

Modeling Tree Mortality Following Wildfire in *Pinus ponderosa* Forests in the Central Sierra Nevada of California

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Abstract. We modeled tree mortality occurring two years following wildfire in *Pinus ponderosa* forests using data from 1275 trees in 25 stands burned during the 1987 Stanislaus Complex fires. We used logistic regression analysis to develop models relating the probability of wildfire-induced mortality with tree size and fire severity for *Pinus ponderosa*, *Calocedrus decurrens*, *Quercus chrysolepis*, and *Q. kelloggii*. One set of models predicts mortality probability as a function of DBH and height of stem-bark char, a second set of models uses relative char height (height of stem-bark char as a proportion of tree height) as the predictor. Probability of mortality increased with increasing height of stem-bark char and decreased with increasing tree DBH and height. Analysis of receiver operating characteristic (ROC) curves indicated that both sets of models perform well for all species, with 83 to 96 percent concordance between predicted probabilities and observed outcomes. The models can be used to predict the probability of post-wildfire mortality of four tree species common in *Pinus ponderosa* forests in the central Sierra Nevada of California.

Keywords: Fire effects; Logistic regression; Ponderosa pine; Wildfire

Introduction

Prediction of postfire tree mortality in relation to fire behavior and resulting injury to trees is important to foresters and ecologists for a variety of purposes. Foresters need to be able to predict mortality following wildfire in order to plan salvage logging and regeneration operations. Mortality predictions are also needed for planning prescribed fires. Knowledge of tree mortality in relation to fire behavior and fire-induced injury facilitates understanding of the effects of fire on the structure and composition of plant communities; therefore postfire mortality prediction models can be an important component in ecosystem process and succession models.

Fire kills trees by the combined effects of heat injury and secondary agents to which injured trees are more susceptible, such as bark beetles and pathogens. Major types of heat injury that kill trees include scorching or consumption of foliage and buds in the crown, cambium kill, and root kill. Resistance of an individual tree to fire-induced mortality depends on morphological characteristics that protect vital tissues from heat injury, and the ability to recover from some degree of injury. Characteristics that reduce crown scorching include an elevated, open crown, and large thick buds that can protect the meristematic tissue (Wagener 1961). Thick, corky bark insulates the cambium (Hare 1965), and trees with deeper rooting habits are less prone to root kill (Brown and Davis 1973). Epicormic sprouting from dormant buds allows many hardwoods and a few conifers to recover from complete crown scorch, provided the cambium is not girdled (Plumb 1980, Plumb and McDonald 1981, Kozlowski et al. 1991). Recovery is typically greater following dormant season fires, when buds have hardened and carbohydrate reserves are greater (Wagener 1961). Vigor also appears to be a factor in a tree's ability to recover from heat injury (Wagener 1961). Within species, the fire resistance associated with morphological traits tends to increase with tree size and age.

Postfire mortality prediction guidelines and models generally include variables reflecting the nature and/or severity of heat injury, and morphological variables reflecting resistance to heat injury. Height of crown scorch can be related to fire intensity (Van Wagner 1973), but has not performed as well in models of postfire tree mortality as other variables, such as percent of prefire live crown length scorched (Wyant et al. 1986), or percent of prefire crown volume scorched (Peterson 1985, Ryan and Reinhardt 1988, Ryan et al. 1988). Several authors have observed that recovery from a high degree of foliage scorch is possible if buds and fine twigs remain relatively uninjured, as can occur during late season wildfires in species with large buds

such as *Pinus ponderosa* (ponderosa pine) (Wagener 1961, Dieterich 1979). Cambial damage has been correlated with mortality through the use of height of stem-bark char (Wyant et al. 1986), depth of char, percent of basal circumference charred (Peterson and Arbaugh 1986), and number of quadrants with dead cambium (Ryan et al. 1988). Bark thickness has been the most widely employed morphological variable used to account for resistance to fire-injury (Harmon 1984, Ryan and Reinhardt 1988, Greene and Schilling 1987), although bark thickness is generally calculated from diameter at breast height (DBH) rather than being measured directly. DBH has also been demonstrated to be negatively correlated with postfire mortality (Harrington 1987, Ryan et al. 1988). Evidence has been found that the insulating ability of bark varies among species, independent of thickness (Hare 1965), but the importance of these differences relative to fairly large interspecies differences in bark thickness is unclear.

The cumulative effect of different types of injury in combination appears to be greater than the effect of any single type of injury alone (Wagener 1961, Peterson and Arbaugh 1986, Wyant et al. 1986, Ryan et al. 1988, Ryan and Reinhardt 1988). Most postfire mortality prediction models utilize variables reflecting either severity of, or resistance to, more than one type of injury.

