redwood from lignotubers, burls, and other carbohydrate storage sources with an active carbon age of up to 21 years (Peltier et al. 2023). Carbohydrate stores within the tree bole, such as vascular tissue surrounding heartwood, may also assist in resprout regeneration. A carbohydrate “physiological equilibrium” following logging has been previously proposed where resprout growth from cut stems relies on carbohydrate reserves until photosynthetic production is equal to carbohydrate requirements (O’Hara et al. 2017; Wiant and Robert 1967). A similar equilibrium may exist for resprouts in a post-fire setting supported by mobilization of carbohydrates from both the bole and lignotubers prior to reaching equilibrium.

Climate Influence on Basal Resprouting

Pre-fire climatic water deficit had a significant influence on resprouting response though of lesser magnitude than fire damage. Post-fire resprouting dynamics have been shown to be more complex than considered measures of fire intensity or damage and are impacted by climatic conditions pre- and post-fire (van Mantgem et al. 2013; Cansler et al. 2024). Reduction of resprouting capacity under drier conditions is known to occur in some lignotuberous shrub species (e.g. Werner et al. 2022), though it has not been previously observed for redwood. Our results did not identify any post-fire climatic influences on resprout response, but our results were constrained by the climate effects present within the CZU fire footprint. Further investigation across the entire gradient of climate conditions within the coast redwood range is still needed to more fully evaluate the effects of climate on redwood resprouting.

Stand Density and Resprouting Response

Stand density metrics were shown to have a subtle influence on resprout response in preliminary variable selection (*Appendix 11, Appendix 13*). Though not included in final top models, canopy openness was also included in similarly explanatory models for total resprout biomass (*Appendix 14*). As canopy openness increases, so does light availability in the understory (e.g. Gersonde et al. 2004). Increases in available light in the understory are associated with increased productivity (e.g. Kerhoulas et al. 2020; Ren et al. 2021) and imply that increased resprout leaf mass can increase the photosynthetic capacity in redwood (Ambrose et al. 2015; Sillett et al. 2010). These findings are supported by previous research that indicates increasing redwood resprout abundance is associated with increased light availability following logging (O’Hara et al. 2007).

Epicormic and Basal Resprouting Link

Basal resprout probability increased with epicormic bole resprout abundance (*Appendix 16*), suggesting that these two responses are potentially linked. Both epicormic and basal resprouting are hormonally controlled and resprouting is

signaled by reduction of auxins as damage is increased (Clarke et al. 2013; Finney 1993; Harris et al. 1971; Kormanik and Brown 1969). While this physiological control likely explains part of the link between epicormic and basal resprouting, it does not explain why the probability of basal resprouting increased with greater abundance of epicormic bole resprouting. In other species, epicormic resprouting utilizes carbohydrates stored in only the stems following wildfire, while basal resprouting is supported by carbon reserves in both the stem and below ground carbon pools (Bowen and Pate 1993; Pate et al. 1990; Smith et al. 2018). Thus, the greater abundance of epicormic resprouts may indicate that heat-caused damage to the vascular system was insufficient to disrupt carbohydrate mobilization from the stem to basal resprouts and that carbohydrate availability was not limited by increased epicormic sprouting. However, further investigation of the link between basal and epicormic resprouting response is necessary.

Conclusions

Two years after wildfire, coast redwood showed extraordinary resilience with no clearly defined threshold of damage where resprouting response declined, and where resprouting response was not a function of tree size. For management, these results suggest that high-severity fire in redwood stands of young to mature secondary stand age (30 + years) does not imply loss of redwood stands, though canopy structure may be severely altered. Our results also suggest that post-fire evaluations should emphasize relative measures of cambial and crown injury when forecasting recovery. Though these trees have demonstrated extreme resilience following the CZU Lightning Complex, further drought stress and fire severity under future climate conditions necessitates continued monitoring of post-fire recovery for redwoods.

