

RESEARCH ARTICLE

PREDICTING POST-FIRE TREE MORTALITY FOR 12 WESTERN US CONIFERS USING THE FIRST ORDER FIRE EFFECTS MODEL (FOFEM)

Sharon Hood* and Duncan Lutes

Fire, Fuel, and Smoke Science Program, Rocky Mountain Research Station, US Forest Service,
5775 Highway 10 W, Missoula, Montana 59808, USA

*Corresponding author: Tel.: +1-406-329-4818; e-mail: sharonmhood@fs.fed.us

ABSTRACT

Accurate prediction of fire-caused tree mortality is critical for making sound land management decisions such as developing burning prescriptions and post-fire management guidelines. To improve efforts to predict post-fire tree mortality, we developed 3-year post-fire mortality models for 12 Western conifer species—white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.), red fir (*Abies magnifica* A. Murray bis), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), incense cedar (*Calocedrus decurrens* [Torr.] Florin), western larch (*Larix occidentalis* Nutt.), lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. ex S. Watson), whitebark pine (*Pinus albicaulis* Engelm.), ponderosa pines (*Pinus ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm and var. *ponderosa* C. Lawson), Jeffrey pine (*Pinus jeffreyi* Balf.), sugar pine (*Pinus lambertiana* Douglas), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *glauca* [Beissn.] Franco)—by pooling data collected from multiple fire-injury studies. Two sets of models were created: one for use in pre-fire planning in which only crown injury and tree

RESUMEN

La predicción precisa de la mortalidad causada por el fuego es crítica para tomar decisiones apropiadas en la gestión de tierras, tales como el desarrollo de las prescripciones de quema y directrices en el manejo post-fuego. Para mejorar los esfuerzos para predecir la mortalidad de árboles post-fuego, desarrollamos modelos de mortalidad de 3 años post-fuego para 12 especies de coníferas del Oeste—abeto blanco (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.), abeto rojo (*Abies magnifica* A. Murray bis), abeto subalpino (*Abies lasiocarpa* [Hook.] Nutt.), libo-cedro de California (*Calocedrus decurrens* [Torr.] Florin), alerce americano (*Larix occidentalis* Nutt.), pino contorta (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. ex S. Watson), pino de corteza blanca (*Pinus albicaulis* Engelm.), dos variedades de pino ponderosa (*Pinus ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm and var. *ponderosa* C. Lawson), pino de Jeffrey (*Pinus jeffreyi* Balf.), pino lambertiana (*Pinus lambertiana* Douglas), picea de Engelmann (*Picea engelmannii* Parry ex Engelm.), y pino oregón (*Pseudotsuga menziesii* [Mirb.] Franco var. *glauca* [Beissn.] Franco) reuniendo datos recolectados de múltiples estudios sobre daños por fuego. Dos conjuntos de modelos fueron creados: uno para planificación pre-fuego, en el cual solo el daño en la copa y en el diámetro a la altura del pecho de los árboles (DAP) fueron las variables potenciales, y el segundo, un modelo óptimo para usar en planificación post-fue-

diameter (DBH) were potential variables, and a second, optimal model for use in post-fire planning that used all significant variables. Predictive accuracy of all models was compared to the accuracy of the general, non-species specific mortality model used in the First Order Fire Effects Model (FOFEM) prior to version 5.7. The new species-specific models improved prediction of fire-caused tree mortality by 0% to 48%. Model accuracy increased the most for red fir, incense cedar, western larch, and whitebark pine, and increased the least for Engelmann spruce. The models in the post-fire option provided higher accuracy compared to the pre-fire models, but also required additional inputs. These new models were added to FOFEM beginning with version 5.7, and the options in the FOFEM Mortality Module were expanded. We describe the new options in FOFEM and how to use the software to predict tree mortality for pre-fire and post-fire planning, as well as modeling limitations and assumptions. The additions to FOFEM offer improved accuracy in predicting post-fire tree mortality for 12 Western conifer species and allow direct inputs of fire injury to increase software applicability to prescribed fire and post-fire forest management.

go que utilizó todas las variables significativas. La precisión en la predicción de todos los modelos fue comparada con la precisión del modelo general de mortalidad que no especifica las especies, utilizado en el Modelo de Efectos del Fuego de Primer Orden (FOFEM por su sigla en inglés), previa a la versión 5.7. Los nuevos modelos especie-específicos mejoraron la predicción de la mortalidad de árboles causada por fuego desde un 0% a un 48%. La precisión del modelo aumentó más para el abeto rojo, el libo-cedro de California, el alerce americano y el pino de corteza blanca, y en menor medida para la picea de Engelmann. Los modelos en la opción post-fuego proporcionaron una precisión más alta comparados con los modelos pre-fuego, pero también requirieron aportes de datos adicionales. Estos nuevos modelos fueron agregados al FOFEM comenzando con la versión 5.7, y las opciones en el Módulo de Mortalidad del FOFEM fueron expandidas. Describimos las nuevas opciones en el FOFEM, y cómo usar el software para predecir la mortalidad de los árboles para la planificación pre-fuego y post-fuego, como así también las limitaciones y supuestos del modelo. Los agregados al FOFEM ofrecieron una precisión mejorada en la predicción de la mortalidad de los árboles post-fuego para 12 especies de coníferas del Oeste, y permitieron incorporar datos sobre daño directo por fuego, aumentando así la aplicabilidad del software para quemas prescriptas y el manejo forestal post-fuego.

Keywords: *Abies*, *Calocedrus*, decision support tools, fire-induced tree mortality, *Larix*, logistic regression, *Picea*, *Pinus*, prescribed fire, *Psuedotsuga*, salvage, validation

Citation: Hood, S., and D. Lutes. 2017. Predicting post-fire tree mortality for 12 western US conifers using the First Order Fire Effects Model (FOFEM). *Fire Ecology* 13(2): 66–84. doi: 10.4996/fireecology.130290243

INTRODUCTION

Accurate prediction of post-fire tree mortality is critical for making sound land management decisions and assessing fire severity

(Reinhardt and Dickinson 2010, Gill *et al.* 2012, Ryan *et al.* 2013). Typically, predicting fire-caused tree mortality is applied in one of two ways: stand-level assessments and individual tree assessments (Hood *et al.* 2007).

Stand-level mortality predictions are used to develop prescribed fire burn plans, post-fire silvicultural prescriptions, and to quantify larger-scale spatial patterns of wildland fire, while individual tree mortality predictions are used to develop post-fire salvage and hazard tree marking guidelines (Reinhardt and Dickinson 2010).

Post-fire tree mortality is influenced by a several factors, with direct death resulting from injury to tissues in the crown, stem, and roots (Dickinson and Johnson 2001, Michaletz and Johnson 2007). Second-order factors, such as bark beetles, disease, competition, and pre-fire and post-fire climate, can also cause substantial levels of additional mortality above first-order, direct fire effects (Hood and Bentz 2007, van Mantgem *et al.* 2013). While the exact mechanisms of tree death are still unknown, even without fire (Anderegg *et al.* 2015), statistical models of fire-caused tree mortality based on fire injuries and tree size are useful and necessary until process-based models are developed (Butler and Dickinson 2010, Kavanagh *et al.* 2010).

Numerous post-fire mortality models have been developed for western US conifers (Woolley *et al.* 2012). Ryan and Reinhardt (1988) developed the original logistic regression mortality model used in today's United States fire behavior and effects software systems, which was then updated by Ryan and Amman (1994) and used in the First Order Fire Effect Model (FOFEM) prior to version 5.7, making it perhaps the most widely used post-fire mortality model in the US (Hood *et al.* 2007). This model also is included in the BehavePlus (Andrews 2009), and the Fire and Fuels Extension to the Forest Vegetation Simulator (FFE-FVS; Reinhardt and Crookston 2003). Hood *et al.* (2007) evaluated the predictive accuracy of the Ryan and Amman model for both stand and individual tree mortality applications for 13 Western conifer species with independently collected post-fire tree mortality data from across the western US.

Predicted stand-level mortality was within $\pm 20\%$ of observed mortality for all species except incense cedar (*Calocedrus decurrens* [Torr.] Florin), western larch (*Larix occidentalis* Nutt.), red fir (*Abies magnifica* A. Murray bis), and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.). Individual tree mortality prediction was most accurate for subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), incense cedar, ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), and Jeffrey pine (*Pinus jeffreyi* Balf.).

