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LETTER

Climatic stress increases forest fire severity across the western United States

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Abstract

Pervasive warming can lead to chronic stress on forest trees, which may contribute to mortality resulting from fire-caused injuries. Longitudinal analyses of forest plots from across the western US show that high pre-fire climatic water deficit was related to increased post-fire tree mortality probabilities. This relationship between climate and fire was present after accounting for fire defences and injuries, and appeared to influence the effects of crown and stem injuries. Climate and fire interactions did not vary substantially across geographical regions, major genera and tree sizes. Our findings support recent physiological evidence showing that both drought and heating from fire can impair xylem conductivity. Warming trends have been linked to increasing probabilities of severe fire weather and fire spread; our results suggest that warming may also increase forest fire severity (the number of trees killed) independent of fire intensity (the amount of heat released during a fire).

Keywords

Climate, fire effects, prescribed fire, tree mortality.

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INTRODUCTION

There is a growing realisation that current warming trends may be associated with increasing forest fire size, frequency and severity (the number of trees killed) across the western United States (US) (Westerling *et al.* 2006; Miller *et al.* 2009; Dillon *et al.* 2011; Williams *et al.* 2013) (but see Miller *et al.* 2012). The mechanism whereby fire severity increases in response to warming is presumed to be through greater probabilities of severe fire weather (higher air temperature and lower relative humidity resulting in lower fuel moisture) (Fried *et al.* 2008). While likely true, this view does not consider the biological context of the fire event. It has been suggested that trees subject to chronic stress are more sensitive to subsequent fire damage (van Mantgem *et al.* 2003; Woolley *et al.* 2011), implying that recent warming trends may lead to a *de facto* increase in fire severity, separate from changes that may increase fire intensity (the amount of heat released during a fire).

Warming trends may already be contributing to increasing stress on forest trees. From the late 1980s, mean annual temperature of the western US increased at a rate of 0.3–0.4 °C decade^{-1}, even approaching 0.5 °C decade^{-1} at the higher elevations typically occupied by forests (Diaz & Eischeid 2007). Warming may increase tree stress by (1) increasing water deficits and thus drought stress on trees (McDowell *et al.* 2008), (2) enhancing the growth and reproduction of insects and pathogens that attack trees (Raffa *et al.* 2008) or (3) both. Warming trends have been implicated in recent episodes of forest die-back (Breshears *et al.* 2005; Allen *et al.* 2010; Williams *et al.* 2013) and rising tree mortality rates in otherwise undisturbed forests (van Mantgem & Stephenson 2007; van Mantgem *et al.* 2009). It is possible that an additional consequence of warming is an increased sensitivity to fire.

Post-fire tree mortality is typically modelled as a function of tree defences (bark thickness) and fire injury (crown scorch extent, stem char height). These empirical models are used to predict fire effects, often as an important tool for fire management planning (e.g. FOFEM, Reinhardt *et al.* 1997). Model performance may be improved by including additional variables, such as season of fire, tree vigour, insects and pathogens, or other local conditions (Woolley *et al.* 2011), although the role of pre- and post-fire climate on tree mortality has yet to be considered.

In this article, we test how climate relates to fire severity (as measured by individual tree mortality probabilities) across coniferous forests of the western US. Previous work suggested a climate–fire severity relationship for a single species in the southern Sierra Nevada mountains of California (van Mantgem *et al.* 2003). Here, we examine if climate influences post-fire tree mortality across broad geographical locations and a variety of species.

MATERIALS AND METHODS

Data sources

In many forest types across the western US, unforeseen increases in fire risks resulting from policies of fire exclusion has led managers to use prescribed fire to reduce understory fuels and small tree densities (Stephens *et al.* 2009). We assembled prescribed fire effects monitoring data from FFI (FEAT/FIREMON Integrated, www.frames.gov/ffi), merging forest plot data across NPS units (National Parks, Monuments and Recreation Areas) in the western US into a single relational database (Fig. 1, Table S1). We included relevant plot data from another national-scale prescribed fire data set, the Fire and Fire Surrogate project (Schwilk *et al.* 2009). Prescribed fire

