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Tree traits influence response to fire severity in the western Oregon Cascades, USA

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ABSTRACT

Wildfire is an important disturbance process in western North American conifer forests. To better understand forest response to fire, we used generalized additive models to analyze tree mortality and long-term (1 to 25 years post-fire) radial growth patterns of trees that survived fire across a burn severity gradient in the western Cascades of Oregon. We also used species-specific leaf-area models derived from sapwood estimates to investigate the linkage between photosynthetic capacity and growth response. Larger trees and shade intolerant trees had a higher probability of surviving fire. Trees that survived fire tended to experience a reduction in growth immediately following fire, with the most pronounced growth suppression found in trees within stands burned at high severity. Radial growth response to fire over time differed markedly as a function of tree size. Smaller trees that survived fire generally experienced enhanced radial growth relative to small trees in unburned stands. Conversely, larger trees that survived fire experienced significant and persistent reductions in growth relative to large trees in unburned stands. There was a linear relationship between diameter and tree leaf area in stands burned at low severity, but a non-linear relationship between diameter and leaf area in stand burned at high severity. Generalized additive models are well suited to modeling non-linear mortality and growth responses to fire. This research provides a better understanding of how fire severity influences tree-growth, forest succession, as well as the long-term resilience of forests to disturbances.

1. Introduction

Wildfire extent and severity have increased in recent decades due to altered fire regimes and a rapidly changing climate (Westerling, 2016; Dennison et al., 2014; Miller and Safford, 2012). Characterizing the ecological effects of contemporary fire is a central concern of forest ecologists and managers. Previous research describes the effects of wildfire on carbon cycling, wildlife habitat, post-fire tree establishment, and other ecosystem responses at spatial scales ranging from a stand to a landscape (e.g., Fontaine and Kennedy, 2012; Campbell et al., 2007; Johnstone and Chapin, 2006; Hoyt and Hannon, 2002; Turner et al., 1997). This study seeks to add to our understanding of disturbance mediated change by examining forest fire effects on mortality, radial growth, and leaf area at the scale of individual trees.

Wildfire injures or kills trees by damaging or consuming crowns, cambial tissue, or roots. The probability of tree survival is a function of fire intensity and tree autoecological traits that protect these sensitive tissues from necrosis (Pausas, 2015; Hood et al., 2010; Stephens and Finney, 2002; Brown and Smith, 2000; Ryan and Reinhardt, 1988). Intuitively, trees that survive fire (residual trees) experience enhanced growth due to reduced competition for light, water, and nutrients (Franklin et al., 1987). However, fire can have a profound effect on future growth of trees by disrupting the acquisition or flow of photosynthates, water, or nutrients within the root, cambium, or leaves; tissues that may need replacement before trees can realize the benefit of reduced competition. For most forests, the degree to which fire severity influences growth patterns in residual trees and the physiological mechanisms that control growth responses are not well understood.

Radial growth of trees is associated with resistance to drought, fire, and insect attack (Vernon et al., 2018; van Mantgem et al., 2003; Waring and Pitman, 1983). Characterizing tree mortality and radial growth patterns following fire may yield insights into the ability of forest stands to maintain their essential structure, function and composition in the face of future change (Lloret et al., 2011). Characterization of individual tree response to fire will also add to our understanding of stand-scale forest successional pathways following disturbance (Dunn and Bailey, 2016).

In this paper, we describe fire effects on tree mortality, post-fire

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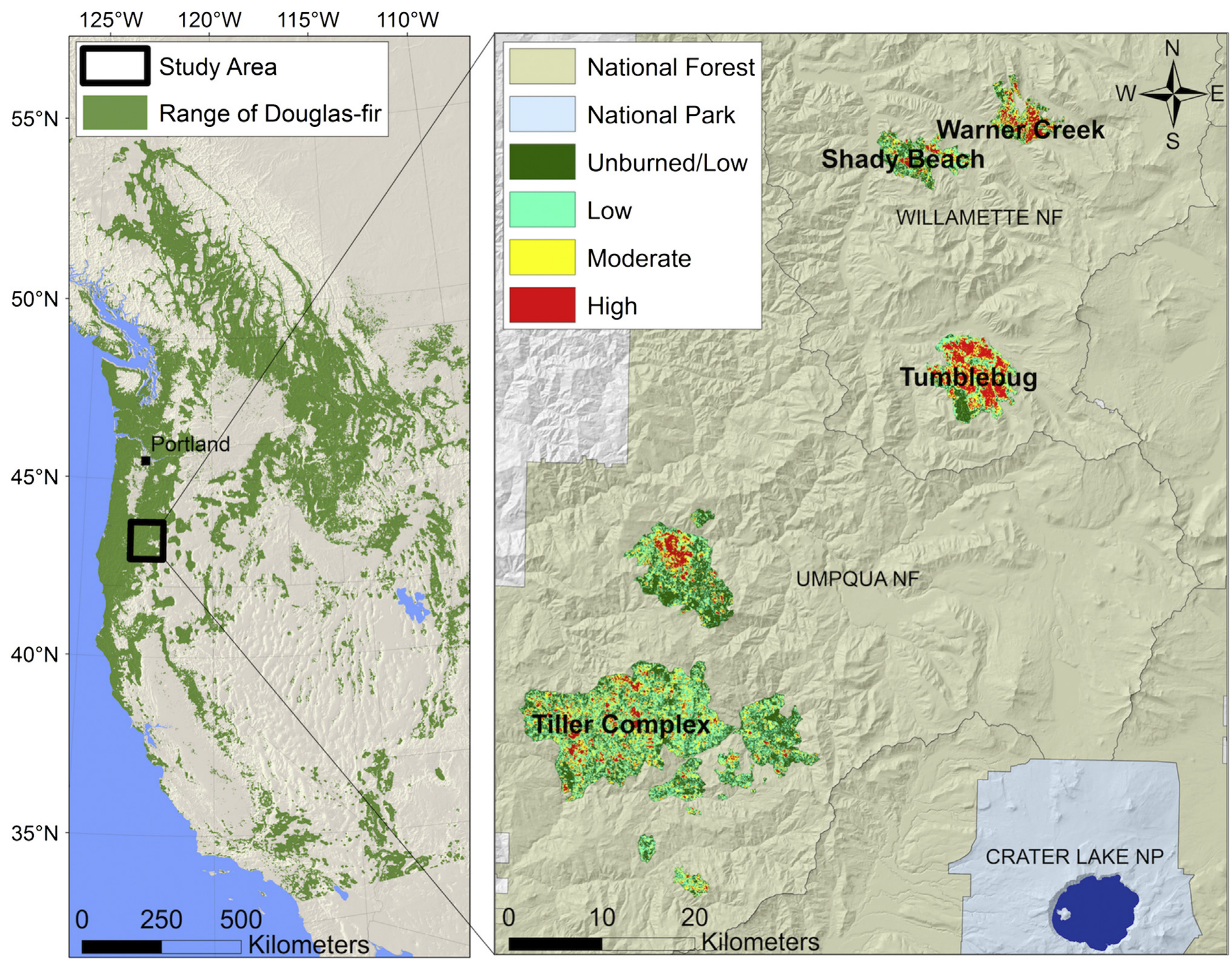

