

Predicting mortality for five California conifers following wildfire[☆]

Sharon M. Hood^{a,*}, Sheri L. Smith^b, Daniel R. Cluck^b

^a USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, 5775 Highway 10W, Missoula, MT 59808, USA

^b USDA Forest Service, Forest Health Protection, Region 5, 2550 Riverside Drive, Susanville, CA 96130, USA

ARTICLE INFO

Article history:

Received 25 February 2010

Received in revised form 18 May 2010

Accepted 25 May 2010

Keywords:

Logistic regression

Bark beetle

Crown scorch

Cambium kill

Crown kill

ABSTRACT

Fire injury was characterized and survival monitored for 5677 trees >25 cm DBH from five wildfires in California that occurred between 2000 and 2004. Logistic regression models for predicting the probability of mortality 5-years after fire were developed for incense cedar (*Calocedrus decurrens* (Torr.) Florin), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), sugar pine (*Pinus lambertiana* Douglas), Jeffrey pine (*P. jeffreyi* Balf.), and ponderosa pine (*P. ponderosa* C. Lawson). Differences in crown injury variables were also compared for Jeffrey and ponderosa pine. Most mortality (70–88% depending on species) occurred within 2 years post-wildfire and had stabilized by year 3. Crown length and crown volume injury variables predicted tree mortality equally well; however, the variables were not interchangeable. Crown injury and cambium kill rating was significant in predicting mortality in all models. DBH was only a significant predictor of mortality for white fir and the combined ponderosa and Jeffrey pine models developed from the McNally Fire; these models all predicted increasing mortality with increasing tree size. Red turpentine beetle (*Dendroctonus valens*) was a significant predictor variable for sugar pine, ponderosa pine, and Jeffrey pine; ambrosia beetle (*Trypodendron* and *Gnathotrichus* spp.) was a significant predictor variable for white fir. The mortality models and post-fire tree survival characteristics provide improved prediction of 5-year post-wildfire tree mortality for several California conifers. The models confirm the overall importance of crown injury in predicting post-fire mortality compared to other injury variables for all species. Additional variables such as cambium kill, bark beetles, and tree size improved model accuracies, but likely not enough to justify the added expense of data collection.

Published by Elsevier B.V.

1. Introduction

Tree mortality after fire can occur over several years as a result of injuries to the crown, bole, and roots, subsequent beetle activity, and weather (Ryan and Amman, 1996). Accurate prediction of tree mortality after fire is critical in pre- and post-fire management decisions. Land managers need accurate predictions of tree mortality based on different weather and fuel scenarios to plan prescribed burns that meet mortality-related objectives. Post-fire management activities, such as salvage, fuels treatments, and reforestation, are based on economical, ecological, and human safety considerations, all of which need to account for current and expected levels of tree mortality.

Substantial research exists documenting the effects of fire on tree mortality in California (Haase and Sackett, 1998; Ganz et al., 2003; Ritchie et al., 2007; Fettig et al., 2008; Maloney et al., 2008); however, few actually predict post-fire tree mortality based on fire-

caused injuries. Those that do have low sample sizes (Mutch and Parsons, 1998; Borchert et al., 2002), provide only generalized tree removal guidelines without supporting data (Wagner, 1961), or relate to low intensity prescribed fire for use in achieving prescribed fire objectives (Stephens and Finney, 2002; Kobziar et al., 2006; Schwilk et al., 2006). Regelbrugge and Conard (1993) modeled post-wildfire mortality for several California species but did not measure crown injury, a variable that almost all other post-fire mortality models include (Fowler and Sieg, 2004). van Mantgem et al. (2003) reported that radial growth was significant in predicting white fir mortality after fire; however, evaluating radial growth is not practical for planning prescribed burns or post-fire management activities, such as salvage or reforestation, which usually requires prediction of tree mortality over large areas at a time.

Crown injury is often the most important factor influencing post-fire tree mortality (Stephens and Finney, 2002; Fowler and Sieg, 2004) for species with thick bark and is quantified by percentage of crown length scorched (Herman, 1954; Storey and Merkel, 1960; Bevins, 1980; Harrington, 1993) or, more commonly, by percentage of crown volume scorched (Ryan and Reinhardt, 1988; Mutch and Parsons, 1998; Borchert et al., 2002; McHugh and Kolb, 2003; Kobziar et al., 2006; Hood and Bentz, 2007). Scorch height and char height are also used as measures of crown injury (Ryan et

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* Corresponding author. Tel.: +1 406 329 4818; fax: +1 406 329 4877.

E-mail address: shood@fs.fed.us (S.M. Hood).

al., 1988; Saveland et al., 1990; Beverly and Martell, 2003; Hély et al., 2003; Sieg et al., 2006). These height variables relate to flame length, a measure of fire intensity, but do not describe the actual amount of crown affected by fire. Thies et al. (2006) used crown scorch as a proportion of total tree height. Percentage crown volume scorched is often cited as more accurate than percentage crown length scorched (Peterson and Arbaugh, 1986; Stephens and Finney, 2002; Kobziar et al., 2006), with Peterson (1985) cited as supporting this claim. However, Peterson (1985) did not compare the predictive accuracy between crown volume scorched and crown length scorched; rather, crown volume scorched versus a calculated crown volume scorch value based on crown length scorched was compared. There is no research that directly compares these two variables and relates them to tree mortality.

Another difference among crown measurement methods is crown scorch versus crown kill. Fire can scorch and kill foliage, kill buds, and consume foliage and buds. For most species, areas of crown needle scorch and bud kill are approximately equal; however, the difference can be substantial for species with large buds, such as ponderosa pine (*Pinus ponderosa* C. Lawson) and Jeffrey pine (*P. jeffreyi* Balf.) (Wagener, 1961; Wade and Johansen, 1986). Preliminary model comparisons of data used in this paper indicated that crown kill was more accurate at predicting tree mortality than crown scorch for ponderosa and Jeffrey pine (Hood et al., 2007a), a finding also supported by Wagener (1961). Other researchers have found including both crown consumption and crown scorch variables improved model predictions of post-fire tree mortality in ponderosa pine (McHugh and Kolb, 2003; Sieg et al., 2006; Breece et al., 2008). Crown kill differs from crown consumption in that crown kill includes all buds killed by fire, either by consumption or indirect heat.

Cambium death caused by lethal heating of the tree bole is another influential factor in tree mortality following fire. Flame exposure for trees with thin bark or long-term smoldering of duff and large fuels around the base of trees with thick bark can kill cambium (Ryan and Frandsen, 1991). Cambium kill in conjunction with crown injury increases the likelihood of tree death (Peterson and Arbaugh, 1989; Hood and Bentz, 2007; Breece et al., 2008). Ryan et al. (1988) monitored trees for 8 years after fire and reported the number of quadrants with dead cambium was the best predictor of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) mortality. The authors concluded that the ability to accurately predict mortality may be greatly limited if cambium kill is not assessed.

Various methods have been used to quantify cambium kill, from direct sampling of the cambial tissue (Bevins, 1980; Ryan et al., 1988; Peterson and Arbaugh, 1989; Ryan and Frandsen, 1991; Hood and Bentz, 2007) to indirect measures such as amount or height of bark scorch or bark char severity (Peterson, 1984; Regelbrugge and Conard, 1993; Borchert et al., 2002; McHugh and Kolb, 2003; Kobziar et al., 2006; Thies et al., 2006). There is a good relationship between bark char severity and actual cambium status for species with thin bark, but not for species with thick bark (Breece et al., 2008; Hood et al., 2008).

Long-term soil heating and high duff consumption can cause root death and affect subsequent tree mortality (Brose and Wade, 2002; Dumm et al., 2008). Swezy and Agee (1991) reported lower fine root biomass and higher mortality rates of old ponderosa pine in prescribed burned units compared to unburned units in Crater Lake National Park, OR. Experimental smoldering prescribed burns around old longleaf pines (*Pinus palustris* Mill.) in Florida reduced coarse root carbohydrate concentrations and likely contributed to observed tree mortality (Varner et al., 2009). Current methods to assess root death are limited to root excavation, soil heating probes, and ground char codes. The first two measures are costly and restricted to research studies. Ground char codes (Ryan, 1982; Ryan and Noste, 1985) provide a general estimation of potential root kill

and are easily assessed in the field. McHugh and Kolb (2003) and Thies et al. (2006) reported average ground char rating was higher for dead trees compared to live trees after fires in ponderosa pine, but it was not significant in predicting ponderosa pine or Douglas-fir mortality (McHugh and Kolb, 2003; Thies et al., 2006; Hood and Bentz, 2007), with the exception of Sieg et al. (2006).