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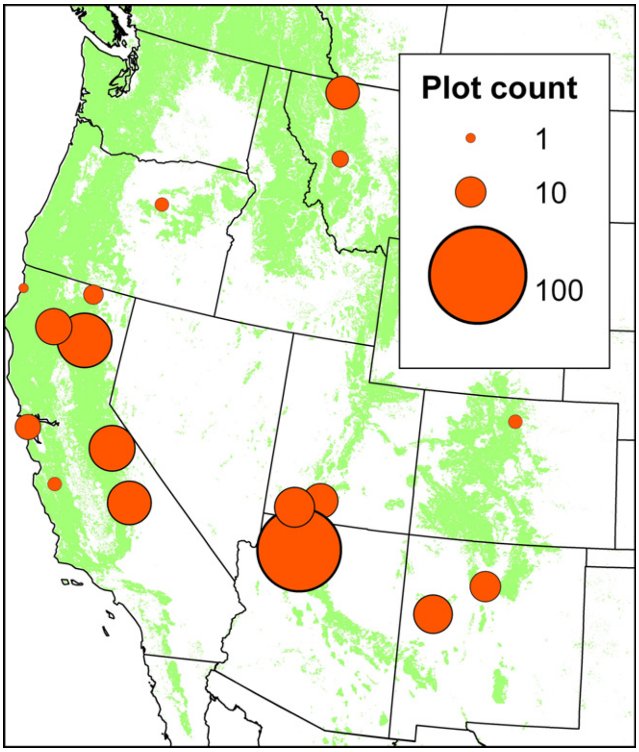

Figure 1 Locations of management units with qualifying pre- and post-burn data. Symbol size is scaled to the number of monitoring plots per management unit. Forest cover is shown in green.

data are particularly well suited to exploring the relationship between climate and fire severity because prescribed fires are conducted over a relatively narrow range of fire weather but over a potentially wide range of interannual climatic conditions.

These surveys captured plot data (0.1 ha for the FFI data set and 1.0 ha for the Fire and Fire Surrogate data set) from 1984 to 2005 where individual trees were tagged, identified to species and measured for diameter (DBH, diameter at breast height, 1.37 m) prior to treating the areas with prescribed fire. The extent of fire-caused injuries [percentage crown volume scorched and stem scorch height (m)] and post-fire mortality were recorded typically within a month following the prescribed fires. We limited our analyses to trees that were recorded as alive prior to burning within plots with 5-year post-fire survey data (3 years for the Fire and Fire Surrogate data set) to capture delayed post-fire tree mortality (van Mantgem *et al.* 2011).

To estimate climate associated with individual sites (most of which lie in complex mountainous terrain without adjacent weather stations), we used the transient 800-m data set from the Parameter-elevation Regression on Independent Slopes Model (PRISM, www.prism.oregonstate.edu) (Daly *et al.* 2008). PRISM uses instrumental observations and a digital elevation model, making adjustments for features such as elevation, aspect, slope and rainshadows. We used the PRISM-derived monthly maximum and minimum air temperature and precipitation to drive a regional water balance model (Basin Characterisation Model, Flint & Flint 2012b) to calculate annual climatic water deficit (annual evaporative demand that exceeds available water). For our estimate of annual climatic water deficit, we downscaled the 800-m PRISM outputs to 270-m using a gradient-inverse-distance-squared approach that incorporates northing, easting and elevation (Flint & Flint 2012a). Climatic water deficit is calculated as potential minus actual evapotranspiration (PET – AET). Potential evapotranspiration is determined hourly using a rigorous energy-balance calculation that includes topographic shading and cloudiness, and then aggregated monthly. Actual evapotranspiration relies on the monthly water balance calculations and is determined on the basis of changes in soil water content. As a result, deep soils provide storage of winter precipitation and maintain lower climatic water deficits during the summer dry season. Shallow soils are limited in their storage capacity, so excess winter precipitation is lost to runoff, resulting in greater annual deficits (Flint & Flint 2012b). The climatic water deficit provides a biologically meaningful index of drought (Stephenson 1990) and is strongly correlated with changing tree mortality rates in unburned forests (van Mantgem & Stephenson 2007; van Mantgem *et al.* 2009).