The reason that the Ryan and Amman mortality model is so widely applied is due to its simplicity. Only two inputs are required to run the model: bark thickness and percent crown volume scorched. Bark thickness is used as a measure of thermal resistance to the cambium in the tree stem (Butler and Dickinson 2010) and is calculated from species-specific coefficients and diameter at breast height (1.37 m above ground; DBH). Bark thickness coefficients are included for 219 species, allowing prediction of fire-induced tree mortality for most forest species in the US. Crown volume scorch is calculated from either flame length or scorch height and crown characteristics. In FOFEM, the user must also enter tree height and live crown ratio, which is then used to calculate live crown length and crown base height, and convert crown length scorched to crown volume scorched (Reinhardt *et al.* 1997). This series of nested models allows mortality prediction for any tree for which bark thickness, tree height, crown ratio, and scorch height are known. The FOFEM graphics option allows easy visualization of general thresholds at which the chance that a tree will die from fire for a given flame length or scorch height begins to sharply increase along the predicted mortality response curve. Thus, FOFEM can be used for pre-fire planning purposes to develop burn prescriptions that help meet specific tree-mortality related objectives. For example, burn objectives often include acceptable limits to mortality of trees over a spe-

cific DBH, or targets to kill a proportion of the smaller-diameter trees that can act as ladder fuels (Ryan *et al.* 2013).

The simplicity of the Ryan and Amman mortality model also limits its usefulness for post-fire planning purposes. In this situation, mortality models are typically applied to an individual tree for which the actual crown volume scorch percentage is known. Directly entering the crown volume scorch value will always provide better estimates of tree mortality than will calculating scorch as described above. In addition, other fire injury variables and secondary effects such as bark beetle attacks may also be known. Expanding the mortality models in FOFEM to allow for direct inputs of fire injury and to account for secondary factors could possibly increase the predictive accuracy of post-fire tree mortality.

Here, we used the same dataset from Hood *et al.* (2007) to describe post-fire tree mortality for 12 widespread western USA conifers: sub-alpine fir, red fir, white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *glauca* [Beissn.] Franco), incense cedar, western larch, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), whitebark pine (*Pinus albicaulis* Engelm.), lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. ex S. Watson), ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm and var. *ponderosa* C. Lawson), Jeffrey pine, and sugar pine (*Pinus lambertiana* Douglas). Our specific objectives were to:

1. Develop species-specific 3-year post-fire mortality models,
2. Compare the species-specific models with the predictive accuracy of the Ryan and Amman model to determine potential improvements to FOFEM, and
3. Update the FOFEM Mortality Module user options to include bark beetle attacks and cambium kill.

We developed new mortality models with improved prediction capability and added these models to FOFEM version 5.7 (Lutes 2012) and ensuing versions. We also updated the user interface in FOFEM to increase prediction options, especially when using the software to model post-fire individual tree mortality. The additions to FOFEM offer improved accuracy in predicting post-fire tree mortality for 12 Western conifer species and allow direct inputs of fire injury to increase software applicability to prescribed fire and post-fire forest management.

METHODS

Site Descriptions

We pooled data from previously published and unpublished fire-injury studies from 23 fires in Arizona, California, Idaho, Montana, and Wyoming, USA. Data included 17 144 sample trees and 12 coniferous species (Table 1). Three-year post-fire tree mortality was used for all fires. Fires occurred between 1982 and 2004 and included both prescribed fires and wildfires. Sample trees covered a broad range of diameters and crown and cambium injury.

Post-Fire Sampling

Field sampling methods were similar across studies; however, not all variables were collected for each fire. Species, DBH, and percentage crown volume scorched or percentage crown length scorched were assessed for each tree within 1 year post fire. Because of morphological and management similarities, ponderosa and Jeffrey pines from fires in California were grouped into one yellow pine category during data collection. Though species-level comparisons for these species would be ideal, it was not possible with the available data. For the majority of trees, cambium kill rating (CKR) and bark beetle attacks were also assessed. All trees were monitored annually

Table 1. Summary of wildfire data included in data analyses for post-fire tree mortality predictions.

Fire name	Location ¹	State	Fire type	Ignition date	Species sampled ²	No. trees ³
Dauber	Coconino NF	AZ	Prescribed	Sep 1995	PP	222
Bridger-Knoll	Kaibab NF	AZ	Wild	Jun 1996	PP	833
Side	Coconino NF	AZ	Wild	May 1996	PP	313
Rodeo-Chediski	Apache-Sitgreaves NF	AZ	Wild	Jun 2002	PP	698
Bucks	Plumas NF	CA	Wild	Aug 1999	RF, WF, SP	236
Storrie	Plumas NF	CA	Wild	Aug 2000	RF, WF	198
Star	Tahoe	CA	Wild	Aug 2001	WF, SP	273
Cone	Lassen	CA	Wild	Sep 2002	JP, PP	1065
McNally	Sequoia NF	CA	Wild	Jul 2002	WF, IC, JP, PP	3872
Power	Eldorado NF	CA	Wild	Oct 2004	SP	719
Lower Priest	Idaho Panhandle NF	ID	Prescribed	Jun 1984	ES, DF, WL	172
Upper Priest	Idaho Panhandle NF	ID	Prescribed	Sep 1983	ES, DF, WL	87
Air Patrol	Northern Cheyenne IR	MT	Wild	Aug 1988	PP	505
Brewer	Custer NF	MT	Wild	Jun 1988	PP	626
Early Bird	Northern Cheyenne IR	MT	Wild	Jun 1988	PP	615
Canyon Creek	Lolo NF	MT	Wild	Sep 1988	WL	69
Mussigbrod	Beaverhead-Deerlodge NF	MT	Wild	Aug 2000	LP, WP, ES, SF, DF	1102
Moose	Flathead NF; Glacier NP	MT	Wild	Aug 2001	LP, WP, ES, SF, PP, DF, WL	1266
Lubrecht	Lolo NF	MT	Prescribed	Apr 2002	LP, PP, DF, WL	1696
Tenderfoot	Lewis and Clark NF	MT	Prescribed	Sep 2002	LP, WP, ES, SF	1750
Slowey	Lolo NF	MT	Prescribed	Mar 1992	PP, DF	241
Green Knoll	Bridger-Teton NF	WY	Wild	Aug 2001	LP, WP, ES, SF, DF	276
Yellowstone	Bridger-Teton NF; Yellowstone NP	WY	Wild	Jun 1988	SF, LP ES, DF	310

¹ IR = Indian reservation; NF = National Forest; NP = National Park.

² Species: LP = lodgepole pine, WP = whitebark pine, ES = Engelmann spruce, RF = red fir, SF = subalpine fir, WF = white fir, IC = incense cedar, JP = Jeffrey pine, PP = ponderosa pine, DF = Douglas-fir, WL = western larch, SP = sugar pine.

³ Tree numbers vary slightly between pre-fire and post-fire analyses based on available data.

for three years post fire for mortality. Trees were considered dead when no green foliage remained in the crown, regardless of beetle attack timing.

Both crown volume scorched and crown length scorched values were visually assessed based on the proportions of the pre-fire crown that were either scorched or consumed (i.e., had pale green, brown, or blackened needles). These variables are not interchangeable (Peterson 1985, Hood *et al.* 2010). Crown volume scorched equals the percentage of the pre-fire crown volume of which needles were either

scorched or consumed and could include areas with live and dead buds. Total tree height, pre-fire crown base height, and the average height of crown scorch were measured to calculate percentage crown length scorched. FOFEM calculates crown volume scorched from crown length scorched (Hood *et al.* 2007); however, for model validation, we used our direct estimates of crown volume scorched that we obtained in the field, as recommended by Peterson (1985).

FOFEM does not differentiate between crown needle scorch and bud kill. While these

variables are approximately equal for most species, the difference can be substantial for some Western conifer species with large or protected buds such as ponderosa pine, Jeffrey pine, and western larch (Dieterich 1979, Hood *et al.* 2010). Both crown bud kill and crown needle scorch were assessed on 5635 ponderosa pine and Jeffrey pine trees to test if accounting for differences in crown kill and scorch improved prediction of tree mortality. Crown bud kill equals the percentage of pre-fire crown volume of which buds were killed either by heated air (i.e., scorched) or consumed by flame contact. Crown scorch equals the percentage of the pre-fire crown volume of which needles were either scorched or consumed and could include areas in the crown with live and dead buds.

Trees assessed for CKR were visually divided at the base into quadrants. Quadrants for most fires were oriented with the slope, with one quadrant on the uphill side, one on the downhill side, and two on the cross-slope. In flat areas and in the California fire sites, quadrants were oriented in the cardinal directions. In the center of each quadrant, cambium status at groundline was visually assessed, as described by Ryan (1982), by removing a small portion of the bark to reveal the cambium. Live cambium is light in color, moist, and pliable. Dead cambium is darker in color and either viscous (i.e., resinosis) or hardened. Cambium kill rating (CKR) was calculated by summing the number of dead cambium samples per tree (0 to 4).