Fig. 1. Location of study area.

radial growth, and leaf area of residual trees within forest stands burned at different severities over the last three decades in the Oregon Cascades. The objectives of this study include: (1) Describing factors influencing survival of individual trees following wildfire; (2) Determining if fire severity classifications calculated at stand scales are associated with distinctive radial growth responses in surviving trees; (3) Describing how fire effects on growth of residual trees varies with size, species, fire severity and time since fire; and (4) Elucidating the relationship between tree photosynthetic capacity and radial growth response to fire.

2. Methods

2.1. Study area

Data for this study were collected within Douglas-fir dominated forests (*Pseudotsuga menziesii* var. *menziesii*) constrained to the distribution of western hemlock in the western central Oregon Cascades (Fig. 1). This study area is characterized by a maritime climate with cool, wet winters and warm, dry summers. Average annual precipitation ranges from 1339 to 1761 mm, with ~75% of precipitation falling from November through April. Average maximum temperatures range from 27.5 °C in August, to 4.3 °C in December, and average minimum temperatures range from 9.1 °C in August to -2.8 °C in December (Daly et al., 2002, www.prismclimate.org). Temperature generally increases and precipitation decreases along a north to south gradient within the study area.

The study area is characterized by mixed conifer forests of species distinguished primarily by shade tolerance. Douglas-fir, a shade intolerant species, is usually the dominant tree species between 500 and 1300 m. Sugar pine (*Pinus lambertiana*), a shade intolerant species, and incense-cedar (*Calocedrus decurrens*), a moderately shade tolerant species, are large, long-lived conifers that are often co-dominant in Douglas-fir stands, particularly in the southern part of the study area or on warmer aspects in the northern part of the study area. Western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), white fir (*Abies concolor*), grand fir (*Abies grandis*), and Pacific yew (*Taxus brevifolia*) are common shade tolerant species that are usually found as understory species. Common understory hardwood trees include golden chinquapin (*Chrysolepis chrysophylla*), bigleaf maple (*Acer macrophyllum*), Pacific madrone (*Arbutus menziesii*) and Pacific dogwood (*Cornus nuttallii*). Silver fir (*Abies amabilis)* was encountered at higher elevations and northeastern aspects while ponderosa pine (*Pinus ponderosa*) occurred at lower elevations and southwestern aspects.

2.2. Field and laboratory procedures

Several large fires burned 76,746 ha within our study area between 1987 and 2014. We collected data within the 2009 Tumblebug Fire, the 2002 Tiller Complex, the 1991 Warner Fire, and the 1988 Shady Beach Fire. Sampling was constrained to mature/old-growth Douglas-fir forests for which there are no records of logging or wildfire over the past 100 years except the 1988–2009 fire events of interest. Each fire was stratified into three severity classes (low, moderate, and high) using