Data quality assurance

The range of each numeric field in our data set was checked to ensure that all values fell within an appropriate range [e.g. stem char height < 75 m, DBH < 500 cm (with the exception of *Sequoia* and *Sequoiadendron*)] and that measurements were taken on a consistent scale (e.g. cm vs. m). Other errors that were identified included trees with multiple species listed on separate records, multiple observations of the same tree recorded on the same day, illogical changes in DBH over repeated measurements and inconsistent measures of tree status through time (i.e. trees listed as live after being listed as dead). Prescribed fire dates were checked for inconsistencies against dates when fire damage was recorded. Once errors were identified, we contacted data managers to correct as many problems as possible. Trees that included errors which could not be corrected were excluded from analysis, representing approximately 10% of the total data set. We were specifically interested in trees that had experienced fire, so we only used data from trees that had complete records for crown volume scorched and stem char height. The final data set included 7117 trees from 251 plots located in 17 separate management units across seven Western states.

Data analysis

We used linear mixed models (Gelman & Hill 2007) to evaluate temporal trends in climate during the years of observation at our plots (1984–2005). We modelled patterns in post-fire mortality probabilities using generalised nonlinear mixed models (GNMM). This approach allowed us to analyse non-normal demographic data [based on tree status, live or dead, (using a logit link function)], and consider both individual-level effects (individual tree characteristics and observations of fire-caused injury) and grouping effects (plot identity).

Mortality probabilities were estimated by annual compounding over the post-fire observation length. Specifically, tree status S_{ij} (0 = live, 1 = dead) of tree i in plot j was modelled as the inverse of an annual survival probability ($1–p_{ij}$) compounded over the years between the initial and final plot survey (t_j):

$$S_{ij} \sim \text{Bernoulli}(1-(1-p_{ij})^{t_j}) \quad (1)$$

Our base model estimated tree mortality probabilities from a combination of linear predictors related to measurements of individual tree defence and fire-caused injury:

$$\text{linpred}_{ij} = \beta^0 + \beta^{BT} \cdot \text{BT}_{ij} + \beta^{PCVS} \cdot \text{PCVS}_{ij} + \beta^{CH} \cdot \text{CH}_{ij} \quad (2)$$

where BT is bark thickness (log transformed), PCVS is percentage crown volume scorch (rounded to 5% values to reduce false precision) and CH is stem char height. Bark thickness was estimated from stem diameter using allometric relationships found in the Forest Vegetation Simulator model (Dixon 2002). We subsequently evaluated improvements to this model with the addition of climatic variables (see below), including interaction effects. For any tree *i*, the regression prediction can be written as follows:

$$p_{ij} = \text{logit}^{-1}(\text{linpred}_{ij} + \alpha_j^{\text{plot}}), \alpha_j^{\text{plot}} \sim N(0, \sigma^2_{\text{plot}}) \quad (3)$$

We also considered varying-intercept, varying-slope models, but these formulations did not improve model performance. Parameters were estimated using a Bayesian approach with Monte Carlo Markov Chains in the R statistical language and JAGS (mcmc-jags.sourceforge.net, accessed June 26, 2012) with the CODA package (Plummer *et al.* 2006). For each model, we used uninformative priors and 31000 iterations of three model chains, with parameters estimated after removing the first 1000 samples and a thinning rate of 0.9666 (yielding 3000 posterior estimates for each parameter). Model convergence was assessed using visual inspection of trace-plots, and from Gelman-Rubin and Geweke's convergence diagnostics. The thinning rate was determined from autocorrelation plots for each parameter.