For ponderosa pine trees from the Air Patrol, Brewer, and Early Bird fires in eastern Montana, cambium status was determined on 307 randomly selected trees (of 1748 total trees) by removing a sample of cambium at groundline from each quadrant using an increment borer and then treating it with 1% orthotolidine vital stain solution in the field to determine visually if the tissue was alive based on a color reaction (see Ryan 1982 for detailed methods).

Beetle assessment varied by tree species and fire-injury study. Ambrosia beetles (*Trypodendron* spp Stephens and *Gnathotrichus* spp. Eichh.) were noted for white fir; red turpentine beetles (RTB; *Dendroctonus valens* LeConte) and mountain pine beetles (*Dendroctonus ponderosae* Hopkins) for sugar pine, ponderosa pine, and Jeffrey pine; engraver beetles (*Ips* spp. De Geer) for ponderosa pine and Jeffrey pine; and Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) for Douglas-fir. For the current analyses, all trees were coded as either attacked or unattacked based on the more detailed attack data collected in the original studies (for details, see Ryan and Amman 1994, McHugh and Kolb 2003, Hood and Bentz 2007, Hood *et al.* 2010). Trees were monitored annually for three years post fire for additional beetle attacks, with the exception of the trees in the California fires. Attacks were only noted one year following the fire for these trees.

Data Analyses

Tree mortality modeling. All trees were coded as either 0 (live) or 1 (dead) based on post-fire year 3 status. The probability of tree death within three years post fire was modeled using general linear models with a binomial error distribution, logit link function specified, and the model form:

$$P_m = \frac{1}{[1 + e^{-(\beta_0 + \beta_1 X_1 + \dots + \beta_t X_t)}]}, \quad (1)$$

where P_m is the probability of mortality; β_0 , β_1 , and β_k are regression coefficients; and X_1 and X_k are independent variables. Model variable screening was performed in SAS using PROC LOGISTIC (version 9.1; SAS Institute, Cary, North Carolina, USA). All final models were developed using either PROC GENMOD or PROC LOGISTIC. Within-subject correlation was accounted for using the REPEATED statement in which trees were grouped into plots

(PROC GENMOD). If trees were not grouped into plots (e.g., California fires), PROC LOGISTIC was used. Only variables with P -values ≤ 0.05 and non-significant Hosmer-Lemeshow goodness of fit tests were retained in the full models.

We first attempted to develop one mortality model for all species, similar to the Ryan and Amman (1994) model in FOFEM. However, this model lacked sufficient predictive accuracy for all species and this effort was discontinued in favor of species-specific models.

Pre-fire and post-fire models were developed for each species, with two exceptions. Lodgepole pine and whitebark pine were grouped because of the small sample size of whitebark pine ($n = 147$) and because there were no statistical differences between DBH, crown volume scorched, and CKR between the two species. Because the ponderosa pines and Jeffrey pines from fires in California were grouped into one yellow pine category during data collection, they were modeled together. The pre-fire model is designed for planning prescribed burns and uses a limited set of variables to predict tree mortality. Candidate variables for the pre-fire mortality model included DBH and crown scorch. The post-fire model is the most accurate model for predicting tree mortality and is likely the most useful in post-fire planning, such as creating individual tree marking guidelines. Candidate variables for the post-fire model included DBH, crown scorch, CKR, and beetle attack. Due to differences in data collection methods among the datasets available for analysis, we developed separate crown volume scorched and crown volume killed models for ponderosa pine and Jeffrey pine and used crown length scorched for white fir, red fir, incense cedar, and sugar pine models, while all other species models used crown volume scorched. Based on plots of the logits, CKR was included as a continuous rather than class variable (Hosmer and Lemeshow 2000).

We cross-validated each final model to obtain a weighted classification table to deter-

mine prediction accuracy. Each species dataset was divided into 10 approximately equal groups for the cross-validation exercise. Groups were assigned based on fires so that each group contained either all of the observations from a given fire or a randomly chosen subset of observations from the same fire. Therefore, each group contained observations from one fire only. We did this in order to compare accuracies both between and within fires. We then ran the logistic regression model 10 times, leaving one group out each a time. Trees with predicted probabilities of mortality ≥ 0.5 were then classified as dead and trees with probabilities of mortality < 0.5 were classified as alive for each model run. We used these classifications to calculate the weighted percentage of trees that were correctly predicted to live and die.

RESULTS

Tree Mortality Modeling

Pre-fire models. We developed models for 12 species from 16838 trees. We could not use all trees for each analysis; therefore, the sampling size differs slightly by analysis. Yellow pine (43%), white fir (14%), lodgepole pine (13%), and Douglas-fir (9%) composed the majority of the total dataset (Table 2). All species except red fir included almost the full range of crown scorch values (0 to 100), while red fir only extended to 89% crown length scorched. Crown scorch median values varied greatly among species, from low values $< 5\%$ for lodgepole pine, whitebark pine, and western larch, to high values of $> 70\%$ for subalpine fir, white fir, and ponderosa pine and Jeffrey pine (Table 2). The smallest trees sampled were generally 10 cm DBH for most species, except for trees in the California dataset (red fir and white fir minimum DBH = 15 cm, and incense cedar and sugar pine minimum DBH = 25 cm). The maximum DBH that was sampled varied widely by species (Table 2).

Table 2. Mean, standard error, median, and range of crown scorch and DBH by species of trees used to develop pre-fire tree mortality predictions models. Species are listed in order of increasing bark thickness using the bark thickness equations in FOFEM.

Species	No. trees	Type ^B	Crown scorch (%)			DBH (cm)		
			Mean ± SE	Median	Range	Mean ± SE	Median	Range
Lodgepole pine	2196	V	19 ± 0.7	0	0 to 100	20.8 ± 0.1	19.6	10.2 to 56.4
Whitebark pine	148	V	24 ± 2.9	2	0 to 100	22.9 ± 0.6	22.5	12.4 to 58.9
Engelmann spruce	223	V	30 ± 2.2	20	0 to 100	33.2 ± 1.1	30.2	12.7 to 85.1
Red fir	209	L	42 ± 1.8	46	0 to 89	42.1 ± 1.2	38.9	15.2 to 104.6
Subalpine fir	947	V	65 ± 1.3	85	0 to 100	19.4 ± 0.2	17.5	10.2 to 75.2
White fir	2304	L	67 ± 0.5	74	0 to 100	59.2 ± 0.4	56.9	15.2 to 152.7
Incense cedar	783	L	40 ± 1.1	38	0 to 98	51.6 ± 0.9	43.7	25.4 to 166.4
Western larch	461	V	26 ± 1.7	5	0 to 100	38.1 ± 0.6	38.1	10.2 to 98.8
Douglas-fir	1539	V	34 ± 0.9	20	0 to 100	33.7 ± 0.4	30.5	10.2 to 105.4
Yellow pine ^A	7309	V	58 ± 0.4	70	0 to 100	41.8 ± 0.3	35.1	6.3 to 178.1
Sugar pine	719	L	40 ± 1.1	41	0 to 98	73.3 ± 1.0	70.4	25.6 to 188.0

^A Includes ponderosa pines and Jeffrey pine.

^B L = crown length; V = crown volume.

The importance of crown scorch and tree size (i.e., DBH) in predicting post-fire mortality varied by species. Crown scorch was a significant variable in all tree-mortality models, with the probability of mortality increasing with increasing crown scorch (Table 3). DBH was only included in the western larch, whitebark pine, and lodgepole pine mortality models. The probability of mortality decreased with increasing DBH. DBH was a significant variable in many of the models; however, the Hosmer-Lemeshow goodness of fit test was significant, indicating a poor model fit. In these cases, DBH was dropped from the model and the Hosmer-Lemeshow goodness of fit test became non-significant.

All pre-fire models were more accurate than the Ryan and Amman model used in versions of FOFEM prior to 5.7 (Figure 1a). Improvement over the current model was primarily because of better prediction of trees that died. Little improvement was made in predicting trees that survived and, in many cases, there was a decrease in accuracy with the new models. Over all species, the new models offer an 11% improvement over the Ryan and Amman model (15% in mortality; 0% in survival).

The models correctly predicted mortality and survival for over 90% of incense cedar, subalpine fir, and western larch using a predicted probability of mortality cutoff value (hereafter cutoff) of 0.5 (Table 4). Prediction of Engelmann spruce survival was poor, with no trees correctly predicted to survive three years post fire.

