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Prescribed fire effects on bark beetle activity and tree mortality in southwestern ponderosa pine forests

C.R. Breece [a], T.E. Kolb [a,*], B.G. Dickson [b], J.D. McMillin [c], K.M. Clancy [d]

[a] School of Forestry, Northern Arizona University, Flagstaff, AZ 86011, United States

[b] Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523, United States

[c] USFS Region 3 Forest Health Protection, Flagstaff, AZ 86001, United States

[d] USFS Rocky Mountain Research Station, Flagstaff, AZ 86001, United States

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Abstract

Prescribed fire is an important tool in the management of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests, yet effects on bark beetle (Coleoptera: Curculionidae, Scolytinae) activity and tree mortality are poorly understood in the southwestern U.S. We compared bark beetle attacks and tree mortality between paired prescribed-burned and unburned stands at each of four sites in Arizona and New Mexico for three growing seasons after burning (2004–2006). Prescribed burns increased bark beetle attacks on ponderosa pine over the first three post-fire years from 1.5 to 13% of all trees, increased successful, lethal attacks on ponderosa pine from 0.4 to 7.6%, increased mortality of ponderosa pine from all causes from 0.6 to 8.4%, and increased mortality of all tree species with diameter at breast height >13 cm from 0.6 to 9.6%. On a per year basis, prescribed burns increased ponderosa pine mortality from 0.2% per year in unburned stands to 2.8% per year in burned stands. Mortality of ponderosa pine 3 years after burning was best described by a logistic regression model with total crown damage (crown scorch + crown consumption) and bark beetle attack rating (no, partial, or mass attack by bark beetles) as independent variables. Attacks by *Dendroctonus* spp. did not differ significantly over bole heights, whereas attacks by *Ips* spp. were greater on the upper bole compared with the lower bole. Three previously published logistic regression models of tree mortality, developed from fires in 1995–1996 in northern Arizona, were moderately successful in predicting broad patterns of tree mortality in our data. The influence of bark beetle attack rating on tree mortality was stronger for our data than for data from the 1995–1996 fires. Our results highlight canopy damage from fire as a strong and consistent predictor of post-fire mortality of ponderosa pine, and bark beetle attacks and bole char rating as less consistent predictors because of temporal variability in their relationship to mortality. The small increase in tree mortality and bark beetle attacks caused by prescribed burning should be acceptable to many forest managers and the public given the resulting reduction in surface fuel and risk of severe wildfire.

Keywords: Arizona; Crown damage; *Dendroctonus*; Insect attack; *Ips*; Logistic regression; *Pinus ponderosa*; Prescribed fire; Tree mortality

1. Introduction

The suppression of wildfires in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests in the southwestern United States has dramatically changed forest structure, composition, and function (Covington and Moore, 1994a,b). Frequent, low-intensity fires were common prior to Euro-American settlement and maintained an open forest structure with a grassy understory (Cooper, 1960; Swetnam and Baisan, 1996; Fulé et al., 1997). These fires limited establishment of non-fire adapted species and kept seedling numbers low (Fulé et al., 1997). In the absence of fire, ponderosa pine forests have become overstocked with pole-size trees and have high fuel loads, resulting in a shift in fire regime from light surface fires to intense, stand-replacing crown fires (Covington and Moore, 1994a).

Prescribed fire is becoming one of the most important tools to manage ponderosa pine forests. Prescribed fire can be used to address many management objectives, such as reducing surface fuels and the consequent risk of high-intensity wildfire (Kilgore and Sando, 1975; Stephens, 1998; Agee and Skinner, 2005; Finney et al., 2005). It can also help restore pre-Euro-American-settlement stand structure and disturbance regime (Covington and Moore, 1994b; Arno et al., 1995) by limiting

* Corresponding author. Tel.: +1 928 523 7491; fax: +1 928 523 1080.
E-mail address: tom.kolb@nau.edu (T.E. Kolb).

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Table 1
Area, mean basal area, and mean tree density of the four study sites in Arizona and New Mexico, measured in 2004

	Kaibab national forest, Arizona[a]			Coconino national forest, Arizona[b]		Apache-Sitgreaves national forest, Arizona[c]			Gila national forest, New Mexico[d]	
	Treatment	Control 1	Control 2	Treatment	Control	Treatment	Control 1	Control 2	Treatment	Control
Area (ha)	396	359	127	405	404	247	186	99	262	245
Mean basal area (m^2 ha^{-1})	24.2	20.4	15.6	16.9	16.9	15.9	19.9	27.9	10.7	13.3
Mean tree density (no. ha^{-1})	221.5	186.5	104.8	335.0	295.6	340.7	488.3	466.7	190.5	237.8

[a] Elevation 2100–2300 m; treatment stand burned October–November, 2003 and March, 2004; dominant tree species *Pinus ponderosa*.
[b] Elevation 2070–2160 m; treatment stand burned September, 2003; dominant tree species *P. ponderosa*, *Quercus gambelii*, *Juniperus deppeana*.
[c] Elevation 2130–2350 m; treatment stand burned October–December, 2003; dominant tree species *P. ponderosa*, *Q. gambelii*, *J. deppeana*.
[d] Elevation 2300–2500 m; treatment stand burned December 2003 and May 2004; dominant tree species *P. ponderosa, Q. gambelii*, *Pseudotsuga menziesii*, *J. deppeana*.

establishment of shade-tolerant species (Mutch et al., 1993), killing seedlings and saplings (Fulé et al., 2002; Perrakis and Agee, 2006) that compete with larger trees, and stimulating understory production (Andariese and Covington, 1986).

