



Tree mortality patterns following prescribed fire for *Pinus* and *Abies* across the southwestern United States

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ABSTRACT

The reintroduction of fire to historically fire-prone forests has been repeatedly shown to reduce understory fuels and promote resistance to high severity fire. However, there is concern that prescribed fire may also have unintended consequences, such as high rates of mortality for large trees and fire-tolerant *Pinus* species. To test this possibility we evaluated mortality patterns for two common genera in the western US, *Pinus* and *Abies*, using observations from a national-scale prescribed fire effects monitoring program. Our results show that mortality rates of trees >50 DBH were similar for *Pinus* (4.6% yr⁻¹) and *Abies* (4.0% yr⁻¹) 5 years following prescribed fires across seven sites in the southwestern US. In contrast, mortality rates of trees ≤50 cm DBH differed between *Pinus* (5.7% yr⁻¹) and *Abies* (9.0% yr⁻¹). Models of post-fire mortality probabilities suggested statistically significant differences between the genera (after including differences in bark thickness), but accounting for these differences resulted in only small improvements in model classification. Our results do not suggest unusually high post-fire mortality for large trees or for *Pinus* relative to the other common co-occurring genus, *Abies*, following prescribed fire in the southwestern US.

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1. Introduction

Across many forest types in the western US fire exclusion has resulted in unforeseen changes, including high fuel accumulations, high densities of small trees and increasing dominance of fire-intolerant species. These changes are particularly acute in forests that historically experienced high frequency and low severity fires (Allen et al., 2002; Brown et al., 2004; Agee and Skinner, 2005; Noss et al., 2006). In response, land managers have used prescribed fire (sometimes in combination with mechanical thinning) to reduce understory fuels and small tree densities. Important to many of these operations is the preservation of large overstory trees, particularly of fire-tolerant species. These trees are key structural elements (Van Pelt and Sillett, 2008; Rambo and North, 2009; Lutz et al., 2012) thought to enhance forest resilience to future fires (Brown et al., 2004; Agee and Skinner, 2005). Prescribed fire has been generally successful at reducing understory fuels (e.g., Stephens et al., 2009), yet there is concern that these management actions may be unintentionally causing high mortality of large

overstory trees, particularly of fire-tolerant species (i.e., *Pinus* species) (Kolb et al., 2007; Hood, 2010).

Large trees are expected to resist fire-caused injuries due to thick bark and high crown base heights (Ryan and Reinhardt, 1988; Hood et al., 2008; Woolley et al., 2011). However, fire exclusion can create conditions that result in lethal fire-caused injuries to large trees, particularly from heavy build-up of duff layers at the base of trees, where smoldering combustion can lead to cambial and root injury (Swezy and Agee, 1991; Varner et al., 2007; Hood, 2010; Nesmith et al., 2010). Other work has suggested that the vascular architecture and metabolic demands of large trees may put them at risk following fire-caused injuries (see references in Kolb et al., 2007). Repeated burning of fire scars (catfaces) on large trees may also lead to cambial damage, potentially increasing mortality probabilities (Hood, 2010). Reduced vigor as a result of dense forest conditions has also been speculated to negatively affect post-fire survivorship (Woolley et al., 2011). Regardless of the cause, the potential loss of large trees represents a barrier to the wider use of prescribed fire.

Independent of tree size, there are also expected differences in fire-tolerances among species. Variability among species in fire-caused mortality rates are thought to be primarily controlled by differences in characteristic bark thicknesses, with fire-tolerant species producing thicker bark at a given stem diameter than fire-intolerant species (Ryan and Reinhardt, 1988; Hood et al.,

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2008). Common *Pinus* species such as ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*) and sugar pine (*P. lambertiana*) tend to have thick bark compared to co-occurring conifers (e.g., white fir, *Abies concolor*) (Reinhardt and Crookston, 2003). Other traits may confer additional resistance, such as the large, fire-resistant buds found in *P. ponderosa* and *P. jeffreyi* which may allow foliage regrowth following fire (see references in Hood, 2010). It is possible that other, more subtle, effects may also partially determine among species differences in post-fire mortality. For example, bark beetles (Coleoptera: Scolytidae) target particular species groups, amplifying fire-caused damage and increasing post-fire mortality (Schwiik et al., 2006; Raffa et al., 2008). Other pathogens such as white pine blister rust (*Cronartium ribicola* J.C. Fisch. ex Raben) may weaken five-needled pines (e.g., *P. lambertiana*), resulting in increased sensitivity to fire [although a recent study did not find evidence of this relationship (Nesmith et al., 2010)]. Managers can use knowledge of these differences in fire tolerances to achieve stand structural objectives in burn plans (e.g., to increase the representation of *Pinus* relative to *Abies* in mixed stands following prescribed fire).