We considered the effect of climate variables (temperature, precipitation and climatic water deficit) in terms of relative changes from long-term averages, calculated by the 5-year interval (pre- or post-fire) divided by the 30 year average (1975 to 2005, 2005 is the year for the most recent fire ignition) for each climate variable. For example, pre-fire relative climatic water deficit (rD) was calculated by dividing the 5-year pre-fire average climatic water deficit by the thirty year average climatic water deficit. Qualitatively similar results were obtained with different reference periods (e.g. 3-year pre-fire interval, 50 year averages) and absolute differences between these periods (e.g. 5-year interval minus the 30 year average). We also considered calendar year of prescribed fire ignition to test for trends in mortality probabilities over time. All numeric predictor variables were standardised by subtracting from the average value to aid model fitting and interpretation. We examined systematic differences among broad geographical regions (California, the Colorado Plateau, and the Rocky Mountains), major genera (*Abies*, *Pinus*, and all other remaining genera) and two tree size classes (< 40 and ≥ 40 cm DBH). Assuming a lognormal distribution of stem sizes, the ≥ 40 cm DBH class approximates the largest 25% of trees in our sample. We used indicator variables to represent these groups in our models, with their importance assessed by estimating interactions with climate variables.

Model selection was done using the Deviance Information Criterion (DIC) (Gelman & Hill 2007), similar to the well-known Akaike Information Criterion (Burnham & Anderson 2002). Differences in DIC (ΔDIC) > 2 were used as evidence of substantial model dissimilarity. We used the area under the receiver operating characteristic curve (AUC) (Saveland & Neuenschwander 1990) to characterise candidate model accuracy (predicted proportions of Type I and Type II errors), with values of AUC > 0.80 suggesting excellent model accuracy (Hosmer & Lemeshow 2000). Model fit was checked by binning the data and plotting average predicted mortality probability against the observed proportion of dead trees (for all models expected average probabilities and observed mortality proportions were highly correlated, $R^2 > 0.9$).

RESULTS

For the years of observations (1984 to 2005) linear mixed models revealed that average climatic water deficits increased ($\beta_{\text{Year}} = 1.42$, 95% Credible Interval = 1.01 to 1.82), largely as a result of increasing average temperatures ($\beta_{\text{Year}} = 0.045$, 95% Credible Interval = 0.043 to 0.048) (trends in precipitation were poorly described by linear models) (Fig. S1). At the study sites this period contained the highest sustained average temperatures and water deficits estimated over the past 50 years.

Although the base model provided excellent discrimination (AUC = 0.90), model selection using DIC suggested models of post-fire mortality were improved by including terms for pre-fire climatic water deficit, relative to the long-term average (rD) (Table 1). The inclusion of a term for pre-fire temperatures provided similar, but less pronounced, improvements to the base model. Terms for post-fire climate did not predict post-fire mortality. Our models suggest that the influence of pre-fire rD on mortality was primarily through positive interactions with crown scorch and char height (Table 2). While the lower boundary of the 95% Credible Interval for the interaction term of char height and rD is negative, the appropriate one-tailed criteria supports the inclusion of this term (i.e. 96% of its estimated distribution is > 0) (Fig. 2). Holding all other variables at average values, our model that includes interactions between crown scorch and rD, along with interactions between stem char height and rD predicts average annual post-fire mortality probability is 3.2%. Under these conditions, increasing pre-fire rD to 2 SD above average conditions our model predicts an average annual post-fire mortality probability of 4.5% (an approximate increase of 41%). Year of ignition was not related to post-fire mortality probabilities ($\beta_{\text{Ignition year}}$ 95% Credible Interval = −0.06 to 0.03), although our data contain a trend towards increasing pre-fire water deficit with ignition year (Fig. S2).

The influence of pre-fire climatic water deficit on post-fire mortality was pervasive throughout our observations. Categorical terms

Table 1 Selection of generalised nonlinear mixed models (GNMM) for post-fire tree mortality using the Deviance Information Criterion (DIC). A difference in DIC (ΔDIC) > 2 was used to determine a substantial difference in model performance. BT represents bark thickness estimated from stem diameter, PCVS represents percentage crown volume scorch, CH represents stem char height, and rD represents relative Deficit (5-year average climatic water deficit relative to the 30 year average, pre- or post-fire ignition)