Current guidelines for estimating postfire mortality in *P. ponderosa* forests in California are based on subjective assessments of several factors influencing mortality (Wagener 1961). The objective of our study was to develop models, based on easily and objectively measured postfire variables, for predicting wildfire-induced tree mortality in *P. ponderosa* forests in California.

Methods

Study area

In the late summer of 1987, the Stanislaus Complex fires burned approximately 60,000 hectares of the Stanislaus National Forest, on the west slope of the Sierra Nevada in central California. We selected 25 stands in which the prefire species composition was dominated by *P. ponderosa*, with no evidence of recent human disturbance. Study stands encompassed a wide range of prefire stand structures and composition (Table 1), with average stand age of 79 years (range 40-180) and average stand height of 24 m. Elevation of these study stands ranges from 800 to 1300 m, and soils are derived from metasedimentary and granitic parent materials. Study stands were affected by a broad range

Table 1. Prefire basal area and number of trees by species for 75 study plots in 25 stands burned in the Stanislaus Complex Fires in the Sierra Nevada of California.

Species	Relative Basal Area			Relative Number of Trees		
	Mean	SD	Range	Mean	SD	Range
	Percent					
<i>Pinus ponderosa</i>	89.7	14.3	32-100	80.1	22.5	12-100
<i>Calocedrus decurrens</i>	3.1	9.5	0-46	3.7	11.0	0-00
<i>Quercus kelloggii</i>	2.6	6.2	0-34	3.7	7.1	0-36
<i>Quercus chrysolepis</i>	1.5	3.7	0-22	7.6	14.3	0-50
<i>Pinus lambertiana</i>	1.5	6.5	0-46	2.8	8.2	0-53
Other Species ¹	1.6	-	-	2.1	-	-
	m ² /ha			trees/ha		
Stand Total	46.4	16.9	20-109	456.3	260.2	125-1975

¹ Other species include *Pinus attenuata*, *Pseudotsuga menziesii*, and *Quercus wislizenii*.

of fire intensity, from low-intensity surface fires to high-intensity crown fires. Botanical nomenclature follows Munz and Keck (1973).

Data

In August and September of 1989, two years after burning, we established 75 plots 400 m² in size in the 25 study stands. For all standing trees on each plot, we measured tree DBH, total height, height of stem-bark char (distance from groundline to the highest point of bole blackening on the uphill or leeward face of the tree), and status of each tree (live, fire-killed, or dead prior to the fire). Trees were considered live if they had any green foliage remaining. Condition of the bark, advanced degree of decay, and lack of fine twigs were used to identify those trees dead before the fire, which were not included in any analyses discussed in this paper. Pertinent comments such as bark beetle infestation were recorded when present. Breast height age was determined on a subsample of trees on each plot.

Since we sampled at the end of the second growing season following fire, sufficient time had passed for the majority of delayed mortality to occur (Wagener 1961, Dieterich 1979); however it was difficult to distinguish scorched foliage from foliage that had simply died sometime after the fires. Therefore we did not include any crown scorch variables in our analysis.

Data analysis

Logistic regression analysis (Walker and Duncan 1967) was used to model the probability of postfire tree mortality as a function of tree size and fire injury variables. The logistic regression model has the form:

$$P(m) = 1/[1 + e^{-(\eta_0 + \eta_1 X_1 + \dots + \eta_K X_K)}] \quad (1)$$

where $P(m)$ is the probability of postfire mortality, X_1 through X_K are independent variables, and η_0 through η_K are model coefficients estimated from the data. The logistic regression model is appropriate for modeling mortality probability because its range is bounded by 0 and 1, and continuous, ordinal, or nominal independent variables may be used to predict binary or ordinal dependent variables, independent of the assumption of multivariate normality (Meter and Maynes 1970, Daniels et al. 1979).

We used DBH, tree height, height of stem-bark char, and relative char height (height of stem-bark char expressed as a proportion of tree height) as independent variables to predict probability of fire-induced mortality for *P. ponderosa* (ponderosa pine), *Calocedrus decurrens* (incense cedar), *Quercus chrysolepis* (canyon live oak), and *Quercus kelloggii* (California black oak). A wide range of tree sizes and fire severity was represented in the data for each of these four species (Table 2). Probability of mortality was hypothesized to be negatively correlated with tree size descriptors, and positively correlated with fire-injury descriptors. Models including various combinations of independent variables were fit to the data; best models were chosen from all candidates on the basis of diagnostic statistics, independent variables being relatively uncorrelated with one another, and accordance with biological theory, as mentioned above. To determine if a general model could be found which was applicable to more than one species, dummy variable regression was used to compare models between species. The SAS LOGISTIC

procedure was used to obtain maximum likelihood estimates of the model coefficients (SAS Institute 1989). Model goodness-of-fit and predictive ability were assessed by the likelihood ratio χ^2 statistic and receiver operating characteristic (ROC) curve analysis (Saveland and Neuenschwander 1990).