In spite of these general patterns there is concern that prescribed fire, frequently conducted as a restoration treatment, may lead to high levels of mortality for large trees, including fire tolerant species. Critically assessing this possibility is fundamental to adaptive management, but has been hindered by the lack of large-scale, long-term monitoring data. The National Park Service (NPS) has a long history of using prescribed fire for fuels and vegetation management and, importantly, has also developed a comprehensive program to monitor outcomes of these treatments (NPS, 2003). These datasets have been created and maintained by individual parks to address local management issues (e.g., Keifer et al., 2006), but surprisingly have not been compiled before to address broad-scale questions. In this paper we use NPS monitoring data from across the southwestern US to test for differences in prescribed fire effects for large and small trees from two important genera, *Pinus* and *Abies*. Specifically, we compare prescribed fire outcomes for these two genera in terms of changes in size structure and mortality patterns, and determine how these patterns vary across tree size classes, broad biogeographical regions, and year of prescribed fire.

2. Methods

2.1. Data sources

We assembled fire effects data from the FFI (FEAT/FIREMON Integrated, www.frames.gov/ffi), merging plot data across NPS units (National Parks, Monuments and Recreation Areas) in the southwestern US into a single relational database. We limited our analyses to NPS units that had records for both *Pinus* and *Abies*, plots with 5-year post-fire survey data (to capture delayed post-fire tree mortality; van Mantgem et al., 2011), and trees ≥ 15 cm DBH (diameter at breast height, 1.37 m) that were recorded as alive prior to burning. We excluded from analyses plots that were established but not burned (i.e., 'control' plots). Year of ignition ranged from 1984 to 2004. The seven NPS units that met these criteria were Bandelier National Monument, Bryce Canyon National Monument, Grand Canyon National Park, Lassen Volcanic National Park, Sequoia National Park, Whiskeytown National Recreation Area, and Yosemite National Park, spanning 5° latitude and 16° longitude (Fig. 1 and Table 1).

Standard NPS fire monitoring protocols include the establishment of 50 × 20 m (0.1 ha) plots at random locations within prescribed fire burn units prior to burning (NPS, 2003). Within each plot all live trees ≥ 15 cm DBH are tagged, measured for diameter,

and identified to species. Immediately following the burn (typically within a few months) crown volume scorch (%) and stem char height (m) are measured for each tagged tree. Trees are assessed for mortality (no green needles) immediately post-fire and 5 years post-fire.

2.2. Data quality assurance

The range of each numeric field was checked to make sure all values fell within an appropriate range (e.g., stem char height < 75 m, DBH < 500 cm) and were measured on the same scale (e.g., cm versus 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 time, and inconsistent measures of tree health status through time (e.g., trees listed as live after being listed as dead). Burn dates were checked against dates when fire damage was recorded for inconsistencies. Once errors were identified, we contacted site managers to correct as many problems as possible. Trees that included errors or missing data were excluded from analysis, comprising approximately 13.5% of trees. Our final data for analysis included 185 plots and 5421 trees, with 2677 *Pinus* and 1694 *Abies*.

2.3. Analyses

We calculated post-fire mortality rates for all species, and for the genera *Pinus* and *Abies*. We did not further consider the effects of burning on less common genera (e.g., *Calocedrus*, *Juniperus*, *Picea*, *Pseudotsuga*, and *Sequoia*) as they lacked large sample sizes or large geographic ranges. We assessed post-fire changes in species composition using χ^2 tests to determine differences in relative abundances of *Pinus* versus *Abies*. We calculated post-fire mortality rates for broad geographic regions (California and Colorado Plateau). We used the same procedures to test changes in species proportions for stems >50 and ≤ 50 cm DBH. The 50 cm DBH cut point roughly corresponds to the 75th percentile of stem diameter using a negative exponential distribution (the 76th and 79th percentile for NPS units in California and the Colorado Plateau, respectively) and allowed for sufficient sample sizes for mortality rate calculations for *Pinus* and *Abies*. We also calculated post-fire mortality rates for trees that were >80 cm DBH, stems that were likely stand dominant or co-dominants (approximately the 90th percentile of stem size for California and Colorado Plateau regions).