Model class	Model predictors	DIC	ΔDIC
Base model	BT + PCVS + CH	4774.9	8.8
Pre-fire climate	BT + PCVS + CH + rD	4772.6	6.5
	BT + PCVS*rD + CH	4768.0	1.9
	BT + PCVS + CH*rD	4767.9	1.8
	BT + PCVS*rD + CH*rD	4766.1	0.0
	BT + PCVS*CH*rD	4768.4	2.3
Post-fire climate	BT + PCVS + CH + rD	4775.4	9.3
	BT + PCVS*rD + CH	4777.9	11.8
	BT + PCVS + CH*rD	4774.3	8.2
	BT + PCVS*rD + CH*rD	4775.1	9.0
	BT + PCVS*CH*rD	4776.2	10.1

Table 2 Individual-level effects of a GNMM model of annualised post-fire tree mortality probabilities, including pre-fire relative Deficit. Names of individual-level effects follow Table 1. Predictor variables were standardised to aid interpretation. Mean parameter estimates, standard deviations and 95% Credible Intervals (CI) were derived from 3000 samples of the posterior distribution

Individual-level effect	Estimate	Std. Dev.	95% CI
BT	−1.57	0.12	−1.82 to −1.34
PCVS	0.02	0.00	0.02 to 0.03
CH	0.09	0.01	0.06 to 0.12
rD	1.25	0.86	−0.47 to 2.97
PCVS*rD	0.02	0.01	0.00 to 0.03
CH*rD	0.16	0.09	−0.02 to 0.34

for geographical region (California, Colorado Plateau and Rocky Mountains) did not influence terms for rD or interactions between fire-caused injury and rD (e.g. $\beta_{rD*Colorado\ Plateau}$ 95% Credible Interval = −2.45 to 3.93, with the California region as the baseline condition). We were unable to detect systematic differences in the influence of climate across major genera (*Abies*, *Pinus*, and all other remaining genera) (e.g. $\beta_{rD*Pinus}$ 95% Credible Interval = −0.43 to 2.34, with all other remaining genera as the baseline condition). Small (< 40 cm DBH) and large trees (≥ 40 cm DBH) were found to have similar sensitivities to pre-fire rD (e.g. $\beta_{rD*Large\ trees}$ 95% Credible Interval = −0.66 to 2.26, with small trees as the baseline condition). In all cases, more than 5% of samples from the posterior distributions for interactions between rD and categorical terms for geographical region, genera and tree size were < 0.

DISCUSSION

Our findings show post-fire tree mortality of coniferous trees was influenced by climate across the western US, describing what appears to be a general, but overlooked, climate–fire relationship. This relationship appeared to be consistent across broad geographical regions, major genera and tree sizes. Climate was predictive of tree mortality after accounting for fire damage and defences, supporting conceptual models of tree mortality that account for combined effects of multiple long- and short-term stressors (Franklin *et al.* 1987; Manion 1991). In our case, longer term climatic stress (5 years prior to fire) predisposed trees to be killed from short-term fire damage. Pervasive warming can be expected to increase the incidence of high severity fire by creating conditions where lower fuel moisture results in fires of higher intensity. An important implication of our results is that chronic stresses on western forests, including continued warming, may also lead to *de facto* increases in fire severity independent of changes in fire intensity.

Our finding that drought stress (measured by climatic water deficit) and fire interact to determine post-fire mortality is supported by recent physiological studies. While the exact mechanisms underlying