Potentially undesirable consequences of prescribed fire include increased bark beetle (Coleoptera: Curculionidae, Scolytinae) activity and tree mortality. Bark beetles can cause mortality in trees that are damaged, but not immediately killed by fire (McCullough et al., 1998; McHugh et al., 2003; Parker et al., 2006; Perrakis and Agee, 2006). Severe crown damage from fire can weaken tree defense (resin production) against bark beetles, making them susceptible to attack (Wallin et al., 2003). Thus, prescribed fire may result in levels of tree mortality that are inconsistent with management goals (Sullivan et al., 2003).

Predicting tree mortality after fire is helpful for determining impacts on wildlife and scenic value, inventorying trees for salvage logging, and evaluating risks of bark beetle attack (Fowler and Sieg, 2004). Many studies have developed models of post-fire tree mortality that include as independent variables measures of fire damage to the crown (Saveland and Neuenschwander, 1990; McHugh and Kolb, 2003; Sieg et al., 2006), bole (Peterson and Arbaugh, 1986, 1989; Regelbrugge and Conrad, 1993; McHugh and Kolb, 2003; Thies et al., 2006), and occasionally the roots (Stephens and Finney, 2002; Thies et al., 2006). Only a few studies have used measures of insect attack in post-fire tree mortality models (Peterson and Arbaugh, 1986; McHugh et al., 2003; Sieg et al., 2006). Validation of models of post-fire tree mortality by testing model predictions against data collected independently is rare (Sieg et al., 2006).

There were four objectives of our study. The first was to document effects of operational prescribed fire on bark beetle attacks and tree mortality in ponderosa pine forests of Arizona and New Mexico. The second was to model tree mortality to provide insight on mechanisms of tree death after prescribed fire, including the role of bark beetle attacks. The third was to compare predictions of tree mortality from three earlier models of ponderosa pine post-fire mortality developed using data from fires in 1995 and 1996 (McHugh and Kolb, 2003; McHugh et al., 2003) to the mortality we measured empirically in prescribed fires in 2003 and 2004. The fourth objective was to compare locations of attack on the bole between *Ips* spp. and *Dendroctonus* spp. bark beetles.

2. Methods

2.1. Study sites

We used four sites for this study, each located in different national forests in Arizona (Kaibab National Forest, Coconino National Forest, and Apache-Sitgreaves National Forest) and New Mexico (Gila National Forest) (Table 1). Each study site was established as part of a larger effort examining the response of forest and bird communities to prescribed fire experiments in ponderosa-pine dominated stands (Saab et al., 2006; Dickson, 2006; www.rmrs.nau.edu/lab/4251/birdsnburns). The dominant tree species of all the sites is ponderosa pine. Other important tree species include Gambel oak (*Quercus gambelii* Nutt.) and alligator juniper (*Juniperus deppeana* Steud.), with occasional Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), pinyon pine (*P. edulis* Englm.), and oneseed juniper (*Juniperus monosperma* (Englm. (Sarg.))).

Each of the four sites includes a stand treated with prescribed fire that is paired with one or two unburned control stands of similar size and stand structure (Table 1). None of the stands were recently thinned prior to the burns. Among the four sites, stands range from 2100 to 2500 m in elevation and mean annual precipitation ranges from 41 to 69 cm, with most precipitation occurring as winter snow and as summer monsoon rains (Sheppard et al., 2002).

The site in the Kaibab National Forest is located near Kendrick Mountain (35.23203, −111.54405), approximately 48 km northwest of Flagstaff, Arizona. The treatment stand was burned in October and November of 2003, and a follow-up burn was used in March of 2004 to complete treatment of the entire stand to desired conditions. The burned stand is paired with two controls. The second control stand was included because it has characteristics similar to the treatment stand, such as large old-growth ponderosa pines, which the first control stand lacks. Both control stands are located about 1 km from the treatment stand.

The site in the Coconino National Forest (34.38423, −111.23512) is located near the town of Happy Jack, Arizona, approximately 64 km southeast of Flagstaff. The treatment stand was burned in September and October of 2003. The control stand is located about 1 km from the treatment stand.

The site in the Apache-Sitgreaves National Forest (34.09786, −109.55295) is located near the town of Lakeside-Pinetop, Arizona, approximately 240 km southeast of Flagstaff. The treatment stand was burned in October through December of 2003. This site has two control stands, and both are located within 8 km of the treatment stand.

The site in the Gila National Forest (33.36257, −108.2832) is located near Collins Park, New Mexico, approximately 483 km southeast from Flagstaff. The treatment stand was burned in December of 2003, with a follow-up burn in May of 2004. The control stand is located about 1 km from the treatment stand.

Prescribed fire treatments were implemented by USDA Forest Service District personnel. Fires were operational broadcast burns of existing fuels and were conducted using methods and under weather conditions typical of prescribed fires in pine-dominated forests in Arizona and New Mexico. Fires burned in a mosaic pattern of varying intensities at all sites (Dickson, 2006).

Each treatment and control stand has a permanent sampling grid of 25–40 sampling stations (hereafter, points; Dickson, 2006). The first grid point was established at random and points thereafter were systematically placed along transect lines which were ≥150 m from the site boundary and ≥250 m from the nearest neighboring point. For each stand, we used a geographic information system and remotely sensed image analysis to determine the total number of point locations that maximized our ability to capture variation in forest canopy cover present on the stand. We calculated average canopy cover within a 100-m radius of a point center using digital orthophotographs and methods developed by Xu et al. (2006). Points were located and permanently marked on the ground using a global positioning system.

2.2. Tree measurements

At each sampling station we established a 10-m radius circular plot (0.03 ha) with the grid point at the center, at the start of the first growing season after burning (June, 2004). We numbered and tagged every tree within all plots and recorded tree species, diameter at breast height (dbh, measured 1.37 m above the ground), tree height, and length of live crown. We calculated the ratio of live crown to tree height, or crown ratio, by dividing the length of live crown by tree height. Trees under 13 cm dbh were not measured because they are rarely attacked by bark beetles.