Bark beetles often contribute to post-fire tree mortality by attacking and killing trees weakened by fire that likely could have survived otherwise (Ryan and Amman, 1996; McHugh and Kolb, 2003; Perrakis and Agee, 2006; Hood and Bentz, 2007). Secondary beetles, such as red turpentine beetles (*Dendroctonus valens*) and ambrosia beetles (*Trypodendron* and *Gnathotrichus* spp.), are not typically considered “tree killers” (Hagle et al., 2003). However, they may interact with fire-caused tree injuries to cause additional mortality or predispose trees to attack by primary bark beetles (Bradley and Tueller, 2001; Ganz et al., 2003).

Our objectives for this study were to: (1) compare differences between crown injury variables that are commonly used to assess fire-caused injury, (2) develop mortality models for five conifer species in California for use in predicting tree mortality within 5 years after wildfire, (3) compare variable importance and model accuracy between full-rank and reduced models in predicting tree mortality after wildfire, and (4) compare the predictive accuracy of our models with previously published California post-fire mortality models. Species included were incense cedar (*Calocedrus decurrens* (Torr.) Florin), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), sugar pine (*Pinus lambertiana* Douglas), ponderosa pine, and Jeffrey pine. These results are a continuation of the study previously reported by Hood et al. (2007a) and are intended to replace the preliminary models presented there. Our results contrast the differences among existing post-fire mortality models in California, including models developed from wildfires and prescribed fires. In addition, our comparisons of crown injury variables and variable importance are useful for understanding the influence of different injury variables on tree mortality after fire.

2. Methods

2.1. Study sites

We selected five wildfires that occurred between 2000 and 2004 for the study. Study sites comprised a wide geographical area in California extending from the southern end of the Cascade Range to the southern end of the Sierra Nevada Range (Table 1; Fig. 1). All fires were in the Sierra Nevada mixed conifer forest type (SAF Type 243; Tappeiner, 1980) with the exception of the Cone Fire, which occurred in the Interior ponderosa pine type (SAF Type 237; Barrett et al., 1980). Personnel from local forest districts identified areas of mixed-severity fire within each fire boundary for possible sampling sites. These areas burned primarily as surface fires, with the majority of trees retaining some green needles, to ensure trees with a wide variation of crown scorch were sampled. No sample trees were cut unless dead (no green needles or living buds) or for a minimum of 5 years post-fire to allow annual monitoring of tree status.

2.2. Sampling

We collected morphological and fire-injury data from five species: incense cedar, white fir, sugar pine, ponderosa pine, and Jeffrey pine (Table 2). Because of the large geographic range of fires, not all species were represented in each fire (Table 1). Ponderosa pine and Jeffrey pine were combined into one group during collection and are referred to as PP/JP hereafter. We did not distinguish ponderosa and Jeffrey pine during data collection because of similar morphological characteristics (Jenkinson, 1990)

Table 1
Wildfire locations and sample size included in analysis of post-fire tree mortality in California.

Description	Wildfire				
	Cone	McNally	Power	Star	Storrie
Longitude	–121°9'45.75"	–118°23'41.96"	–120°15'15.37"	–120°29'11.74"	–121°17'36.21"
Latitude	40°45'18.51"	36°4'4.64"	38°30'28.62"	39°5'46.88"	40°2'1.16"
Ownership	Lassen NF	Sequoia NF	El Dorado NF	Tahoe NF	Lassen NF
Ignition date	September, 2002	July, 2002	October, 2004	August, 2001	August, 2000
Forest type ^a	Interior ponderosa pine	Sierra Nevada mixed conifer	Sierra Nevada mixed conifer	Sierra Nevada mixed conifer	Sierra Nevada mixed conifer
Species (sample size) ^b	PP/JJP (926)	IC (783) WF (1878) PP/JJP (1079)	SP (644)	WF (196) SP (70)	WF (101)

^a Eyre, 1980.

^b IC = incense cedar; WF = white fir; SP = sugar pine; PP/JJP = ponderosa and Jeffrey pine.

Table 2
Mean, standard deviation (SD), and range of tree characteristics collected from five California wildfires by species. N.A. indicates where no data was collected. PP/JJP includes ponderosa pine and Jeffrey pine. Cambium kill rating is the number of quadrants with dead cambium.

	Incense cedar, n = 783			White fir, n = 2175			Sugar pine, n = 714			PP/JJP, n = 2005		
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
DBH (cm)	51.6	24.6	25.4–166.4	60.4	20.9	25.4–152.7	73.3	26.5	25.7–188.0	62.9	26.3	25.4–160.8
Tree height (m)	16.3	6.8	4.6–43.9	25.0	6.9	7.0–59.8	34.8	9.6	7.6–66.5	24.8	7.3	7.3–53.7
Pre-fire crown ratio	0.72	0.11	0.27–0.94	0.68	0.15	0.19–0.96	0.61	0.13	0.26–0.93	0.67	0.10	0.16–0.90
Crown length killed (%)	40	31	0–98	68	26	0–99	40	30	0–98	64	24	0–99
Crown volume killed (%)	44	34	0–95	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	69	24	0–95
Crown length scorched (%)	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	85	19	0–100
Crown volume scorched (%)	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	87	17	0–100
Cambium Kill Rating (CKR)	2.12	1.31	0–4	2.06	1.26	0–4	2.36	1.37	0–4	2.35	1.38	0–4



Fig. 1. Locations of wildfires in California, USA that were included in this study.

and fire-adaptations (Habeck, 1992; Morgan, 1994; Gucker and Corey, 2007). These two species are especially hard to differentiate after fire when the lower bole is charred and cones on the ground have been consumed. In addition, USDA Forest Service personnel in California do not differentiate between the two species for management purposes (Bill Oliver, USDA Forest Service, personal communication). The Cone Fire generally had more ponderosa pine than Jeffrey pine, and the McNally Fire more Jeffrey pine than ponderosa pine, but both species were abundant within the two fire perimeters.

For the Cone, McNally, and Power Fires, we selected individual fire-injured trees to fill a matrix of different crown and cambium injury levels, size classes, and species. Crews were instructed to sample 30 trees from each category within the fire boundary. Specific categories included DBH (diameter at breast height, 1.37 m above ground) classes from 25–50 cm, 51–76 cm, and >77 cm; crown kill ranges <10%, 11–50%, 51–60%, 61–70%, 71–80%, 81–90%, and 91–100%; and cambium kill categorical ratings of 0, 1, 2, 3, and 4. We sampled trees with <10% crown kill because of interest in mortality rates of trees with low crown injury across the range of cambium kill. We targeted trees between 50 and 100% crown kill more than trees with 11–50% crown kill based on previous literature indicating trees with higher crown kill have a higher probability of mortality (Van Wagner, 1973; Fowler and Sieg, 2004). At each site, crews selected trees that fit the criteria as they were encountered until the category was filled or all trees were sampled. Although the target of 30 trees for every category was not met, this sampling gave us a broad range of fire injuries and size classes for analysis. For the Star and Storrie Fires, crews selected trees with higher levels of crown kill but were given no size or cambium injury selection criteria. All trees were alive at the time of selection. We did not select trees that initially showed signs of attack by primary bark beetles (*Dendroctonus jeffreyi*, *D. brevicornis*, *D. ponderosae*, or *Scolytus ventralis*).

We completed initial assessments of tree condition during the summer of the year following each fire. For PP/JJP, initial assessment

occurred after bud break to more accurately distinguish between crown kill and crown scorch, as recommended by Wagener (1961). For each tree, we recorded species, DBH, tree height, pre-fire crown base height, post-fire crown base height, percent crown volume killed (McNally and Cone only), cambium kill rating (CKR; categorical variable between 0 and 4), and post-fire beetle attacks. We also recorded crown length scorched and percent crown volume scorched for PP/JP.

Crown kill refers to the portion of the crown that no longer has living tissue. It includes both tissue consumed by flames and tissue killed by convective heating during the fire. Pre-fire compacted crown base was estimated by the presence of scorched needles or partially consumed needles and fine branches that indicated live areas of the crown before the fire, as described in Ryan (1982). Variations in crown kill pattern were averaged to obtain one post-fire crown base value. Lengths were measured using a clinometer or laser hypsometer to the nearest 0.3 m. We calculated pre-fire crown length and crown length killed from the estimated pre-fire crown base height, post-fire crown base height, and tree height measurements. We calculated the percentage of pre-fire crown length killed by dividing the crown length killed by the pre-fire crown length.

Percent crown volume killed was also determined for trees in the McNally, Cone, and Power Fires. We visually estimated the volumetric proportion of crown killed compared to the space occupied by the pre-fire crown volume to the nearest 5% (Ryan, 1982). Obtaining both a length measurement and a volume estimate for crown kill enabled us to compare the two variables for incense cedar, sugar pine, and PP/JP and allowed comparison of our models with previously published California post-fire mortality models that use volume estimates.