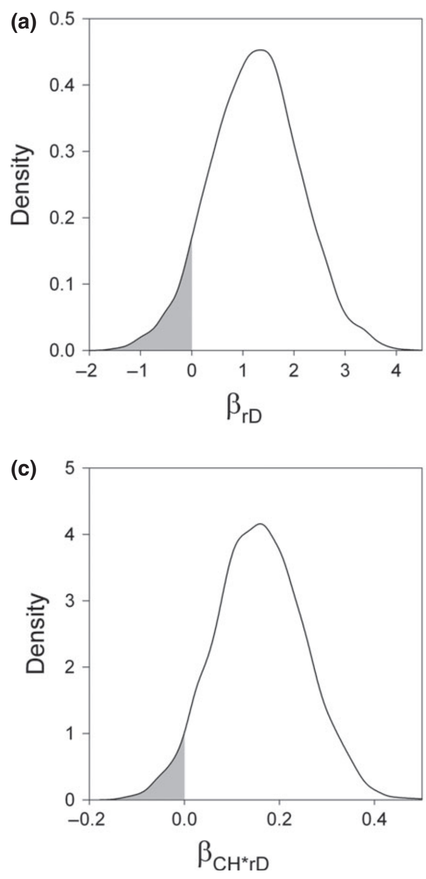

Figure 2 Densities of 3000 samples from the posterior distributions of GNMM parameters (β) relating post-fire tree mortality probability to pre-fire average climatic water deficit, relative to the 30 year average (rD). The main effect (β_{rD}) had 93% of samples > 0 (a), while density distributions for interactions between percentage crown volume scorched and pre-fire rD (PCVS*rD) (b) and stem char height and pre-fire rD (CH*rD) (c) had over 95% of samples > 0. Grey regions show density of samples where β < 0.

drought-induced tree mortality are unclear (McDowell 2011), evidence from trembling aspen (*Populus tremuloides*) shows that multi-year drought leads to compromised repair of xylem elements (a process termed 'cavitation fatigue') and increased susceptibility to subsequent drought (Anderegg *et al.* 2013). While heat from fires causes direct necrosis of plant tissues, Michaletz *et al.* (2012) have shown that fire may also lead to reductions in water conductivity within trees due to cavitation and deformation of xylem elements. In addition, Kavanagh *et al.* (2010) suggest that heat plumes from fires increase evaporative demand to an extent where cavitation may occur in the xylem of canopy branches. These processes imply that when water deficits are high, trees may be more prone to loss of xylem function (cavitation) from fire because xylem repair mechanisms may be compromised and/or water supply may be insufficient to compensate for high rates of moisture loss from leaves. Understanding the linkages among climate, tree health, fire damage and pathogen activity remains an unresolved barrier in our ability to predict the effects of fire in coming decades (although progress has been made in creating physiologically based models of fire-caused tree mortality, Michaletz & Johnson 2008).

Other factors, not considered here, will also determine post-fire tree mortality. Bark beetles and pathogens may respond directly to climatic changes, and may amplify the effects of drought stress and fire (Raffa *et al.* 2008). Competitive effects from neighbouring trees may weaken trees prior to fire (Woolley *et al.* 2011), an effect that may be particularly acute in forests that have experienced long-term fire exclusion. A potential limitation of our data set is that it was derived entirely from prescribed fires, requiring further work to verify these relationships in unmanaged fires. A more complete description of post-fire tree mortality will likely require not only additional measurements but also a more complex modelling framework that accommodates direct and indirect effects. Climatic effects will be a partial determinant of overall pre-fire tree health, which will also be influenced by other local conditions (e.g. neighbourhood crowding, light and soil environment, pathogen pressures).

Disturbance is a common feature of natural systems, but escalating frequency of tree mortality from fire may lead to substantial changes in forest structure and function, including increased carbon emissions (Meigs *et al.* 2009). These emissions represent a potentially large positive feedback to current warming trends (Bowman *et al.* 2009). The warming experienced so far across much of our study region is small compared to expected future conditions (Seager & Vecchi 2010), so even small contributions of the current climate to fire severity has profound implications for forest conservation. For example, these relationships are not built into current fire planning tools (Reinhardt *et al.* 1997) such that mounting climatic stress and subsequent fire-caused mortality may lead to inadvertent occurrences of prescribed fire with more severe effects than expected. Higher severity fire may not be a negative outcome in all cases. In many areas, fire exclusion has likely allowed the establishment of high numbers of small trees (e.g. Lydersen & North 2012). It may be possible for managers to intentionally increase tree mortality from prescribed fires to meet forest structural objectives if ignitions are timed to coincide with drier conditions. Of equal importance, our study highlights the need to maintain plot-based forest monitoring networks to assess effects on individual trees, which complement remotely sensed fire monitoring efforts (Key 2006). Our work suggests that ongoing environmental changes are contributing to chronic and acute stress to forests, consistent with other findings worldwide (Lewis *et al.* 2004; van Mantgem *et al.* 2009; Allen *et al.* 2010).

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STATEMENT OF AUTHORSHIP

All authors designed the study and organised data. PvM and JN analysed the data. PvM wrote the article with contributions from all authors.

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