We measured 2819 trees over all sites of which 72% ($n = 2091$) were ponderosa pine. Of the ponderosa pine, 994 were located in burned stands and 1097 were in unburned control stands. We restricted all statistical analyses to ponderosa pine, except for tree mortality, for which we also used all trees species in our analysis.

At the burned stands we measured the extent of fire damage on each tree as bole char severity, char height and direction, percent of the bole circumference charred, percent of crown scorched by fire, and percent of crown consumed by fire using the same procedures described in McHugh and Kolb (2003). We determined bole char severity by examining the first 0.5 m of the bole where char height was highest. We used the bole char severity rating system created by Ryan (1983): 0 = no char, 1 = light char on edges of bark plates, 2 = bark uniformly black with the exception of inner depths of prominent fissures and bark characteristic discernable, and 3 = bark deeply charred and bark characteristics not discernable. We measured char height for the lowest and highest points on the tree in which char was found on the bole and recorded the azimuths for these two points. At the base of the tree we visually estimated the percent of bole circumference charred. For crown measurements we estimated the length of the pre-fire live crown and the percent of the crown volume with green needles, brown needles (scorched by fire), and needles that were black or consumed by the fire. The same two observers took the measurements at all sites except the Coconino site, where 50% of the measurements were taken by a crew of four Forest Service personnel. To ensure consistency, these measurements were checked for accuracy by the two observers responsible for all sites.

2.3. Bark beetle attacks and tree mortality

Each spring and fall of 2004, 2005, and 2006, we examined each tree for bark beetle activity (pitch tubes, entrance or exit holes, or boring dust) at 0–2 m above the ground. We assigned each tree a bark beetle attack rating as defined by McHugh et al. (2003): 0 = no evidence of bark beetle activity, 1 = bark beetle activity in <75% but >0% of the bole circumference (partial attack), and 2 = bark beetle activity in ≥75% of the bole circumference (mass attack).

If a tree had a bark beetle attack rating of 1 or 2 (partial or mass attack), and ≥75% or more of the crown was fading, we cut out a 30 cm × 30 cm section of the bark on the north side of the tree at heights of 1, 3, 5, and 7 m above the ground. We examined each bark sample for bark beetles and galleries and, if possible, identified the species of bark beetle that made the galleries (Wood, 1982). We recorded presence or absence of bark beetle species identified in each bark sample. When identification to species was not possible, we identified only the beetle genus.

We recorded ponderosa pine mortality during the bark beetle surveys. We defined any tree as dead if ≥75% of the needles in the post-fire crown were yellow or brown. The post-fire crown was defined as the green portion of the crown that remained after the burn treatments. All trees classified as dead using this criterion in the first 2 years of the study were found to have no green needles in the third year of the study and showed no evidence of being alive. Thus, trees with ≥75% yellow or brown needles in the post-fire crown appeared to survive no more than a few months.

2.4. Statistical analysis

We used a randomized block analysis of variance (ANOVA; JMP v. 5.1; SAS Inc.) to compare mean number of bark beetle attacks between burned and unburned stands. We blocked by site ($n = 4$ blocks) in order to remove variation among sites from the experimental error. For each stand, we transformed data on the proportion of trees attacked using an arcsine transformation (Neter et al., 1996) to stabilize variances. We used ANOVA to test for differences between burned and unburned stands in the proportion of trees successfully attacked by bark beetles (resulting in tree death), and for all trees (live or dead) attacked by bark beetles.

We used the GLIMMIX macro of SAS 9.1 (SAS Institute, 2002) to test for associations between tree height and attack by bark beetle genus (*Ips* or *Dendroctonus*). The GLIMMIX macro allows for distributions that are not normal and for potentially correlated data, such as observations of bark beetle occurrence at different heights on the same tree. We grouped bark beetles by genus since sample size for each species was low.

2.5. Tree mortality models

We used multiple logistic regression to model post-fire tree mortality (live vs. dead) as function of independent predictor variables (Hosmer and Lemeshow, 1989). The model form we used is

$$P(\mathrm{m}) = \frac{1}{1 + \exp(-(\beta_0 + \beta_1 X_1 + \ldots + \beta_n X_n))}$$

where $P(\mathrm{m})$ is the response variable logit-transformed to represent the estimated probability of mortality, β_0, β_1, and β_n are regression coefficients, and X_1 and X_n are independent variables.

We screened independent variables for use in the model by conducting two-sample t-tests to identify which variables differed significantly ($p < 0.10$) between live and dead trees. Those variables that differed significantly were then evaluated for the model using forward stepwise selection (Hosmer and Lemeshow, 1989) using a significance level of 0.05 in χ^2-tests for including independent variables. The final model we obtained using forward stepwise selection was the same as the final model obtained using backwards stepwise selection ($p > 0.01$ to remove variables from the model).

We assessed model fit using Nagelkerke's max-rescaled R^2 (Nagelkerke, 1991), and the Hosmer and Lemeshow (1989) Goodness-of-Fit test. We used the Wald statistic to determine the statistical significance of each independent variable. We assessed model performance using receiver operating characteristic (ROC) curves (Saveland and Neuenschwander, 1990). All statistical operations were implemented using SPSS version 14.0 (SPSS, Chicago, IL, USA).