We determined differences in stem diameter distributions for *Pinus* and *Abies* before and 5 years following burning using a departure index, M , similar to the Gini coefficient, but able to distinguish both the magnitude and direction of change (Menning et al., 2007), written as:

$$M = \left(\frac{2}{k-1} \right) \sum_{i=0}^n \left[\left(\frac{\hat{f}_i}{n_f} - \frac{f_i}{n_f} \right) (k+1-i) \right] \quad (1)$$

where k is the number of bins (size classes), f_i is the count of trees in bin i for the test distribution, n_f is the total count of trees in all bins in the test distribution (\hat{f} and n_f represent these values for the reference distribution). We calculated M for pre-fire versus the 5-year post-fire censuses. Changes in *Pinus* and *Abies* diameter class distributions were compared using a paired permutation test.

We modeled patterns in post-fire mortality probabilities for *Pinus* and *Abies* using generalized linear mixed models (GLMM) (Gelman and Hill, 2007). This modeling approach allowed us to analyze non-normal demographic data [based on tree status, live or dead, (using a logit link function)], considering both individual-level variables (characteristics of individual trees and fire-caused injury) and group-level variables (plots nested within NPS

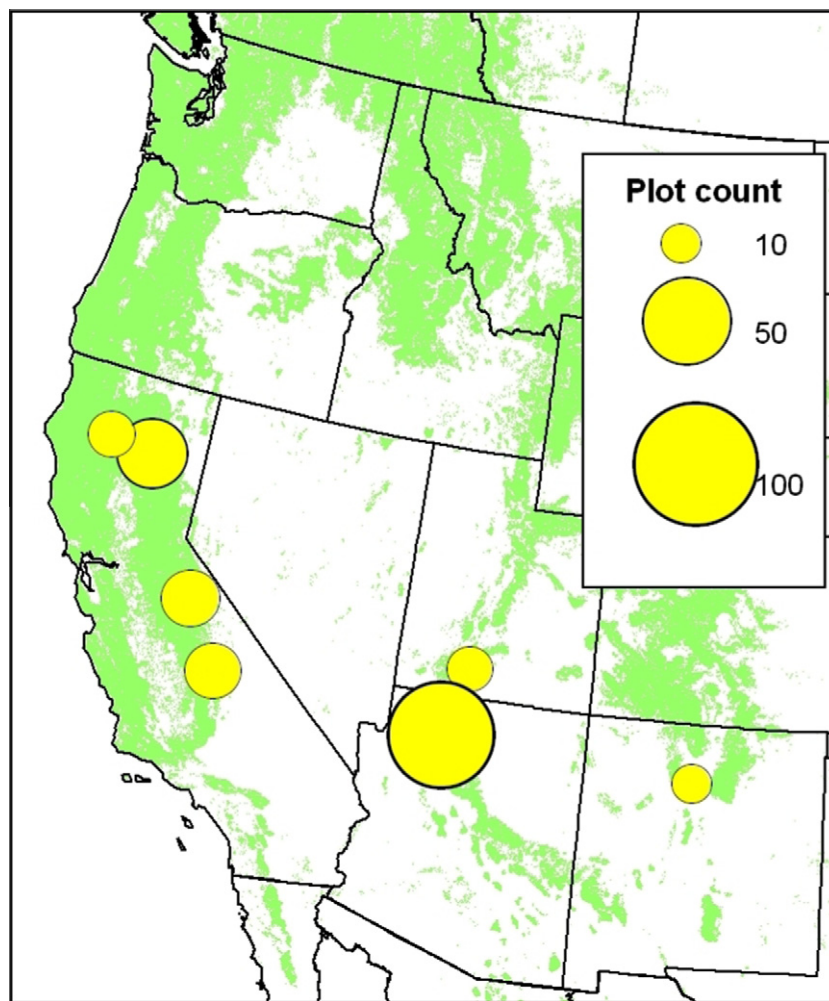


Fig. 1. Locations of NPS units with qualifying pre- and post-burn data for *Pinus* and *Abies*. Symbol size is scaled to the number of monitoring plots per NPS unit. Forest cover is shown in green. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

unit). We were specifically interested in differences in fire-caused mortality between *Pinus* and *Abies*, so we only used observations that had complete records for stem char height and crown volume scorch. One large (66.2 cm DBH) *Abies* that died following fire was excluded from this analysis because it was found to have a disproportionate influence on model fit (though very similar results were obtained when this tree was included). For predictors of individual tree mortality we used bark thickness estimated from species specific equations in Reinhardt and Crookston (2003), crown volume scorch (rounded to 10% values to avoid false precision), measurements of stem char height, and genera (*Pinus* or *Abies*). We also tested terms for geographic region (California and Colorado Plateau) and for calendar year of prescribed fire ignition. We conducted additional analyses on *P. ponderosa* and *P. jeffreyi*, which were found to have significant differences in patterns of post-fire mortality independent of tree size compared to other members of the *Pinus* group. Numeric values for individual-level predictors of mortality were standardized by subtracting by the sample mean. As a visual aid to our analyses, we graphed changes in mortality rate over time, with plot records grouped into 5-year bins to obtain a sufficient number of trees to calculate rates. Note that these graphs use different sampling plots over time to determine mortality rates, so that trends can arise from several different causes (i.e., there is a possible site-switching bias, Hall et al., 1998).