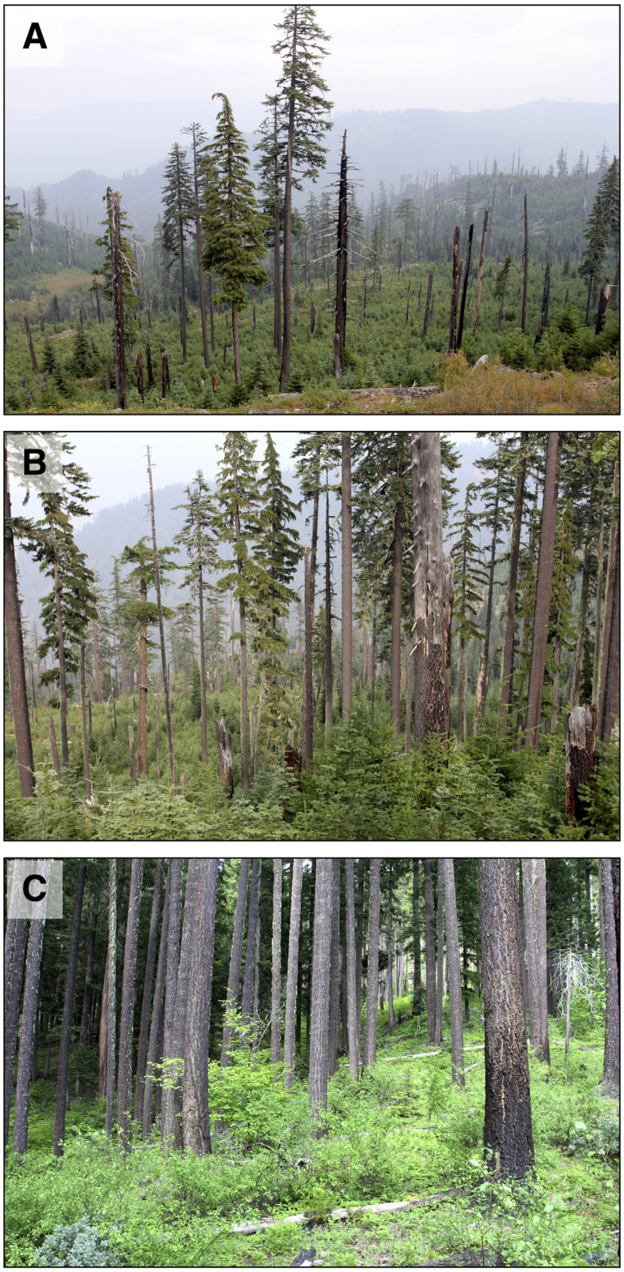

Fig. 2. Examples of severity classes sampled. Panel A = high severity, Panel B = moderate severity, Panel C = low severity. All photos were taken in 2018 within the Warner Creek fire perimeter, 27 years post-fire.

Monitoring Trends in Burn Severity classified maps (MTBS; www.mtbs.gov). We combined the MTBS very low and low severity classes because we observed similar fire effects in these areas during field reconnaissance. These three severity classes generally corresponded to < 25%, 25–50%, and > 75% basal area mortality, although our field estimates suggest delayed mortality likely contributed to higher mortality by the time we sampled these fires.

In 2012 and 2013 we randomly located 57 1-ha circular plots, each with four 0.10 ha circular subplots, within burned and unburned stands within and around each fire perimeter (Fig. 2). All plots within a given severity class were separated by a minimum distance of 400 m to ensure that we sampled over a broad area and to limit spatial autocorrelation (van Mantgem and Schwilk, 2009). We only sampled plots located in an area having a consistent severity class with an extent greater than our 1-ha plot to limit the influence of variability in fire effects on tree response. We sampled six plots in each MTBS fire severity class within the 1991 Warner Creek Fire (total $n = 18$ plots, 72 subplots, sampled in 2013) and 2002 Tiller Complex Fires (total $n = 18$ plots, 72 subplots, sampled in 2012). We also sampled in stands that were burned at high severity and subsequently salvaged logged within the 2002 Tiller Complex ($n = 6$ plots, 24 subplots, sampled in 2012) and within the 1988 Shady Beach fire ($n = 6$ plots, 24 subplots, sampled in 2012). In 2013, we also sampled one plot in each severity class within the 2009 Tumblebug Fire. We also sampled unburned forests ($n = 6$ plots, 24 subplots) adjacent to sampled fires that had similar tree structural and compositional characteristics observed in burned areas.

Within each nested subplot, we recorded diameter at breast height (DBH) and species of all live and dead trees. To evaluate whether MTBS data had correctly classified stands, we calculated fire severity by differencing dead tree basal area and total live and dead basal area and computed correlations between these field observations of fire severity and our MTBS severity classifications.

We used a hand-powered increment borer to extract cores from two randomly selected live trees in each of four size classes from every species present within each subplot. We cored trees ≥2.54 to 10 cm DBH within a 5.64 m radius of subplot center, trees ≥10 to 40 cm DBH within 8.92 m radius of subplot center, and trees ≥40 within 17.84 m radius of subplot center. We applied chemical stains immediately following the removal of each core to delineate the boundary between sapwood and heartwood and used digital calipers to measure sapwood width to the nearest mm from inside bark to the boundary of sapwood and heartwood (Kutscha and Sachs, 1962).

All cores were transported in paper straws to the dendrochronology lab at Oregon State University College of Forestry where they were mounted, sanded, and visually cross-dated using standard methods (Stokes and Smiley, 1968). Tree cores were measured to 0.001 mm precision using a computer controlled Velmex system (Velmex, Inc., Bloomfield NY). After verifying cross-dating accuracy using COFECHA software (Grissino-Mayer, 2001), annual ring widths were converted to basal area increment by calculating the difference between basal area calculated from inside the bark radius of each tree core and basal area calculated from radius minus each tree ring width.

2.3. Analysis of tree survival

We modeled the influence of fire severity and tree characteristics on tree mortality using generalized additive models (GAMs) implemented in R's mgcv package (Wood, 2006). GAMs are generalized linear models in which one or more covariates are replaced by the sum of a smooth non-parametric function. Smooth functions automatically balance goodness-of-fit and overfitting via a cross-validation procedure that minimizes the average squared difference between the full data set and predicted values of omitted data (Andersen, 2009; Wood, 2004; Hastie and Tibshirani, 1986). The use of flexible smoothers in a GAM framework is well suited to modeling the influence of fire on mortality because this response may be non-linear. For instance, we hypothesized that probability of mortality from fire may increase with fire severity up to a certain point past which probability of mortality would plateau.

We estimated the probability of tree survival using a GAM with a binomial distribution. We tested a wide variety of forest environmental, structural, and compositional attributes as potential predictor variables (see Table 1). Fire event and plot were included as nested random effects to account for potential spatial dependency in model residuals. We created separate GAM models for shade tolerant and shade intolerant species because we hypothesized that these species would exhibit different responses to fire. A small proportion of the dead trees we measured in the field (1.6% of total trees) could not be reliably identified to species and were excluded from this analysis. We evaluated prospective GAM models by manual forwards and backwards stepwise variable selection. We selected final models with the lowest Akaike's Information Criterion (AIC) and lowest generalized cross-validation (GCV) scores. Like AIC, lower GCV scores indicate a model that minimizes

Table 1
Variables evaluated as potential explanatory variables of mortality and radial growth in GAM models.

