PRESCRIBED FIRE CAN INCREASE MULTI-SPECIES, REGIONAL-SCALE RESILIENCE TO INCREASING CLIMATIC WATER DEFICIT

By

Emma Clare Williams

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Abstract

Dry mixed conifer forests of southwestern North America are projected to be particularly vulnerable to ongoing persistent warm drought conditions, and related increases in wildfire frequency, size and severity, due in part to consequences of over a century of fire exclusion. Prescribed fire is applied actively in many landscapes to reduce hazardous fuel loads and continuity, restore forest community composition and structure, and increase tree resilience to drought stress. However, fire can also adversely affect tree growth by damaging cambial, root, and canopy tissues, leading to tradeoffs in the use of fire as a tool for forest resilience. Radial growth is an indicator of climatic and ecological stress and can thus provide a relative measure of resilience to stress and disturbances; but, the mechanisms driving tree resilience to prescribed fire and concurrent drought are poorly understood. Thinning effects of prescribed fire may increase tree resilience to drought by increasing water, light and nutrient availability and production of defense mechanisms. However, trends over the last century indicate warming temperatures are increasing tree sensitivity to fire by reducing post-fire growth (lower resilience) and increasing the likelihood of mortality. Trees can be resistant to fire exposure, and where growth changes occur they can be transient or persistent. We studied the interactions between tree- and stand-level fire effects on the growth responses of surviving *Abies concolor, Pinus jefferyi, Pinus ponderosa,* and *Pseudotsuga menziesii* over 24 years of variable climatic conditions in ten National Parks across the western and southwest United States. We used linear mixed effects models to identify mechanisms influencing resistance and resilience responses to fire and interannual climate, using climatic water deficit (CWD) as an index of climatic stress. Compared to pre-fire growth, trees exposed to fire increased growth during periods of greater water deficits. Tree growth responses were variable among and within species and size classes, but contingent on time-since-fire and the climate during the recovery period. Negative fire effects on tree resistance were generally transient, while climate and pre-existing stand conditions were persistent controls on tree resilience. These results suggest that antecedent and subsequent climate conditions modulate post-fire forest response. Consideration of climate variation could improve the strategic use of prescribed fire for tree resilience to drought, and a deeper understanding of factors contributing to prefire growth may elucidate the mechanisms driving post-fire growth responses.

Keywords: Abies; Climatic Water Deficit; Dendroecology; Douglas fir; Drought; Fire Effects; Growth Response; Ponderosa; Prescribed Fire; Resilience.

1.0 Introduction

Ongoing warm drought conditions across the western United States have increased the vulnerability of forest trees to water stress, bark beetle attack, and fire-related mortality (Westerling et al 2006; Allen et al 2010; van Mantgem et al 2013; Westerling et al 2016). These vulnerabilities are particularly pressing in the southwestern United States, where dry ponderosa pine and mixed conifer forests, historically maintained in dynamic equilibrium by frequent, low-severity fire regimes (Swetnam & Baisan 1996; Scholl & Taylor 2010), have experienced long-term fire exclusion and suppression (Covington et al 1997; Knapp et al 2013). In response to these trends, national policy directions such the National Fire Plan of 2000 and the Healthy Forests Restoration Act of 2003 have been implemented in an effort to increase forest resilience to the interacting forces at play (Stephens & Ruth 2005).

The past two decades have brought about increased wildfire size accompanied by severities exceeding the historical range of variability known to dry mixed conifer forests, resulting in record fire suppression costs (Stephens et al 2014). Of the greatest wildfire area burned years since 1960, nine occurred between 2000 and 20015 (NIFC 2016). Warming temperatures have been implicated in these trends through expansion of the fire season (Westerling et al 2016) and increasing fuel aridity (Abatzoglou & Williams 2016). Concurrently, fire severity has been increasing due to greater probabilities of extreme fire weather (Fried et al 2008), accumulation of hazardous fuels (Agee & Skinner 2005), and increased likelihood of fire-caused mortality in drought-stressed trees (van Mantgem et al 2013).

Prescribed and managed wildfire have become increasingly proposed and practiced to mitigate these consequences by restoring ecological processes to fire-adapted forests of western North America (Falk 2006; North et al 2012; North et al 2015). *Resilience* is the capacity to withstand a disturbance and recover pre-event function (Walker et al 2005). Prescribed fire may increase fire-adapted tree resilience to drought by increasing water, light and nutrient availability, thereby increasing vigor (Battipaglia et al 2015; Certini 2005; but see Lloret et al 2011), and ability to resist bark beetle attacks (Hood et al 2015). However, drought-related tree mortality under future climates may be underestimated and top-down climate effects could overwhelm bottom-up management of forest structure (Allen et al 2015). This project seeks to test the effect of prescribed fire on climate sensitivity and describe how post-fire recovery period climatic and ecological conditions influence Southwest conifer resilience to fire.

Tree radial growth, an indicator of tree vitality, is sensitive to inter-annual climatic and ecological variability (Dobbertin 2005). Tree resilience can be estimated by comparing growth during and after an event to pre-disturbance levels (Lloret et al 2011; Martinez-Vilalta et al 2012). Drought is a top-down process, with temporally synchronized effects on annual growth during an event, occurring across a regional scale (Adams & Kolb 2005; Fritz 1976). In comparison, heterogeneity in fuel conditions, topography, and fire weather during the burn period creates strong variability in fire effects within the stand scale (Falk et al 2011). By studying individual tree responses to disturbance across a regional network, interactions between tree-, stand-, and regional-scale controls on recovery can be analyzed over time (Falk et al 2011).

We propose a framework for assessing resilience in terms of magnitude, direction, and persistence of a response trajectory following a disturbance (Figure 1). Stable systems function within a range of variability around an equilibrium (Walker et al 2004), and are *resistant* (*R*) if they remain within this range during and after a disturbance (Lloret et al 2011). If the magnitude of post-disturbance response exceeds this range the system is not resistant. Transient positive (+*T*) or negative (-*T*) trajectories initially shift functional level, but return to the antecedent range over time, indicating resilience. Persistent positive (*+P*) and negative (*-P*) trajectories experience a phase change, functioning at a new baseline of variability. *–P* trajectories are neither *resistant* nor *resilient*. Response trajectories will be influenced by cross-scale interactions effecting ecosystem function (Figure 2) (Walker 2004).

Precipitation and temperature are the prevailing regional-scale tree growth limitations in montane Southwest dry-conifer forests (Fritz 1974; Williams et al 2013). Biophysical properties modulate the extent of these limitations. For example, low elevation stands experience greater evaporative demand, compared to cooler, high elevation sites, which also benefit from snowpack persisting later into the growing season (Adams & Kolb 2005; Flint & Flint 2011; van Mantgem & Sarr 2015). Taken together, the effect of these factors on annual growth can be estimated with climatic water deficit (CWD), a biologically-meaningful measure of drought that accounts for soil depth, and the timing of energy and water inputs (Stephenson 1998; Flint and Flint 2011). van Mantgem and others (2013) found that increased CWD reduced tree *resistance* to fire, in terms of survivorship, even after accounting for fire damage. Drought during the post-fire recovery period can have strong impacts on resilience (Slack et al 2016). Drought magnitude and persistence would likely influence response trajectories, however, this has not been assessed under a range of climatic conditions.