Post-fire models. We developed models for 12 species from 13 284 trees. The sample size was reduced from the pre-fire model dataset because not all studies assessed CKR. As in the pre-fire model development, yellow pine (31%), white fir (17%), lodgepole pine (15%), and Douglas-fir (11%) composed the majority of the total dataset (Table 5).

Crown scorch and CKR were significant in all post-fire tree mortality models, but the importance of DBH varied by species (Table 6). The probability of mortality increased with increasing crown scorch and CKR. DBH was only significant for explaining white fir, whitebark pine, lodgepole pine, and Douglas-fir mortality ($P \leq 0.05$). The probability of mortality decreased with increasing DBH for whitebark pine and lodgepole pine. For white fir, however, the probability of mortality in-

Table 3. Predicted post-fire tree probability of mortality equations for use in pre-fire planning (i.e., only crown scorch and DBH are potential variables). CLS = crown length scorched (%); CVS = crown volume scorched (%); DBH = diameter at breast height (cm).

Species	Predicted probability of mortality equation
White fir	$P_m = \frac{1}{[1 + e^{-(-3.5083 + (CLS \times 0.0956) - (CLS^2 \times 0.00184) + (CLS^3 \times 0.000017))}]}$
Subalpine fir	$P_m = \frac{1}{[1 + e^{-(-1.6950 + (CVS \times 0.2071) - (CVS^2 \times 0.0047) + (CVS^3 \times 0.000035))}]}$
Red fir	$P_m = \frac{1}{[1 + e^{-(-2.3085 + (CLS^3 \times 0.000004059))}]}$
Incense cedar	$P_m = \frac{1}{[1 + e^{-(-4.2466 + (CLS^3 \times 0.000007172))}]}$
Western larch	$P_m = \frac{1}{[1 + e^{-(-1.6594 + (CVS \times 0.0327) - (DBH \times 0.0489))}]}$
Whitebark pine and lodgepole pine	$P_m = \frac{1}{[1 + e^{-(-0.3268 + (CVS \times 0.1387) - (CVS^2 \times 0.0033) + (CVS^3 \times 0.000025) - (DBH \times 0.0266))}]}$
Engelmann spruce	$P_m = \frac{1}{[1 + e^{-(-0.0845 + (CVS \times 0.0445))}]}$
Sugar pine	$P_m = \frac{1}{[1 + e^{-(-2.0588 + (CLS^2 \times 0.000814))}]}$
Ponderosa pines and Jeffrey pine	$P_m = \frac{1}{[1 + e^{-(-2.7103 + (CVS^3 \times 0.000004093))}]}$
Douglas-fir	$P_m = \frac{1}{[1 + e^{-(-2.0346 + (CVS \times 0.0906) - (CVS^2 \times 0.0022) + (CVS^3 \times 0.000019))}]}$

creased with increasing DBH. For Douglas-fir, probability of mortality decreased with increasing DBH for unattacked trees, but increased for attacked trees. DBH was a significant variable in many of the other models, but was not included due to significant values for the Hosmer-Lemeshow goodness of fit test. For ponderosa pine and Jeffrey pine, the crown volume kill model was about 5% more accurate than the crown volume scorched model (Table 4; Figure 1b).

All post-fire models were more accurate than the Ryan and Amman model in versions of FOFEM prior to 5.7 (Figure 1b). Increased

accuracy over the older versions of FOFEM was primarily because of better prediction of trees that died, an improvement of over 40% for some species. As in the pre-fire models, mortality prediction was improved more than survival prediction. Over all species, the new models offer a 15% improvement over the Ryan and Amman model (22% in mortality, 4% in survival).

The models correctly predicted mortality and survival for over 90% of incense cedar, subalpine fir, and western larch using a cutoff of 0.5 (Table 4). Including CKR in the models improved prediction, especially for spruce

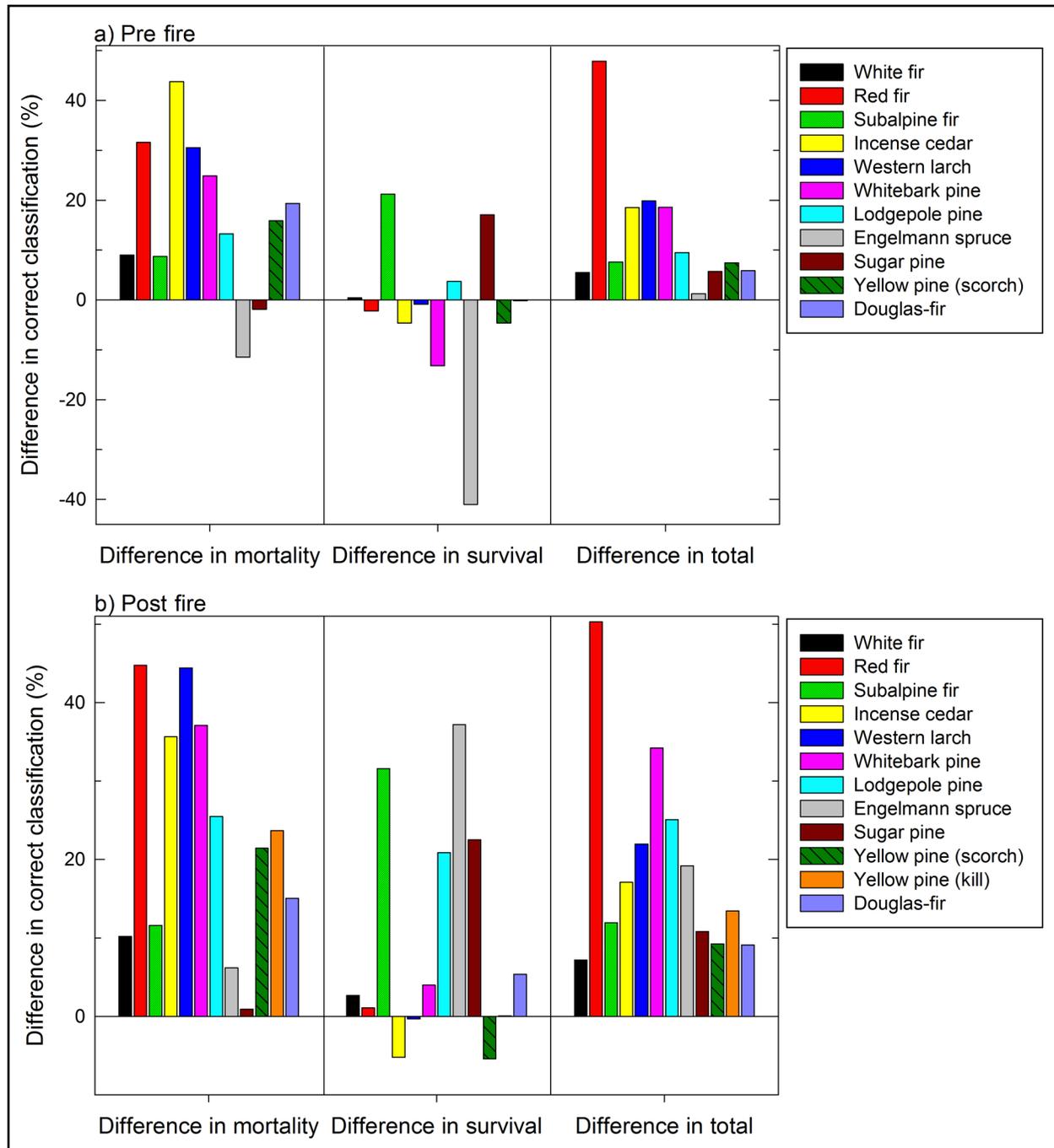


Figure 1. Percent change in mortality model accuracies by species between the Ryan and Amman FOFEM model and new A) pre-fire and B) post-fire mortality models. Positive numbers reflect an increase in accuracy over FOFEM; negative numbers reflect a decrease in accuracy. For evaluating how well the model classified trees as either live or dead, we assumed that a tree with a predicted probability of mortality value greater than or equal to 0.5 was dead and less than 0.5 was alive (i.e., cutoff = 0.5).

Table 4. Classification accuracy and difference by species of pre-fire and post-fire tree mortality models. Cutoff = 0.5. NA = not applicable.