2.6. Validation of previous models of tree mortality

McHugh and Kolb (2003) and McHugh et al. (2003) developed logistic regression models of the probability of ponderosa pine mortality after fires that occurred in 1995–1996 in northern Arizona. They constructed a model for each of three fires – a fall prescribed fire, a spring wildfire, and a summer wildfire – and also derived a model for data pooled across fires. Our methods for measuring tree characteristics, fire damage, and insect attack, and for model development and calculation, were identical to McHugh and Kolb (2003) and McHugh et al. (2003). We compared empirical measurements of tree mortality 3 years after the 2003–2004 prescribed burns in our study with the probability of mortality predicted from each of the three models developed from fires in 1995–1996, namely (1) McHugh and Kolb (2003) model based on data pooled over fires with total crown damage and bole char severity as independent variables, (2) McHugh and Kolb (2003) model based on a fall prescribed fire with total crown damage and bole char severity as independent variables, and (3) McHugh et al. (2003) model based on a fall prescribed fire with total crown damage and insect attack rating as independent variables.

We used a linear regression model of observed tree mortality versus predicted probability of tree mortality to evaluate prediction accuracy of the previously published models. The slope and R^2 of the regression measures the predictive ability of the model (Howlin et al., 2004; McDonald et al., 2006; Suring et al., 2006). A good model has a slope that is close to 1 and a confidence interval that excludes 0 and includes 1. A higher R^2 value in the regression indicates greater predictive ability (Howlin et al., 2004). We performed the regressions for data consisting of the predicted probability of tree mortality from the earlier models and the observed proportion of dead trees for each of 10 total crown damage classes (0, 10, 20, 30, 40, 50, 60, 70, 80, and 90%) from our study. This approach compares directly the predicted probability of mortality from models with observed mortality calculated as a proportion from a large population, and does not require the assignment of a specific predicted probability of mortality as a "cut-point threshold" (Fielding and Bell, 1997) that distinguishes live and dead trees. We used data from only the burned stands and pooled data over the four sites for the validation analyses. Because proportion data often requires transformation ($2\times$ arcsine ($\sqrt{}$ (proportion)) to stabilize variances (Neter et al., 1996), we performed the regressions with both untransformed and transformed data. The transformation improved variance homogeneity, but had little effect on regression slopes, R^2 values, and interpretation of the results. Thus, we present results from the regressions on the untransformed data to facilitate interpretation.

3. Results

3.1. Bark beetle attacks

Most (80%) trees attacked by bark beetles were attacked by more than one species of beetle. The most common species were western pine beetle (*Dendroctonus brevicomis* LeConte), southern pine beetle (*D. frontalis* Zimmermann), pine engraver (*Ips pini* (Say)), Arizona five-spined ips (*I. lecontei* Swaine), and western pine engraver (*I. latidens* (LeConte)). Other species included red turpentine beetle (*D. valens* LeConte), the

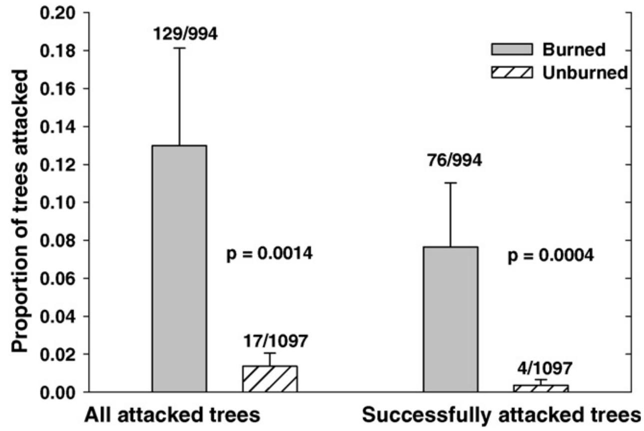

Fig. 1. Proportion of ponderosa pine trees attacked by bark beetles (*Dendroctonus* and *Ips* spp. pooled) in burned and unburned stands in Arizona and New Mexico pooled over three post-fire growing seasons (2004–2006). Numbers above the bars are the total number of trees attacked out of the total number of surveyed trees. All attacked trees include trees killed by bark beetle attacks and beetle-attacked trees that were still alive in the third growing season (2006) after burning. Successfully attacked trees were attacked by beetles and died. The *p*-values are from ANOVA comparing the proportion of attacked trees on burned vs. unburned stands.

roundheaded pine beetle (*D. adjunctus* Blandford), and six-spined ips (*I. calligraphus* (Germar)).

A significantly greater proportion of trees were attacked by bark beetles in burned stands (0.13 or 13% of burned trees) compared to unburned stands (0.015 or 1.5% of unburned trees) ($F = 40.75$; d.f. = 1, 5; $p = 0.001$) (Fig. 1). This proportion includes trees killed by bark beetles, as well as live trees with sign of beetle attack, such as pitch tubes and frass. The proportion of trees successfully attacked by bark beetles (i.e., attacks leading to tree death) in the burned stands was nearly 21 times the proportion in the unburned stands (Fig. 1; 7.6% of burned trees and 0.36% of unburned trees; $F = 71.42$; d.f. = 1, 5; $p < 0.001$). Approximately 80% of these trees were attacked successfully within the first post-fire season, 8% were attacked in the second year, and 12% were attacked in the third post-fire year. The proportion of trees with bark beetle attacks generally increased as total crown damage increased for each study site (Fig. 2).

Attacks by *Ips* spp. were more common in the middle and upper bole than the lower bole and increased with increasing height on the bole ($p = 0.01$). The odds ratio of an attack by *Ips* spp. was 3.7 (95% CI 1.4–9.9), indicating that, on average, the odds of an attack increased 3.7 times for every 2 m increase in height on the bole. In contrast, *Dendroctonus* spp. attacks were not associated with height on the bole ($p = 0.17$) and occurred at mid-range bole diameters, whereas most attacks by *Ips* species occurred at smaller tree diameters (Fig. 3).