Model selection was done using the Akaike information criterion adjusted by sample size (AIC_c) (Burnham and Anderson,

2002). A difference >2 in AIC_c was used as the cut-point to indicate substantial improvement in model performance. Standard deviations, P -values, and 95% confidence intervals for parameter estimates were created from 1000 bootstrapped samples of the final models. We used the area under the receiver operating characteristic (ROC) curve (Saveland and Neuenschwander, 1990) to determine the sensitivity [the number of correctly classified trees (predicted live or dead) versus the number of type I and type II errors] of the candidate models, with values for the area under the ROC curve (AUC) >0.80 suggesting excellent model discrimination (Hosmer and Lemeshow, 2000).

3. Results

Averaged across all seven NPS units, the *Pinus* group was dominated by *P. ponderosa*, accounting for 71% of all individuals (Table 1). Other *Pinus* species and their respective stem density percentages were *P. edulis* (10%), *P. contorta* (6%), *P. attenuata* (5%), *P. lambertiana* (5%), and small numbers of *P. jeffreyi* and *P. flexilis* ($\leq 2\%$). The *Abies* group was dominated by *A. concolor* (97%), but also included *A. magnifica* (2%) and small numbers of *A. lasiocarpa* (1%). *P. ponderosa* was the dominant species in terms of stem density at two of the three NPS units in the Colorado Plateau region, whereas *A. concolor* dominated three of the four NPS units in the California region (Table 1). Other than differing dominant conifer

Table 1

Characteristics of National Park Service (NPS) units, with among plot averages and range (in parentheses) for stem diameters, fire injuries, and year of prescribed fire ignitions.

NPS unit	Latitude	Longitude	Plot count	Live tree count ^a	DBH (cm)
Bandelier	35.78	–106.33	10	203	26.6 (15–60)
Bryce Canyon	37.58	–112.18	13	380	28.6 (15–80)
Grand Canyon	36.18	–112.67	74	2036	32.9 (15–120)
Lassen Volcanic	40.49	–121.41	32	1234	32.4 (15–170)
Sequoia	36.51	–118.58	20	566	41.6 (15–296)
Whiskeytown	40.61	–122.60	14	445	29.5 (15–143)
Yosemite	37.85	–119.56	22	557	39.9 (15–179)

NPS unit	Crown volume scorch (%)	Stem char height (m)	Burn year
Bandelier	37 (0–100)	1.5 (0–11)	1994 (1994–1998)
Bryce Canyon	28 (0–100)	1.1 (0–18)	1996 (1995–2001)
Grand Canyon	22 (0–100)	2.4 (0–30)	1998 (1992–2004)
Lassen Volcanic	25 (0–100)	2.0 (0–20)	1996 (1990–2002)
Sequoia	21 (0–100)	2.4 (0–27)	1991 (1984–1995)
Whiskeytown	14 (0–100)	1.4 (0–20)	1995 (1994–1996)
Yosemite	25 (0–100)	1.2 (0–13)	1995 (1991–2002)

NPS unit	Species comprising ≥1% of stems ^b
Bandelier	PINPON 89%, ABICON 6%, PSEMEN 4%
Bryce Canyon	ABICON 49%, PINPON 22%, PSEMEN 22%, PINFLE 5%, JUNSCO 2%
Grand Canyon	PINPON 67%, ABICON 9%, PINEDU 9%, JUNOST 7%, POPTRE 4%, PICENG 2%, ABILAS 1%, PSEMEN 1%
Lassen Volcanic	ABICON 50%, PINPON 28%, PINCON 12%, CALDEC 5%, PINJEF 4%
Sequoia	ABICON 43%, CALDEC 16%, PINLAM 15%, SEQGIG 13%, PINPON 9%, ABIMAG 2%, QUEKEL 2%
Whiskeytown	PINATT 30%, QUEKEL 25%, ABICON 19%, PINPON 12%, PINLAM 10%, QUECHR 2%, PSEMEN 1%
Yosemite	ABICON 35%, CALDEC 19%, PINPON 19%, QUEKEL 10%, ABIMAG 7%, PINLAM 7%, PINJEF 1%, PSEMEN 1%

^a Count of live trees pre-fire.