Species	Pre-fire model accuracy			Post-fire model accuracy			Difference		
	Correctly predicted mortality (%)	Correctly predicted survival (%)	Total correct (%)	Correctly predicted mortality (%)	Correctly predicted survival (%)	Total correct (%)	Mortality difference	Survival difference	Total difference
Lodgepole pine and whitebark pine	76.7	71.4	73.1	88.9	88.6	88.7	+12.2	+17.2	+15.6
Engelmann spruce	71.0	0.0	68.2	88.7	78.2	86.1	+17.7	+78.2	+17.9
Red fir	50.0	84.1	82.8	63.2	87.4	85.2	+13.2	+3.3	+2.4
Subalpine fir	93.4	79.1	90.6	96.3	89.5	95.0	+2.9	+10.4	+4.4
White fir	80.0	74.8	77.6	81.2	77.1	79.3	+1.2	+2.3	+1.7
Incense cedar	75.7	93.4	91.7	67.5	92.8	90.3	-8.2	-0.6	-1.4
Ponderosa pines and Jeffrey pine—scorch	79.3	80.5	80.1	84.8	79.8	81.8	+5.5	-0.7	+1.7
Ponderosa pines and Jeffrey pine—kill	NA	NA	NA	87.1	85.3	86.0	NA	NA	NA
Douglas-fir	85.8	76.9	78.9	81.5	82.4	82.1	-4.3	+5.5	+3.2
Western larch	54.5	93.2	90.5	68.4	93.8	92.5	+13.9	+0.6	+2.0
Sugar pine	81.4	80.4	80.8	84.2	85.8	85.1	+2.8	+5.4	+4.3

Table 5. Mean, standard error, median, and range of crown scorch and DBH by species of trees used to develop post-fire (i.e., optimal) tree mortality prediction models. Species are listed in order of increasing bark thickness using bark thickness equations in FOFEM.

Species	No. trees	Type ^B	Crown scorch (%)			DBH (cm)		
			Mean ± SE	Median	Range	Mean ± SE	Median	Range
Lodgepole pine	2038	V	19 ± 0.7	0	0 to 100	20.5 ± 0.1	19.3	10.2 to 54.9
Whitebark pine	148	V	24 ± 2.9	2	0 to 100	22.9 ± 0.6	22.5	12.4 to 58.9
Engelmann spruce	223	V	30 ± 2.2	20	0 to 100	33.2 ± 1.1	30.2	12.7 to 85.1
Red fir	209	L	42 ± 1.8	46	0 to 89	42.1 ± 1.2	38.9	15.2 to 104.6
Subalpine fir	947	V	65 ± 1.3	85	0 to 100	19.4 ± 0.2	17.5	10.2 to 75.2
White fir	2304	L	67 ± 0.5	74	0 to 100	59.2 ± 0.4	56.9	15.2 to 152.7
Incense cedar	783	L	40 ± 1.1	38	0 to 98	51.6 ± 0.9	43.7	25.4 to 166.4
Western larch	389	V	15 ± 1.3	0	0 to 100	38.8 ± 0.7	39.4	10.2 to 98.8
Douglas-fir	1409	V	33 ± 0.9	20	0 to 100	33.2 ± 0.5	30.0	10.2 to 105.4
Yellow pine ^A	4115	V	62 ± 0.6	80	0 to 100	47.1 ± 0.4	40.1	9.7 to 178.1
Sugar pine	719	L	40 ± 1.1	41	0 to 98	73.3 ± 1.0	70.4	25.6 to 188.0

^A Includes ponderosa pines and Jeffrey pine.

^B L = crown length; V = crown volume.

Table 6. Post-fire predicted probability of tree mortality equations (i.e., all significant variables included, $P \leq 0.05$). Variable definitions: CLS = crown length scorched (%); CVS = crown volume scorched (%); CVK = crown volume killed (%); DBH = diameter at breast height (cm); CKR= cambium kill rating; beetle presence or absence: white fir, sugar pine: 1= attacked, -1 = unattacked; Douglas-fir, Jeffrey pine, and ponderosa pine: 1= attacked, 0 = unattacked¹ (see methods for complete descriptions of variables).

Species	Predicted probability of mortality equation
White fir	$P_m = \frac{1}{[1 + e^{(-(-3.5964+(CLS^3 \times 0.00000628)+(CKR \times 0.3019)+(DBH \times 0.019)+(beetles \times 0.5209))}]}$
Subalpine fir	$P_m = \frac{1}{[1 + e^{(-(-2.6036+(CVS^3 \times 0.000004587)+(CKR \times 1.3554))}]}$
Red fir	$P_m = \frac{1}{[1 + e^{(-(-4.7515+(CLS^3 \times 0.000005989)+(CKR \times 1.0668))}]}$
Incense cedar	$P_m = \frac{1}{[1 + e^{(-(-5.6465+(CLS^3 \times 0.000007274)+(CKR \times 0.5428))}]}$
Western larch	$P_m = \frac{1}{[1 + e^{(-(-3.8458+(CVS^2 \times 0.0004)+(CKR \times 0.6266))}]}$
Whitebark pine and lodgepole pine	$P_m = \frac{1}{[1 + e^{(-(-1.4059+(CVS^3 \times 0.000004459)+(CKR^2 \times 0.2843)-(DBH \times 0.0485))}]}$
Engelmann spruce	$P_m = \frac{1}{[1 + e^{(-(-2.9791+(CVS \times 0.0405)+(CKR \times 1.1596))}]}$
Sugar pine	$P_m = \frac{1}{[1 + e^{(-(-2.7598+(CLS^2 \times 0.000642)+(CKR^3 \times 0.0386)+(beetles \times 0.8485))}]}$
Ponderosa pines and Jeffrey pine ²	$P_m = \frac{1}{[1 + e^{(-(-4.1914+(CVS^2 \times 0.000376)+(CKR \times 0.513)+(beetles \times 1.5873))}]}$
	$P_m = \frac{1}{[1 + e^{(-(-3.5729+(CVK^2 \times 0.000567)+(CKR \times 0.4573)+(beetles \times 1.6075))}]}$
Douglas-fir	$P_m = \frac{1}{[1 + e^{(-(-1.8912+(CVS \times 0.07)-(CVS^2 \times 0.0019)+(CVS^3 \times 0.000018)+(CKR \times 0.584)-(DBH \times 0.031)-(beetles \times 0.7959)+(DBH \times beetles \times 0.0492))}]}$

¹ Beetle species in presence or absence data: white fir, attacked by ambrosia beetle; sugar pine, attacked by red turpentine or mountain pine beetle; Jeffrey pine and ponderosa pines, attacked by mountain pine beetle, red turpentine beetle, or ips beetle; Douglas-fir, attacked by Douglas-fir beetle.

² First equation uses crown volume scorched and second equation uses crown volume killed or consumed.

(+18%) and lodgepole pine and whitebark pine (+16%). The additional model variables offered a 2% to 4% increase in accuracy for the other species, except incense cedar. The incense cedar pre-fire model was slightly more

accurate (1%) than the post-fire model at classifying live and dead trees using the cutoff 0.5 (Table 4).

DISCUSSION

Predicting Fire-Caused Tree Mortality

The species-specific models presented here offer improved accuracy to the Ryan and Amman model embedded in the FOFEM mortality module prior to version 5.7. The Ryan and Amman model is based on data from seven conifer species, with the majority of the data coming from Douglas-fir. The Ryan and Amman model does not include data for several of the species included here—whitebark pine, red fir, white fir, incense cedar, ponderosa pine, Jeffrey pine, nor sugar pine. The models generally predict mortality better than survival. The species models for red fir, incense cedar, and western larch offer over 20% improvement in predicting which trees will die within three years post fire for the simplest, pre-fire models, and over 30% improvement for the post-fire models that take into account cambium injury. The new pre-fire models increased accuracy over the Ryan and Amman model by <10% accuracy for white fir, sugar pine, ponderosa pine, and Jeffrey pine, which is somewhat surprising considering that no data for these species was used for model development. Additional species need evaluation, as currently FOFEM predicts post-fire mortality for approximately 205 species that have no data supporting model development. We note that our grouping of ponderosa pine and Jeffrey pine and also whitebark pine and lodgepole pine could mask differences in fire responses between these species. Additional research is needed to determine if species groups are suitable for predicting post-fire mortality. We reasoned that grouping similar species was warranted in developing empirical models geared towards management purposes. However, we advise that studies of the mechanistic causes of tree death should likely not group species without prior testing.