3.2. Tree mortality

By the end of the third post-burning growing season (fall 2006), mortality of ponderosa due to all causes (e.g., bark beetles plus other factors) increased from 0.6% in unburned stands to 8.4% in burned stands ($F = 39.7$; d.f. = 1, 5; $p = 0.002$). The majority (72%) of ponderosa pine mortality due to all causes occurred within the first post-fire growing season, 13% occurred within the second season, and 15% occurred within the third season. For data pooled over stems ($\geq$13 cm dbh) of all tree species, burning increased mortality

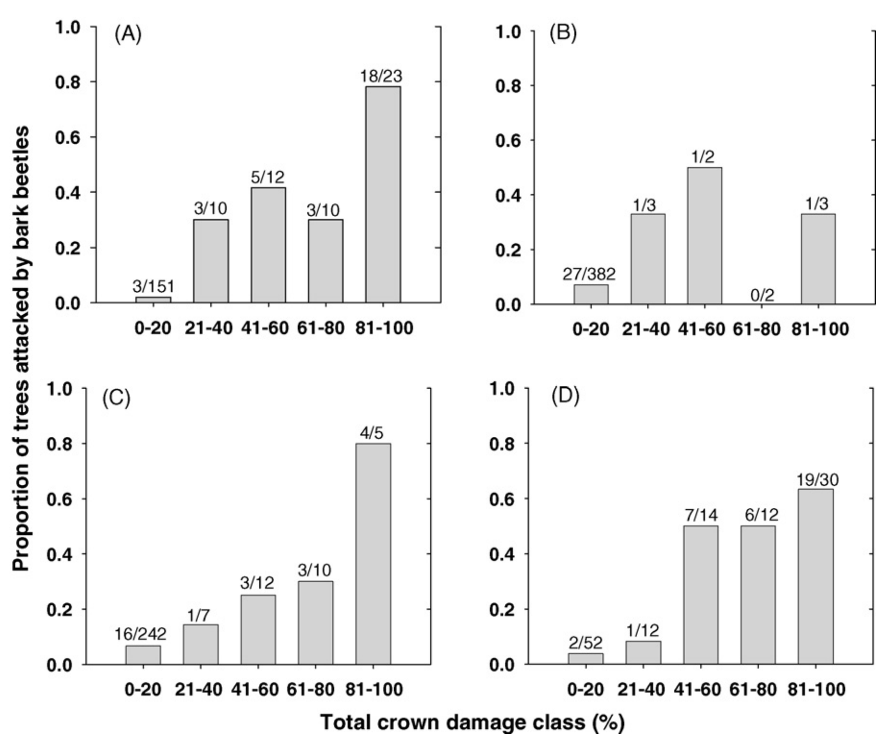

Fig. 2. Proportion of ponderosa pine trees attacked by bark beetles (species pooled) by total crown damage (TCD) class for each site (A–D). Numbers above the total number of trees attacked out of the total number of surveyed trees in each TCD class. A: Kaibab; B: Coconino; C: Apache-Sitgreaves; D: Gila.

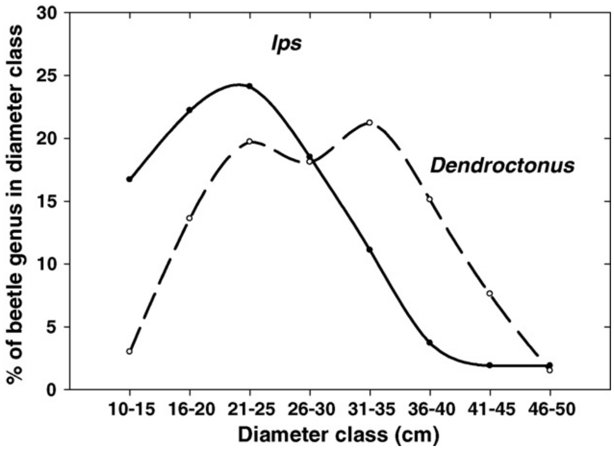

Fig. 3. Percentage of bark beetles in *Ips* and *Dendroctonus* genera in samples from all sampled ponderosa pine bole diameter classes.

from 0.6% in unburned stands to 9.6% in burned stands over the first three post-fire growing seasons ($F = 28.2$; d.f. = 1, 5; $p = 0.003$).

3.3. Mortality models

Two variables, dbh ($p = 0.479$) and tree height ($p = 0.522$), did not differ significantly between live and dead trees, and thus were not considered for the model of post-fire tree mortality. Variables considered for the model were live crown ratio, total crown damage, crown scorch, crown consumption, leeward bole char height, windward bole char height, bole char severity, and bark beetle attack rating. We did not include crown scorch or consumption in models with total crown damage because both were correlated with total crown damage (total crown damage = scorch + consumption). However, we evaluated differences between models that included total crown damage and models that included scorch and consumption separately without total crown damage.

Significant variables in model of post-fire tree mortality included total crown damage ($p < 0.0001$), bark beetle attack rating ($p < 0.0001$), and bole char severity ($p = 0.0003$) (Table 2). Despite the significance of bole char severity, we deleted it from the final model, which included only total crown damage and bark beetle attack rating, because: (1) the Hosmer–Lemeshow test indicated significant lack of fit (Table 2), (2) the negative coefficient for bole char severity is inconsistent with previous studies (McHugh and Kolb, 2003) and seems biologically unlikely because it implies less mortality with an increase in char severity, (3) improvement in R^2 (0.81 compared with 0.79) was marginal, and (4) ROC was identical to the model with only total crown damage and bark beetle attack rating (Table 2). The model with only total crown damage and bark beetle attack rating as independent variables was highly significant ($\chi^2 = 407.74$; d.f. = 2; $p < 0.0001$), and accurately described variation in tree mortality based on multiple tests of model fit (Table 2).