For PP/JP, we also assessed percent crown length scorched and percent crown volume scorched. Crown scorch refers to the portion of the crown where needles are heat-killed; however, the buds may be dead or alive. For most species, kill and scorch are nearly equal (Ryan, 1982). However, the buds of ponderosa and Jeffrey pine are larger and more protected by needle clusters than the smaller buds of true firs and incense cedar and, consequently, often survive fire even when the surrounding needles are scorched (Wagener, 1961; Van Wagner, 1973; Dieterich, 1979; Ryan, 1982; Ryan and Reinhardt, 1988; Michaletz and Johnson, 2006). These pines are capable of surviving 100% crown scorch if little to no crown kill occurs (Dieterich, 1979; Harrington, 1993). Following Wagener (1961), we assumed crown kill and crown scorch were equivalent for other species in the study, which have much smaller buds than PP/JP.

We estimated cambium kill by first visually dividing the tree bole into quadrants oriented to cardinal directions (Ryan et al., 1988; Hood and Bentz, 2007). We then sampled cambium in the center of each quadrant by drilling through the bark to the sapwood, within 7.5 cm of ground-line, using a power drill equipped with a hole saw bit 2.5 cm in diameter (Hood et al., 2007b). Each sample was visually inspected in the field for color and condition of the tissue. Dead cambium is darker in color, often resin soaked and hard or gummy in texture. Live cambium is lighter in color, moist and rather pliable. Dead cells in the cambium zone also lose their plasticity which may allow the bark and wood to separate more easily (Ryan, 1982). A cambium kill rating (CKR) between 0 and 4 was recorded for each tree by summing the number of quadrants with dead cambium.

Beetle activity was recorded for each tree the first year after fire. For white fir, the circumference of the bole with ambrosia beetle boring dust was recorded to the nearest 10%. We recorded the number of red turpentine beetle pitch tubes on the boles of PP/JP and sugar pines. Beetle assessments were limited to visual signs on tree boles and no bark was removed to determine attack success. Bark beetle attacks after the first post-fire year were only recorded

for sugar pines. Mountain pine beetle attacks on a subset of dead sugar pines in the Power Fire were confirmed after no green foliage remained in the crown by removing a section of bark 4 and 5 years post-fire to inspect gallery patterns. The subset of dead sugar pines included those that had not been harvested, 210 of the original 267 trees.

We revisited all trees annually in the fall for 5 years following each fire to monitor tree condition (alive or dead). Trees were recorded as dead if no green foliage or living buds remained or if trees had either fallen or snapped off.

2.3. Data analysis and model development

We used 2-sample Wilcoxon–Mann–Whitney tests to examine differences in fire injury and tree size between live and dead trees by species. We considered p -values ≤ 0.05 statistically significant.

We modeled the probability of tree death using logistic regression by coding all trees as either 0 (live) or 1 (dead) based on their status 5 years after fire using the model form:

$$P_m = \frac{1}{1 + \exp(-(\beta_0 + \beta_1 X_1 + \dots + \beta_k X_k))}$$

where P_m is the probability of mortality 5-years post-fire, β_0 , β_1 , and β_k are regression coefficients, and X_1 and X_k are independent variables (SAS Institute Inc. version 9.2). We developed separate mortality models for incense cedar, white fir, sugar pine, and PP/JP. An optimal model was developed for each species based on the following candidate predictor variables: DBH, percent crown length killed, CKR, and beetle presence (1) or absence (0). Presence or absence of beetle attack (i.e., pitch tubes or boring dust) was used after determining that it performed equally well in the model compared to using the percent of the bole circumference with boring dust or number of pitch tubes, as initially assessed.

Additional models using percent crown volume killed in lieu of percent crown length killed were developed for PP/JP and incense cedar. We did not develop white fir or sugar pine models using crown volume killed because we did not have volume measurements for all trees for these species. Additional PP/JP models using percent crown length scorched and percent crown volume scorched in place of percent crown length killed and percent crown volume killed were also developed. Developing models with different crown injury variables allowed examination of the predictive accuracies among the different variables. CKR was included as a continuous rather than a categorical variable based on plots of proportion dead by CKR value for all species except sugar pine (Hosmer and Lemeshow, 2000). For sugar pine, these plots showed little differences in proportion of dead trees for CKR values 0–3, after which the proportion dead rose dramatically. An ANOVA, followed by the Tukey–Kramer multiple comparison test of least squares means (SAS Institute Inc. version 9.2) showed post-fire year 5 status was only significantly different when CKR=4, with no differences in year 5 status for CKR values ≤ 3 . Therefore, CKR was modeled as a categorical variable for sugar pine, with CKR ≤ 3 equal to 1 and CKR = 4 equal to 2.

Independent variable screening for inclusion into the tree mortality models was performed using univariate logistic regression. Only variables that differed between live and dead trees ($p \leq 0.1$) were retained for model development. Once all candidate variables were screened, only variables with $p \leq 0.05$ were retained in the full model. We then plotted the relationship between the logit and retained variables to determine the correct scale of each variable for the multivariate model (Hosmer and Lemeshow, 2000).

Performance of all models was evaluated using the area under the receiver operating characteristic curve (ROC) and classification tables, as have been used in previous post-fire mortality model-

Table 3
Mean, standard deviation (SD), and range of ponderosa and Jeffrey pine (PP/JP) tree characteristics and differences between live and dead trees 5 years post-wildfire by fire. Red turpentine beetle attacks were recorded for the first year after fire only. *p*-values are results of Wilcoxon two-sided *t*-tests between live and dead trees by fire. N.A. = not applicable.

	Cone fire						McNally fire					
	n = 926			Live n = 375	Dead n = 551	<i>p</i> -value	n = 1079			Live n = 131	Dead n = 948	<i>p</i> -value
	Mean	SD	Range				Mean	SD	Range			
DBH (cm)	42.4	12.8	25.4–104.4	44.5	41.0	0.0007	80.5	21.8	40.1–160.8	71.9	81.7	<0.0001
Crown length killed (%)	57	27	0–99	31	74	<0.0001	70	19	0–99	48	73	<0.0001
Cambium Kill Rating (CKR)	2.14	1.48	0–4	1.0	2.9	<0.0001	2.54	1.25	0–4	2.1	2.6	0.0002
Attacked (%) ^a	65	N.A.	N.A.	24	94	<0.0001	36	N.A.	N.A.	5	41	<0.0001

^a Red turpentine beetle.

ing (e.g., Saveland and Neuenschwander, 1990). The ROC reflects the accuracy of the model in classifying live and dead trees, with a value of 0.5 being no better than chance and 1.0 indicating a perfect fit. ROC values equal to 0.5 suggest no discrimination, values between 0.7 and 0.8 are acceptable discrimination, between 0.8 and 0.9 are excellent discrimination, and greater than 0.9 are considered outstanding discrimination (Hosmer and Lemeshow, 2000). Model accuracy is typically reported using the threshold value 0.5, but the most appropriate threshold will vary with management objectives (Freeman and Moisen, 2008).

We cross-validated each final model to obtain a weighted classification table to determine model accuracy. Each species dataset was divided into 10 approximately equal groups for the cross-validation exercise. We then ran the logistic regression model ten times, leaving one group out at a time, to calculate the probability of mortality for each tree in each left out group. Trees with predicted probabilities of mortality ≥ 0.5 were classified as dead, and trees with probabilities < 0.5 were classified as live for each model run to calculate the weighted average percentage of trees that were correctly predicted to live and die. The classification results presented for the models display the cross-validated accuracy using a cutoff of 0.5 of the percent of trees that each model correctly predicted to die (true positive) and the percent of trees that each model correctly predicted to live (true negative).

Ideally, we would have also used data from another fire to further test model predictive accuracy (Sieg et al., 2006; Hood and Bentz, 2007; Hood et al., 2007c; Breece et al., 2008). However, we chose to retain all data for model development in order to ensure adequate sample size and increase the power of our models (Hosmer and Lemeshow, 2000). This follows the methods used in the majority of post-fire tree mortality models, including all studies conducted in California (Regelbrugge and Conard, 1993; Mutch and Parsons, 1998; Borchert et al., 2002; Stephens and Finney, 2002; Kobziar et al., 2006; Schwilk et al., 2006).

We created reduced models to assess the importance of the CKR, beetle attack, and DBH variables in predicting tree mortality after each optimal mortality model was developed. We began by removing the CKR variable to create a second reduced model. If the optimal model included a significant beetle attack variable, a third reduced model was developed without the beetle attack variable. We then removed both CKR and the beetle attack variables. Lastly, where DBH was significant in the optimal model, we also removed it to include a reduced model predicting post-fire mortality based on crown injury alone.