The Ryan and Amman model uses DBH to predict bark thickness, which functions as

semi-mechanistic variable of heat resistance in the model. Bark thickness is the largest factor influencing the rate of heat transfer to the underlying cambium, but other bark properties are also involved, such as fissures, moisture content, density, and thermal conductivity (Dickinson and Johnson 2001, Chatziefstratiou *et al.* 2013). Because of the importance of bark thickness in protecting the stem during fire, the original model may perform satisfactorily for species with accurate bark thickness coefficients, especially for species with thicker bark (i.e., high basal heat resistance). The accuracy of bark thickness coefficients is largely unknown for most species and requires additional research. In one of the only studies examining the bark thickness equations used in FOFEM and other fire effects models, Zeibig-Kichas *et al.* (2016) reported bark thickness was underpredicted for several conifers. In addition, bark thickness does not always increase linearly with DBH (Jackson *et al.* 1999), as is assumed in FOFEM, which could lead to overprediction of bark thickness for large-diameter trees.

The new pre-fire models also offer little improvement for the conifers used to develop the Ryan and Amman model: subalpine fir, lodgepole pine, Engelmann spruce, and Douglas-fir. In particular, the pre-fire Engelmann spruce model was worse in predicting both mortality and survival compared to the Ryan and Amman model. In versions prior to 5.7, FOFEM calculated all species of spruce using the Ryan and Amman equation, but then constrained mortality to at least 80%, highlighting the difficulty that has surrounded predicting Engelmann spruce mortality (Lutes 2012).

Crown injury is often the most important predictor of post-fire tree mortality, and most logistic regression-based models use some measure of crown injury (Sieg *et al.* 2006, Woolley *et al.* 2012). Consistent with this, crown scorch or crown kill is included in all the species-specific models presented here. This is not surprising as tree survival is highly

dependent on the amount of needles available for carbon acquisition via photosynthesis, and reductions in crown after fire reduce net photosynthesis and stomatal conductance (Sparks *et al.* 2016), even though water use efficiency can increase (Wallin *et al.* 2003). FOFEM predicts scorch height from flame length using the model in Van Wagner (1973), and this model does not distinguish between needle kill and bud kill (see Dickinson and Johnson 2001 for detailed processes involved in modeling crown tissue death). This difference can be substantial for ponderosa pine and Jeffrey pine (Hood *et al.* 2010) and indicates areas of the crown that can potentially recover if only the needles are scorched, but buds and branches are not killed (Dieterich 1979, Fowler *et al.* 2010). Our post-fire crown kill model is about 5% more accurate than the crown scorch model, and we recommended using the crown kill model when possible for ponderosa pine and Jeffrey pine, especially when large differences exist in crown scorch and crown kill. Further research into the factors affecting plant hydraulic integrity (West *et al.* 2016) and thermal tolerance of bud and foliage tissues due to physical and physiological properties is needed to better understand and model crown injury from fire (Hare 1961, Dickinson and Johnson 2001). Michaletz and Johnson (2006) developed a crown scorch model capable of predicting differences in scorch and bud kill heights. This model deserves additional examination and validation as a possible replacement for the Van Wagner (1973) model in FOFEM.

Tree size or DBH is a common variable in post-fire mortality models (Woolley *et al.* 2012). This contrasts with our findings that DBH was influential in predicting post-fire tree mortality for only a few species: whitebark pine, lodgepole pine, western larch, white fir, and Douglas-fir. Predicted mortality increases with increasing DBH for white fir and, if attacked by bark beetles, for Douglas-fir. The interaction between bark beetles and DBH

is consistent with the findings of Hood and Bentz (2007), as Douglas-fir beetle is known to preferentially attack larger trees (Furniss 1965). Though many studies report a positive correlation between tree size and resistance to fire, others have reported either a negative or no relationship with DBH and resistance (Swezy and Agee 1991, Stephens and Finney 2002, McHugh and Kolb 2003, Varner *et al.* 2007, Hood *et al.* 2010, Lerch *et al.* 2016). Several reasons may account for the conflicting results in the literature between DBH and post-fire mortality. Biological reasons include indirect effects such as reductions in tree vigor with age, bark-beetles attack preferences, and deep duff layers that can cause long-term smoldering (Hood 2010). The range of data used to develop models will also heavily influence variable importance, and the size range of trees varies widely in studies of post-fire tree mortality.

The new post-fire models that include cambium kill and bark beetle attack increase predictive accuracy in FOFEM by approximately 10% to 50% compared to the Ryan and Amman models. However, for most species, the new post-fire models increased accuracy <5% over the new pre-fire models, and this small increase is likely not enough to justify the extra time needed to assess these additional variables. However, assessing cambium injury for whitebark pine, lodgepole pine, and Engelmann spruce increases model accuracy by over 15% compared to the new pre-fire models. The large improvement when cambium injury is accounted for is most likely because these three species all have very thin bark and low-intensity fire burning around the tree bases will kill these trees even with little to no crown scorch (Hood *et al.* 2008).

FOFEM Updates

We replaced the Ryan and Amman model with our new species-specific mortality models in FOFEM version 5.7 (Lutes 2012).

While not the focus of this paper, it should be noted that the models were also added to BehavePlus 4.5 and later versions. BehavePlus only uses pre-fire models, while FOFEM uses both pre-fire and post-fire models. To use the post-fire models, users can now check a “Post Fire Injury” radio button in the Mortality module (Figure 2). The species drop-down menu changes to only include the 12 Western conifers studied here, and their synonyms and varieties. Required inputs are listed parenthetically after each species name, to denote if crown volume or crown length scorched or bark beetle attack information is required. The user then sets the probability mortality cutoff level (0 to 1) to determine the predicted mortality level (Figure 2). For example, if a cutoff of

0.5 is chosen, the mortality report will list the number of trees killed that have a predicted probability of mortality ≥ 0.5 . The mortality graph shows the cutoff value as a red line to denote the threshold of crown damage that must be exceeded to cause mortality. This is different from how mortality is reported in the pre-fire option, which kills the percentage of trees of a given species, DBH, height, and crown ratio equal to the predicted probability of mortality (e.g., if 15 white fir are entered and the $P_m = 0.19$, the pre-fire mortality report will list three dead trees, while the post-fire mortality report will list zero dead trees because they are all under the cutoff value of 0.5). The post-fire option allows an easy comparison of how bark beetles or cambium kill

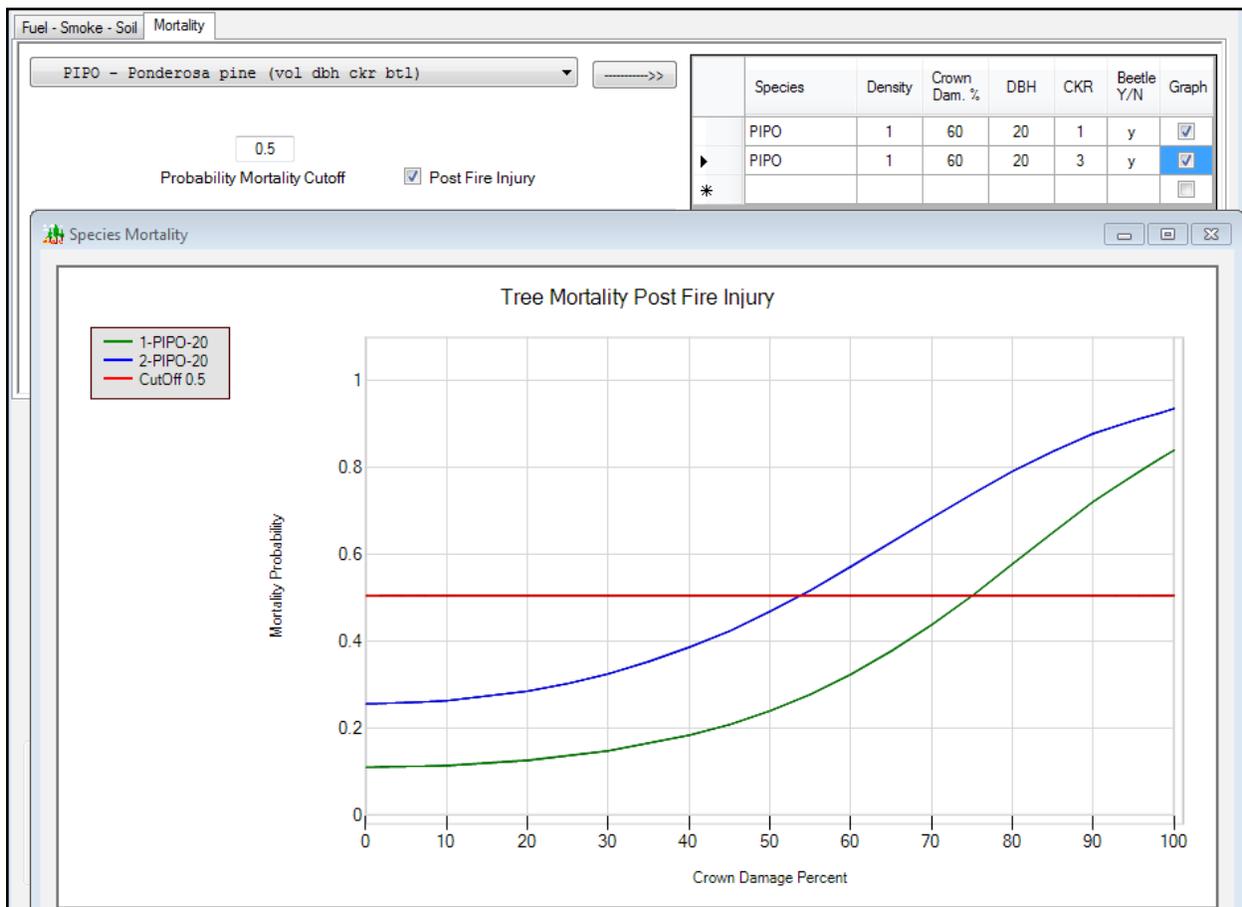


Figure 2. Screen shot of FOFEM version 6.4 using the Post Fire Injury option. The curves show predicted probability of mortality for 20 inch (50.8 cm) ponderosa pines with a CKR of 1 and 3 and a cutoff of 0.5. Crown damage above the red cutoff line indicates a high likelihood of tree death.