Replacing total crown damage with its components, crown scorch and crown consumption, did not improve model accuracy. Tests of model performance were almost identical between the two-variable model with total crown damage and bark beetle attacking rating and the three-variable model with crown scorch, crown consumption, and bark beetle attack rating (Hosmer–Lemeshow test $p = 0.81$ vs. 0.81; Nagelkerke's R^2 0.79 vs. 0.79; ROC 0.98 vs. 0.98; for two- and three-variable models, respectively). Also, crown consumption was not statistically significant ($p = 0.112$) in the three-variable model, which also included crown scorch and bark beetle attack rating.

The modeled probability of tree mortality varied with total crown damage and bark beetle attack rating (Fig. 4). Trees with no bark beetle attack had a low probability of mortality at all levels of crown damage. Trees with partial attacks had a mostly linear increase in probability of mortality with an increase in total crown damage. Trees with mass attacks had a high probability of mortality at all levels of crown damage.

Table 2
Parameter estimates and diagnostic tests for three logistic regression models of post-fire ponderosa pine mortality

Model[a]	b_0	b_1 BBAR	b_2 TCD	b_3 BCS	H-L[b] p-value	Nagl.[c] R^2	ROC[d]
BBAR[e], TCD[f]	−5.841	3.896	3.166	n/a	0.81	0.79	0.98
S.E.	0.510	0.396	0.586				
Wald test p-value	0.000	0.000	0.000				
TCD, BCS[g]	−3.239	n/a	4.832	−0.476	0.03	0.39	0.84
S.E.	0.365		0.450	0.269			
Wald test p-value	0.000		0.000	0.0772			
BBAR, TCD, BCS	−4.401	4.422	4.748	−1.631	0.02	0.81	0.98
S.E.	0.566	0.488	0.789	0.454			
Wald test p-value	0.000	0.000	0.000	0.000			

Standard errors and p-values for the Wald test are beneath each parameter estimate.
[a] Model is in the form: $P(\mathrm{m})=1/[1+\exp(-(b_0+(b_1\mathrm{BBAR})+(b_2\mathrm{TCD})+(b_3\mathrm{BCS})))]$.
[b] H-L *p*-value is for the Hosmer–Lemeshow goodness-of-fit test.
[c] Nagl. R^2 is the Nagelkerke's R^2 value.
[d] ROC is the area under the receiver operating characteristic curve.
[e] BBAR is bark beetle attack rating: mass attack = 2, partial attack = 1, no attack = 0.
[f] TCD, or total crown damage, is the sum of the percent crown volume scorched and percent crown volume consumed by fire.
[g] BCS is bole char severity: 0 = none; 1 = low; 2 = medium; 3 = high.

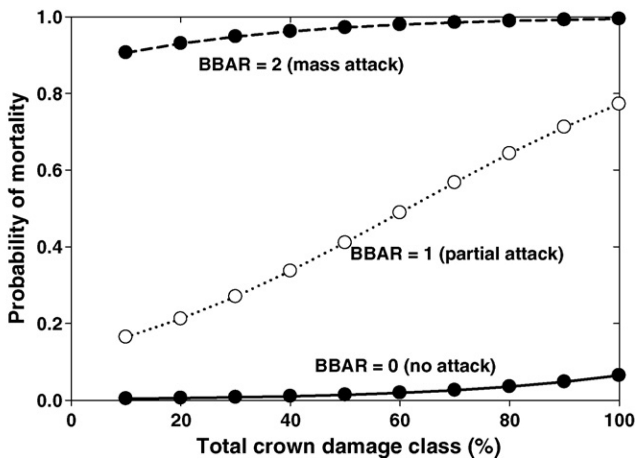

Fig. 4. Graphical representation of the model for probability of ponderosa pine mortality for each bark beetle attack rating (BBAR) and total crown damage (TCD) class. Model coefficients are shown in Table 2 (BBAR and TCD model).

We also developed a model with total crown damage and bole char severity as independent variables because this model provided the best fit to McHugh and Kolb (2003) data on post-fire mortality of ponderosa pine following fires in northern Arizona in 1995–1996. However, this model did not perform well with our data in the Hosmer–Lemeshow test for goodness-of-fit and Nagelkerke's R^2 (Table 2). Moreover, bole char severity was not a significant variable in the model (Table 2). The ROC value was lower than other models we evaluated (Table 2), but the value of 0.84 indicates correct classification of mortality for 84% of trees because of the dominant influence of total crown damage as a predictor of mortality.

3.4. Validation of previous models of tree mortality

The three models developed by McHugh and Kolb (2003) and McHugh et al. (2003) were moderately accurate for predicting broad patterns of tree mortality in our data. The regression of observed versus predicted mortality for each model had a slope that was close to 1 and a confidence interval that included 1, but excluded 0 (Fig. 5). The model from McHugh and Kolb (2003) using pooled data across all fires and with total crown damage and bole char severity as independent variables was the most accurate (Fig. 5A). Predictions of the probability of mortality from this model were close to observed proportions of mortality for trees with low total crown damage as shown by the cluster of points in the lower left of Fig. 5A. The model overestimated mortality by 10–20% for trees with 70 and 80% total crown damage as shown by the points below the 1:1 line in Fig. 5A. The model underestimated mortality by about 20% for trees with 90% total crown damage as shown by the point in the upper right of Fig. 5A above the 1:1 line. These deviations from the 1:1 line also generally occurred for the other two models (Fig. 5B and C).

Using only the total crown damage and bark beetle attack rating variables, we compared our model of post-fire tree mortality in 2003–2004 to a model developed by McHugh et al. (2003) using data from a fall prescribed fire in 1995 (Fig. 6). In the absence of bark beetle attacks, our model shows very low tree mortality with increasing total crown damage whereas the McHugh et al. (2003) model shows a large increase in mortality as total crown damage exceeds 60% (Fig. 6A). With partial bark beetle attacks, our model shows a nearly linear relationship between total crown damage and mortality whereas the McHugh et al. (2003) model shows a sharp increase in mortality when total crown damage exceeds 50% (Fig. 6B). With mass bark beetle attacks, our model shows high mortality at all levels of total crown damage whereas the McHugh et al. (2003) model shows a large increase in mortality when total crown damage exceeds 30% (Fig. 6C).