Analysis of PP/JP potential model variables revealed large differences in data ranges between the Cone and McNally Fires (Table 3). The majority of trees died on the McNally Fire (88%), compared to 60% of trees on the Cone Fire. Sampled trees were much larger on average on the McNally Fire than the Cone Fire, with little overlap (Fig. A.1). Also, crown kill in general was high regardless of DBH on

the McNally Fire; only 6% of the trees had crown length kill $\leq 40\%$. The high crown kill across all size ranges for the McNally Fire and little overlap in DBH between the two fires caused the variable effect of DBH in predicting tree mortality to be inconsistent (Fig. A.1). Therefore, we felt that combining the two fires for model development was inappropriate and developed separate PP/JP models for each fire.

2.4. Model comparisons

We used our independent data to test the prediction accuracy of incense cedar, white fir, sugar pine, and PP/JP using the mortality models of Stephens and Finney (2002) and Mutch and Parsons (1998) and the survival criteria of Wagener (1961). Only the Stephens and Finney models using percent crown volume scorched (PCVS) and DBH as predictor variables were tested, as those were the variables common to both datasets. For the trees that we had crown volume injury, we calculated the probability of mortality using the equations in Stephens and Finney (2002) and Mutch and Parsons (1998). Crown volume killed was not collected for all fires; therefore, the total number of trees used in the model accuracy assessment differs from that used to develop the mortality models. We then classified all trees with a probability of mortality ≥ 0.5 as dead and trees < 0.5 as alive to obtain classification accuracies by species. Our system of evaluating cambium injury did not exactly match Wagener's cambium injury definitions. Therefore, we used the following rule set for classifying trees: light rating for trees with CKR = 0 and a moderate rating for trees with CKR ≥ 1 for all species except sugar pine. Sugar pines with CKR ≤ 2 were given a

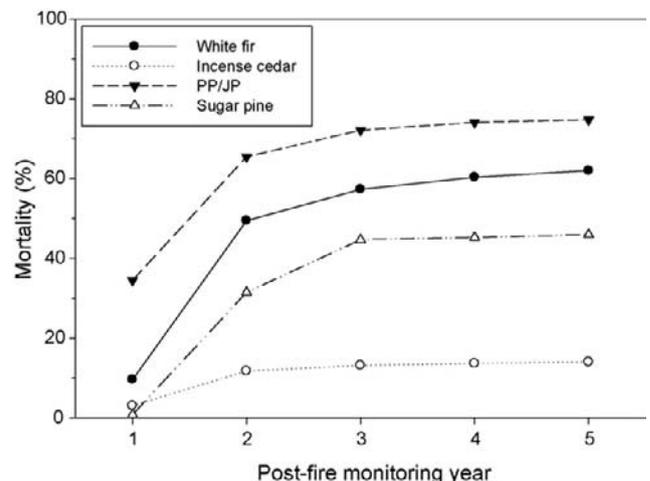


Fig. 2. Annual post-fire mortality (%) for five California wildfires by tree species. PP/JP = ponderosa and Jeffrey pine.

Table 4

Mean DBH, crown injury, and cambium kill rating for live and dead trees 5 years post-wildfire by species. N.A. indicates variable not applicable or where no data was collected. Beetle attacks were recorded for the first year after fire only. *p*-values are results of Wilcoxon two-sided *t*-tests. PP/JP includes ponderosa pine and Jeffrey pine.

	Incense cedar			White fir			Sugar pine			PP/JP		
	Live <i>n</i> = 673	Dead <i>n</i> = 110	<i>p</i> -value	Live <i>n</i> = 827	Dead <i>n</i> = 1348	<i>p</i> -value	Live <i>n</i> = 386	Dead <i>n</i> = 328	<i>p</i> -value	Live <i>n</i> = 506	Dead <i>n</i> = 1499	<i>p</i> -value
DBH (cm)	52.0	49.0	0.1629	55.7	63.2	<0.0001	77.2	68.8	<0.0001	51.6	66.7	<0.0001
Crown length killed (%)	33	79	<0.0001	49	80	<0.0001	22	61	<0.0001	36	74	<0.0001
Crown volume killed (%)	37	85	<0.0001	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	42	79	<0.0001
Crown length scorched (%)	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	69	90	<0.0001
Crown volume scorched (%)	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	74	91	<0.0001
Cambium Kill Rating (CKR)	2.0	2.8	<0.0001	1.8	2.9	<0.0001	1.8	3.1	<0.0001	1.3	2.7	<0.0001
Attacked (%) ^a	N.A.	N.A.	N.A.	5	13	<0.0001	23	78	<0.0001	19	60	<0.0001

^a White fir = ambrosia beetle; PP/JP and sugar pine = red turpentine beetle.

light rating, and CKR > 2 were given a moderate rating. No modifications were made for different seasons, site quality, or growth vigor. We followed this same classification method to evaluate PP/JP data from the McNally Fire for the Cone Fire PP/JP model and vice versa.

3. Results

3.1. Tree characteristics

Most mortality (70–88%) of sampled trees occurred within 2 years after fires and leveled off after year 3 (Fig. 2). DBH was not significantly different between live and dead trees for incense cedar. In contrast, dead white fir and PP/JP were larger than live white fir and PP/JP, and dead sugar pine were smaller than live sugar pine (Table 4). Trees that died had greater crown and cambium injury than surviving trees for all species studied (Table 4).

3.2. Crown measurement differences

PP/JP crown scorch was higher than crown kill for both volume and length measurements (Fig. 3A, only length shown). Average crown length scorched equalled 85% compared to 64% crown length killed for PP/JP (Table 2). Average PP/JP crown volume scorched equalled 87% compared to 69% crown volume killed (Table 2). Differences between crown volume and crown length measurements were smaller (Table 2, Fig. 3B). Percent crown volume killed and scorched was higher than percent crown length killed and scorched for all species tested (Table 2).

3.3. Mortality models

3.3.1. Incense Cedar

The optimal models for predicting incense cedar mortality included percent crown kill cubed and CKR (Table A.1). ROC values were identical for optimal models using percent crown length kill and percent crown volume killed, and classification accuracies were also similar (Table 5). DBH was not a significant predictor of incense cedar mortality ($p = 0.2303$). Predicted probability of mortality increased positively with crown kill (both length and volume) and CKR (Fig. 4; Fig. A.2). The addition of CKR had relatively little effect on model classification accuracy (Table 5). The models were very accurate (>92%) in predicting surviving trees, but predicted mortality accuracy varied from 65 to 74% (Table 5).

3.3.2. White fir

The optimal model for predicting white fir mortality included percent crown length kill cubed, CKR, DBH, and ambrosia beetle attacks (Table A.1). Predicted probability of mortality increased as each of the model variables values increased (Fig. 5); however, the addition of other variables after accounting for crown kill caused little improvement in overall prediction accuracy (Table 5).

3.3.3. Sugar pine

The optimal model for predicting sugar pine mortality included percent crown length kill cubed, CKR, and red turpentine beetle (Table A.1). DBH was not a significant predictor of mortality in any sugar pine model ($p = 0.471$). Predicted probability of mortality increased with beetle attack, crown kill, and CKR (Fig. 6). The

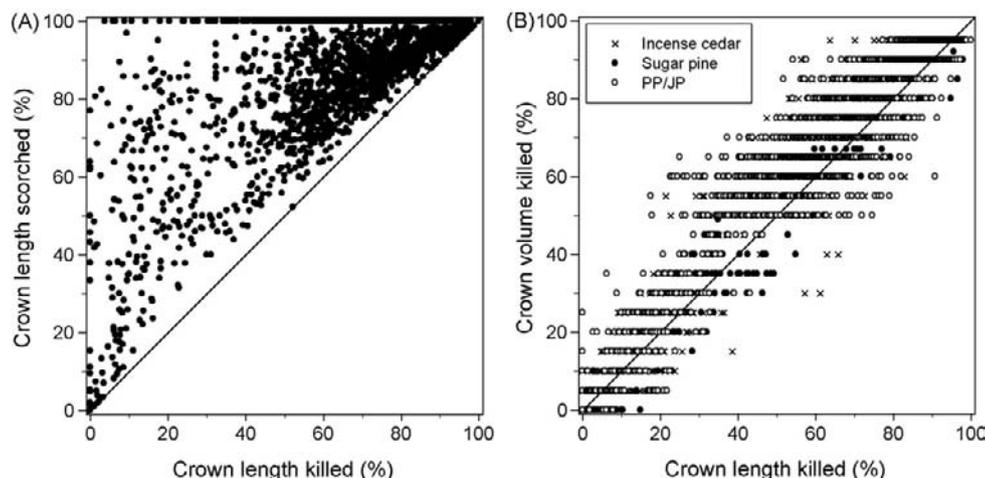


Fig. 3. A comparison of crown injury variables after wildfires in California. A) Ponderosa and Jeffrey pine (PP/JP) crown length killed (%) values compared to PP/JP crown length scorched values (%). B) Crown length killed (%) values compared to crown volume killed values (%) for incense cedar, sugar pine, PP/JP. Solid lines denote 1:1.