Tree demography, stand conditions, and pests are finer-scale controls on tree growth and, when filtered by fire, influence the magnitude of first- (e.g. injury) and second-order (e.g. pests) fire effects (Figure 2). *Abies concolor* (Gordon & Glend.) Lindl. Ex Hildebr. (ABCO), *Pinus jeffreyi* Grev. & Balf. (PIJE), *Pinus ponderosa* P. Lawson & C. Lawson (PIPO), and *Pseudotsuga menziesii* (Mirdb.) Franco (PSME) are four common mid-elevation conifer species in western forests. Although large individuals of each species have thick fire-resistant bark,

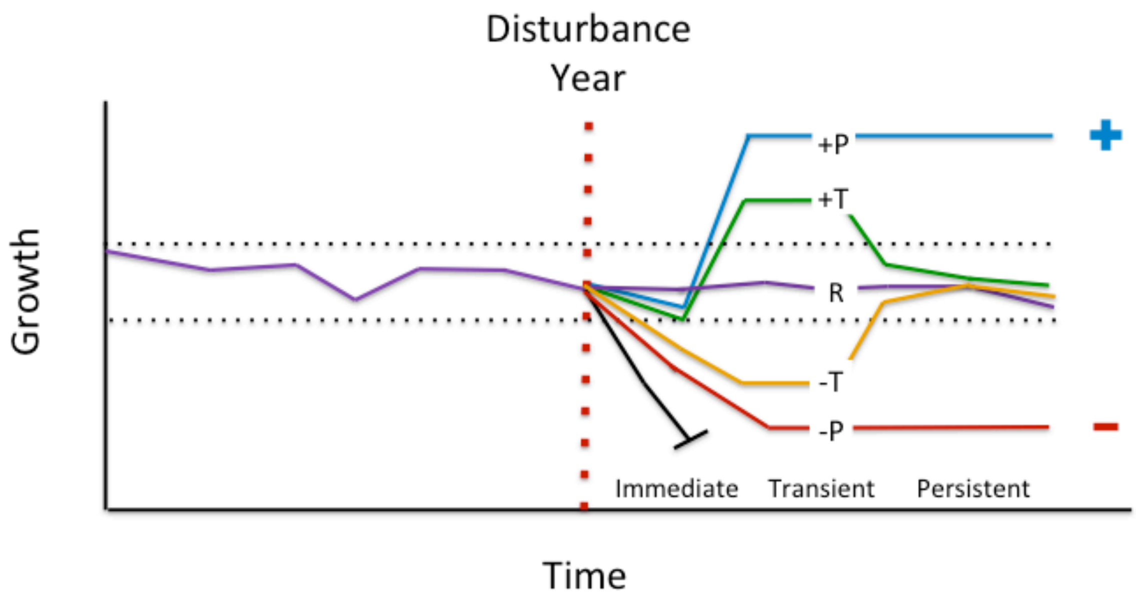

Figure 2: Post-disturbance response trajectories are typified by magnitude, direction, and persistence of change from antecedent conditions. Resistance (R) is marked as an ability to remain unchanged. Persistent (P) positive and transient (T) responses characterize resilience, the ability to exceed or return to antecedent conditions. Persistent negative (-P) responses indicate a loss and function unrecovered over time.

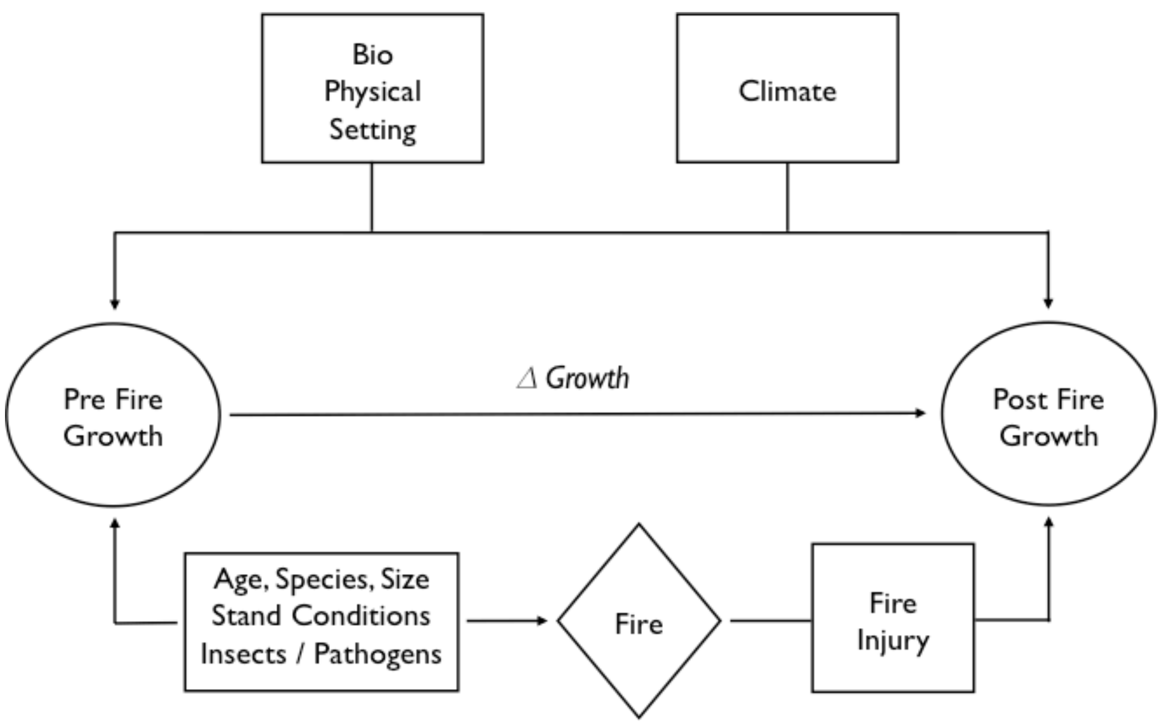

Figure 2 Controls on southwest conifer growth before and after fire. The overall prefire growth condition is regulated by tree life history, stand conditions, pests, and climate. Prefire growth is an important predictor of post fire growth. However, fire related injury, changes in stand level competitive pressure, increased vulnerability to insects and pathogens, and changing climate can influence individual tree growth responses.

thinner bark of small ABCO can increase susceptibility to fire caused injury (e.g. crown volume scorch and char height) (van Mantgem & Schwarts 2003). Each species hosts an array of specific pests and pathogens. Background levels of mistletoe and insect pests affect growth negatively by reducing tree cambial conductivity and water regulation (Sanguesa-Barreda et al 2013). PSME and PIJE experience elevated bark beetle attack rates after fire (Bradley & Tueller 2001; Hood & Bentz 2007).

Stand conditions (live and dead fuel composition and structure) drive competitive interactions and influence fire behavior (Hood 2010; Sanchez-Salguero et al 2015). Thinning effects through fire-caused mortality yield variable responses. Reinhardt & Ryan (1988) found that change in plot basal area increased growth in *Larix occidentalis* eight years after fire but not for co-occurring *Pseudotsuga menziesii*. Likewise, *Pinus ponderosa* in Arizona did not respond to fire-caused thinning (Sutherland et al 1991; Peterson et al 1994), but growth remained lower in stands with greater competition (Sutherland et al 1991). Thinning can yield longer-term changes in tree growth, particularly in large trees (Kerhoulas et al 2013).