Variable	Description
Species	One of ABAM, ABCO, ACMA, ARME, CACH, CADE, CONU, PILA, PIPO, PSME, TABR, THPL, or TSHE
DBH	Diameter at breast height (cm)
Height	Height of tree (m)
CBH	Crown base height—the lowest height above the ground of live foliage (m)
CR	Crown ratio—The ratio of crown length to total tree height (%)
MTBS Severity Class	One of Uunburned, Low, Moderate, or High
BA Mortality	Ratio of basal area of dead trees estimated to have been killed by fire to live tree basal area
Elevation	Height above sea level of trees sampled (m)
Aspect	Aspect, transformed to a continuous variable ranging from 0 to 2 (aspect = 1 + cos(45° – aspect) (Beers 1966)
Slope	Steepness of slope (%)
Heatload	Index of potential direct incident radiation adjusted for aspect and slope (McCune and Dylan 2002)
Easting	x-coordinate in Universal Transverse Mercator North American Datum 1983 projection
Northing	y-coordinate in Universal Transverse Mercator North American Datum 1983 projection
Residual Trees QMD	Quadratic mean diameter of trees surviving fire (cm)
Residual Trees Density	Density of trees surviving fire (trees ha^{-1})
Residual Trees BA	Basal area of trees surviving fire (m^2 ha^{-1})
Snag Density	Density of snags (trees ha^{-1})
Snag BA	Basal area of snags (m^2 ha^{-1})

smoothed predictor terms while maximizing model explanatory power (Wood et al., 2015; Wood, 2011).

We evaluated concurvity of model terms using several indices available in mgcv (Wood, 2006). Concurvity refers to the degree to which a smooth model term can be approximated by one or more smooth model terms. Like multicollinearity in a linear modeling framework, concurvity can complicate statistical inference using GAMs. All mgcv concurvity indexes are calculated on a scale of 0 to 1, with 0 indicating no concurvity and 1 indicating a total lack of identifiability. We rejected model terms with concurvity indices that exceeded 0.3. This threshold was arbitrary but successfully eliminated all model terms in which Pearson's r correlation exceeded 0.50 or -0.50, which we believe represents a conservative approach to model specification.

2.4. Fire effects on tree growth

Previous research indicates that tree radial growth can be suppressed following fire, and we hypothesized that trees within stands burned at low, moderate, and high severity would be suppressed to different degrees relative to unburned stands (Arabas et al., 2008; Rubino and McCarthy, 2004). To test this hypothesis, we compared basal area increment (BAI) in the year following fire to BAI in the year before fire for trees within plots burned at different severities using the independence test function in R's coin package (Hothorn et al., 2008).

The coin package independence test is analogous to a *t*-test or a Wilcoxon Signed Rank test in that it compares the mean of two sets of dependent variables. A test statistic is provided by approximating a null distribution via conditional Monte Carlo resampling with 10,000 replications. This procedure is appropriate for non-normally distributed data and unequal sample sizes (Hothorn et al., 2008; Hothorn et al., 2006; Strasser and Webber, 1999). We also used the independence test to compare BAI of trees in unburned stands in the year following fire to BAI of trees in stands burned at low, moderate, and high severity.

It is possible that differences in annual BAI before and after fire could be attributable to differences in climate between years. In all statistical analysis of tree growth undertaken for this study, we simultaneously evaluated time before and after fire for four fires that burned at different times over three decades. We anticipated that compositing the time variable in this fashion would dampen the specific influence of climate on BAI and allow us to generalize about the effects of time since fire, fire severity, and other variables independent of climate influences on tree physiological responses. Our inferences about the effects of fire on tree radial growth are based on same year comparisons of trees within plots burned at different severities and unburned trees, which also controls for the effect of climate on tree growth.

2.5. Modeling residual tree radial growth response to fire over time

We used GAMs to model residual tree BAI as a function of time since fire, fire severity, and a wide variety of forest environmental, structural, and compositional attributes (see Table 1). Like the mortality response, we expected the radial growth response to be nonlinear. For instance, we hypothesized that tree growth would be suppressed immediately following fire but recover over time and might exceed pre-fire BAI as a result of reduced competition for resources. We also hypothesized that the effect of fire severity on BAI might vary by tree size, and so we modeled BAI response separately for four different DBH bins containing an approximately equal number of observations. Fire event and plot were included as nested random effects to account for spatial dependency in model residuals. Temporal autocorrelation of model residuals was evaluated with Durbin-Watson tests and by examining partial autocorrelation plots.

The use of flexible smoothers permits easy visualization of BAI change over time. But smoothing functions do not produce parametric coefficients that allow straightforward interpretation of the effect of fire severity on the BAI response. To quantify the effect of fire severity on BAI response over time, we fit varying coefficient models with fire severity classifications as parametric categorical variables. We considered the effect of fire severity to be a significant influence on post-fire BAI when 95% confidence intervals for the parametric BAI estimate in unburned plots did not overlap with 95% confidence intervals for the parametric BAI estimate of the severity class tested.

2.6. Evaluating the relationship between tree radial growth and leaf area

We hypothesized that any observed reductions in BAI would be associated with the death of tree photosynthetic material as a result of wildfire. We modeled leaf area based on the pipe theory model in which the area of sapwood at crown base height relates proportionally to tree leaf area (Marshall and Waring, 1986; Waring et al., 1982). First, we estimated diameter inside bark using species and regional specific equations (Larsen and Hann, 1985; Pillsbury and Kirkley, 1984). Second, we used species and regional specific taper equations (Walters and Hann, 1986) and field derived estimates of crown base height to estimate diameter inside bark at crown base height. We assumed minimal decrease in sapwood width to this point based on previous research (Dunn and Bailey, 2015), and calculated sapwood area at crown base height using sapwood width estimated from tree cores. We then applied species-specific sapwood to leaf area ratios to quantify individual tree leaf area at the time of sampling (Gersonde et al., 2004; Turner et al., 2000; Urban, 1993; Waring et al., 1982; Waring et al., 1977).