ROC curve analysis is an analytical technique derived from signal detection theory, which provides methodology for assessing the performance of diagnostic systems, characterized by a stimulus, a response, and a state of nature (Swets and Pickett 1982, Saveland and Neuenschwander 1990). In evaluating tree mortality prediction models, the observed status of a tree is the stimulus, the model prediction is the response, and the agreement between the two is the outcome. The comparison of observed status and that predicted by the model can have four possible outcomes; hit, miss, false alarm, or correct rejection (for example, a hit is both predicted and observed dead, while a false alarm is observed live but predicted dead) (Saveland and Neuenschwander 1990). The conditional probability of each outcome is calculated by dividing the number of occurrences in a cell (outcome) by the total number of occurrences in that column (observed status) (Saveland and Neuenschwander 1990).

Because the logistic mortality model predicts continuous mortality probabilities in the interval [0,1], whereas observed status is dichotomous (live or dead), some threshold mortality probability (decision criterion) must be chosen to decide to predict whether a tree will live or die. This decision criterion may be set arbitrarily, or based on some information such as the relative expected values of various possible outcomes (Saveland and Neuenschwander 1990). The condi

Table 2. Characteristics of trees used to develop and validate models for predicting postfire tree mortality following the Stanislaus Complex Fires in the Sierra Nevada of California.

Species	Postfire Status	Trees		DBH(cm)		Tree Height(m)			Height of Stem-Bark Char(m)			Relative Char Height ¹		
		n	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
<i>Pinus ponderosa</i>	Live	275	41.8	17.3	13-114	28.9	8.3	9-55	5.6	4.5	0-21	0.19	0.14	0-0.72
	Dead	550	29.4	14.7	9-89	23.5	7.8	3-50	16.5	8.5	0-40	0.71	0.30	0-1
<i>Calocedrus decurrens</i>	Live	34	36.4	11.6	16- 64	20.0	6.2	7- 35	4.8	4.3	0- 20	0.27	0.24	0- 1
	Dead	17	27.8	21.9	11- 76	16.5	13.3	6- 44	8.5	5.3	2- 16	0.58	0.29	0.25 -1
<i>Quercus chrysolepis</i>	Live	14	27.5	12.2	15-51	10.7	3.3	6-16	0.5	0.52	0-1	0.06	0.06	0-0.17
	Dead	73	14.1	4.9	9-35	8.0	4.6	4-25	5.1	3.1	0.3-15	0.70	0.36	0.03-1
<i>Quercus kelloggii</i>	Live	10	34.2	17.3	14-71	18.3	9.5	6-32	1.9	1.8	0-6	0.08	0.06	0-0.21
	Dead	28	25.4	15.5	10-69	13.7	6.5	6-33	7.0	5.0	0-18	0.58	0.38	0-1
Validation Dataset ²														
<i>Pinus ponderosa</i>														
	Live	79	43.7	19.6	16-98	29.5	9.2	15-54	6.1	5.0	0-21	0.20	0.13	0-0.65
	Dead	193	27.3	16.0	10-112	22.6	8.3	2- 47	16.0	8.8	1 -36	0.71	0.31	0.05 -1

¹ Relative Char Height = Char Height/Total Tree Height.

² Approximately 25 percent of the *Pinus ponderosa* sample trees were randomly selected and removed prior to model fitting to be used for model validation.

tional probabilities of the four possible outcomes will vary according to the decision criterion; as decision criteria approach 0 the rate of hits and false alarms increases, and decision criteria closer to 1 result in higher rates of misses and correct rejections. The ROC curve is generated by plotting the hit rate versus the false alarm rate as the decision criterion varies from 0 to 1 (Egan 1975). The area under the the ROC curve is useful for assessing overall model performance: the greater the area under the ROC curve, the better the performance (Saveland and Neuenschwander 1990). When the dependent variable is binary, rather than polychotomous, the area under the ROC curve is closely related to the Mann-Whitney U statistic (Bamber 1975, Leach 1979) and is also equivalent to the index C (Hanley and McNeil 1982).

The index C measures association between predicted probabilities and observed conditions and is calculated as the proportion of concordant pairs of observations plus one-half the number of ties (Harrell 1986). Concordant pairs are defined as follows. Take two observations having different values of observed status (live or dead). If the observation that died has a greater predicted probability of mortality than the one that lived, then the two observations form a concordant pair (Harrell 1986). Although it may be derived from

either the proportion of concordant pairs or as the area under the ROC curve, C is useful for evaluating model predictive ability, and is independent of any arbitrarily chosen decision criterion (Harrell 1986, Saveland and Neuenschwander 1990).

To evaluate further the performance of the mortality models for *P. ponderosa*, a subsample of 272 trees (approximately 25 percent) of the *P. ponderosa* dataset was randomly selected and removed from the dataset prior to fitting, to be used for validation purposes. Agreement between the model predictions and observed outcomes in the validation dataset was evaluated using ROC curve analysis (Saveland and Neuenschwander 1990).