First entry prescribed fires can cause elevated injury to trees through consumption of long accumulated soil litter and duff layers (Hood 2010). Surface fires consume the litter layer quickly and can burn at intensities capable of releasing enough radiant heat to injure the cambium or scorch needles and buds (Hood 2010). Height of stem char estimates cambial damage (max char) while percent crown volume scorch (%CVS) estimates foliage loss, and each have shown consistently negative controls on post-fire growth (Busse et al 2000; Feller and Klenner 2011). Ground fires consume the duff layers, causing cambial and root injury (Hood 2010). Increases in depth of forest floor consumed can temporarily limit conductance through fine root mortality and correlates negatively with growth response in PSME and PIPO (Busse et al 2000; Feller and Klenner 2011). Combustion of litter, duff, and herbaceous vegetation may have positive effects on growth through transient nutrient pulses (Busse et al 2000). Negative effects of %CVS and max char, and positive effects of nutrient mineralization, are generally reported to have short-term, 1- to 4-year, negative effects on growth (Harrington & Reukema 1983; Busse et al 2000; Cerinti 2005; Hood 2010).

The objective of this study is to assess the growth resilience of dominant southwestern conifers to prescribed fire under a range of climatic, biophysical, and stand conditions over time. First, we employ linear mixed effects models to test the importance of individual and interacting influences on tree resistance and resilience. We then assess reoccurring patterns in growth trajectories using the described framework (Figure 1). We take advantage of the detailed FEAT and FIREMON Integrated (FFI) database and US Geological Survey (USGS) Tree Demography plots for pre- and post-fire monitoring data collected repeatedly over wide spatial and temporal scales (USDI, 2003). The trees analyzed in this project are a fire surviving subset sampled for an investigation on how interactions between drought and fire influence tree mortality (van Mantgem et al, *in prep*).

2.0 Materials and Methods

2.1 Study Site Selection

2.1.1 Park Selection

The National Park Service has been integrating prescribed fire into management programs since 1968 (USDI 1968). In 2003, the Fire Monitoring Handbook (FMH) was established to standardize and define the plot-based monitoring program already in place at many parks (USDI 2003). Macroplot plot (20 x 50 m) locations are randomly assigned within Park burn units. All living pole-sized and overstory trees are given unique tag numbers and locations are sometimes recorded on stem maps. Plots are measured prior to burns as a baseline for comparison with re-visits the same year, one-, two-, five-, and ten-years after each fire. Tree diameter at breast height (DBH) and survivorship is recorded and tree, shrub, and herb density is measured. Fixed Brown transects are used to remeasure woody fuel loads with every visit. Once the plot has cooled and less than a year after the burn, qualitative burn severity is assessed, along with %CVS, max char, and scorch height (USDI 2003). Optional measurements of live crown position and evidence of tree damage are variably recorded. All data is entered into the online FFI database.

Fire effects data were available from 20 Southwestern National Parks and Monuments. We queried the FFI database to filter out potential errors (i.e. missing values in required fields or fire injury data collected > 1 year after fire) and subset plots containing tagged ABCO, PIJE, PIPO, or PSME meeting the following criteria: burned >2 years and <25 years before 2014, pre fire DBH > 15cm, and crown volume scorch and stem char > 0. Plots containing these trees were located in Bandelier National Monument (BAND), Bryce Canyon National Park (BRCA), Crater Lake National Park (CRLA), El Malpais National Monument (ELMA), Grand Canyon National (GRCA), Lava Bed National Monument (LABE), Lassen Volcanic National Park (LAVO), Sequoia and Kings Canyon National Parks (SEKI), Yosemite National Park (YOSE), and Zion National Park (ZION). We sampled all viable parks to include as wide a range of variability in biophysical and stand conditions as possible

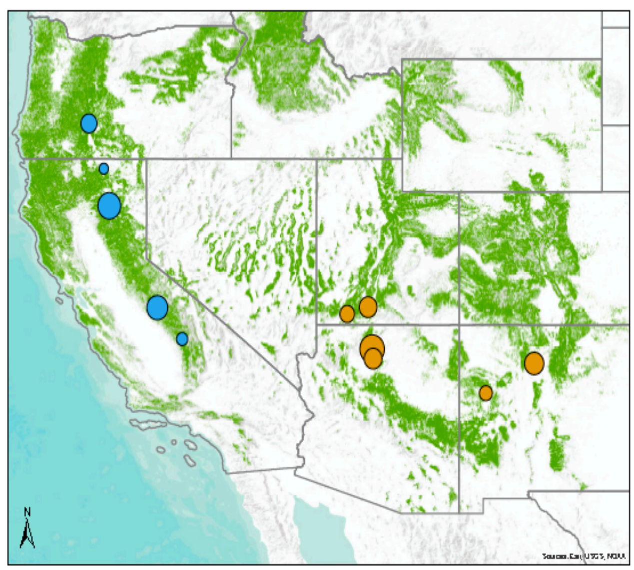

Figure 3: Map of park locations with points scaled to number of trees sampled. The Grand Canyon NP North and South rims were treated as separate sides due to discontinuities in elevational range, forest type, and fuels.

(Figure 3).

2.1.2 Plot and Tree Selection

We employed a modified stratified random sampling approach to achieve a balanced sample of trees from three size classes (DBH 15 – 30cm, >30 – 60cm, >60cm). At each park, plots containing a minimum of four trees meeting our criteria were blocked by dominant target species. Limited plots containing ABCO or PSME >60cm DBH were selected preferentially, while the remaining plots were selected at random from each block. The number of plots visited at each park was weighted by variability in topographic conditions and availability (Table 1).

Park	Plot Count	Tree Count	Stand Density (Trees/ha)	Elevation (m)	Slope (%)	Burn Years 1990	1992	1993	1994	1995	1997	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2012
Pacific Southwest (PSW)																								
CRLA	8	37	170 - 420	1547 - 1624	0 - 45									X		X				X			X	
LABE	2	5	80 - 380	1451 - 1461	0 - 3											X								
LAVO	12	49	210 - 710	1785 - 1862	0 - 27	X				X														
SEKI	8	17	NA	1985 - 2191	11 - 20	X								X										
YOSE	8	48	130 - 570	1307 - 1765	0 - 30						X					X				X	X			X
Total	*38*	*156*																						
Interior Southwest																								
BAND	10	45	210 - 1020	2684 - 2922	0 - 45								X								X			
BRCA	13	40	70 - 530	2462 - 2776	0 - 21					X			X	X							X			
ELMA	5	19	50 - 250	2285 - 2371	0 - 5						X	X				X			X					
GRCA – NR	13	52	220 - 610	2446 - 2764	4 - 36		X	X			X		X	X			X			X				X
GRCA – SR	8	40	110 - 410	2049 - 2274	0			X	X		X							X	X	X		X		
ZION	6	21	120 - 700	1964 - 2411	0 - 30					X	X				X		X							
Total	*55*	*6*																						
Grand Total	*93*	*162*				2	1	2	1	3	5	1	3	4	1	4	2	1	2	4	3	1	1	2

Table 1: Range of conditions measured in sample plots in Interior Southwest (ISW) and Pacific Southwest (PSW). Parks: Bandelier National Monument (BAND), Bryce Canyon National Park (BRCA), Crater Lake National Park (CRLA), El Malpais National Monument (ELMA), Grand Canyon National Park North Rim (GRCA-NR) and South Rim (GRCA-SR), Lava Bed National Monument (LABE), Lassen Volcanic National Park, Sequoia and Kings Canyon National Parks (SEKI), Yosemite National Park (YOSE), and Zion National Park (ZION). Stand density is measured in trees/hectare. Years between 1990 and 2012 with prescribed burns occurring in each park are checked with an 'X'. Total Plots = 93. Total Trees =373.