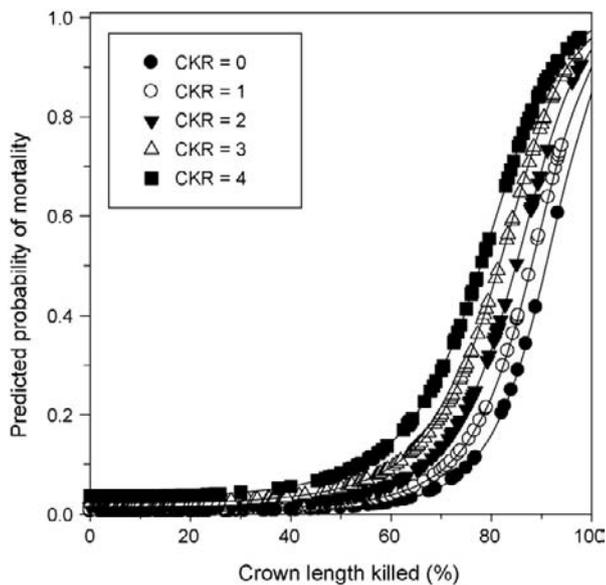


Fig. 4. Incense cedar predicted probability of mortality 5 years post-fire using full rank model 1 (Table A.1). Symbols display tree data collected from the McNally wildfire, California. Lines denote logistic regression model curves. CKR = cambium kill rating.

reduced models without either CKR or red turpentine beetle caused only slight decreases in predictive accuracies compared to the optimal model. Larger decreases were observed in the reduced model that contained only crown length killed (Table 5). Mountain pine beetles attacked 81% of the subset of sugar pines that subsequently died on the Power Fire (170 of 210 assessed trees).

3.3.4. Ponderosa and Jeffrey pine group (PP/JP)

There were distinct differences in the models developed from the Cone Fire and those from the McNally Fire. The Cone Fire optimal model to predict PP/JP mortality, regardless of crown injury type, included crown injury squared, CKR, and red turpentine beetle as variables (Table A.2). DBH was not significant in any Cone PP/JP model, regardless of what crown injury variable was used ($p=0.2970$, crown length killed model). Models using length estimates compared to volume estimates had similar predictive accuracy based on ROC, true positive, and true negative values (Table 5). Crown kill and crown scorch variables performed

similarly for the Cone Fire PP/JP models. Predicted probability of mortality increased with increasing crown injury, CKR, and beetle attacks (Fig. 7). Crown kill was the most significant model variable and the reduced crown kill models resulted in only slight decreases in predictive accuracies (Table 5).

Unlike the Cone Fire, the McNally Fire optimal model to predict PP/JP mortality included DBH as a significant variable (Table A.2). Predicted probability of mortality increased with increasing DBH, crown injury, CKR, and beetle attacks (Fig. 8). Crown injury was not squared as in the Cone Fire models. Accuracies among the optimal PP/JP crown injury models for McNally were very similar, and mortality was predicted much more accurately than survival (Table 5). Using the Cone Fire PP/JP crown length killed model, correctly predicted PP/JP mortality on the McNally Fire was 94% (804 of 851 trees correctly predicted to die). Correctly predicted survival was low, with only 37% of the trees predicted to survive actually alive 5 years after fire (84 of 228 trees correctly predicted to survive). Using the McNally Fire crown length killed model, correctly predicted PP/JP mortality on the Cone Fire was 84% (536 of 637 trees) and correctly predicted survival was 95% (274 of 289 trees). The McNally Fire PP/JP trees were on average much larger than the PP/JP trees on the Cone Fire, with higher crown kill and CKR (Table 3).

3.4. Comparisons with previous post-fire mortality models

Incense cedar model accuracy was very similar between the models presented in this study (Table 5) and the Stephens and Finney model, while Wagener's criteria greatly overestimated incense cedar mortality (Table 6). Only 18% of the trees predicted to die using Wagener's criteria actually died. The incense cedar mortality curve for trees 50 cm DBH, the mean size of trees in our study, was almost identical between our crown volume killed model and Stephen and Finney's model when cambium kill rating was 0 (Fig. A.2).

The Stephens and Finney model overestimated white fir tree survival in our study (Table 6). Fifty-three percent of the white fir trees the model predicted to survive were dead by year 5. Correctly predicted white fir mortality was much higher, with 88% of the trees correctly predicted to die. Model accuracy was very similar for the Mutch and Parsons white fir model and Wagener's criteria: both predicted survival better than mortality. The Mutch and Parsons white fir model had a 94% correctly predicted survival rate and a 69% correctly predicted mortality rate, compared to Wagener's 95%

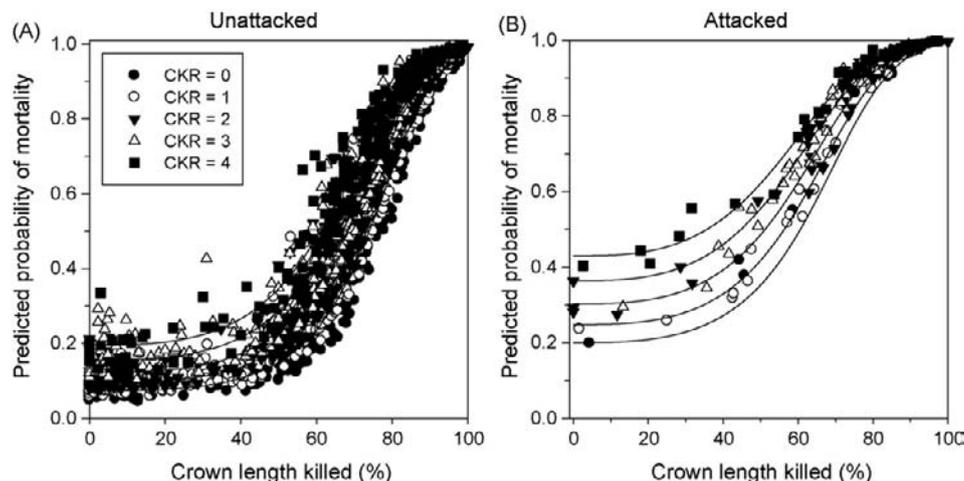


Fig. 5. White fir predicted probability of mortality 5 years post-fire by ambrosia beetle attack status ((A) unattacked and (B) attacked) using full rank model 1 (Table A.1). Ambrosia beetle attacks were recorded for the first year after fire only. Symbols display tree data collected from the McNally, Star, and Storrie wildfires, California. Lines denote logistic regression model curves by CKR when DBH = 60 cm. CKR = cambium kill rating.

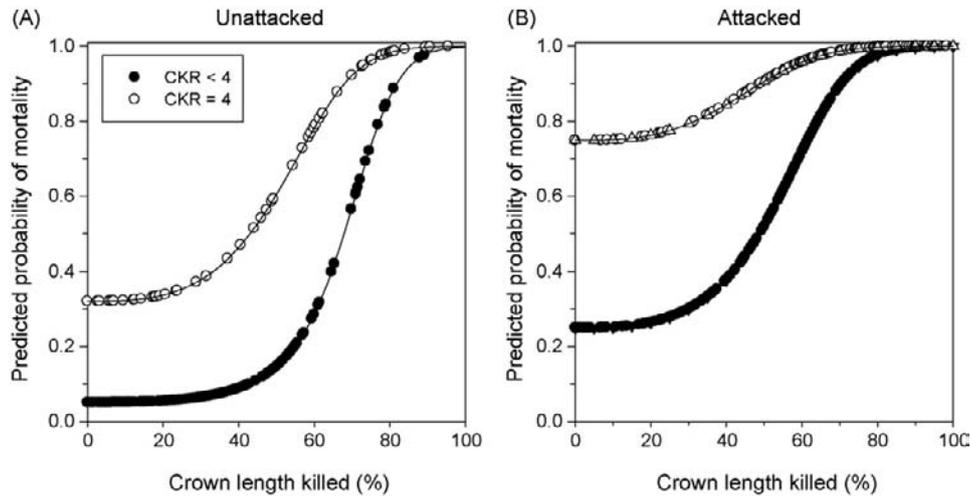


Fig. 6. Sugar pine predicted probability of mortality 5 years post-fire by red turpentine beetle attack status ((A) unattacked and (B) attacked) using full rank model 1 (Table A.1). Red turpentine beetle attacks were recorded for the first year after fire only. Symbols display tree data collected from the Power wildfire, California. Lines denote logistic regression model curves. CKR = cambium kill rating.

and 65%, respectively. Accuracy of our white fir model(s) was in-between the other models- they predicted mortality similarly to the Stephens and Finney model, but survival prediction accuracy was lower than the Mutch and Parsons model and Wagener’s criteria (Tables 5 and 6).