We modeled leaf area using a GAM with fire severity as a varying coefficient parametric categorical variable. As with the tree mortality and residual tree BAI response, we evaluated potential predictor variables using AIC and GCV. We hypothesized that leaf area response may be influenced by interactions of tree structural attributes and fire severity. We tested for potential interactions by constructing separate models with smooth functions of two covariates using mgcv's tensor product smooth function (Wood et al., 2013). This function combines the model matrices associated with different smooth functions into a single model matrix (with penalties for each original matrix), a procedure roughly analogous to multiplication of two covariates in an interaction term of a simple linear model. Modeling the interaction of covariates requires both terms to be continuous variables. Unlike previous models which modeled fire severity using categorical MTBS classifications, in this case we used proportion basal area mortality recorded in the field as an explanatory variable. To visualize the interaction of tree structural attributes and fire severity, we created three-dimensional graphics that allow interpretation of response surfaces (Wood, 2006).

3. Results

3.1. Tree survival

We modeled the probability of survival using 1,631 live and 2,674 dead trees of 11 different species in 51 plots that had experienced fire (Table 2). Basal area mortality in plots ranged from 10% to 100%. There was good agreement between our field observed mortality calculations and MTBS severity classes ($R^2 = 0.76$, $p = < 0.01$). We used MTBS severity classes in most subsequent statistical analysis because (1) results were similar using either MTBS classifications or field observed severity; (2) MTBS severity classifications are widely used by researchers and managers and their use permits comparisons between the present paper and future research; and, (3) MTBS severity classes are derived from differences in vegetation measured typically within the year following fire and so may provide a more objective measurement of how fire intensity influences mortality than our field measurements, which reflect an unknown degree of lagged mortality effects over the 4–25 years between fire occurrence and the completion of field measurements.

The best GAM models for shade tolerant and shade intolerant survival as evaluated with AIC and GCV included species, fire severity, and tree diameter as predictor variables with plot and fire event as random effects. Other environmental and tree characteristic variables (elevation, tree height, time since fire, etc.) were either non-significant or introduced significant concurvity in the model.

As we expected, shade tolerance and size of trees had a significant influence on probability of survival. Even quite large (100–150 cm DBH) shade tolerant species had no better than a 50–75% chance of surviving low and moderate severity fire, while medium-sized (50–100 cm DBH) shade intolerant species had a 75–90% chance of surviving low and moderate severity fire (Fig. 3). Shade tolerant species had almost no chance of surviving high severity fire—we found only two live shade tolerant individuals in high severity fire plots (a Pacific madrone and an incense cedar). Shade intolerant trees exhibited a distinctive response to fire severity that depended on the size of trees. Small shade intolerant trees (< 25 cm DBH) were vulnerable to low, moderate, and high severity fire. Shade intolerant trees > 50 cm DBH usually survived low and moderate severity fire. Only very large shade intolerant trees (> 175 cm DBH) had more than a 25% chance of surviving high severity fire (Fig. 3).

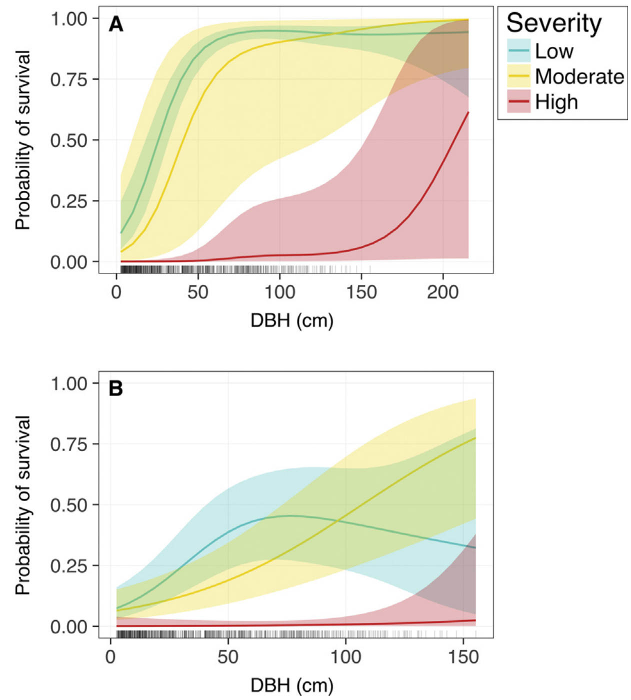

Fig. 3. Probability of survival of shade intolerant species (A) and shade tolerant species (B) by diameter. Tick marks on x axis represent individual tree DBH observations. Note different scale of x-axis. Refer to Tables 2 and 3 for information about shade tolerance.

3.2. Fire effects on tree growth

We modeled residual tree growth using tree cores from 779 live trees of 10 species in 48 plots with live trees present (Table 3). As expected, BAI was suppressed following fire, with stands burning at higher severity experiencing a greater reduction in growth.

Table 2
Sample population evaluated in survival probability models.

Code	Species	Common name	Shade tolerant	*n*
PILA	*Pinus lambertiana*	Sugar pine	N	186
PIPO	*Pinus ponderosa*	Ponderosa pine	N	3
PSME	*Pseudotsuga menziesii*	Douglas-fir	N	3194
ABCO	*Abies concolor*	White fir	Y	174
ACMA	*Acer macrophyllum*	Bigleaf maple	Y	3
ARME	*Arbutus menziesii*	Pacific madrone	Y	3
CADE	*Calocedrus decurrens*	Incense cedar	Y	203
CHCH	*Chrysolepis chrysophylla*	Golden chinquapin	Y	67
TABR	*Taxus brevifolia*	Pacific yew	Y	39
THPL	*Thuja plicata*	Western red cedar	Y	204
TSHE	*Tsuga heterophylla*	Western hemlock	Y	232

Table 3
Sample population evaluated in radial growth response models.