Six to ten sample trees were randomly selected in each plot from lists stratified by species and size class. Although trees were burned 1 to 3 times between 1990 and 2012, this study only includes response to the first documented entry burn. The nested design sampled 597 tagged trees within 122 plots from 10 parks. Because we are interested in the range of transient and persistent responses of survivors, we have included 373 trees that were either alive at the time of sampling or with an outer ring formed more than five years after the burn (Table 1).

2.2 Field and Laboratory Techniques

Sample trees were located in the field by tag number from FFI plot records. We photographed each plot and recorded geographic coordinates, aspect, slope, and sample date. The following tree demographic and stand condition measurements were recorded: tag number, species, survivorship status, DBH, canopy position, max char height, presence/absence of bark beetle evidence, non-fire related damage (i.e. lightening scar), basal area with prism BAF 20 or 30, DBH and distance of largest neighbor within 15m in four cardinal point quadrants. We followed FMH overstory tree monitoring protocols to verify species identity, and to evaluate current survival status, DBH, canopy code, and to categorize observed environmental damage (USDI 2003). Because some burn dates were up to 24 years prior to these competition measures, and we were interested in testing the influence of fire-caused change in stand density, we only used FFI measurements of pre- and immediate post-fire stand density and basal area for our analyses. FFI measurements were collected by NPS fire effects monitoring crews using standard FMH protocols (USDI 2003). Fire-caused change in competitive pressure was quantified by subtracting post-fire stand density (cSD) and basal area (cBA) from the respective pre-fire measurements.

Up to three increment cores were collected from each sample tree at approximately 50cm bole height and perpendicular to the direction of slope. When rot, fire injury, or other physical damage to the bole required, we sampled above 50cm from the lowest height possible. Live and dead trees were sampled with 5.12mm and 12mm diameter increment borers, respectively.

In the laboratory, increment cores were mounted and sanded with progressively finer grits to a 400 grit resolution (Pilcher, 1990; Speer, 2010). When available, cores were crossdated by visually comparing patterns of ring width anomalies as pointer years in an existing chronology for that area (Yamaguchi, 1991). Chronologies were exported from the International Tree Ring Database (https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring) and skeleton-plotted using dplR (Bunn 2010). Chronologies of ABCO were unavailable at BAND, BRCA, CRLA, LAVO, GRCA, and ZION, so we created them using a subset of the oldest trees sampled at each of these sites, using the package dplR in R Studio© (Bunn 2010). Narrow rings were the primary cross dating markers in cores from the interior Southwest, due to the prevailing moisture limitation on tree growth (Fritz 1974). Wide rings and distinctive latewood characteristics were additionally employed as cross dating markers in cores from Lassen, Yosemite, and Crater Lake National Parks (Schweingruber 1989). Rings were measured to a precision of .005 mm with a Velmex measuring system and recorded into the Tellervo tree-ring measurement and archiving software (http://www.tellervo.org/). Cross dating among all cores from a given species and park was verified statistically with the program COFECHA (Holmes et al 1986). Any core flagged with low interseries correlation (<0.328), or a higher correlation at a different date position, was visually inspected for dating errors and remeasured. After the first iteration of crossdating quality control, problem cores were removed and the remaining verified sample were analyzed together in COFECHA. The average interseries correlation values for each 25 year segment was recorded as a dating quality standard. All cores were analyzed together in a second iteration of crossdating quality control, and those with segment intercorrelation values over 10% less than the verified segment average were inspected and remeasured. Additionally, cores with an interseries correlation over 10% less than that of another core from the same tree were inspected and remeasured.

Growth in a given year and tree was calculated by averaging ring widths among replicate cores per tree. Trees growing in open stands often exhibit size-related negative growth trend that could bias post-fire growth response calculations (Cook et al 1990). Each tree's ring width series was inspected visually for biological growth trends, and the nearest decade following the stabilization of an asymptotic growth phase was recorded (Keeling and Sala 2012). The earliest common decade excluding negative size-related trends was identified as 1970 and each series was truncated to the period from 1970 to outer ring date. We converted ring widths to a unitless ring width index (RWI) with a mean of one to standardize differences in absolute growth among trees (Carnwath & Nelson 2016). RWI was calculated by dividing an individual's annual ring width by its mean radial growth from 1970 to the outer year. Standardizing width to mean growth emphasizes interannual variability caused by climate and retains lower frequency variability such as ecological disturbance responses that may be removed by detrending methods (Carnwath & Nelson 2016).

2.3 Analytical methods.

2.3.1 Quantifying Resistance and Resilience

In the context of this study, immediate (1 - 4yr), transient (5 - 8yr), and persistent (9-12yr) responses can be quantified as the respective ratios of growth following disturbance to antecedent growth. We define the antecedent growth condition as the individual's five-year pre-fire growth mean. Standardizing to five-year pre-fire growth allows inclusion of multiple years of interannual variability, while reducing the potential for comparison of post-fire growth against low-growth periods driven by other causes. For a given tree, growth response index (*Response*) was calculated annually as RWI for each post-fire year (k) divided by its five-year pre-fire mean RWI ($RWI_{pre(m)}$):

$$Response = RWI_{post(k)} / RWI_{pre(m)}$$

Response indices were subset into immediate, transient, or persistent observations by post-fire year. Because the growth reference period includes the period of prescribed burns, and related growth impacts, *Response* should be considered a conservative estimate. Including the post-fire period allows us to account for the 2000s drought effects on growth and has been used in studies measuring growth impacts from other disturbance types (Carnwath and Nelson 2016).

2.3.2 Climate and Pre-fire Growth Variable Selection

Climate data were derived from the Parameter-elevation Regression on Independent Slopes Model (PRISM, www.prism.oregonstate.edu) (Daly et al, 2008). PRISM estimates of monthly maximum and minimum air temperature and precipitation were downscaled to 270-m grid cells with a gradient-inverse-distance-spared approach (Flint & Flint, 2012). Climatic water deficit (CWD) is the difference between potential and actual evapotranspiration and represents a biologically-meaningful estimate of drought with consideration of local topography and edaphic traits (Stephenson, 1990; Flint and Flint, 2012). Pearson correlation coefficients were used to evaluate the growth sensitivity of the 20-year pre-fire period to annual maximum temperature, annual cumulative precipitation, and CWD. To make values comparable among plots in different regions, CWD was converted to an index (aCWD) normalized to the 1970 to 2014 mean CWD. Values of aCWD >1 indicate years more water limited than the mean, while years with aCWD <1 are less water limited (Figure 4). Relative CWD (rCWD) is the ratio of annual post-fire water deficit to the mean five-year pre-fire period of comparison. Using rCWD allows us to account for change climate conditions in the pre- vs. post-fire periods.