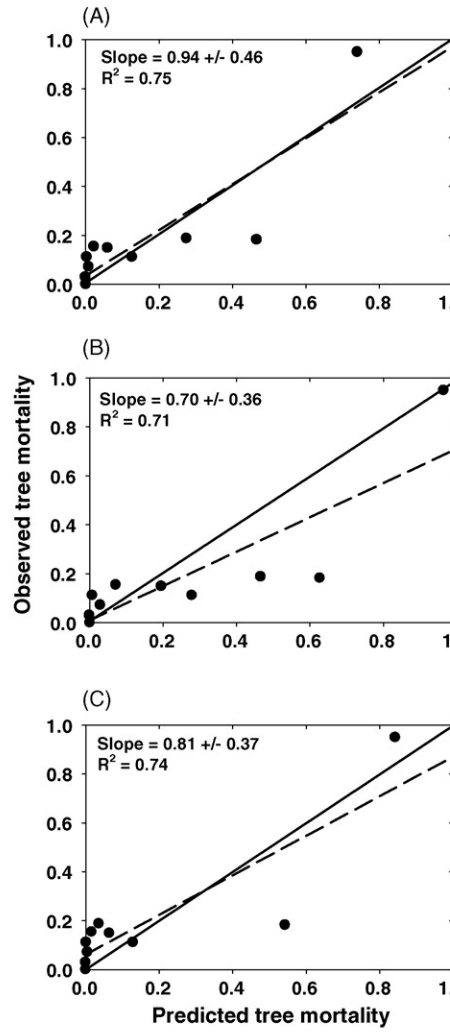

Fig. 5. Linear regression (dashed line) of observed ponderosa pine tree mortality (year) from this study ($n = 10$) vs. the tree mortality predicted by the models developed by McHugh et al. (2003) (B) and McHugh and Kolb (2003) (A and C), for each of 10 total crown damage (TCD) classes (0, 10, 20, 30, 40, 50, 60, 70, 80, and 90%). BBAR is bark beetle attack rating, TCD is total crown damage, and BCS is bole char severity. The solid line indicates a 1:1 relationship. The slope, 95% CI for the slope, and R^2 value are shown for each relationship. A: pooled fire model with TCD and BCS; B: prescribed fire model with TCD and BBAR; C: prescribed fire model with TCD and BCS.

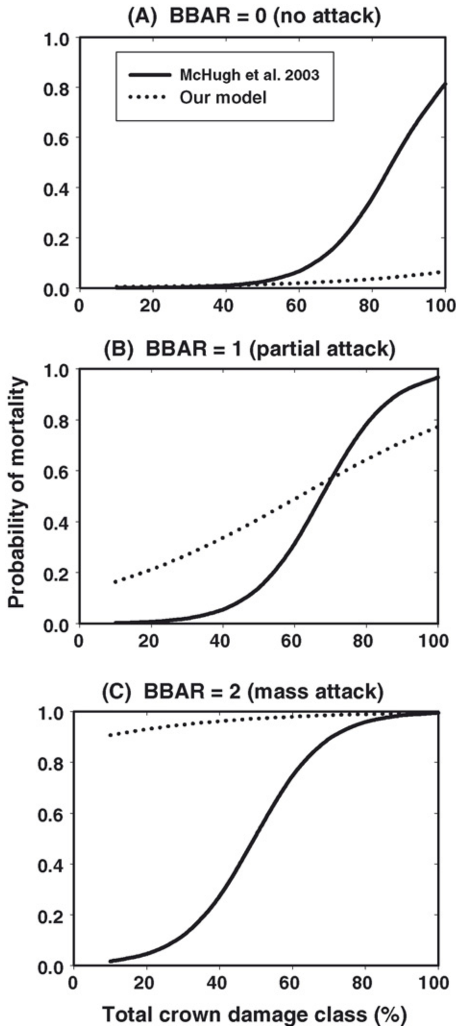

Fig. 6. A comparison of our multiple logistic regression model developed with data from prescribed fires in 2003–2004 with the model developed by McHugh et al. (2003) developed with data from a 1995 prescribed fire. Each model used only total crown damage (TCD) and bark beetle attack rating (BBAR; 0, 1, 2) as predictor variables (A–C).

4. Discussion

Our results demonstrate that prescribed fire can increase bark beetle activity in southwestern ponderosa pine forests, and support the caution that Parker et al. (2006) raised concerning possible unintended effects of prescribed fire on bark beetle activity in coniferous forests of the interior western U.S. Though prescribed fire treatments in the Southwest U.S. tend to result in lower levels of severity than many wildfires (Dickson, 2006), crown damage due to these treatments can increase tree susceptibility to bark beetle attack. Heavy crown damage may result in the loss of whole-canopy photosynthate and reduce carbon allocation to resin production, the primary defense of trees against initial bark beetle attacks (Wallin et al., 2003). Of the dead trees in burned stands in our study, 96% were attacked by bark beetles. Trees that died after prescribed fire in our study had an average of 62% total crown damage from fire, and the bark beetle attack rating and total crown damage were the most significant variables in all of our tree mortality models.