Results

The best mortality prediction model for all species used DBH and height of stem-bark char as predictor variables (Table 3). The Likelihood Ratio χ^2 was highly significant for all species ($P \leq 0.001$), and the coefficients for both DBH and height of stem-bark char were also significant ($P \leq 0.01$) for all species (Table 3). Dummy variable regression indicated that the coefficients for the *Q. chrysolepis* model did not differ

Table 3. Logistic regression models for predicting tree mortality following late-season wildfire in *Pinus ponderosa* forests in the central Sierra Nevada of California. * and ** = parameter estimate differs from zero at $\alpha = 0.05$ and at $\alpha = 0.01$, respectively (Wald's χ^2 test).

Two Variable Model						
$P(m) = 1/[1+e^{-(\eta_0+\eta_1X_1+\eta_2X_2)}]^{1/}$						
Species	η_0	η_1	η_2	LRS ²	$P(\Omega)^2$	C
<i>Pinus ponderosa</i>	1.0205**	-0.0933**	0.2858**	509.8	0.0001	0.930
<i>Calocedrus decurrens</i>	-0.1148	-0.0713**	0.2642**	15.5	0.0004	0.844
	2.1327*	-0.1676**	1.3328**	75.9	0.0001	0.968
One Variable Model						
$P(m) = 1/[1+e^{-(\eta_0+\eta_3X_3)}]^{1/}$						
Species	η^0	η^3	LRS ²	$P(\Omega)^2$	C ³	
<i>Pinus ponderosa</i>	-2.2697**	7.5662**	487.3	0.0001	0.914	
<i>Calocedrus decurrens</i>	-2.3205**	4.0242**	13.1	0.0003	0.830	
	-2.3240**	20.2875**	74.2	0.0001	0.961	

Where: $P(m)$ = predicted probability of fire-induced mortality (mortality refers to top-kill for *Quercus* spp.)

X_1 = tree diameter at breast height (DBH, cm)

X_2 = height of stem-bark char (m)

X_3 = relative char height (height of stem-bark char I tree total height)

β^3 = model coefficients estimated from the data

e^i = the base of the natural logarithm

LRS = Likelihood Ratio Statistic, a χ^2 statistic for assessing model goodness of fit, with df = number of parameters in the model. Statistical significance of LRS indicated in column labeled $P(\Omega)$.

C is the proportion of concordant pairs, and is a measure of association between predicted probabilities and observed outcomes. It is also equal to the area under the Receiver Operating Characteristic (ROC) curve.

Quercus spp. includes *Quercus chrysolepis* and *Q. kelloggii*. Separate models for these two species were compared and found to not differ significantly ($P > 0.15$ for both models), so single models were fit to the combined data.

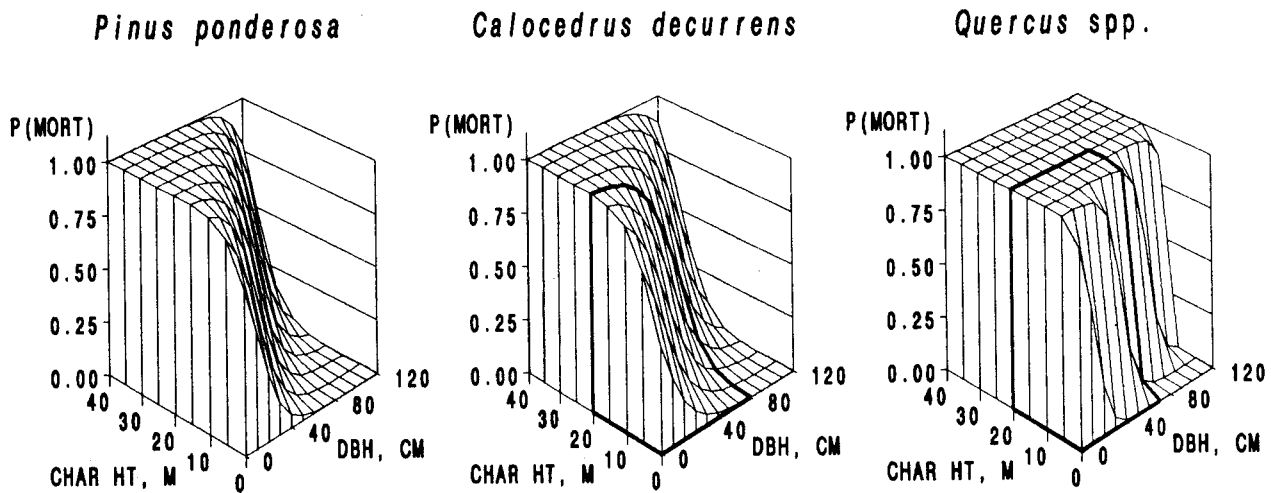


Figure 1. Response surfaces for logistic regression models of probability of postfire mortality as a function of DBH and height of stem-bark char for individual trees of four species common in *Pinus ponderosa* forests in the Sierra Nevada of California. *Quercus* spp. includes *Quercus chrysolepis* and *Q. kelloggii*. Surfaces are plotted on a common scale for visual comparison. The heavy solid lines on the *Quercus* and *C. decurrens* surfaces delineate the narrower range of the data for these species.