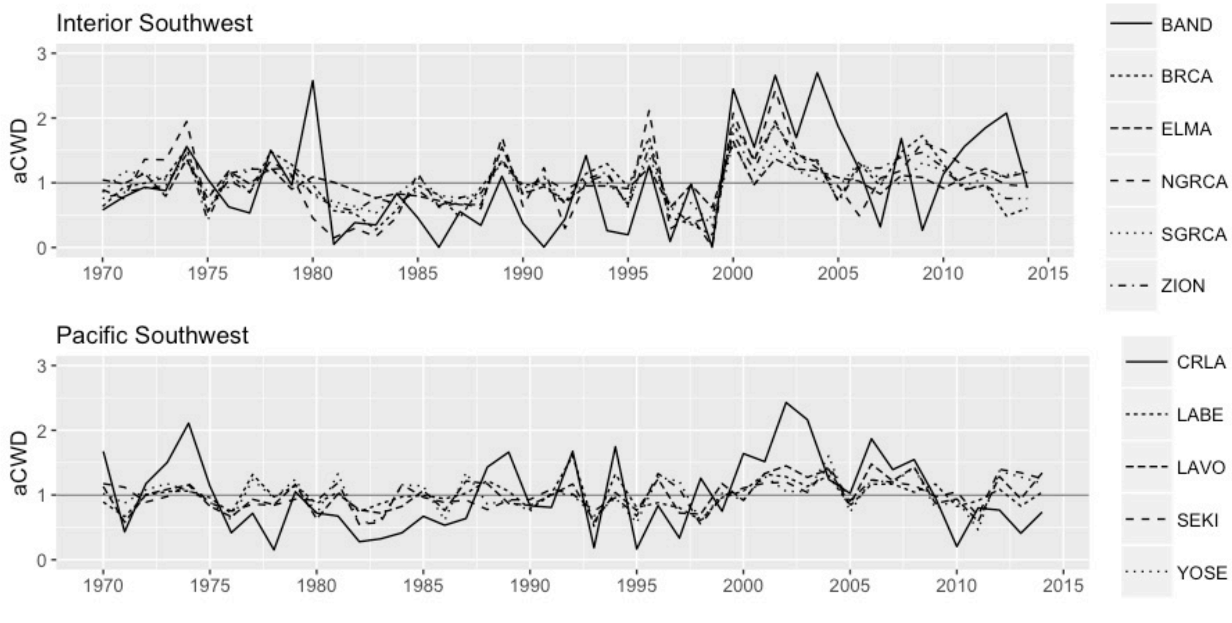

Figure 4: Time series of mean annual climatic water deficit index (aCWD) at each interior and pacific Southwest park during the reference period.

Pre-fire tree growth was defined in terms of trend and the number of abrupt declines, which have been identified as predictors of tree growth and mortality responses to drought (Das et al, 2007; Martinez-Vilata et al 2012). Pre-fire trend, the rate and direction of growth, was calculated as the slope estimate from a regression of tree raw ring widths over a 10- and 25- year pre-fire period. Abrupt declines were identified as reductions in ring width >0.05mm and >50% from the prior year and counted over the 10- and 25-year pre-fire period. The four periods (5, 10, 25, and 50 years) of trend and abrupt declines were plotted against growth response to determine which relationship was strongest. Although growth rate is a common measure for pre-fire growth in studies using basal area increment, we did not include it in analysis because 5-year pre-fire growth rate is used to calculate the response variable.

2.3.3 Model Selection

We developed four mixed effects models to test mechanistic controls on individual tree growth to fire in the immediate, transient, and persistent periods using the nlme package in R (Pinheiro et al 2016). Mixed effects models allow spatial autocorrelation associated with a nested sampling design to be corrected for within random effects (Zuur et al, 2009). We applied an AR-1 autocorrelation structure, and used the prewhitened RWI series for all analyses, to meet assumptions of temporal independence using the 'chron' function in dplR (Yamaguchi 1986; Bunn 2010). The first model fit a climate-growth relationship to test for fire-related changes in drought sensitivity.

$$RWI_{i(jy)} = \beta_0 + \beta_1 \bullet aCWD_{yi} + \beta_2 \bullet Treatment + \beta_3 \bullet (aCWD_{yi} \bullet Treatment_{ji}) + \alpha_k + \gamma_{0k(j)} + \varepsilon_{k(jy)}$$

Equation 1: With β_0 as the population intercept and β_1- β_3 as the parameter estimates for the relationships between prewhitened 10-year pre- to 10-year post-burn RWI and aCWD index, prescribed burn treatment, and their interaction, where *(j)* is an individual tree nested in a plot (*i*) in a park *(p)* in a given year *(k)*. *α* and *γ* are random effects parameter estimates of slope and intercept, respectively.

In the immediate, transient, and persistent response models, a square root transformation was applied to rCWD to achieve an even spread of model residuals. Numerical predictors were centered on a mean of zero to simplify comparisons among parameter estimates. By including all variables of hypothesized importance in the fixed effects component of the full model (Eq 2), we tested alternative random effects structures with restricted maximum likelihood estimates and determined the best fit model (penalized for model complexity) using Akaike's Information Criteria (AIC) (Zuur et al, 2009). Models were determined improved if a change in random structure reduced AIC by greater than two (Anderson & Burnham, 2002).

$$Response_{i(jk)} = \beta_0 + \beta_1 \bullet \sqrt{(rCWD_{i(k)}} + \beta_2 \bullet trend10_{\,i(jk)} + \alpha_{i/j} + \gamma_{0i(j)} + \varepsilon_{\,i(jk)}$$

Equation 2: Base Fixed Effects model: β_0 is the population intercept and β_1- β_2 are parameters adjusting the fixed effects (see Table 2 for description of all fixed factors tested in the model), *i* is the index for plot, *i*(*j*) is the index for tree nested in plot, *k* is the index for the year of measurement. *α* and *γ* are random effects parameter estimates of slope and intercept, respectively.

Fixed effects were selected for each model using maximum likelihood estimates (Zuur et al, 2009). Fixed effects were sequentially added to the base model using the forward stepwise selection method. Fixed effects were determined to improve the model if the AIC was reduced.

Measurement Scale	**Predictor**	**Origin of Measurement**	**Unit**
Tree	Species	Field Collection	Category (ABCO, PIPO, PSME, PIJE)
Tree	Size Class	Field Collection	Category (DBH >15-40.6cm or >40.6cm)
Tree	Trend 10	Tree Ring Time Series	Regression Slope (ratio)
Tree	Max Char Ht	FFI Database	Length (m)
Tree	% Crown Volume Scorch	FFI Database	Percentage
Stand	rCWD	Calculated from PRISM Data	Annual Index
Stand	Stand Density Change	FFI Database	Count
Stand	Post-fire Stand Density	FFI Database	Count
Stand	Basal Area Change	FFI Database	Numeric
Stand	Post-fire Basal Area	FFI Database	Numeric
Stand	Time Since Fire	Tree Ring Time Series	Annual
Stand	Region	-	Category (ISW, PSW)
Tree	MaxCharHt * Size Class	-	Interaction
Stand	rCWD * Basal Area Change	-	Interaction

Table 2: List of fixed effects terms included in full model used to test each random effects structure.

2.3.4 Classifying Trajectories in Transient and Persistent Growth Responses

We classified each tree's post-fire growth response into one of the five potential resilience trajectories by visually inspecting each 12-year pre- and post-fire RWI series. Trees that burned in 2012, or that burned again within 5 years of the first burn, were not included due to short series length. A two-year moving average was applied to RWI series to smooth interannual climate variability and clarify longer-term trends following the burn year. Post-fire RWI trajectories remaining within the range of pre-fire variability (< 0.25 from mean) were considered unchanged, and the most resistant. Positive or negative responses were classified if a tree's post-fire growth extended out of the range of pre-fire variability for 2 or more years. To allow expected lag in response, trees that initiated a positive or negative change before year five and maintained growth >0.25 from the pre-fire mean through year 12 were classified as persistent. Trees that returned to this range of variability within 12 years were classified as transient. A composite series was then developed for each trajectory class. Mean pre- and post-fire aCWD was calculated in terms of difference from the 1970 – 2014 mean. An analysis of variance was conducted to test effect of aCWD on growth trajectories

3.0 Results

3.1 Treatment Effect on Climate – Growth Relationships

Six trees with negative age-related growth trends extending past 1970 were excluded from further analysis to avoid potential bias in the resistance and resilience index calculations. The standardization period for RWI calculations includes severe drought years in the 1970s and 2000s (Figure 4), in addition to the fire-related disturbance during the prescribed fire periods in the 1990s and 2000s.