Abbreviations

AIC – Akaike Information Criterion

AICc – Akaike Information Criterion corrected for small sample size

BCR – Bole char ratio (bole char height / total tree height)

BCH – Bole char height

BRT – Boosted regression trees

CBH – Crown base height

CDH – Crown damage height

CWD – Climatic water deficit

CV – Cross-validation

CV-NRMSE – Cross-validated normalized root mean squared error

DBH – Diameter at breast height

dNBR – Differenced normalized burn ratio

GLM – Generalized linear model

GLMM – Generalized linear mixed-effects model

NRMSE – Normalized root mean squared error

RdNBR – Relative delta normalized burn ratio

RI – Relative influence

RMSE – Root mean squared error

Declarations

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Figures

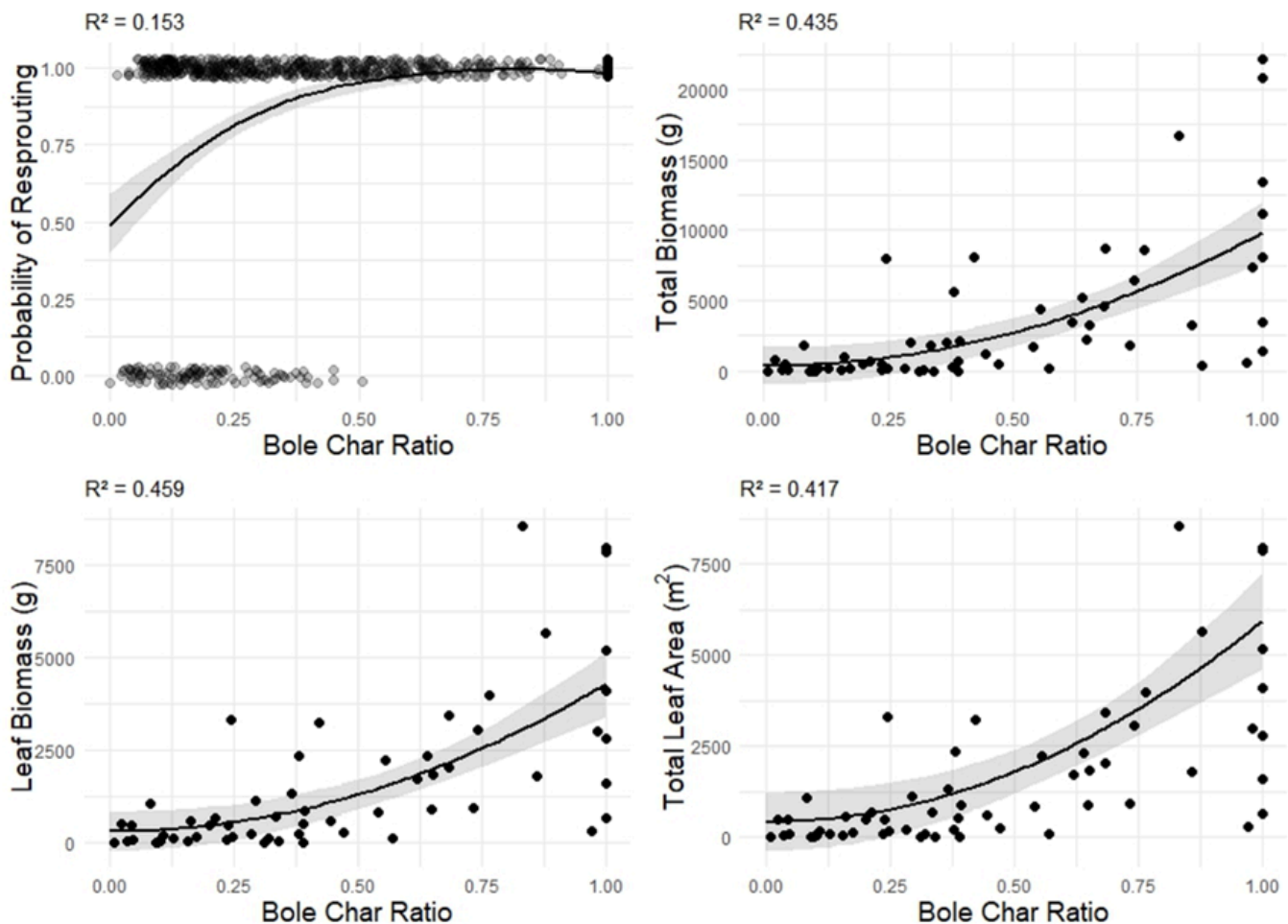


Figure 1

Univariate models for respective resprout responses using the top damage predictor of bole char ratio (BCR) with 95% (2 standard deviations) confidence intervals. Raw data jittered as points along with plotted model.