Code	Species	Common name	Shade tolerant	*n*
PILA	*Pinus lambertiana*	Sugar pine	N	31
PIPO	*Pinus ponderosa*	Ponderosa pine	N	3
PSME	*Pseudotsuga menziesii*	Douglas-fir	N	424
ABCO	*Abies concolor*	White fir	Y	82
ACMA	*Acer macrophyllum*	Bigleaf maple	Y	3
CADE	*Calocedrus decurrens*	Incense cedar	Y	82
CHCH	*Chrysolepis chrysophylla*	Golden chinquapin	Y	7
TABR	*Taxus brevifolia*	Pacific yew	Y	14
THPL	*Thuja plicata*	Western red cedar	Y	56
TSHE	*Tsuga heterophylla*	Western hemlock	Y	77

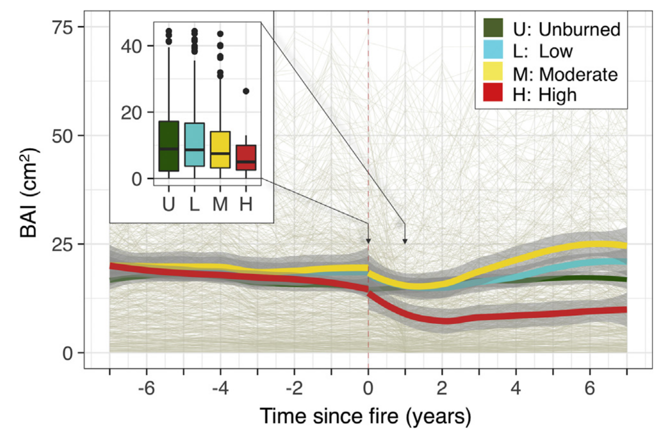

Fig. 4. Tree radial growth response to different fire severities. Light brown lines in main panel are individual tree BAI for seven years before and after fire. Heavy colored lines show smoothed means of BAI for each severity class in the years before and after fire (shown by the dashed red vertical line). Because the means are smoothed for a period before and after fire, the end point of each heavy line is not the mean of that year (see text for pre- and post-fire means). The inset box shows BAI of individual trees (cm^2) within plots burned at different severities in the year following fire (a total of 16 outlying observations are included in the calculation of means but are not shown for ease of visual interpretation). There was a statistically significant difference in mean BAI of trees burned at high severity and other severity classes ($p < 0.01$).

Independence tests indicated a statistically significant difference between pre-fire and post-fire BAI across all severity classes ($p < 0.01$). Mean BAI in unburned stands went from 16.2 cm^2 in the year before fire to 14.2 cm^2 in the year following fire, a 12% decrease. Mean BAI in stands burned at low and moderate severity went from 20.0 cm^2 to 14.6 cm^2 (a 27% decrease) and from 21.4 cm^2 to 14.4 cm^2 (a 33% decrease), respectively. Mean BAI in stands burned at high severity went from 21.1 cm^2 to 7.1 cm^2, a 66% decrease (Fig. 4).

Although there were statistically significant differences between most pairwise comparisons of BAI over time, there was no statistically significant difference between BAI of trees in unburned stands and trees in stands burned at low or moderate severity ($p \geq 0.10$) in the year following fire. There was a significant difference between BAI of trees in unburned plots and trees in plots burned at high severity ($p < 0.01$), and between trees in plots burned at low or moderate severity and trees in plots burned at high severity ($p < 0.01$).

3.3. Residual tree radial growth response to fire over time

BAI response varied significantly among different diameter classes. Small diameter (2.54–29 cm DBH) residual trees in low, moderate, and high severity plots experienced significantly greater growth as measured by BAI than trees in unburned plots, with the greatest growth response in high severity plots. Medium diameter (30–55 cm DBH) trees in plots burned at low and moderate severity experienced the same or slightly greater growth than trees in unburned plots, although this difference was not statistically significant. Medium sized trees in plots classified as high severity experienced reductions in BAI relative to unburned plots, although this difference was also not statistically significant. Large (56–80 cm) and very large (81–185 cm) trees experienced significant reductions in BAI following fire. The largest difference between BAI in burned and unburned trees was in very large trees burned at high severity, which had significantly less BAI than trees in unburned plots for up to twenty years following fire (Fig. 5).

3.4. Relationship between tree radial growth and leaf area

The best model for leaf area as evaluated with AIC and GCV included DBH, species, and severity class with fire event and plot as random effects. As expected, shade intolerant species generally had lower leaf area than shade tolerant species (Fig. 6). There was no significant difference between leaf area of trees in low severity, moderate severity, and unburned plots, but there was a statistically significant difference between leaf area in trees burned at high severity and all other severity classes after accounting for DBH and species ($p < 0.01$) (Fig. 7).

Interactions between fire severity and DBH modeled with tensor products suggested non-symmetrical relationships between fire severity and leaf area in different sized trees. There was a roughly linear relationship between tree diameter and leaf area in trees within areas burned at lower severities. In areas burned at high severity, leaf area increased as diameter increased until a certain diameter at which point leaf area declined (Fig. 8).

4. Discussion

4.1. Tree mortality and growth response to wildfire

In this paper we show that wildfire acts as an ecological filter both during and well after fire occurs, first by selecting trees for survival, and second by selecting trees for enhanced or diminished utilization of available resources for many years after fire. Specifically, fire preferentially kills shade tolerant species and smaller trees. Small trees that survive fire will experience augmented growth whereas larger residual trees generally experience growth reductions as result of fire. Fire severity classifications are useful heuristic devices, but it is often unclear to what degree different severity bins correspond to meaningful and distinctive ecological effects. We show that a widely used severity classification (MTBS) explains meaningful differences in tree-scale responses, with the most significant differential tree growth response among different sized trees observed as fire severity increases (Figs. 5 and 8).