Sugar pine mortality predicted by the Stephens and Finney model was extremely accurate (95%), but it overpredicted conifer survival (Table 6). The reverse pattern was true for both the Mutch and Parsons model and Wagener’s criteria. Accuracy of our sugar pine models was in between: the models predicted mortality

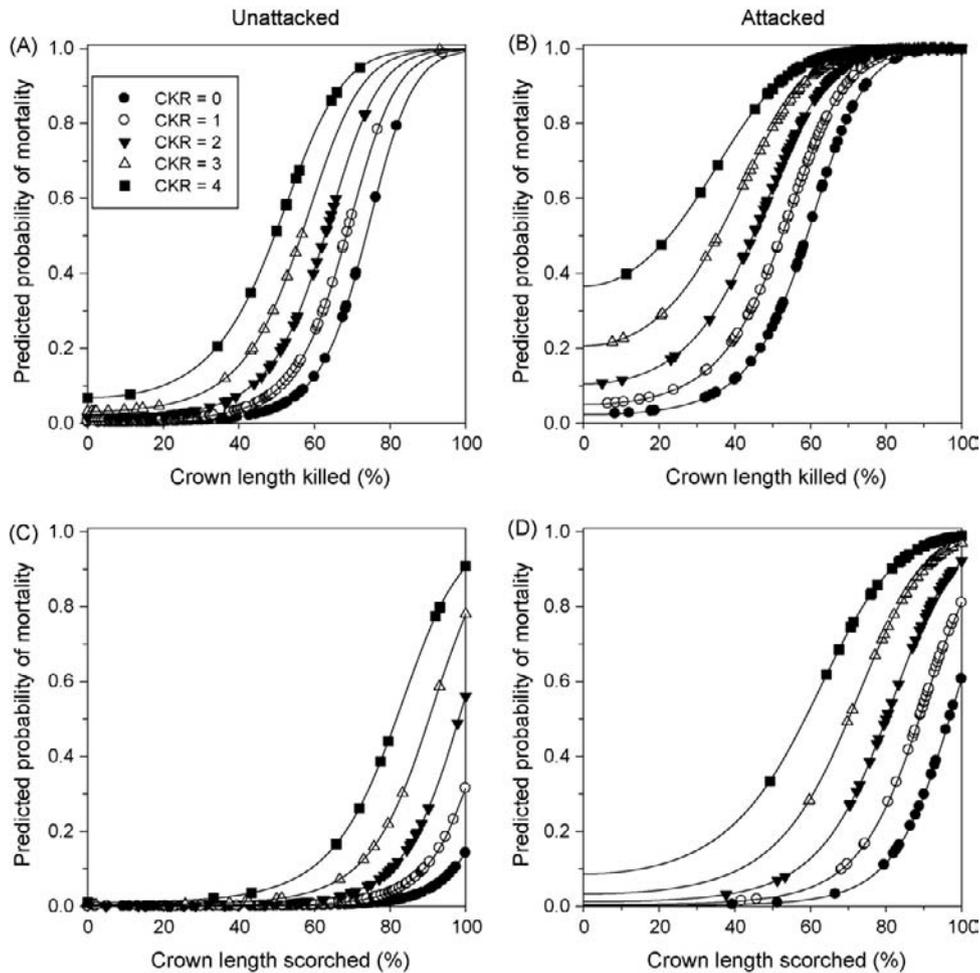


Fig. 7. Cone fire predicted probability of mortality 5 years post-fire for ponderosa and Jeffrey pine (PP/JF) by red turpentine beetle attack status ((A) unattacked and (B) attacked) using crown length killed (A, B) and crown length scorched (C, D) using full rank model 1 (Table A.2). Red turpentine beetle attacks were recorded for the first year after fire only. Symbols display tree data collected from the Cone wildfire, California. Lines denote logistic regression model curves. CKR = cambium kill rating. Note lack of attacked trees below 40% crown length scorched (D).

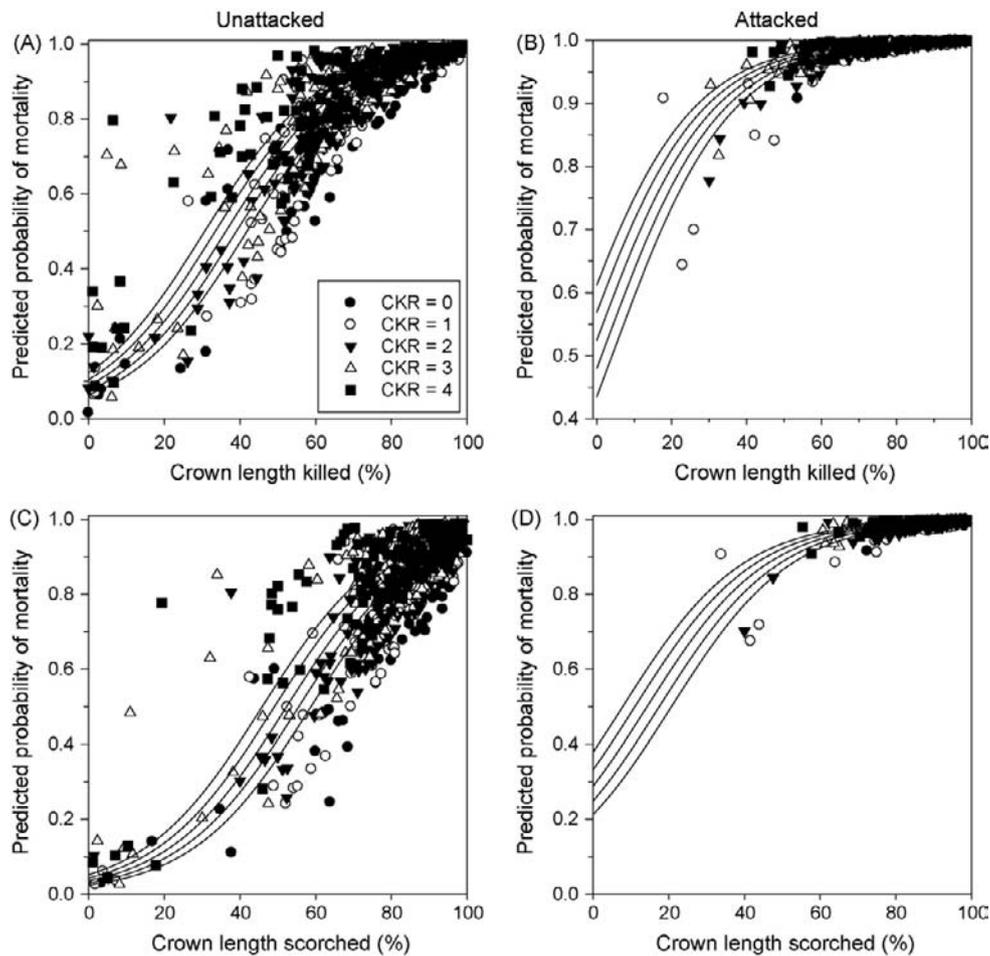


Fig. 8. McNally fire predicted probability of mortality 5 years post-fire for ponderosa and Jeffrey pine (PP/JP) by red turpentine beetle attack status ((A) unattacked and (B) attacked) using crown length killed (A, B) and crown length scorched (C, D) using full rank model 1 (Table A.3). Red turpentine beetle attacks were recorded for the first year after fire only. Symbols display tree data collected from the McNally wildfire, California. Lines denote logistic regression model curves. CKR = cambium kill rating. Note lack of attacked trees for low crown length killed (B) and crown length scorched (D) values.

slightly worse than the Stephens and Finney model but better than the others, while predicting survival better than the Stephens and Finney model but worse than the others (Tables 5 and 6).

Survival of PP/JP was substantially overpredicted using the Stephens and Finney model with only 28% of the trees predicted to survive actually surviving to year 5 (Table 6). Wagener's criteria performed similarly to our models for PP/JP, with an approximately 10% lower mortality prediction accuracy than the models presented here (Tables 5 and 6). The mortality curves between our PP/JP crown volume scorched models and Stephens and Finney's ponderosa model are quite different, especially for the McNally Fire, where DBH is included in the model (Figs. A.3C, A.4C). Our McNally PP/JP models predict mortality to increase with tree size, while the Stephens and Finney model predict the opposite relationship. Therefore, the differences in predicted values are striking when trees are large (average PP/JP DBH for McNally Fire = 80 cm; Fig. A.4C), but are approximately the same when DBH equals 35 cm.