from those of the *Q. kelloggii* model ($P < 0.05$ for both DBH and char height), so data for these two species were combined to estimate the parameters of a model for mortality probability for *Quercus* spp. (Table 3). In our analysis, mortality of *Quercus* spp. refers to top-kill, not complete mortality of each individual. One hundred percent of top-killed *Q. chrysolepis* and 89 percent of top-killed *Q. kelloggii* sprouted from the root collar. The response surfaces for postfire mortality probability as a function of DBH and height of stem bark char for *P. ponderosa*, *C. decurrens*, and *Quercus* spp. are shown in Figure 1. Probability of mortality increases with increasing char height, and decreases with increasing DBH (Table 3, Figure 1), as hypothesized.

Relative char height (height of stem-bark char as a proportion of tree height) was also found to be a good predictor of mortality. Models predicting mortality as a function of relative char height were highly significant ($P < 0.0003$ for all species), and the slope coefficients indicate that probability of mortality significantly increases with increasing relative char height for all species ($P < 0.01$) (Table 3). Figure 2 illustrates the models predicting probability of mortality as a function of relative char height for *P. ponderosa*, *C. decurrens*, and *Quercus* spp.: once again, the models for the two *Quercus* spp. did not differ, so a single model for both species is presented (Table 3).

C was quite high for all species for both the model based on DBH and char height, and the relative char height model, ranging from 0.83 to 0.968 (Table 3). The relationship between C and the ROC curves is demonstrated in Figure 3. The mortality probability

model based on DBH and char height for the *P. ponderosa* fitting dataset has a C of 0.93, and $C = 0.914$ for the relative char height model (Figure 3). Both models perform quite well, with fairly high hit rates at low false alarm rates. ROC curves are not shown for the other species; C can be used to assess model performance (Table 3).

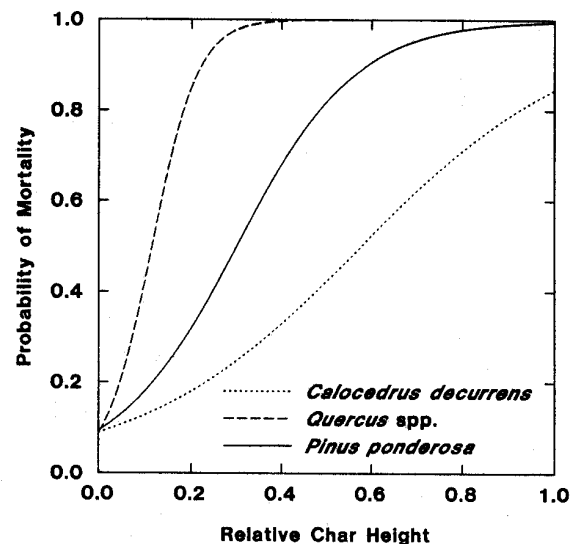


Figure 2. Probability of post-wildfire mortality as a function of relative char height (height of stem-bark char / tree height) for individual trees of four species common in *Pinus ponderosa* forests in the Sierra Nevada of California. *Quercus* spp. includes *Quercus chrysolepis* and *Q. kelloggii*.

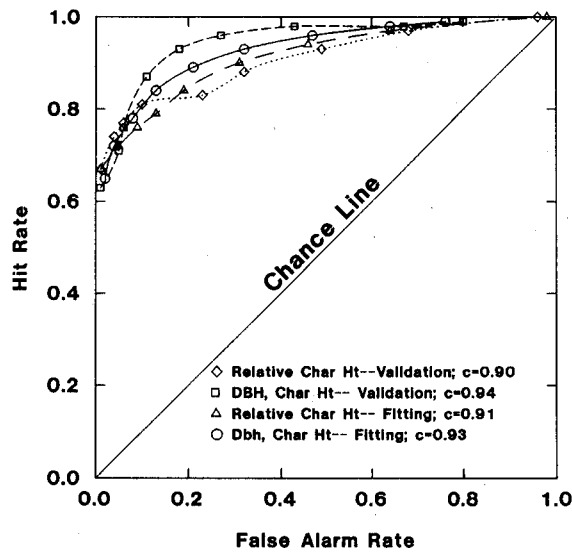


Figure 3. Receiver Operating Characteristic curves for logistic post-wildfire mortality probability models for *Pinus ponderosa*. ROC curves are based on the performance of two mortality prediction models on the estimation (fitting) dataset and for a validation dataset. Post-wildfire mortality probability is predicted as a function of DBH and char height, and as a function of relative char height (char height as a proportion of tree height).