We observed modest and short-term residual tree radial growth response to low and moderate severity fire. Our study area is dominated by Douglas-fir, and these findings suggest that Douglas-fir trees quickly recover pre-fire productivity following non-stand replacing fire. Residual trees in stands burned at high severity, in contrast, experienced significant and persistent growth reductions. Taken as a whole, our findings suggest fundamentally different ecosystem responses when fire intensity exceeds a certain threshold in Douglas-fir forests of the western Cascades.

Reduced growth in large diameter trees that survive fire is evident in our estimates of leaf area 10- and 25-years post-fire. Although radial growth suppression in residual trees following fire may be associated with root or cambial damage, this paper suggests that long-term reductions in growth are most strongly related to loss of photosynthetic material (Hood et al., 2010; Stephens and Finney, 2002). Long-term growth reductions related to crown damage are most pronounced in larger trees, presumably because trees that are at or near their maximum height do not recover photosynthetic material lost in fire as readily as younger trees that add foliage as they increase in height (Fig. 9).

GAM models are well suited to modeling complex tree radial growth responses over time in response to different fire severities. Long-term data analyzed with flexible smoothers will likely reveal important patterns in data that are obscured by short term data fit to linear models. For instance, our findings show that estimates of future forest productivity based on tree growth trends in the immediate aftermath of fire may overestimate future productivity because initial tree growth recovery trajectories may terminate below pre-fire levels and/or decline following an initial recovery.

4.2. Post-fire succession

Although focused on tree-scale ecological effects of fire, this

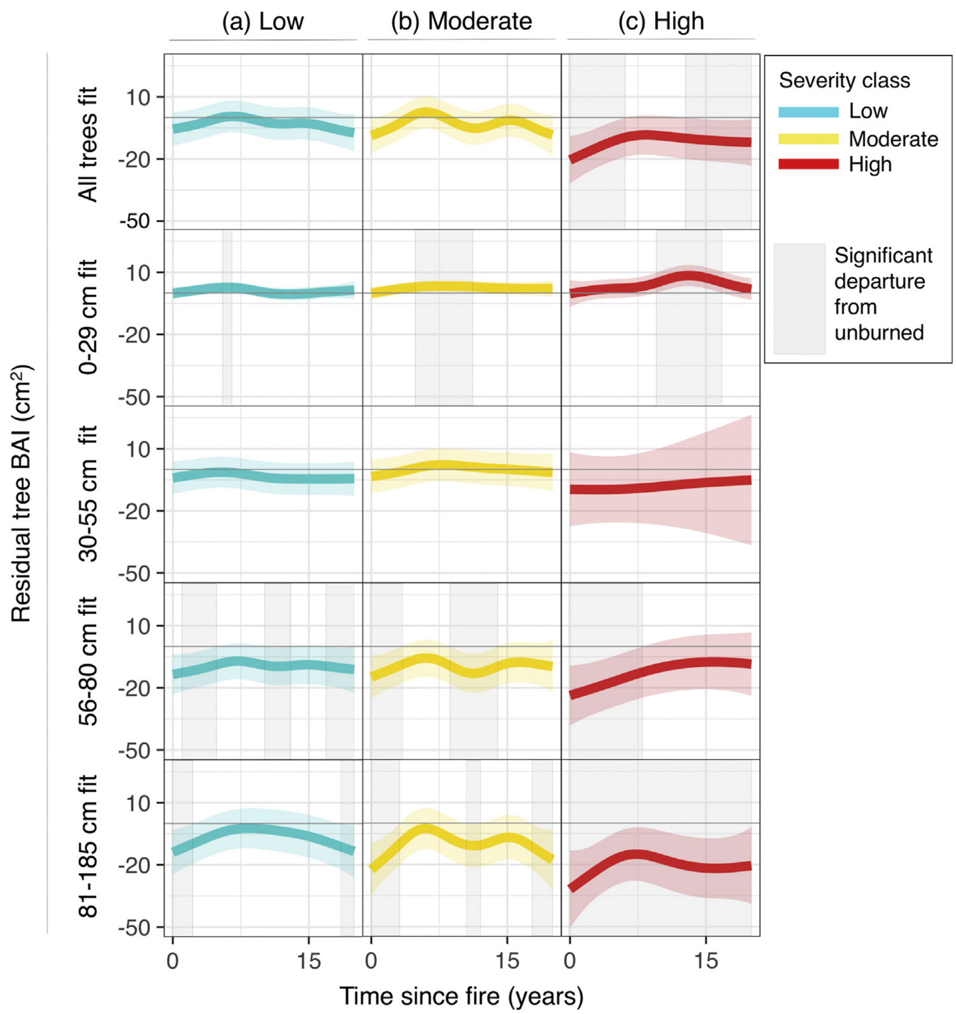

Fig. 5. Difference in modeled BAI between trees in unburned plots and residual trees within plots burned at low, moderate, and high severity within different DBH classes. The y-axis shows the basal area response fit in cm^2 by different diameter classes. Grey shaded areas indicate the time period during which different diameter classes experienced modeled radial growth that was significantly greater or less than the same diameter class of trees in unburned stands.

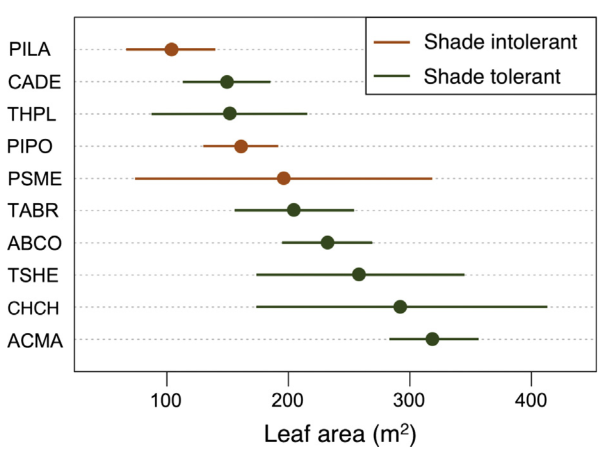

Fig. 6. Modeled leaf area of different residual tree species after accounting for DBH, fire severity, and with fire event and plot as random effects. See Table 3 for species codes and sample sizes.