The climate growth model included aCWD and treatment as fixed effects and park as a random effect with random slope and intercept. RWI had a strong negative relationship with aCWD (Figure 5), further supporting that water stress limits growth in these forests. Treatment with prescribed fire weakened the relationship between RWI and aCWD, with burned trees showing greater growth in years with higher water deficit (Figure 5, Table 3, $p<0.001$). The marginal R^2 indicates that the fixed effects account for 22% of the growth variance and the conditional R^2 shows the combined fixed and random effects account for 38% of the variance.

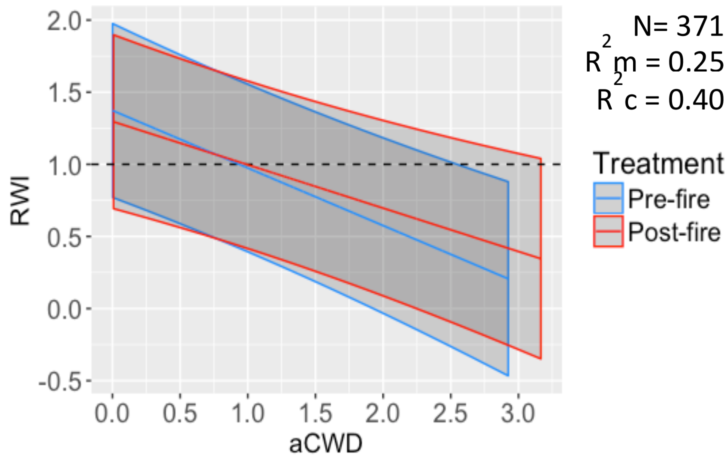

Figure 5: Climate-growth relationship before (blue) and after (red) prescribed fire. Growth after fire is less sensitive to increasing climatic water deficit than before. Wide confidence bands illustrate high variability among years and trees. R^2m and R^2m account for the fixed effects and combined fixed and random effects, respectively.

Table 3: Summary of mixed effects climate-growth relationships before and after treatment

Variable	***Coef***	***SE***	***df***	***P***
(Intercept)	1.37	0.08	8054	<0.001
aCWD	-0.40	0.08	8054	<0.001
Treatment	-0.08	0.02	8054	<0.001
aCWD*Treatment	0.10	0.01	8054	<0.001

3.2 Immediate, Transient, and Persistent Term Controls on Growth Response

3.2.1 Random Effects Structure

The optimal structure of the random effects terms in the immediate and transient term mixed effects models were the same. Both models best accounted for variation by nesting Tree within Plot and adding a random intercept and slope. The models were further improved by allowing growth response to vary by park (Table 4). The persistent term model also used a nested Tree in Plot random effects structure, but did not improve with a random slope.

Model	**Random Structure**	**df**	**AIC**
1	Full + No Random Effects	19	800.00
2	Full + (Intercept | Park)	20	793.60
3	Full + (Intercept | Plot/Tree)	21	745.22
4	Full + (Intercept | Park/Plot/Tree)	22	746.71
5	Full + (Intercept | Plot/Tree), weights = var(~1 | Park)	30	638.18
6	Full + (Intercept | Plot/Tree), weights = var(~1 + rCWD | Park)	30	638.18
7	Full + (Intercept + rCWD | Plot/Tree), weights = var(~1 | Park)	34	637.34

Table 4: Random effects structure selection. Model 7 achieved the best fit with the greatest degrees of freedom.

3.2.2 Controls on Growth Response

Individual tree and stand scale controls on growth response to prescribed fire varied in significance and magnitude over the 12 year post-fire study period (Table 5). Relative climatic water deficit, the ratio between pre- and post-fire CWD, exerted a negative control on growth response during each term, indicating response is conditional on water availability in both the pre- and post-fire periods. The negative effect of rCWD on growth response was weakest in the

	Variable	Immediate	Parameter Estimate Transient	Persistent
Stand & Regional Controls				
	Intercept	0.97	0.72	0.93
	rCWD	-0.34	-0.58	-0.13
	rCWD*Trend.10	-	-	0.77
	Post-fire BA	-0.11	0.10	-
	Years Post-fire	0.04	0.03	-
	Region (PSW)	-0.11	-	-
Tree Demographics				
	Species (pipo)	0.08	-	-
	Size (small)	-	-	-0.08
	Trend.10	-0.66	-0.99	-0.73
Tree Injury				
	%CVS	-0.002	-	-
	MaxChar*Size(small)	-0.02	-0.02	-0.05
Model Fit				
	Sample Size	268	206	128
	marginal R^2	0.22	0.21	0.12
	conditional R^2	0.45	0.49	0.3

Table 5 Significant fixed effects terms and parameter estimates for immediate, transient, and persistent term linear mixed effects models ($p < 0.05$). Relative climatic water deficit (*rCWD*) is the ratio between annual post fire CWD and the 5 year pre fire mean. Pacific Southwest (PSW) is compared to interior Southwest (ISW) region. Trees >40.6cm DBH (large) are compared to trees <40.6cm DBH (small). Percent crown volume scorch (%CVS), maximum stem char height (MaxChar), and post fire basal area (BA) were measured immediately post-fire. Ten year pre-fire growth trend (10 Yr Trend) calculated as the slope of growth over time.

9-12yr persistent term, and strongest in the 5-8yr transient term. A cross-scale positive interaction between stand rCWD and tree 10yr pre-fire growth trend indicates, for a given change in climatic condition, increasing pre-fire trends increased post-fire growth response. Surprisingly, however, 10yr pre-fire trend consistently had the strongest negative relationship with growth response during every term. Basal area, and indicator of stand-level competition and productivity, was the only predictor reversing direction of control on growth over time. While post-fire basal area had a negative effect during the immediate post-fire term, the relationship became positive in the transient term. At the regional scale, trees growing in the pacific Southwest tended to have lower immediate growth responses to fire than those in the interior Southwest. This indicates some condition occurring above the plot scale was not taken into account in the random effects.

First order fire effects were measured at the individual tree scale. Crown volume scorch negatively influenced immediate growth response, however it appears trees were able to recover to this injury by the transient period. In small trees (<40.6cm DBH), injury associated with stem char continued exerting a negative effect on post-fire growth over 12 years. Difference in responses between small and large trees was detectible during the persistent period, when large trees responded more positively. Species was only significant in the immediate term, when PIPO responded more positively to fire than ABCO.

Tree sample size for a post-fire term was limited by the proximity of the burn year to the 2015 sampling year. Fixed effect variables explained 22% of the variance in growth response in the immediate term model (n = 268), 21% in the transient term (n = 206), and 12% in the persistent term (n=128). While the predictors in the persistent term are strongly related to post-fire growth response in our sample trees, we do not have high confidence that these relationships can be applied to another set of trees.

3.3 Classification of post-fire growth trajectories

A total of 319 trees were included in the growth trajectory classification exercise (Figure 6,Table 6). Resilient trees, responding with a persistent positive (+P, 12%), transient positive (+T, 12%), or transient negative (-T, 24%) growth trajectory accounted for 46% of the trees.