4. Discussion

4.1. Crown injury assessments

Crown injury can be assessed using a variety of methods. However, operational fire behavior and effects models such as BehavePlus, Farsite, and FOFEM (Reinhardt et al., 1997; Finney, 1998; Andrews, 2009) are unable to predict bud kill, relying on

the assumption that scorch height equals both foliage and bud kill. These models use flame length estimates to first calculate scorch height and then to convert crown length scorch to crown volume scorch. While we found a good relationship between crown length and crown volume estimates, these calculations introduce additional error into the predictions of mortality. Furthermore, the difference between crown scorched and crown killed varied widely in the ponderosa and Jeffrey pine trees sampled. Application of mortality models based on observed crown injury instead of predicted crown injury will improve model accuracy. New physics-based fire behavior models have the potential to more accurately model needle consumption, bud kill, and needle scorch to increase our capability of predicting fire effects from anticipated fire behavior (Linn et al., 2005; Mell et al., 2009).

4.2. Mortality modeling and variable importance

Measures of crown injury were the most important predictor of post-fire tree mortality for all species, a finding consistent with almost all other post-fire tree mortality studies (Fowler and Sieg, 2004). Incense cedar seems more tolerant of high levels of crown injury than the other species tested, a finding corroborated by Stephens and Finney (2002). Predicted mortality was typically less than 0.5 for trees with crown kill <50% that were unattacked (ambrosia beetle in white fir; red turpentine beetle in PP/JP and sugar pine) for all species. Predicted mortality then rose sharply

Table 5

Accuracy statistics for incense cedar, white fir, sugar pine, and ponderosa pine/Jeffrey pine (PP/JP) mortality models 5 years post-wildfire in California as shown by the receiver operating characteristic curve value (ROC), true positive (percentage of trees predicted to die that were dead by post-fire year 5), and true negative (percentage of trees predicted to live that were alive through post-fire year 5). Model 1 is the statistically best, optimal model for each species. Subsequent models are reduced models with variables left out (2 = no CKR; 3 = no beetles; 4 = no CKR or beetles; 5 = no CKR, beetles, or DBH). Accuracy cutoff = 0.5. CKR = cambium kill rating (i.e., number of dead cambium quadrants). Full models are included in Appendix A.

Model	ROC	True positive (%)	True negative (%)
Incense cedar			
Crown length killed			
1	0.92	70	92
2	0.90	74	93
Crown volume killed			
1	0.92	73	93
2	0.91	65	95
White fir			
Crown length killed			
1	0.87	82	74
2	0.86	82	73
3	0.87	82	74
4	0.86	82	73
5	0.85	81	72
Sugar pine			
Crown length killed			
1	0.93	87	85
2	0.91	85	82
3	0.91	85	83
4	0.88	84	79
JP/PP Cone fire			
Crown length killed/crown length scorched			
1	0.97/0.96	92/90	89/91
2	0.96/0.93	89/88	88/87
3	0.96/0.95	90/89	86/85
4	0.95/0.87	88/81	85/85
5	N.A.	N.A.	N.A.
Crown volume killed/crown volume scorched			
1	0.97/0.96	92/90	90/90
2	0.96/0.93	89/88	90/87
3	0.97/0.95	91/91	86/85
4	0.95/0.96	89/81	85/87
5	N.A.	N.A.	N.A.
PP/JP McNally fire			
Crown length killed/crown length scorched			
1	0.89/0.87	91/91	64/68
2	0.89/0.87	91/90	70/69
3	0.86/0.83	91/90	65/61
4	0.86/0.83	90/90	65/65
5	0.82/0.79	90/90	70/63
Crown volume killed/crown volume scorched			
1	0.90/0.89	90/90	63/63
2	0.90/0.88	90/90	65/66
3	0.87/0.85	90/90	67/63
4	0.86/0.84	90/90	72/74
5	0.81/0.78	90/90	79/81

Table 6

Classification accuracy of Stephens and Finney (2002) mortality models, Mutch and Parsons (1998) mortality models, and Wagener (1961) survival criteria for incense cedar, white fir, sugar pine, and PP/JP (i.e., ponderosa and Jeffrey pine) using data collected from five wildfires in California. *N* = total number of trees tested. True positive = percentage of trees predicted to die that died. True negative = percentage of trees predicted to live that lived. N.A. = not applicable. Accuracy cutoff = 0.5.

Species	<i>N</i>	Stephens and Finney ^a		Mutch and Parsons		Wagener	
		True Positive	True Negative	True Positive	True Negative	True Positive	True Negative
Incense cedar	783	71	90	N.A.	N.A.	18	100
White fir	1878	88	47	69	94	65	95
Sugar pine	644	95	68	54	89	61	90
PP/JP	2005	99	28	N.A.	N.A.	81	94

^a Only the models using percent crown volume scorched (PCVS) and DBH as predictor variables were tested.

with increasing crown kill after this point. With the exception of the McNally Fire PP/JP models, squaring the crown injury variables for the Cone Fire PP/JP and cubing them for the other species reflects this sensitive, steep nonlinear relationship between crown injury and tree mortality. The causal mechanism of this observed pattern is likely due to the increased photosynthetic capacity lost with high levels of crown scorch. Photosynthate production is lower in the middle and lower portions of the crown compared to the upper portions (Aubuchon et al., 1978); therefore, when crown scorch is less than 50% it does not equate to a 50% loss in photosynthetic capacity. However, as scorch increases to the upper portions of the crown, it begins to have substantial impacts on photosynthate production, which translates into higher rates of tree mortality (Stephens and Finney, 2002).

Crown injury was the most influential predictor of tree mortality, yet we found virtually no difference in predictive accuracy between the incense cedar and PP/JP models developed with percent crown length variables versus models developed with percent crown volume variables. This differs from conclusions drawn by other authors suggesting that a volume estimate is more accurate (Peterson, 1985; Stephens and Finney, 2002; Kobziar et al., 2006). We suggest that percent crown length and percent crown volume measurements of crown injury are both strong predictors of post-fire tree mortality, and that the selection of one crown injury variable over another can be based on the assessor's preferred method. Crown volume estimates are useful for factoring in crown shape, particularly for tree crowns that are very conical. However, volume estimates are more objective and require training to achieve consistent results among crew members. Crown length estimates do not account for crown shape, but are more objective because they are based on measurements of tree height and crown base height. Regardless of which variable is chosen, crown volume and length estimates are not interchangeable in the mortality models.

Attacks by red turpentine beetle or ambrosia beetle were associated with increased tree mortality. While neither beetle is considered a primary bark beetle capable of attacking and killing healthy trees, their signs may be good external indicators that a conifer sustained substantial injuries from fire. Kelsey and Joseph (2003) reported increased ethanol production in fire-injured trees, which was associated with increased red turpentine beetle landing rates compared to control trees. Short-term decreases in resin flow immediately after fire was cited as the possible mechanism leading to increased attacks by *Ips* beetles in fire-injured red pine (*Pinus resinosa* Aiton) (Lombardero et al., 2006).

Trees in this study were deliberately selected not to include those attacked by primary bark beetles within the first year after fire. However, we did assess a portion of dead sugar pine after the first year and found that 81% were attacked by mountain pine beetles. The high incidence of mountain pine beetle attack, although not useful for predicting mortality immediately after fire, provides insight into the high level of mountain pine beetle activity in fire-injured trees in the area. Ponderosa pine could have been attacked

by western or mountain pine beetles or Jeffrey pine by Jeffrey pine beetles two or more years post-fire and contributed to mortality. Bark beetle activity was not assessed after the first year for most trees for two reasons: (1) post-fire management decisions are usually based on immediately observable fire injuries and (2) many of the trees that died in the study were immediately harvested and therefore could not be assessed for attacks (only trees with no remaining green needles were harvested).

Predicted tree mortality increased with increasing cambium kill rating (CKR). Our method of evaluating cambium injury using four points sampled at the tree base provides greater accuracy in predicting post-fire tree mortality compared to not sampling cambium. Hood et al. (2008) found that direct sampling of cambium to obtain CKR did not lead to increased post-fire ponderosa pine mortality in Montana, USA and was a more accurate predictive variable than bark char codes developed by Ryan (1982) for species with thick bark. Given similar levels of crown injury, mortality would be underpredicted for trees with high levels of cambium kill and overpredicted for trees with low levels of cambium kill if CKR is not assessed. Holding crown injury constant, sugar pine mortality increased only slightly until all cambium quadrants sampled were dead (CKR=4), which follows past findings that sugar pine is capable of withstanding more extensive cambial injury than other California conifers (Wagener, 1961).

The PP/JP crown kill models were more accurate than the crown scorch models in general. However, the difference was minimal. Crown kill is much more easily determined by waiting until the first bud break after the fire (Wagener, 1961). However, predicting mortality of pine trees prior to bud break may be useful for making management decisions immediately after the fire in order to limit wood deterioration. Thirteen percent of PP/JP with 100% crown length scorched (61 of 473 trees) survived for 5 years following fire. This statistic and the PP/JP scorch mortality curves (Figs. 7 and 8C, D) show that some trees are capable of surviving high levels of scorch if the amount of cambium kill and bud kill is low, a finding also reported by several others (Wagener, 1961; Dieterich, 1979; Wade and Johansen, 1986; Harrington, 1993; Hanson and North, 2009). However, beetle attacks and increasing levels of crown kill and cambium injury lower the chance of survival. These results imply that mature trees with large buds can survive moderate intensity, low severity fires if they are not subsequently attacked by bark beetles.