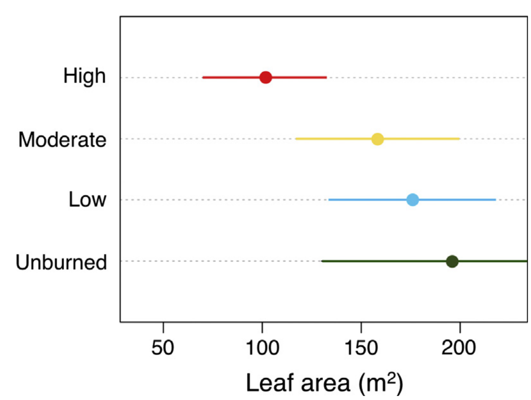

Fig. 7. Difference in leaf area modeled at time trees were sampled at different MTBS fire severities after accounting for DBH, species, and with fire event and plot as random effects. There is no statistically significant difference between modeled leaf area of trees within stands burned at moderate severity, low severity, and unburned stands ($p > 0.05$), but a significant difference between trees within stands burned at high severity and the other three severity classes ($p < 0.01$).

research has implications for stand and landscape-scale successional dynamics. The results we present suggest that fire severity alters forest stand structure not only through mortality but also via individual tree physiological responses. Slower growth in residual trees that results from fire damage may render these trees more vulnerable to mortality in the face of additional stressors (Cailleret et al., 2016; van Mantgem et al., 2003).

Conversely, slower growth rates may increase the longevity of trees

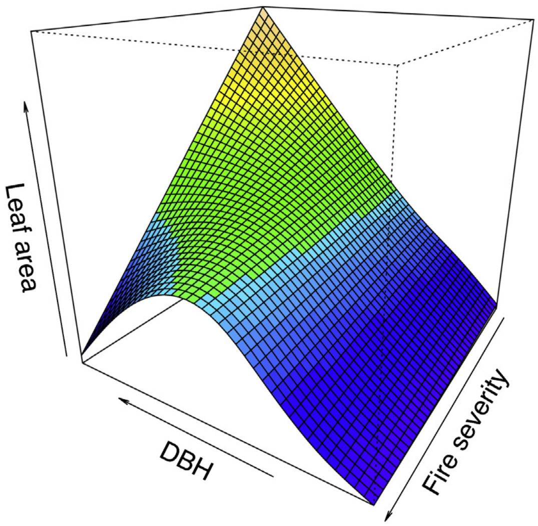

Fig. 8. Influence on leaf area index of tensor product interaction of DBH and fire severity (continuous basal area mortality) calculated for the year trees were sampled. There is a roughly linear increase in leaf area in small trees as fire severity increases. There is a strongly non-linear relationship between leaf area and fire severity in larger sized trees.

by encouraging parsimonious use of resources (Johnson and Abrams, 2009; Black et al., 2008). It is possible that the exceptional life span of Douglas-fir in our study area (trees routinely exceed 500 years of age) may be because of and not in spite of periodic fire damage. Our growth estimates come from data collected 10 and 25 years post-fire, suggesting trees that survive fire may be present long into the future as stands develop. Crown damage from moderateintensity disturbance results in complex canopy structure that may simultaneously facilitate increased growth in understory trees and the persistence of older trees (Van Pelt et al., 2016). Forest complexity that results from fire damage is potentially an important component of forest resilience to future change.

It is possible that the differential response to fire severity observed between smaller and larger trees is due to the fact that small trees are more common and small trees that exhibited a positive response to fire simply escaped significant fire effects. The time elapsed between fire and field observations makes it difficult to determine the degree to which the spatial pattern of fire influenced individual tree response to fire. However, live trees of all sizes were equally likely to have bole scorch recorded by field crews.

We believe it is most likely that fire has a more pronounced long-term effect on radial growth of tall-statured and large diameter trees than smaller trees because recovery of a tree's leaf area following disturbance is achieved primarily through height growth and the addition of new branches. Large trees at or near their maximum height potential have limited capacity to recover in this fashion, instead relying on the creation of epicormic branches and more complex crown structures to add leaf area without exceeding the tensile strength of the water columns (Van Pelt and Sillett, 2008; Ishii and Ford, 2001; Waring et al., 1982). This has important implications for wildlife species reliant on complex crown or branch structure for nesting, such as northern spotted owl or marbled murrelet (Bond et al., 2009; Ritchie, 1988; Franklin et al., 1981). Fire disturbance may be an important mechanism for creating these features and the persistence of these species in the Pacific Northwest (Fig. 9).

Although we show that MTBS severity classifications are associated with distinctive tree-scale effects, the differential response to fire of trees of different sizes and species suggests that it is important to contextualize field measured or satellite-derived severity metrics by forest structural and compositional attributes. The same fire severity as measured by standard indexes may have different implications for

Fig. 9. Fire damage to tree canopies in stands burned at high severity. Incense cedar in the Tumblebug Fire perimeter in 2018, nine years post-fire (Panel A). Douglas-fir in the Warner Creek Fire perimeter in 2018, 27 years post-fire (Panel B). Note significant loss of photosynthetic material in older trees at or near their maximum potential height. Note also that extensive crown damage appears to significantly augment the wildlife habitat potential of old trees (creating branch platforms, breakage, dead boles, etc.).

future forest dynamics depending on residual tree structure and composition. Fire intensity and individual tree resistance drive residual tree structure and composition following fire. As we continue to develop heuristics and management strategies based on fire severity maps, it becomes increasingly important that we find ways to quantify pre-fire forest structure to better understand the future trajectory of forests following disturbance.

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