^b Species composition for stems ≥15 cm DBH pre-fire. Percentages may not add to 100 due to rounding. ABICON = *Abies concolor*, ABILAS = *Abies lasiocarpa*, ABIMAG = *Abies magnifica*, CALDEC = *Calocedrus decurrens*, JUNOST = *Juniperus osteosperma*, JUNSCO = *Juniperus scopulorum*, PICENG = *Picea engelmannii*, PINATT = *Pinus attenuata*, PINCON = *Pinus contorta*, PINEDU = *Pinus edulis*, PINFLE = *Pinus flexilis*, PINJEF = *Pinus jeffreyi*, PINLAM = *Pinus lambertiana*, PINPON = *Pinus ponderosa*, POPTRE = *Populus tremuloides*, PSEMEN = *Pseudotsuga menziesii*, QUECHR = *Quercus chrysolepis*, QUEKEL = *Quercus kelloggii*, SEQGIG = *Sequoiadendron giganteum*.

species, the Colorado Plateau and California datasets were generally similar in other aspects including number of plots (97 and 88 plots respectively), average DBH (31.8 and 35.3 cm), average percentage crown volume scorch (24% and 23%), average stem char height (2.2 and 1.9 m), and average burn year (1997 and 1995).

The 5-year post-fire annualized mortality rate of trees >50 cm DBH was 4.6% yr^{–1}, and rates were similar for large *Pinus* (4.6% yr^{–1}) and *Abies* (4.0% yr^{–1}). Mortality rates were also low for likely stand dominants or co-dominants (trees >80 cm DBH) for sites in California (6.2% yr^{–1}) and the Colorado Plateau (4.2% yr^{–1}) (note there were few trees of this size, $n_{\text{California}} = 158$, $n_{\text{Colorado Plateau}} = 31$). In contrast, the mortality rate of trees ≤50 cm DBH was 7.1% yr^{–1}, and differed between *Pinus* (5.7% yr^{–1}) and *Abies* (9.0% yr^{–1}). The overall mortality rate of all trees combined was 6.7% yr^{–1}, with lower rates for *Pinus* (5.5% yr^{–1}) compared to *Abies* (8.3% yr^{–1}), so that by 5 years post-fire 25% of *Pinus* and 35% of *Abies* had died. Mortality rates for major species within each group were similar (*P. ponderosa* = 4.0% yr^{–1}, *A. concolor* = 8.1% yr^{–1}). Differences in mortality rates translated into changes in proportions of *Pinus* and *Abies* before fire versus 5 years post-fire (all stem sizes, $\chi^2 = 9.65$, df = 1, $P = 0.0018$), a trend driven by differences in mortality of trees ≤50 cm DBH ($\chi^2 = 11.21$, df = 1, $P = 0.0008$; stems >50 cm DBH, $\chi^2 = 0.04$, df = 1, $P = 0.847$).

Patterns in post-fire mortality rates between major genera were reflected by changes in stem diameter class distributions. Prior to burning both the *Pinus* and *Abies* groups were heavily dominated by small trees (Fig. 2). Following burning both *Pinus* and *Abies* stem diameter distributions shifted towards larger individuals, indicating the preferential survival of large trees (average $M_{\text{Pinus}} = +0.004$, range of $M_{\text{Pinus}} = -0.153$ to 1.847; average $M_{\text{Abies}} = +0.024$, range of $M_{\text{Abies}} = -0.115$ to 1.885). As a result, average stem diameters

increased in the post-fire interval by 1.4% for *Pinus* and 7.5% for *Abies*. The shift in stem diameter distributions was significantly smaller for *Pinus* versus *Abies* (M_{Pinus} and M_{Abies} paired permutation test, $P = 0.008$), due to lower mortality rate of small *Pinus* compared to *Abies*.