Tree size is widely recognized as an important factor in resistance to fire injury due to an increase in crown base height and bark thickness as tree height and diameter increase (Ryan et al., 1988). However, tree diameter was only significant in the white fir and McNally Fire PP/JP models and they predict mortality to increase with increasing DBH. This is contrary to most other post-fire tree mortality models and those reported by Stephens and Finney (2002) and Mutch and Parsons (1998) for white fir. An increase in the predicted mortality as DBH increases has only previously been reported for ponderosa pine (Ryan and Frandsen, 1991; McHugh and Kolb, 2003), Douglas-fir (Hood and Bentz, 2007), and longleaf pine (Varner et al., 2007). Discrepancies in tree sizes between studies may explain observed differences in DBH and tree mortality for white fir. The Stephens and Finney white fir model was developed using data from trees between 5–65 cm DBH, with a mean DBH of 20.3 cm compared to 25.4–152.7 cm with a mean diameter of 60.4 cm for white fir in this study. Data from white fir used to develop the Mutch and Parsons model also included much smaller trees than our study. While Mutch and Parsons (1998) did not give specific diameter ranges by species, they sampled trees greater than 1.4 m tall and up to 180 cm DBH. Other explanations may be larger trees can have greater duff accumulations, leading to increased smoldering times and the potential for more root injury (Swezy and Agee, 1991; Sackett and Haase, 1998; Kolb et al., 2007;

Varner et al., 2007). Larger trees may also be less vigorous than smaller trees, reducing their capability to recover from fire-caused injuries (McHugh and Kolb, 2003).

Our finding that DBH was not significant in predicting tree mortality for most species evaluated is corroborated by Mutch and Parsons (1998) and Stephens and Finney (2002) for sugar pine and van Mantgem et al. (2003) for white fir. McHugh and Kolb (2003) reported their ponderosa pine mortality model using bole char severity and crown injury was more accurate than the model using DBH and crown injury. This may be due a U-shaped mortality distribution following fires with smaller and larger diameter trees having higher mortality than mid-diameter trees (Swezy and Agee, 1991; McHugh and Kolb, 2003; Varner et al., 2005; Kolb et al., 2007; Varner et al., 2007). However, logistic regression does not adequately model U-shaped distributions (Hosmer and Lemeshow, 2000).

Another reason for conflicting reports of the role of tree diameter in predicting post-fire tree mortality is differences in tree sizes that were used to develop the mortality equations. Studies rarely encompass the entire range of possible tree sizes, especially in conjunction with a full range of crown and cambium injury. For example, our study focuses on medium to large diameter trees, with a minimum DBH of 25.4 cm (Table 2). Many prescribed fire studies include very small trees with high crown injury, but they have few large trees with high levels of crown injury in the sample because of objectives to limit overstory tree mortality while reducing fuel loadings and ingrowth of smaller trees (Mutch and Parsons, 1998; Stephens and Finney, 2002; Kobziar et al., 2006).

4.3. Model Accuracy Comparisons

Wagener's (1961) evaluation criteria are the same for incense cedar, white fir, and sugar pine. However, in our study and Stephens and Finney (2002), incense cedar were able to survive higher levels of crown kill compared to other species, a difference not reflected in Wagener's criteria. Based on our accuracy assessment, Wagener's criteria should not be used for predicting post-fire incense cedar mortality.

Both the Stephens and Finney model and the Mutch and Parsons model were developed for prescribed fire use. Their data were collected after prescribed fires and the majority of the observed mortality was in the smaller size classes, as would be expected when burning under typically mild prescribed fire conditions. In contrast, our data were collected from wildfires. Information about the development of Wagener's criteria is limited, but likely also came from wildfires. Tree mortality is associated with fire intensity (Schwilck et al., 2006), so the separation of wildfire versus prescribed fire should not be the only factor determining what model to use. Rather, managers should select models based on which ones best match the fire intensity and tree sizes used to develop the model. Many prescribed fire studies do not have many observations with high levels of crown kill and cambium kill; therefore, applying the models to areas that experience mixed to high severity fire are likely to underpredict tree mortality. Conversely, models developed from wildfires, such as the ones in this study, may not have as many observations in the low to mid crown kill ranges and could overpredict mortality for prescribed fires.

Based on the McNally Fire, it appears that large diameter PP/JP trees have lower survival rates than mid-diameter trees, a finding also reported by others (McHugh and Kolb, 2003; Perrakis and Agee, 2006; Varner et al., 2007). Even with few trees in the lower crown injury range and little DBH overlap between the two fires, the McNally Fire PP/JP model predicted Cone Fire PP/JP survival and mortality very well. Additional evaluation is needed, but caution should be used when applying our Cone Fire PP/JP model to large trees with high crown kill. The McNally Fire PP/JP models appear

to do better for a wider range of diameters than the Cone Fire PP/JP models. However, the McNally PP/JP model is not recommended for large diameter trees (>80 cm DBH) with crown length kill less than 40%. For these trees, the model greatly overpredicts mortality. The dramatic differences in the predicted probabilities of mortality for larger trees between our model and the Stephens and Finney model (Fig. A.4C) and our evaluation of the PP/JP on the McNally and Cone Fires illustrates the concern of extrapolating beyond the data used for model development and also highlights the need for further evaluation of mortality models with independent data.

5. Conclusions

Land managers need the ability to predict mortality following wildfires to plan tree removal and regeneration projects, determine future stocking levels, and plan fuels treatments. These models enable managers to select a desired level of predicted probability of mortality, based on land management objectives, to develop site specific land management plans (see Hood et al., 2007b for detailed explanation). The predictive accuracies for reduced models are also provided to demonstrate the decrease in accuracy when significant variables are removed. While beetle attack and CKR increased model accuracy, the improvement was negligible for most species (Table 5). Each variable in a model requires additional time for assessment in the field. Estimating crown injury takes the least amount of time and was the most important variable to predict tree mortality after fire. Sampling the cambium in each quadrant is the most time consuming. In most instances the extra time required to assess these additional variables is likely not worth the effort for the marginal improvement in predictive accuracy.

We based our accuracy assessment using a 0.5 cutoff in order to more easily compare models. Model accuracy will change based on the cutoff chosen (Freeman and Moisen, 2008), with higher cutoffs resulting in fewer false positives (i.e., trees predicted to die but actually surviving) and more false negatives (i.e., trees predicted to survive but actually dying). There are a multitude of ecological and economic objectives related to post-fire forest management. The models presented here are intended to be used in conjunction with other objectives to meet overall management goals. Managers can tailor their management guidelines by choosing an appropriate cutoff level and augmenting their decision criteria after determining average post-fire tree injury characteristics and considering local environmental and tree physiological factors.

Numerous empirical post-fire mortality models exist (Fowler and Sieg, 2004; Fernandes et al., 2008), yet few models are evaluated to determine their range of applicability for other fires. Because we did not have independent data to evaluate each model's predictive capability other than PP/JP, the accuracies reported are likely to be lower for other fires and warrant further investigation. Hood et al. (2007c) concluded that species specific models are more accurate than generalized models that include species specific terms, such as used in the First Order Fire Effects Model (FOFEM; Reinhardt et al., 1997) and BehavePlus (Andrews, 2009). A systematic evaluation of these and other existing post-fire mortality models' predictive accuracies is needed, such as the ones conducted here and elsewhere (Sieg et al., 2006; Hood et al., 2007c; Breece et al., 2008). These evaluations could then be used to improve post-fire tree mortality predictive software to aid users in objectively selecting the best model for their location.

Acknowledgments

The Forest Service, U.S. Department of Agriculture, Region 5, Natural Resource Management program and Forest Health Protection program provided funding for data collection and analysis.

We also acknowledge funding from the Joint Fire Science Program under Project JFSP 05-2-1-105. We greatly appreciate the support and cooperation from personnel on the Eldorado, Lassen, Sequoia and Tahoe National Forests. Kevin Ryan assisted with the study design and Dave Turner provided statistical advice. We thank M. Ahearn, M. Berry, K. Bowdoin, J. Egan, S. Emmert, C. Evanoff, E. Frolli, L. Galland, S. Hack, R. Mahnke, S. McFarland, J. Morris, M. Murphy, S. Muse, D. Olson, K. Patterson, J. Paul, K. Pavlica, E. Smith, B. Strom, and R. Turcotte for their assistance with field data collection and J. Maddox and R. Bennett for data entry. The comments of Charles McHugh and two anonymous reviewers greatly improved previous versions of this manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.05.033.

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