will affect mortality over a range of crown damage using the graphing option.

CONCLUSIONS

Versions of FOFEM starting with 5.7 offer improved accuracy in predicting 3-year post-fire tree mortality for white fir, subalpine fir, red fir, incense cedar, western larch, lodgepole pine, whitebark pine, Engelmann spruce, sugar pine, Douglas-fir, ponderosa pine, and Jeffrey pine. FOFEM now allows users to directly enter crown scorch, cambium injury, and beetle attacks to improve model accuracy for these species. The updated FOFEM User Guide includes a description of all mortality models used in the application. BehavePlus and versions of the Fire and Fuels Extension to the Forest Vegetation Simulator posted after 2013 also include the pre-fire mortality equations for the 12 species listed above.

These models and all other post-fire mortality models in FOFEM are empirically based. Therefore, extrapolations beyond the data used for model development will always be constrained, with uncertainties in accuracy (Butler and Dickinson 2010, Woolley *et al.* 2012). Improvements to process models may allow replacement of empirical models for some applications in the future (Dickinson and Johnson 2001, Michaletz and Johnson 2007, Butler and Dickinson 2010, Kavanagh *et al.* 2010, Michaletz *et al.* 2012, Woolley *et al.* 2012). However, it is difficult to envision process models completely subsuming empirical models anytime soon, as empirical models and decision support tools serve foundational roles for land management in predicting tree responses to fire because process models are often too complex for practical application.

While research into mechanisms of post-fire mortality is important, we also see the value in continued research to improve empirical

models of post-fire mortality and test model accuracy. FOFEM continues to use the Ryan and Amman mortality model for the majority of species not described in this paper. With 219 species included in FOFEM, this means that more than 90% of species have no data to support the mortality predictions generated. Future research should validate the Ryan and Amman model in FOFEM for these species to determine predictive accuracy and to explore improved model development. Very few models exist that include data from trees <10 cm DBH. There is a dire need for further research on fire-induced mortality for seedlings and saplings, such as was done by Battaglia *et al.* (2009) for ponderosa pine, and by Engber and Varner (2012) for Douglas-fir. Such data on smaller-tree resistance to fire can help plan treatment timelines that may achieve mortality targets using only fire, rather than combined mechanical and fire treatments. FOFEM does not account for differences in phenology, burn season, or fire type (e.g., prescribed or wild-fire), and we did not examine these factors in our analyses. While such factors have been shown to affect tree mortality (Harrington 1987, 1993), our data did not allow separation by additional factors, while still retaining the same range of other variables such as DBH, crown scorch, and CKR. Therefore, it would be impossible to know if any differences in model results would be due to fire type, season, or a simply a change in data distribution. Woolley *et al.* (2012) detailed additional knowledge gaps and areas of future research needed to improve predictions of post-fire mortality for western North American conifers. Many of these gaps apply to other geographic regions as well. Incorporation of new research findings into fire effects software should occur routinely to ensure that managers can easily apply the most accurate science to fire-related land management decisions.

ACKNOWLEDGEMENTS

We acknowledge funding from the Joint Fire Science Program under Project JFSP #05-2-1-105 and #16-01-04-8. We would like to thank R. King for help with the statistical analysis. S. Smith, D. Cluck, K. Ryan, and C. McHugh contributed data for model validation and development. We thank the three anonymous reviewers that improved a previous version of the manuscript.

LITERATURE CITED

- Anderegg, W.R.L., J.A. Hicke, R.A. Fisher, C.D. Allen, J. Aukema, B. Bentz, S. Hood, J.W. Lichstein, A.K. Macalady, N. McDowell, Y. Pan, K. Raffa, A. Sala, J.D. Shaw, N.L. Stephenson, C. Tague, and M. Zeppel. 2015. Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist* 208: 674–683. doi: [10.1111/nph.13477](https://doi.org/10.1111/nph.13477)
- Andrews, P. 2009. BehavePlus fire modeling system, version 5.0: variables. General Technical Report RMRS-GTR-213WWW, revised. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Battaglia, M., F.W. Smith, and W.D. Shepperd. 2009. Predicting mortality of ponderosa pine regeneration after prescribed fire in the Black Hills, South Dakota, USA. *International Journal of Wildland Fire* 18: 176–190. doi: [10.1071/WF07163](https://doi.org/10.1071/WF07163)
- Butler, B.W., and M.B. Dickinson. 2010. Tree injury and mortality in fires: developing process-based models. *Fire Ecology* 6: 55–79. doi: [10.4996/fireecology.0601055](https://doi.org/10.4996/fireecology.0601055)
- Chatziefstratiou, E.K., G. Bohrer, A.S. Bova, R. Subramanian, R.P. Frasson, A. Scherzer, B.W. Butler, and M.B. Dickinson. 2013. FireStem2D—a two-dimensional heat transfer model for simulating tree stem injury in fires. *PloS ONE* 8: e70110. doi: [10.1371/journal.pone.0070110](https://doi.org/10.1371/journal.pone.0070110)
- Dickinson, M., and E. Johnson. 2001. Fire effects on trees. Pages 477–525 in: E.A. Johnson and K. Miyanishi, editors. *Forest fires: behavior and ecological effects*. Academic Press, New York, New York, USA.
- Dieterich, J.H. 1979. Recovery potential of fire-damaged Southwestern ponderosa pine. Research Note RM-379, US Department of Agriculture, Forest Service, Fort Collins, Colorado, USA.
- Engber, E.A., and J.M. Varner. 2012. Predicting Douglas-fir sapling mortality following prescribed fire in an encroached grassland. *Restoration Ecology* 20: 665–668. doi: [10.1111/j.1526-100X.2012.00900.x](https://doi.org/10.1111/j.1526-100X.2012.00900.x)
- Fowler, J.F., C.H. Sieg, J. McMillin, K.K. Allen, J.F. Negron, L.L. Wadleigh, J.A. Anhold, and K.E. Gibson. 2010. Development of post-fire crown damage mortality thresholds in ponderosa pine. *International Journal of Wildland Fire* 19: 583–588. doi: [10.1071/WF08193](https://doi.org/10.1071/WF08193)
- Furniss, M.M. 1965. Susceptibility of fire-injured Douglas-fir to bark beetle attack in southern Idaho. *Journal of Forestry* 63: 8–14.
- Gill, A.M., S.L. Stephens, and G.J. Cary. 2012. The worldwide “wildfire” problem. *Ecological Applications* 23: 438–454. doi: [10.1890/10-2213.1](https://doi.org/10.1890/10-2213.1)
- Hare, R.C. 1961. Heat effects on living plants. Occasional paper 183, US Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana, USA. doi: [10.5962/bhl.title.127760](https://doi.org/10.5962/bhl.title.127760)
- Harrington, M.G. 1987. Ponderosa pine mortality from spring, summer, and fall crown scorching. *Western Journal of Applied Forestry* 2: 14–16.
- Harrington, M.G. 1993. Predicting *Pinus ponderosa* mortality from dormant season and growing season fire injury. *International Journal of Wildland Fire* 3: 65–72. doi: [10.1071/WF9930065](https://doi.org/10.1071/WF9930065)