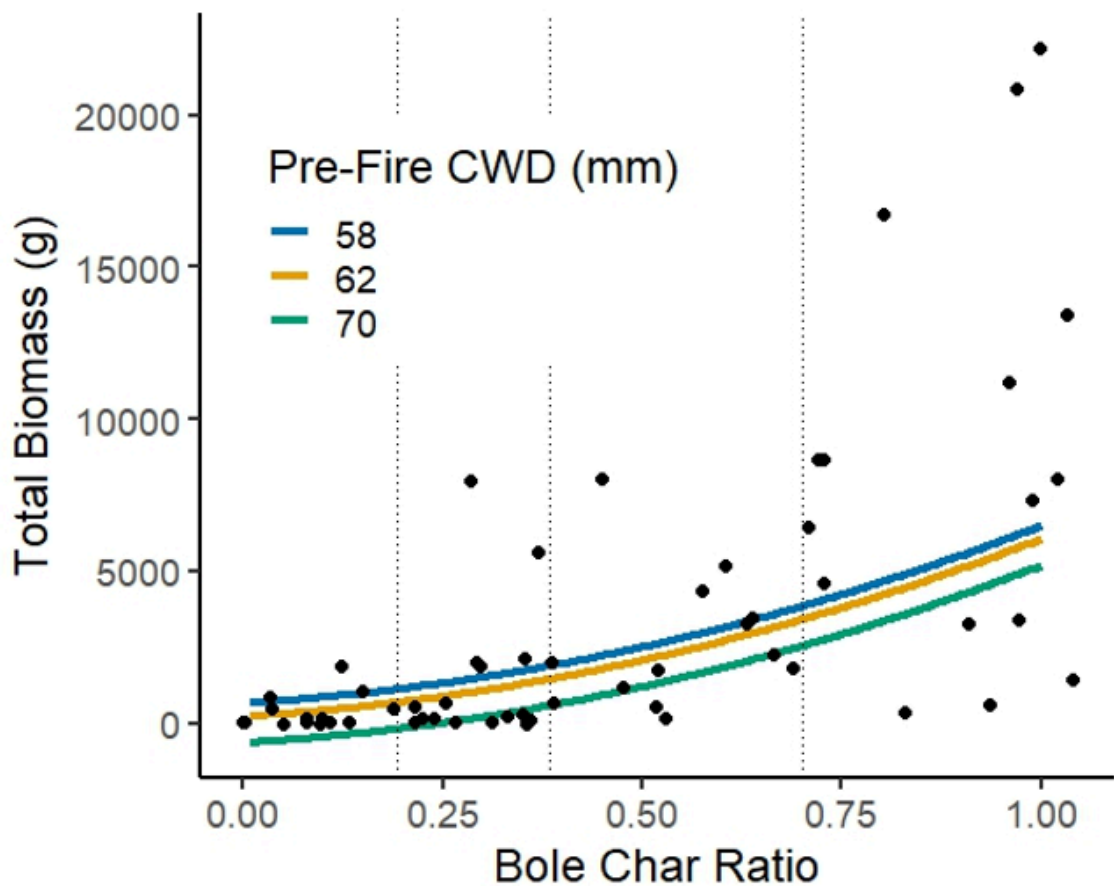


Figure 2

Top selected model of total resprout biomass (g) for secondary redwood two years following fire. Bole Char Ratio = bole char height to total tree height ratio, Pre-Fire CWD = partial water year climate water deficit pre-fire (mm). Modeled CWD values were representative of observed Q1, median, and QIII values rounded to the nearest whole mm. Vertical dotted lines represent QI, median, and QIII breaks for BCR distributions. Relationship for other measured metrics of resprout abundance, leaf mass and leaf area, were nearly identical (*Appendix 15*).

Supplementary Files

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- [SupplementarymaterialCarrasco2026.docx](#)