Models of tree mortality that used total crown damage (percentage of crown volume scorched plus consumed) had similar performance in describing variation in tree mortality in our data to models that used its components, crown scorch and consumption. This finding is consistent with a previous report for wild- and prescribed-fires in northern Arizona ponderosa pine forests (McHugh and Kolb, 2003). Sieg et al. (2006) concluded from a study of wildfires in Arizona, Colorado, South Dakota, and Montana that classification of post-fire mortality of ponderosa pine with logistic regression was more accurate when crown scorch and consumption were used as separate independent variables compared with the use of total crown damage. However, tests of model performance in that study were only slightly different between models with crown scorch and consumption ($R^2 = 0.79$; ROC = 0.963; % correct classification = 89.9%) and models with total crown damage ($R^2 = 0.77$; ROC = 0.958; % correct classification = 89.5%). Because of only minor improvements found in the study by Sieg et al. (2006), and no improvement in our study, efforts to separate the effects of crown scorch and consumption on ponderosa pine post-fire mortality may not be warranted.

In contrast to an earlier recommendation by McHugh and Kolb (2003), we do not recommend the use of Ryan (1982, 1983) bole char severity rating in post-fire mortality models of ponderosa pine. Although we found a higher frequency of damaged cambium in trees rated with light and moderate char compared with no char in a related study (Breece, 2006), the majority of trees in the light (71%) and moderate (58%) char classes had no cambium damage in four samples from around the tree circumference. Moreover, the negative relationship between bole char severity and tree mortality that we estimated is not consistent with the results of McHugh and Kolb (2003). For example, the coefficient was positive in the models reported by McHugh and Kolb (2003), indicating higher mortality with greater bole scorch severity. Their result is consistent with an experimental study that showed the importance of stem damage during fire to mortality of young ponderosa pine (Van Mantgem and Schwartz, 2004). However, other experimental studies have shown little effect of partial girdling of the bole by heating on physiological processes and mortality in other pine species (Ducrey et al., 1996). Because of these differences, the broader influence of bole char severity, as measured in our study, on mortality of mature ponderosa pine is unclear.

Results of our study and McHugh et al. (2003) highlight important temporal variation in the role of bark beetle attacks in post-fire mortality of ponderosa pine in the southwestern U.S. Bark beetle attack rating was more strongly associated with tree mortality in our study than in McHugh et al. (2003). This difference between studies may be due to temporal changes in bark beetle populations. Our study occurred in 2004–2006, just after a peak in activity of western pine beetle and *Ips* in the Southwestern region (USDA Forest Service, 2005), whereas the study by McHugh et al. (2003) occurred in 1996–1999, when activity of these beetles was low and no major populations were located near the study sites. Moreover, trees in the McHugh et al. (2003) study were attacked mostly by the red turpentine beetle, whereas the majority of trees in our study were attacked by other *Dendroctonus* and *Ips* species. The red turpentine beetle frequently attacks fire-damaged trees (McHugh et al., 2003), but seldom kills them directly; however it may predispose trees to fatal attack by other beetle species (Bradley and Tueller, 2001). In contrast, the *Dendroctonus* species common in our study, western pine beetle and southern pine beetle, and *Ips* spp. are primary tree-killing bark beetles in the southwestern U.S. (Furniss and Carolin, 1997). Thus, our model likely predicted higher mortality of trees at the mass attack level of the bark beetle attack rating than the model of McHugh and Kolb (2003) because trees in our study were attacked more often by primary tree-killing *Dendroctonus* and *Ips* species.

The variable effect on tree mortality of the three-class bark beetle attack rating (none, partial, moderate) over different studies in the same region using identical methods (our study, McHugh et al., 2003; Fig. 6) raises caution about the robustness of this rating in predicting ponderosa pine mortality when bark beetle populations and species composition vary temporally and spatially. While bark beetle attacks often increase tree mortality at a given level of fire damage to the crown (McHugh et al., 2003; Sieg et al., 2006), the magnitude of the increase appears to vary between endemic and outbreak populations of the primary tree-killing beetle species. Future models of post-fire tree mortality might be improved by using measures of abundance of primary tree-killing beetles, such as western pine beetle, as an independent variable, rather than the three-class system that pooled attacks over species which we used.

Patterns of attack in relation to height on the bole differed between *Dendroctonus* and *Ips* genera. We found no association between *Dendroctonus* spp. attacks and height on the bole. However, our sampling may have underestimated the presence of red turpentine beetles, which can attack the bole at or below ground level (Smith, 1971). Also, the maximum height above which attacks by *Dendroctonus* spp. do not occur may have been undersampled. Attacks by *Ips* spp. increased with bole height between 1–7 m above ground, and were greatest where bole diameter was small (Fig. 3) and bark was thin, similar to reports for *I. pini* on ponderosa pine in northern Arizona (Kolb et al., 2006). Kolb et al. (2006) suggest that *I. pini* attack thin bark so as to avoid competition with bark beetles that attack portions of the tree with thicker bark, or to avoid the energy expenditure associated with attacking thicker bark.

In summary, our results indicate that operational, cool-season prescribed fires in 2003–2004 in four National Forests in Arizona and New Mexico increased bark beetle attacks on ponderosa pine (>13 cm dbh) from 1.5% of all trees in unburned stands to 13% of all trees in burned stands over the first 3 years after burning. This difference in bark beetle attacks increased ponderosa pine mortality on a per year basis from 0.2% per year in unburned stands to 2.8% per year in burned stands. Post-fire tree mortality was significantly related both to crown damage from prescribed fire and bark beetle attacks. Models of post-fire tree mortality developed by McHugh and Kolb (2003) and McHugh et al. (2003) based on fires that occurred in northern Arizona in 1995 and 1996 were moderately successfully at predicting broad patterns in tree mortality following fires in 2003 and 2004 in our study, but predictions were off by up to 20% for trees with heavy crown damage. The small increase in tree mortality and bark beetle attacks caused by prescribed burning should be acceptable to many forest managers and the public given the well-documented effects of such burning on reducing surface fuels and the risk of severe wildfire (e.g., Pollet and Omi, 2002; Finney et al., 2005).

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