The best fit model of post-fire mortality probabilities included terms for bark thickness, crown volume scorch, stem char height, genera (*Pinus* or *Abies*), and an interaction of crown volume scorch and genera (Table 2). As expected, tree mortality probabilities were negatively correlated with bark thickness and positively correlated with crown volume scorch, and char height (Table 3). Beyond the well-known allometric relationships with bark thickness, there were significant differences between genera in terms of mortality probability and the influence of crown volume scorch. Model results suggest *Pinus*, relative to *Abies*, was slightly more resistant to equivalent levels of crown volume scorch (Fig. 3). However, including a term for genera resulted in only a very slight improvement in model discrimination ($\text{AUC}_{\text{without genera}} = 0.901$, $\text{AUC}_{\text{with genera}} = 0.903$). Further testing revealed that *P. ponderosa* and *P. jeffreyi* experienced lower probabilities of mortality compared to other members of the *Pinus* group (model term for species identity [95% bootstrapped CI]: $\beta_{P. ponderosa} = -2.93$ [–4.89 to –0.84]; $\beta_{P. jeffreyi} = -4.43$ [–8.34 to –1.31]). Accounting for these difference did not, however, improve model performance ($\text{AUC} = 0.91$ with and without terms for within *Pinus* species identity). No differences were found within the *Abies* group. Including a term for geographic region in these models showed significant regional differences for *Pinus*, but not *Abies*. *Pinus* mortality varied between regions primarily as a result of lower mortality probabilities for *P. ponderosa* in the Colorado Plateau ($P < 0.0001$). Graphs of mortality by ignition year of fire visually suggested increasing mortality over time

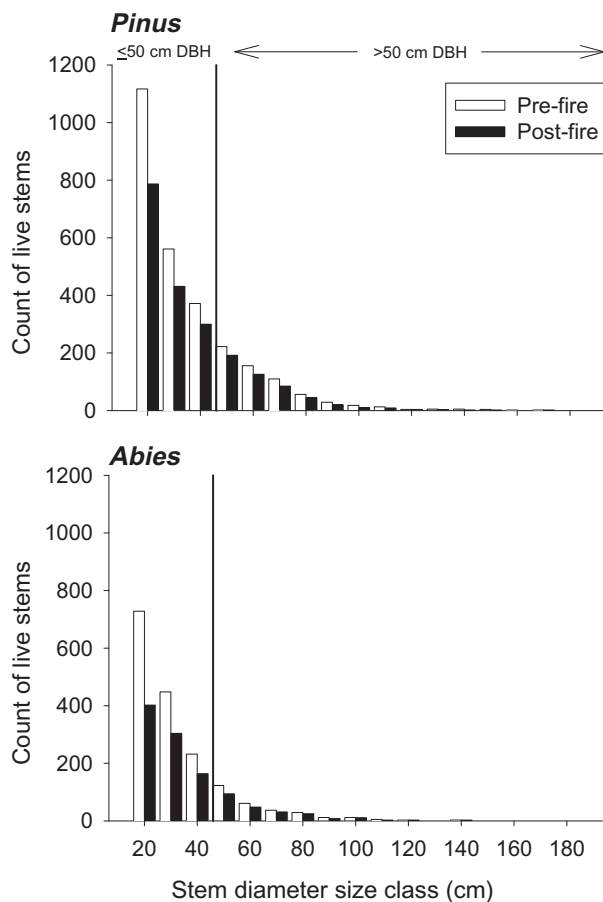


Fig. 2. Stem diameter distributions of live trees pre-fire and 5 years post-fire for *Pinus* and *Abies*.

in response to prescribed burning for *Abies*, but not *Pinus* (Fig. 4). However, year of fire ignition was not a significant predictor of individual tree post-fire mortality ($P=0.211$), and differences among sites may be responsible for any observed trend.

4. Discussion

Across the southwestern US we did not find evidence for unusually high post-fire mortality of trees >50 cm DBH or differential mortality of *Pinus* and *Abies* in this size class. The mortality rate of $\sim 4\% \text{ yr}^{-1}$ for trees >50 cm DBH is comparable to other reports of large tree mortality rates following prescribed fires in the western US (van Mantgem et al., 2011). Although these rates are low, they are higher than background mortality rates for large trees in stands in the western US that have not recently burned (approximately $0.5\text{--}1\% \text{ yr}^{-1}$) (van Mantgem et al., 2009, 2011). However, elevated post-fire mortality rates will be transient, likely persisting only up to 5 years post-fire (van Mantgem et al., 2011).

Even with these relatively low mortality rates, the question remains if this constitutes an acceptable loss of large trees. To address this question one must weigh periodic increases in mortality rates following low-severity prescribed fire against background mortality and the probability of infrequent but extreme (100%) mortality rates following stand-replacing crown fire. For example, assume that for large trees prescribed fire results in a 4% mortality rate up to 5 years post-fire, returning to background mortality rate of 1%. The application of three fires with a 20 year fire return interval to a starting population of 1000 large trees would result in an additional 199 tree deaths above unburned background levels, or a 31% increase in dead trees (this simple calculation assumes a consistently high post-fire mortality rate with repeated burning). However, repeated burning would create stand conditions that would allow remaining trees to avoid crown fire (Stephens et al., 2009), and thus avoid losses of large trees (Stephens and Moghaddas, 2005).