The two *P. ponderosa* mortality models were applied to the validation dataset consisting of 272 trees which were randomly selected for removal prior to model fitting. Model predictions for the validation dataset were quite consistent with observed mortality for both models (Table 4). ROC curves were also used to assess model performance on the validation dataset, and to compare the behavior of the models between the fitting and validation dataset (Figure 3). *C* was 0.94 for the DBH and char height model, and 0.90 for the relative char height model (Figure 3). ROC curve analysis indicates that both models give close agreement between predicted mortality probabilities and

observed status two years following wildfire, with the model based on DBH and char height performing somewhat better (Figure 3).

Discussion

Model evaluation

Our results agree with those of many researchers that DBH is negatively correlated with postfire tree mortality (Table 3, Figures 1 and 2) (Wyant et al. 1986, Harrington 1987, Ryan et al. 1988). The greater fire resistance of trees with larger diameter is generally attributed to increased insulation of the cambium by the thicker bark of larger trees. Several researchers have used bark thickness as a predictor of postfire mortality (Hannon 1984, Ryan and Reinhardt 1988); however, few researchers have actually measured bark thickness (Peterson and Arbaugh 1986). Bark thickness is generally computed as a function (often linear) of DBH, with different bark thickness functions by species (Hannon 1984, Ryan and Reinhardt 1988). A consequence of this approach is that variation in bark thickness due to site differences and random variability is artificially removed from the data. Also, any linear relationship of bark thickness to DBH can be accounted for directly in the coefficients of the logistic mortality model. The insulating efficiency of bark also varies by species and age, independent of thickness, according to bulk density, proportion of cork, and ratio of outer bark to inner bark (Hare 1965, Spalt and Reifsnnyder 1962). Direct measurements of cambial injury in relation to fire behavior, bark thickness, and bark thermophysical properties would be necessary to understand fully the contribution of bark to fire resistance. DBH, used either directly or to calculate estimated bark thickness, and measured bark thickness both perform well for predicting postfire mortality for practical applications

Table 4. Classification table comparing observed and predicted postfire status¹ of a validation sample² of 272 *Pinus ponderosa* for validation of logistic regression models predicting probability of wildfire-induced mortality in the Sierra Nevada of California.

Model: $P(\text{mort}) = f(\text{DBH, Char Height})$				Model: $P(\text{mort}) = f(\text{Relative Char Height})^3$			
<u>Observed Status</u>				<u>Observed Status</u>			
<u>Predicted Status</u>	Dead	180	14	<u>Predicted Status</u>	Dead	160	18
	Live	13	65		Live	33	61
Total number observed		193	79	Total number observed		193	79

¹ For this analysis, 0.5 was chosen a priori as the decision criterion. That is, trees with predicted probability of mortality ≥ 0.5 are predicted dead.

² Prior to model fitting, approximately 25 percent (272 trees) of the *Pinus ponderosa* dataset were randomly selected and removed from the fitting dataset to be used for model validation.

³ Relative Char Height = Height of Stem-Bark Char/ Total Tree Height.

(Loomis 1973, Hannon 1984, Peterson and Arbaugh 1986, Ryan and Reinhardt 1988, Saveland and Neuenschwander 1990), although DBH is more easily and rapidly measured.

Crown scorch has been implicated as the primary cause of postfire mortality in conifers, largely due to killing of buds (Wagener 1961, Dieterich 1979, Wyant et al. 1986, etc.), and ocular estimates of percent of crown volume scorched have been used to predict mortality with good success (Ryan and Reinhardt 1988, Ryan et al. 1988, Saveland and Neuenschwander 1990). Variables reflecting stem char have also been used to estimate mortality of conifers (Storey and Merkel 1960, Wyant et al. 1986) and upland oaks in the eastern United States (Loomis 1973, Regelbrugge 1988). In our study, both absolute and relative height of stem bark char were demonstrated to be significant predictors of mortality following wildfire (Table 3). Height of crown scorch has been related to fire intensity, flame length, ambient temperature, and wind speed (Van Wagner 1973). Height of stem-bark char, while not a good estimator of absolute flame length or fire intensity, may be useful to estimate relative differences in flame length and fire intensity (Cain 1984). Percent of crown volume scorched will be determined by the height of scorch, and the elevation and shape of the crown. It seems likely that height of crown scorch (absolute or percent of prefire live crown length), percent crown volume scorched, and height of stem-bark char would be correlated; however this information is rarely found in the literature. If compared on the basis of C, or by computing the percentage of trees correctly classified at an arbitrarily chosen decision criterion, such as 0.5, our model based on char height and DBH appears to have comparable performance to other published models (based on these and other variables) for different species and geographical locations (Peterson and Arbaugh 1986, Wyant et al. 1986, Ryan and Reinhardt 1988, Ryan et al. 1988, Saveland and Neuenschwander 1990).