- Hood, S.M. 2010. Mitigating old tree mortality in long-unburned, fire-dependent forests: a synthesis. RMRS-GTR-238, US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Hood, S.M., and B. Bentz. 2007. Predicting post-fire Douglas-fir beetle attacks and tree mortality in the northern Rocky Mountains. *Canadian Journal of Forest Research* 37: 1058–1069. doi: [10.1139/X06-313](https://doi.org/10.1139/X06-313)
- Hood, S.M., D.R. Cluck, S.L. Smith, and K.C. Ryan. 2008. Using bark char codes to predict post-fire cambium mortality. *Fire Ecology* 4: 57–73. doi: [10.4996/fireecology.0401057](https://doi.org/10.4996/fireecology.0401057)
- Hood, S.M., C. McHugh, K.C. Ryan, E. Reinhardt, and S.L. Smith. 2007. Evaluation of a post-fire tree mortality model for western US conifers. *International Journal of Wildland Fire* 16: 679–689. doi: [10.1071/WF06122](https://doi.org/10.1071/WF06122)
- Hood, S.M., S. Smith, and D. Cluck. 2010. Predicting tree mortality for five California conifers following wildfire. *Forest Ecology and Management* 260: 750–762. doi: [10.1016/j.foreco.2010.05.033](https://doi.org/10.1016/j.foreco.2010.05.033)
- Hosmer, D.W., and S. Lemeshow. 2000. Applied logistic regression. Second edition. John Wiley and Sons, New York, New York, USA. doi: [10.1002/0471722146](https://doi.org/10.1002/0471722146)
- Jackson, J.F., D.C. Adams, and U.B. Jackson. 1999. Allometry of constitutive defense: a model and a comparative test with tree bark and fire regime. *The American Naturalist* 153: 614–632. doi: [10.1086/303201](https://doi.org/10.1086/303201)
- Kavanagh, K.L., M.B. Dickinson, and A.S. Bova. 2010. A way forward for fire-caused tree mortality prediction: modeling a physiological consequence of fire. *Fire Ecology* 6: 80–94. doi: [10.4996/fireecology.0601080](https://doi.org/10.4996/fireecology.0601080)
- Lerch, A.P., J.A. Pfammatter, B.J. Bentz, and K.F. Raffa. 2016. Mountain pine beetle dynamics and reproductive success in post-fire lodgepole and ponderosa pine forests in northeastern Utah. *Plos ONE* 11: e0164738. doi: [10.1371/journal.pone.0164738](https://doi.org/10.1371/journal.pone.0164738)
- Lutes, D. 2012. FOFEM 6.0 User Guide. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- McHugh, C., and T.E. Kolb. 2003. Ponderosa pine mortality following fire in northern Arizona. *International Journal of Wildland Fire* 12: 7–22. doi: [10.1071/WF02054](https://doi.org/10.1071/WF02054)
- Michaletz, S.T., and E.A. Johnson. 2006. A heat transfer model of crown scorch in forest fires. *Canadian Journal of Forest Research* 36: 2839–2851. doi: [10.1139/x06-158](https://doi.org/10.1139/x06-158)
- Michaletz, S.T., and E.A. Johnson. 2007. How forest fires kill trees: a review of the fundamental biophysical processes. *Scandinavian Journal of Forest Research* 22: 500–515. doi: [10.1080/02827580701803544](https://doi.org/10.1080/02827580701803544)
- Michaletz, S.T., E.A. Johnson, and M.T. Tyree. 2012. Moving beyond the cambium necrosis hypothesis of post-fire tree mortality: cavitation and deformation of xylem in forest fires. *New Phytologist* 194: 254–263. doi: [10.1111/j.1469-8137.2011.04021.x](https://doi.org/10.1111/j.1469-8137.2011.04021.x)
- Peterson, D.L. 1985. Crown scorch volume and scorch height: estimates of postfire tree condition. *Canadian Journal of Forest Research* 15: 596–598. doi: [10.1139/x85-097](https://doi.org/10.1139/x85-097)
- Reinhardt, E., and N. Crookston. 2003. The fire and fuels extension to the forest vegetation simulator. RMRS-GTR-116, US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.
- Reinhardt, E.D., and M.B. Dickinson. 2010. First-order fire effects models for land management: overview and issues. *Fire Ecology* 6: 131–142. doi: [10.4996/fireecology.0601131](https://doi.org/10.4996/fireecology.0601131)
- Reinhardt, E.D., R.E. Keane, and J.K. Brown. 1997. First Order Fire Effects Model: FOFEM 4.0 user's guide. INT-GTR-344, US Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, Utah, USA.

- Ryan, K.C. 1982. Techniques for assessing fire damage to trees. Pages 1–11 in: J. Lotan, editor. Proceedings of the symposium: Fire, its field effects. Intermountain Fire Council, 19–21 October 1982, Jackson, Wyoming, USA.
- Ryan, K.C., and G.D. Amman. 1994. Interactions between fire-injured trees and insects in the greater Yellowstone area. Pages 259–271 in: D.G. Despain, editor. Plants and their environments: proceedings of the first biennial scientific conference on the greater Yellowstone ecosystem. Technical report NPS/NRYELL/NRTR, US Department of the Interior, National Park Service, Natural Resources Publication Office, Denver, Colorado, USA.
- Ryan, K.C., E.E. Knapp, and J.M. Varner. 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. *Frontiers in Ecology and the Environment* 11: e15–e24. doi: [10.1890/120329](https://doi.org/10.1890/120329)
- Sieg, C.H., J.D. McMillin, J.F. Fowler, K.K. Allen, J.F. Negrón, L.L. Wadleigh, J.A. Anhold, and K.E. Gibson. 2006. Best predictors for postfire mortality of ponderosa pine trees in the Intermountain West. *Forest Science* 52: 718–728.
- Sparks, A., C. Kolden, A. Talhelm, A. Smith, K. Apostol, D. Johnson, and L. Boschetti. 2016. Spectral indices accurately quantify changes in seedling physiology following fire: towards mechanistic assessments of post-fire carbon cycling. *Remote Sensing* 8: 572. doi: [10.3390/rs8070572](https://doi.org/10.3390/rs8070572)
- Stephens, S.L., and M.A. Finney. 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. *Forest Ecology and Management* 162: 261–271. doi: [10.1016/S0378-1127\(01\)00521-7](https://doi.org/10.1016/S0378-1127(01)00521-7)
- Swezy, D.M., and J.K. Agee. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. *Canadian Journal of Forest Research* 21: 626–634. doi: [10.1139/x91-086](https://doi.org/10.1139/x91-086)
- van Mantgem, P.J., J.C.B. Nasmith, M. Keifer, E.E. Knapp, A. Flint, and L. Flint. 2013. Climatic stress increases forest fire severity across the western United States. *Ecology Letters* 16: 1151–1156. doi: [10.1111/ele.12151](https://doi.org/10.1111/ele.12151)
- Van Wagner, C.E. 1973. Height of crown scorch in forest fires. *Canadian Journal of Forest Research* 3: 373–378. doi: [10.1139/x73-055](https://doi.org/10.1139/x73-055)
- Varner III, J.M., J.K. Hiers, R.D. Ottmar, D.R. Gordon, F.E. Putz, and D.D. Wade. 2007. Overstory tree mortality resulting from reintroducing fire to long-unburned longleaf pine forests: the importance of duff moisture. *Canadian Journal of Forest Research* 37: 1349–1358. doi: [10.1139/X06-315](https://doi.org/10.1139/X06-315)
- Wallin, K.F., T.E. Kolb, K.R. Skov, and M.R. Wagner. 2003. Effects of crown scorch on ponderosa pine resistance to bark beetles in northern Arizona. *Environmental Entomology* 32: 652–661. doi: [10.1603/0046-225X-32.3.652](https://doi.org/10.1603/0046-225X-32.3.652)
- West, A.G., J.A. Nel, W.J. Bond, and J.J. Midgley. 2016. Experimental evidence for heat plume-induced cavitation and xylem deformation as a mechanism of rapid post-fire tree mortality. *New Phytologist* 211: 828–838. doi: [10.1111/nph.13979](https://doi.org/10.1111/nph.13979)
- Woolley, T., D.C. Shaw, L.M. Ganio, and S.A. Fitzgerald. 2012. A review of logistic regression models used to predict post-fire tree mortality of western North American conifers. *International Journal of Wildland Fire* 21: 1–35. doi: [10.1071/WF09039](https://doi.org/10.1071/WF09039)
- Zeibig-Kichas, N.E., C.W. Ardis, J.-P. Berrill, and J.P. King. 2016. Bark thickness equations for mixed-conifer forest type in Klamath and Sierra Nevada mountains of California. *International Journal of Forestry Research* 2016: 10. doi: [10.1155/2016/1864039](https://doi.org/10.1155/2016/1864039)