Prescribed fire had similar effects for both *Pinus* and *Abies*, although our models of post-fire mortality probabilities also support the idea that some species in the *Pinus* group (*P. ponderosa* and *P. jeffreyi* in particular) may be slightly more resistant to fire-caused crown injuries (see references in Hood, 2010). While models of post-fire mortality probabilities demonstrated statistically significant differences between *Pinus* and *Abies*, these differences were biologically trivial (i.e., model discrimination – the relative frequency of type I and II errors – improved only slightly with the inclusion of a term for genera). This result supports models that ignore taxonomic group when predicting fire effects (after accounting for bark thickness patterns) (i.e., FOFEM, FVS-FFE; Ryan and Reinhardt, 1988; Reinhardt and Crookston, 2003) unless an extremely high degree of precision is needed for estimates of fire effects.

Depending on management objectives, differences among species might still be important. For example, after controlling for individual differences in bark thickness, crown volume scorch, and stem char height there appeared to be differences in tree mortality probabilities between the California and Colorado Plateau regions. A likely explanation for this finding is differences in species composition. *Pinus* in the Colorado Plateau region was heavily dominated by fire-tolerant *P. ponderosa* (84%), while the proportion of *P. ponderosa* in the California region in the *Pinus* group was much lower (50%). However, models of post-fire mortality probabilities for *P. ponderosa* alone still identify regional differences in outcomes, perhaps due to systematic differences in fuels (e.g. fuel amount, arrangement, and moisture content), fire weather or ignition technique. More detailed work is needed to test these possibilities.

Defining and achieving precise goals for forest structure using prescribed fire will remain elusive due to limited control over fire effects and persistent information gaps (Stephenson, 1999). Important information gaps regarding large tree survivorship include unknown post-fire mortality rates for large trees prior to disruptions of fire regimes, the effects of ongoing environmental changes that may influence large tree mortality (Lutz et al., 2009; van Mantgem

Table 2

Selection of generalized linear mixed models (GLMM) for post-fire mortality of *Pinus* and *Abies* using the Akaike information criterion adjusted by sample size (AICc). ΔAICc and AICcWt represent differences among models and model weights. BarkTh represents bark thickness estimated from DBH, PCVS represents percentage crown volume scorch, CharHt represents stem char height, and Genus represents the taxonomic group (either *Pinus* or *Abies*).

Model	K	AICc	ΔAICc	AICcWt	LL
BarkTh + BarkTh ² + PCVS + CharHt + Genus + PCVS * Genus	9	3399	0	0.67	–1690.5
BarkTh + BarkTh ² + PCVS + CharHt + Genus + PCVS * Genus + CharHt * Genus	10	3400	1.4	0.33	–1690.2
BarkTh + BarkTh ² + PCVS + CharHt + Genus	8	3413	14.1	0	–1698.6
BarkTh + BarkTh ² + PCVS + CharHt + Genus + CharHt * Genus	9	3415	15.6	0	–1698.3
BarkTh + BarkTh ² + PCVS + CharHt	7	3418	18.9	0	–1702.0

Table 3
Fixed effects for GLMM model of post-fire tree mortality probabilities of *Pinus* relative to *Abies*. Names of fixed effects follow Table 3. Predictor variables were standardized to aid interpretation. *P*-values and 95% confidence intervals (CIs) for each estimated parameter derived from 1000 bootstrapped samples.

Fixed effect	Estimates	Std. error	<i>P</i>	95% CI
BarkTh	−0.687	0.069	<0.0001	−0.829 to −0.549
BarkTh ²	0.091	0.012	<0.0001	0.067 to 0.116
PCVS	0.037	0.003	<0.0001	0.032 to 0.043
CharHt	0.169	0.022	<0.0001	0.126 to 0.213
Genus _{Pinus}	0.404	0.148	0.0062	0.092 to 0.725
PCVS * Genus _{Pinus}	−0.013	0.003	<0.0001	−0.019 to −0.007