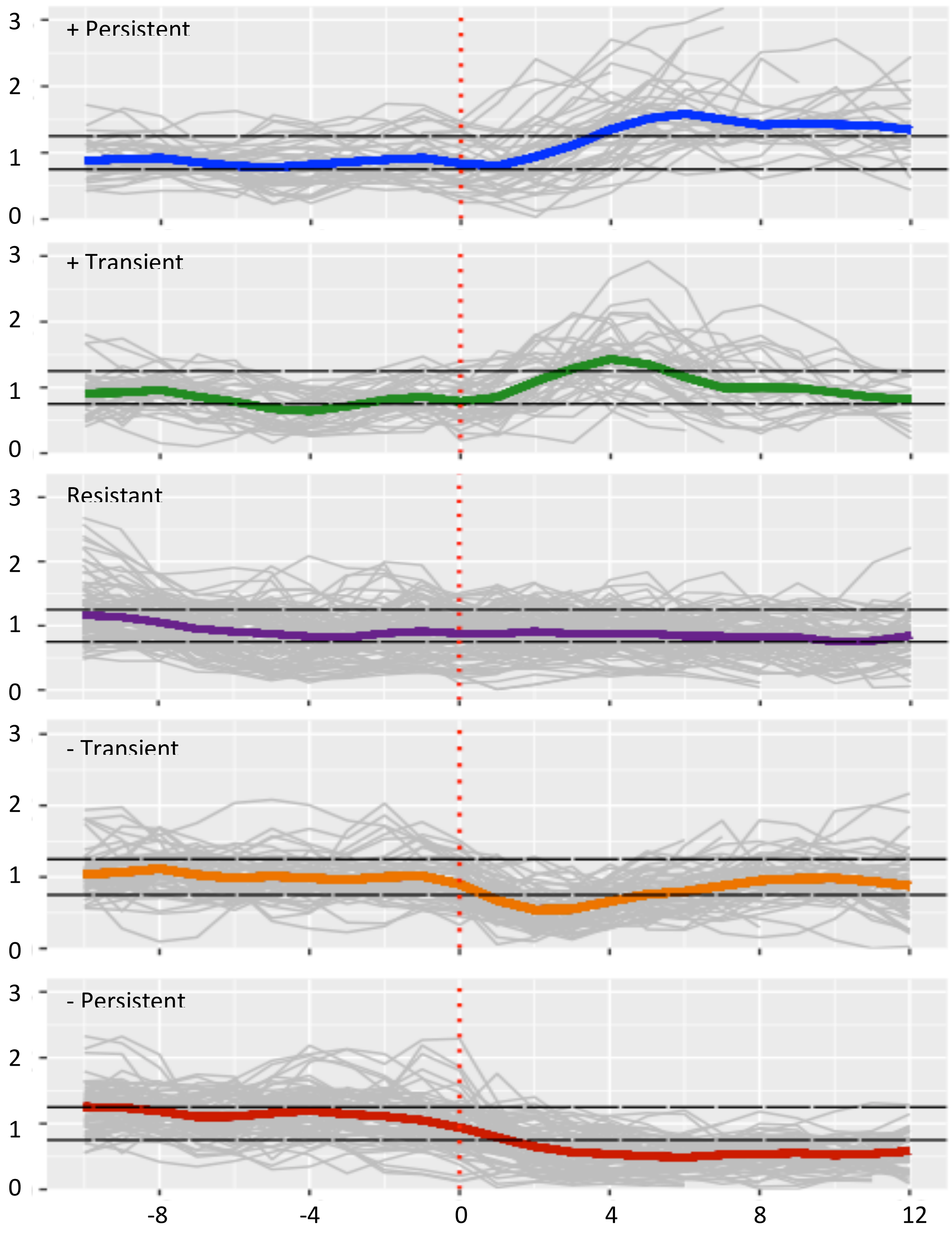

Figure 6: Spaghetti plots of five resilience trajectories from all parks, species, and burn years. The average annual growth is highlighted in blue (+P), green (+T), purple (R), orange (-T), and red (-P).

Trees resistant to change in the post fire period (R) accounted for 34% of the sample and the remaining 24% were not resilient (-P). Surprisingly, ANOVA results indicate trees responding with negative growth trajectories experienced lower pre-fire water deficits than those responding positively (Table 7; Figure 7). While the post-fire period was generally more water-limited compared to the 1970—2014 mean (Figure 7), trees responding with persistent positive (+P) and transient negative (-T) growth were more water-limited in the post-fire period compared to the other trajectories. Some trees displayed a lag in response, with resistance to the immediate effects followed by either a decline or increase in growth after 3 years (Figure 6).

Trajectory	Tree Count
+ Persistent	38
+ Transient	39
Resistant	108
- Transient	58
- Persistent	76
Not Determinable	11
Total Trees	338

Table 6: Number of trees classified under each post-fire growth response trajectory.

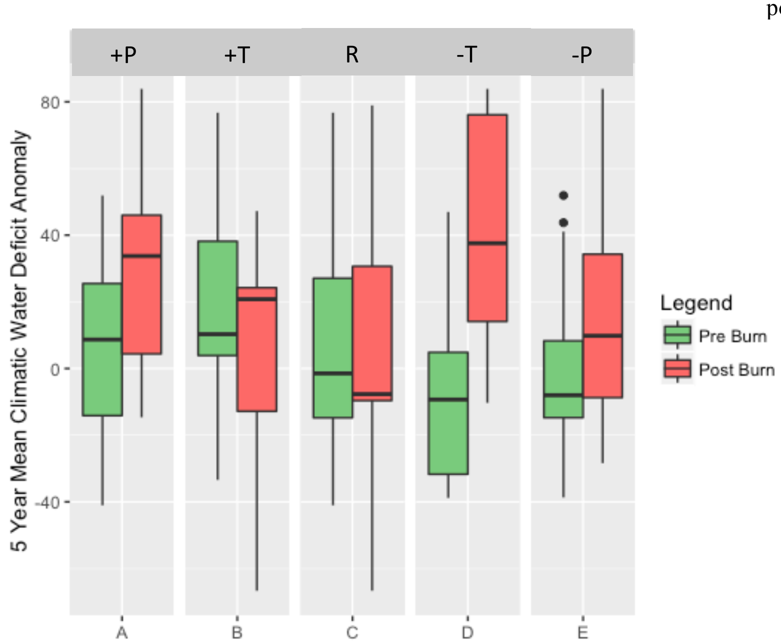

Figure 7: Comparison between pre- and post-fire 5 year mean climatic water deficit anomaly for each growth trajectory.

	5 Year Prefire aCWD			5 Year Posfire aCWD		
	Estimate	*SE*	*P*	Estimate	*SE*	*P*
(Intercept)	8.13	4.30	0.06	29.895	4.975	<0.01
+ Transient	11.17	6.00	0.06	-20.1	6.945	<0.01
Resistant	-2.02	5.03	0.69	-25.148	5.816	<0.01
- Transient	-18.47	5.52	<0.01	6.955	6.389	0.28
- Persistent	-11.47	5.27	0.03	-11.041	6.093	0.07

Table 7: ANOVA summary comparing parameter estimates for aCWD between pre- and post-fire growth trajectories. Each estimate is relative to the estimate for + Persistent growth response.

4.0 Discussion

4.1. Effect of Prescribed Fire on Climate Sensitivity

Tree growth was less sensitive to increasing climatic water deficit after fire, suggesting the treatment increased tree resilience to drought. Consistent with previous work, water availability and evaporative demand were the primary limitations on Southwest conifer growth (Fritts 1974; Williams et al 2013). Climatic water deficit explained a greater amount of the growth variance than precipitation, suggesting it is better representative of water stress experienced by the organism. The wide confidence intervals (Figure 5) show high variability in the pre- and post- fire climate-growth relationships. We took a temporally explicit approach to further understand effect of climate on growth response.