The postfire mortality probability model based on relative char height also performs comparably to previously published models, but does not perform quite as well as the model based on DBH and char height, as indicated by the ROC curves and C (Figure 3, Table 3, Table 4). Relative char height was found to be a better single variable predictor than absolute height of stem-bark char, but was not used in conjunction with DBH for several reasons. Models based on DBH and relative char height were found not to yield significant improvement over the DBH and char height model in terms of goodness of fit, and area under the ROC curve. Also, DBH did not always make a significant contribution to the model in the presence of relative char

height, as indicated by the Wald χ^2 test for significance of individual parameters. Most of our stands were relatively even-aged, and composed of fairly shade-intolerant species; therefore it was not surprising to find that DBH was strongly correlated with tree height (r ranged from 0.69 for *Q. chrysolepis* to 0.87 for *P. ponderosa*). This fact resulted in DBH also being fairly well correlated (negatively) with relative char height. We did not consider the model using DBH and relative char height to be very useful due to this collinearity, and the corresponding lack of significant improvement over the DBH and char height model.

Percent of crown scorched, either expressed as volume or length, has been demonstrated to be a better predictor of mortality than absolute height of crown scorch (Peterson 1985, Wyant et al. 1986, Ryan et al. 1988), indicating that probability of mortality is determined by the actual injury sustained by a tree rather than the fire-caused environmental conditions. In headfires (common in wildfires on steep slopes) our model based on relative char height accounts for this concept directly. Because DBH is positively correlated with height, the model based on DBH and char height indirectly accounts for resistance to crown scorching arising from a higher crown, as well as accounting for resistance to cambium kill resulting from thicker bark. Although height of stem-bark char may not explicitly quantify fire-injury, our data provide evidence that stem char height may be an empirical predictor of the degree of fire-injury in certain situations. Other studies have also found DBH and height of stem-bark char to be related to postfire mortality of several hardwood species (Loomis 1973, Plumb 1980, Regelbrugge 1988) and conifers (Storey and Merkel 1960, Wyant et al. 1986).

Several factors that affect postfire mortality are not explicitly accounted for by our models. Season of burning can affect fire resistance. Many tree species (e.g., *P. ponderosa*) appear to be more susceptible to mortality following early growing season burns than to late growing season or dormant season burns (Harrington 1987). Early in the growing season bark moisture content is higher, increasing thermal conductivity, vulnerable tissues such as elongating meristems are exposed, and carbohydrate reserves are decreased (Wagener 1961). Insulation of meristematic tissue by well-developed buds in species with large buds, such as *P. ponderosa*, is believed to facilitate survival of trees with high degrees of foliage scorch (Wagener 1961, Dieterich 1979). The models presented in this paper are most applicable to late season wildfires, as the study stands were burned in late August and September.

Delayed mortality can be affected by insect infestation and disease incidence, both of which were present in our study areas. We observed bark beetle infestations on both living and dead trees in our study, but did not quantify the effect of insect infestation on mortality. The majority of insect-induced delayed mortality is likely to have occurred by the end of the second postfire growing season (Wagner 1961, Dieterich 1979), when our sampling occurred, so our models may indirectly account for the interactions between fire injury and insect infestation and disease incidence.

Tree vigor influences resistance to fire injury, but we did not quantify vigor directly. Only to the extent that vigor is correlated with tree size is vigor accounted for by our models. The vigor of many trees in our sample may have been somewhat reduced by a long-term drought which occurred during the course of our study.

One other factor influencing mortality that we were unable to account for is variation in residence time of fire related to smoldering combustion of large fuels, and in areas with a thick forest floor. The long duration of smoldering combustion can result in cambial girdling and root kill, increasing the likelihood of mortality for trees with relatively little crown scorch. Our mortality prediction models do not account for injury related to increased duration of heating.

Species comparisons

Species-specific differences in fire resistance can be evaluated using these postfire mortality prediction models. Both models indicate that *P. ponderosa* and *C. decurrens* are more resistant to fire-induced mortality than are *Q. chrysolepis* and *Q. kelloggii* (Figures 1 and 2). Unlike most conifers, *Quercus* spp. may survive 100 percent crown scorch by producing epicormic sprouts from dormant buds on branches in the crown, if the cambium is not girdled (Plumb 1980, Plumb and McDonald 1981). We observed many surviving individuals of both *Quercus* species with much (if not all) of their foliage originating from postfire epicormic sprouting. However, these *Quercus* species appear more susceptible to cambial damage than *P. ponderosa* and *C. decurrens* due to thinner, denser bark. Following top-kill due to cambial girdling, the majority of *Quercus* in our study sprouted vigorously from the root collar, which is consistent with previous studies which note the high frequency of basal sprouting following cutting or burning of various *Quercus* spp. (Plumb 1980, Plumb and McDonald 1981, Regelbrugge 1988 and Paysen et al. 1991). Basal sprouts originate from dormant buds, which sprout in