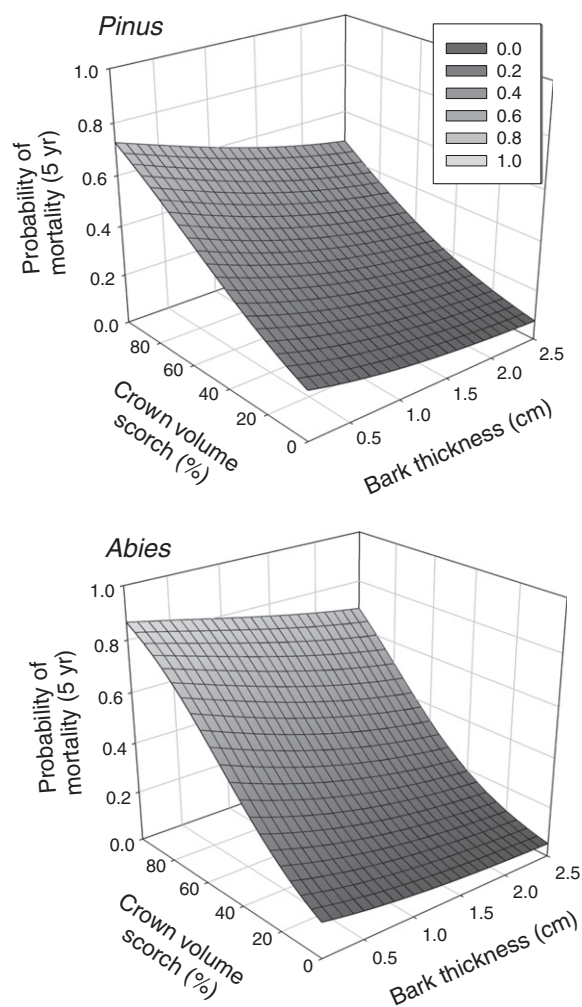


Fig. 3. Modeled relationships among bark thickness, crown volume scorch and probability of individual tree mortality (5 years post-fire) for *Pinus* and *Abies*. Stem char height was held constant at the median value of 0.5 m for both genera.

et al., 2009), the effects of repeated burning, and the potential for enhanced reproduction and growth of surviving trees in the post-fire environment (but see Keeling and Sala, 2012). If large tree survivorship is an important goal, there are management actions that could reduce the incidence of fire-caused injuries (e.g., raking fuels away from the base of large trees) (Hood, 2010; Nesmith et al., 2010), although these treatments might not always be effective and may be prohibitively expensive to apply across large areas. Plots of mortality rates over time presented in this study (Fig. 4) visually imply trends towards increasing post-fire mortality for *Abies*. This trend was not significant and the data cannot account

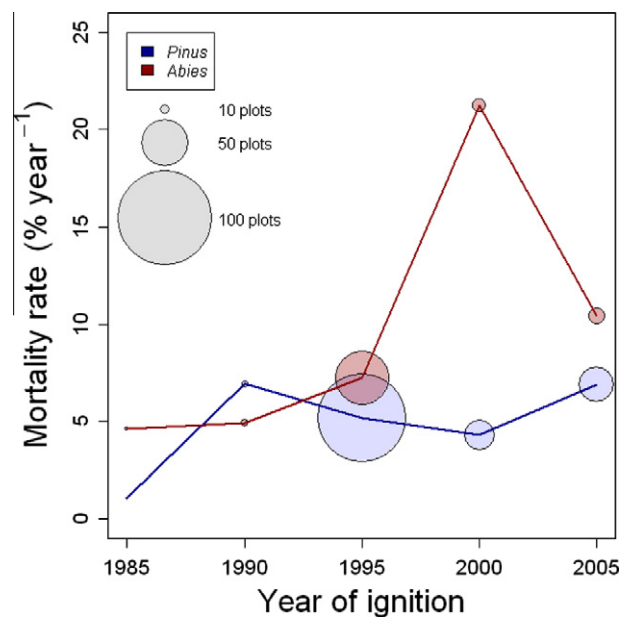


Fig. 4. Average mortality rate for *Pinus* and *Abies* 5 years post-fire versus calendar year of prescribed fire ignition. Symbol size is scaled to the number of monitoring plots used to calculate mortality rate. These plots use different sampling sites over time to determine mortality rates and analyses indicate that trends are not statistically significant.

for a potential site-switching bias (i.e., different plots were used over time to assess trends). However, across the western US background mortality rates in unmanaged forests have been increasing rapidly in recent decades (van Mantgem et al., 2009), and it is possible that environmental stress (e.g., climatic warming, air pollution) coupled with dense forest conditions may increase the expected mortality response to prescribed burning (Woolley et al., 2011). Future analyses testing these possibilities will be greatly facilitated by the existence of the FFI databases and others like it. These monitoring records are invaluable, and maintaining, and even expanding, these databases should remain a priority.

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