4.2. Top-Down Controls on Growth Response to Prescribed Fire

Relative climatic water deficit allows us to consider how growth response to fire is influenced by pre fire drought. When rCWD is >1, a tree is expected to be recovering in more favorable annual climatic conditions compared to the antecedent condition, while rCWD < 1 indicates more water limited post fire years. Resistance and resilience were expected to increase if water were less limited in the post fire period and thus we expected a positive relationship between response and rCWD. On the contrary, the modeled negative relationship suggests antecedent water availability may be more important to resistance and resilience than water limitation in the post fire recovery period. This is consistent with findings that antecedent drought increases fire related mortality (van Mantgem 2013) and increasingly negative growth responses to fire (Keeling & Sala 2012). However, the climatic patterns among growth trajectories suggest that trees experiencing greater water deficits in both the pre and post fire periods were the most resilient while those experiencing lower antecedent deficits were the least resilient. Partitioning seasonality of water limitation among localities, rather than over the course of the water year, may provide finer resolution insights on where and when water limitation effects resistance and resilience.

Although plot and park were included in the random effects terms, geographic region of growth was still an important influence on resistance. These two regions receive moisture at different times of the year and from different storm tracks. The California parks experience a more Mediterranean precipitation distribution, with winter precipitation dominating the hydrograph (van Mantgem & Sarr 2015). The interior southwest is driven by a bimodal precipitation distribution with late summer monsoon and winter precipitation dominating water availability (Sheppard et al 2002). The interior Southwest sites were higher in elevation and tended to show more variable annual climatic water deficits, even within and among parks (Figure 5). Biophysical adjustments along aridity gradients, such as elevation, at both the tree and stand scales may compensate for water availability and thus tree growth (Martinez-Vilalta et al 2012; van Mantgem & Sarr 2015).

4.3 Bottom-up Controls on Growth Response to Prescribed Fire

Immediate response to prescribed fire was negatively influenced by fire injury (crown scorch and char height), post-fire basal area, and pre-fire growth trend. Practitioners often use fire to thin understory trees, so it is not surprising that smaller trees, with thinner bark, were more strongly affected by potential cambial injury (Hood 2010). Our results indicate a moderately significant negative effect of max char when considering all of the study species, which are all thick barked at maturity. %CVS and max char were only immediate negative controls, indicating that surviving trees recover from related injury after three years and are then primarily influenced by effects at the stand scale. We did not assess the effects of litter or duff combustion, which may have accounted for fine root mortality, cambial damage, or nutrient turnover (Busse et al 2000). First entry burns after extended periods of exclusion can have particularly severe tree level effects when fuels have been building up in mounds around the bole (Hood et al 2010). The negative effect of basal area on growth response indicates that more dense stands limit immediate growth, potentially due to stronger competition. However, the reversal of this relationship in the transient term indications site conditions facilitating higher basal areas could improve tree recovery.

Declining growth trends are understood as a symptom of biological or physical stressors (Franklin et al 1987), taking into account several environmental factors. Ten year prefire trend was an important predictor for the entire post-fire period but, surprisingly, the negative relationship show trees decreasing in growth rate responded more positively than those with increasing growth rates. Trend has been associated with competitive pressure, species life history, and an ability individual's ability to persist in a declining state (Bigler and Bugmann 2003; Das et al 2007). Surviving trees growing in the understory, with declining growth due to canopy suppression, may respond more favorably to fire of it results in gaps in the canopy. Conversely, Linares and other (2010) determined that long term climatic patterns drove growth trends in *Abies pinsapo* Boiss. while relative growth rates were modulated by competition. While the interaction between rCWD and change in stand density was a poor predictor of growth response, exploring interactions between growth trend and climatic trend, canopy position, stand density, or tree species could help describe the mechanisms behind these patterns.

Fire cause reductions in stand density did not appear to be high enough to contribute to a positive growth response reported by others (Reinhardt & Ryan 1988; Mutch & Swetnam 1993). However, absolute post-fire basal area was significant. Prescribed fires are employed to maintain thinned or relatively thin stands and are not designed to kill large overstory trees, disproportionate contributors to stand basal area (Hood 2010). Burning in overstocked stands with a large amount of ladder fuels could result in difficult to control fire behavior and high severity fire (Ryan et al 2013). Because of this, prescribed fire cannot replicate the full range of conditions that trees and stands experience during the even more heterogeneous process of wildfire (Ryan et al 2013). From an experimental standpoint, however, ability to make pre-fire measurements and constraints on fire weather and behavior afforded by prescribed fire are useful in making general assumptions needed for statistical testing. The wealth of data available from FFI contributes to making prescribed fire a valuable proxy for understanding fire effects. However, small plot size (20 x 50m) likely cause less accurate estimates in stand density and basal area when compared to a more detailed neighborhood competition accounting for competition outside of the plot. With due care to sample under a range of stand and climatic conditions, comparisons against unburned stands can help us better understand the mechanistic underpinnings of tree response to fire and make inferences on cross-scale resilience (Angeler et al 2010).

4.4 Application of Resilience Framework

Restoring resilience to ecosystems occurs across a range of spatial and temporal scales (Peterson). The increasing use of prescribed fire has been followed by a breadth of scientific investigations questioning the directionality and relative importance of fire effects on trees and forest ecosystems. The heterogeneity in fire behavior drives extreme variability in fire effects and disentangling interactions on forest growth is not a trivial matter. Annual observations of tree growth are useful for quantifying mechanistic drivers of growth responses under a variety of conditions. However, trees operate over longer time scales and trends before and after the event should complement the study to account for response lags (Skov et al 2005; Das et al 2007; D'Amato et al 2013; Kerhoulas et al 2013). We suggest that classifying predominant patterns in reorganization after a disturbance can assist researchers and managers in understanding how individual drivers may interact over time to influence the outcomes of resilience objectives.

In this study we used tree growth to estimate resilience to prescribe fire. Growth responses clearly separated out into five trajectories defined by directionality and persistence. The most resilient trees were able to resist fire during periods of heightened water stress and shift functional growth to an elevated level. Scale dependent self-organization hypothesizes that forest trees operate within the same niche space and can therefore effect each other's ability to garner resources and thus increase radial growth (Peterson et al 1998; Angler et al 2010). Therefore, one may hypothesize that an initial growth decline of all foundational species studied allowed for a synergistic recovery period and reduce the ability of a single species to capitalize on newly available resources and maintain dominance (Cavin et al 2013). In competitive stands, the ability to resist fire injury, particularly when a strong competitor's capacity to uptake resources is compromised, can provide a competitive edge. This edge may be transient or persistent depending on whether the competitor may recover. When constrained within an operational unit, the distribution of trajectories itself may suggest resilience in that unit over a given period of time.

Trees with positive growth persistence did so in spite of increasing water limitations and appear to be both drought and fire resilient. Additional measurements and statistical tests are needed to determine whether persistent positive growth responses were facilitated by release from competition, elevated water use efficiency, or other drivers (Soule & Knapp 2006). Designating classification criteria is necessary for constraining growth responses to immediate first and second order fire effects. Unburned control trees experiencing similar climatic conditions are essential to confirm response stimulus and partition the relative importance of climatic drivers (Sutherland et al 1991; Lloret et al 2011; Keeling & Sala 2012; Kerhoulas et al 2013).

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