response to decreased levels of inhibitory growth regulating hormones, which are produced in the crown and translocated to the root system. In our study, 36 percent of *Q. chrysolepis* and 60 percent of *Q. kelloggii* which were not top-killed produced basal sprouts. Although some background sprouting of undisturbed trees has been noted (Paysen et al. 1991), the frequency of this type of sprouting has not been well-documented. This sprouting may have been caused by these trees receiving enough cambial and/or crown damage to disrupt the production of growth regulating hormones which normally inhibit sprouting of dormant buds. Increased insolation on the tree boles may also initiate sprouting from dormant buds (Paysen et al. 1991).

The postfire mortality prediction model based on DBH and char height, and the model based on relative char height, did not differ between the two *Quercus* species (Table 3), and general models fit to the two species combined appeared to have good performance for both species. Although a more extensive sample may reveal differences in fire resistance between these two species, in our study there was much overlap in the ranges of tree size and fire injury between these species, and both species exhibited similar mortality (top-kill) responses. Differences in fire resistance have been found among various *Quercus* spp. in the eastern United States (Loomis 1973, Regelbrugge 1988).

According to the relative char height model, *C. decurrens* appears more fire resistant than *P. ponderosa* (Figure 2), although this difference is not evident in the mortality response in relation to DBH and char height (Figure 1). In our sample, *C. decurrens* tended to be shorter than *P. ponderosa*, relative to DBH. Therefore, a *C. decurrens* with a given DBH and char height would have a greater relative char height than would a *P. ponderosa* with the same DBH and char height. It is unclear which model more accurately demonstrates relative fire resistance of these two species. *P. ponderosa* is believed to be one of the most fire resistant conifers of the western United States (Brown and Davis 1973). When young, *C. decurrens* has thin bark and is believed to be quite fire susceptible, although bark thickness and fire resistance are believed to increase significantly with size and age (Powers and Oliver 1990). *C. decurrens* may also be less prone to postfire insect attack than *P. ponderosa* (Powers and Oliver 1990). More data are needed to determine the relationships between tree size, age, and relative fire resistance between these species.

Model application

Several considerations are important in applying these models. The predicted probability of mortality

may be interpreted as the probability of postfire mortality of an individual tree with given DBH and char height (or relative char height), or the proportion of trees likely to die in a given DBH and char height (or relative char height) class. If the models are applied to individual trees, then a decision criterion must be chosen to predict mortality. The optimum decision criterion will vary depending on the relative values of certain outcomes and on a given user's objectives. One objective may be to maximize the percent of correct classification, which would be accomplished for our *P. ponderosa* models with a decision criterion of 0.5. There are times when different outcomes may not have equal values, for example false alarms may be more costly than misses, in which case one would accept more false alarms in order to increase the hit rate. Saveland and Neuenschwander (1990) provide an excellent discussion of considerations and strategies for choosing optimum decision criteria.

Both logistic mortality models provided good fits to the data for all species studied, and the *P. ponderosa* models predicted well for the validation dataset (Tables 3 and 5). This indicates that our models reflect factors important in determining postfire mortality even though they do not directly quantify the mechanisms responsible for this mortality.

Conclusions

We developed models for predicting probability of post-wildfire mortality for four tree species common in *P. ponderosa* forests throughout California. The models are based on DBH, maximum height of stem-bark char, and height of stem-bark char expressed as a proportion of tree height. All of the variables can be easily and consistently measured without any subjective judgements. The models based on DBH and char height require more information than those based on relative char height, but give somewhat better performance. These models should be viewed as preliminary, as they have not been tested against independent data. However, due to the wide range of tree sizes and fire behavior represented in the data, and the good performance of the *P. ponderosa* models when applied to the validation dataset, we believe these models will provide reasonable estimates of post-wildfire mortality probability in *P. ponderosa* forests in California. These models are most applicable to *P. ponderosa* forests in the central Sierra Nevada with stand structure and composition similar to those in this study, and which are burned by late-summer wildfires.

These models should be useful to forest managers planning post-wildfire salvage logging and regenera-

tion operations, and to ecologists interested in the role of wildfire in determining the structure and composition of forest communities. They may be useful in assessing mortality following prescribed fires as well.

The process by which trees die as a result of fire-induced injury is still poorly understood. Better understanding of the relationships between fire behavior, fire-injury to individual trees, and the physiological response of trees to these injuries will improve our understanding of fire-induced tree mortality, and its influence on the structure and function of forest communities.

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