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An experimental demonstration of stem damage as a predictor of fire-caused mortality for ponderosa pine

Phillip van Mantgem and Mark Schwartz

Abstract: We subjected 159 small ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) to treatments designed to test the relative importance of stem damage as a predictor of postfire mortality. The treatments consisted of a group with the basal bark artificially thinned, a second group with fuels removed from the base of the stem, and an untreated control. Following prescribed burning, crown scorch severity was equivalent among the groups. Postfire mortality was significantly less frequent in the fuels removal group than in the bark removal and control groups. No model of mortality for the fuels removal group was possible, because dead trees constituted <4% of subject trees. Mortality in the bark removal group was best predicted by crown scorch and stem scorch severity, whereas death in the control group was predicted by crown scorch severity and bark thickness. The relative lack of mortality in the fuels removal group and the increased sensitivity to stem damage in the bark removal group suggest that stem damage is a critical determinant of postfire mortality for small ponderosa pine.

Résumé : Nous avons soumis 159 jeunes pins ponderosa (*Pinus ponderosa* Dougl. ex P. & C. Laws.) à des traitements destinés à tester l'importance relative de différents types de dommages au tronc pour prédire la mortalité après feu. Les traitements incluaient un groupe où l'écorce à la base du tronc avait été artificiellement enlevée, un deuxième groupe où les combustibles présents à la base du tronc avaient été enlevés et un groupe témoin. La sévérité des dommages à la cime était semblable chez tous les groupes après avoir effectué un brûlage dirigé. La mortalité après feu était significativement moins fréquente dans le groupe où les combustibles avaient été enlevés comparativement à celui où l'écorce avait été enlevée et au groupe témoin. Il était impossible de modéliser la mortalité dans le groupe où les combustibles avaient été enlevés parce que les arbres morts représentaient <4 % des arbres étudiés. La mortalité dans le groupe où l'écorce avait été enlevée était le plus adéquatement prédite par la sévérité du roussissement du tronc et de la cime tandis que la mortalité dans le groupe témoin pouvait être prédite par la sévérité du roussissement de la cime et l'épaisseur de l'écorce. L'absence relative de mortalité dans le groupe où les combustibles avaient été enlevés et la sensibilité accrue aux dommages au tronc dans le groupe où l'écorce avait été enlevée indiquent que les dommages au tronc sont un facteur déterminant de mortalité après feu chez les jeunes pins ponderosa.

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Introduction

The data typically used in creating models of fire-caused tree mortality present two distinct problems. First, many studies are opportunistic (e.g., Peterson 1985; Peterson and Arbaugh 1986, 1989; Regelbrugge and Conard 1993), and the nonrandom selection of sampling units can lead to fire effects being mediated by unmeasured site differences. Second, most models depend on observational data that cannot reliably isolate the effects of the predictor variables. For example, stem diameter is related to both crown height (Yuancai and Parresol 2001) and bark thickness (Hengst and Dawson 1994; van Mantgem and Schwartz 2003), and its use in fire-caused mortality models confounds our understanding of how trees escape and resist damage. Experimental approaches, when possible, may help overcome both of these problems.

The role of stem damage in the process of postfire mortality is particularly unclear. Past research has generally found stem injury to be a less important predictor of postfire mortality than crown scorch severity but still a factor that greatly enhances the predictive ability of the models (e.g., Peterson and Arbaugh 1986, 1989; Peterson and Ryan 1986; Wyant et

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al. 1986; Ryan and Reinhardt 1988). However, successful models have been created that only consider stem damage and stem defenses (Regelbrugge and Conard 1993), and Ryan et al. (1988) found the extent of cambial necrosis to be the single best predictor of postfire mortality for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Other models ignore the effects of stem damage altogether, although stem diameter is often modeled as a proxy for stem defenses (e.g., bark thickness) (e.g., Mutch and Parsons 1997; Stephens and Finney 2002; van Mantgem et al. 2003).

The objective of this study was to experimentally identify the role of stem damage as a determinant of postfire tree mortality for small (≤15 cm diameter at breast height) ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.). We focus on small trees because they are sensitive to fire-caused damage and their removal is often a goal of prescription burning.

Materials and methods

We conducted this experiment at Calaveras Big Trees State Park (38.2719°N; 120.2867°W) in the low-elevation mixed conifer forests of the central Sierra Nevada, California. The climate of this area is Mediterranean, with long, dry summers and wet, snowy winters. A large proportion of the precipitation in these forests arrives in the form of snow (Major 1977). The average January and July air temperatures for this region are 2 and 22 °C, respectively. Our measurements were collected in a haphazardly selected stand of ponderosa pine, which contained occasional individuals of white fir (*Abies concolor* (Gord. & Glend.) Lindl.) and California black oak (*Quercus kelloggii* Newb.). Our sample population consisted of 159 ponderosa pine individuals, with diameter at breast height (DBH) of approximately 5–15 cm. We randomly assigned trees to one of three treatments: (*i*) partial basal bark removal; (*ii*) basal fuels removal; and (*iii*) control. For the partial bark removal treatment, we moved aside litter and duff and carefully removed the basal 5 cm of outer bark, using a wood chisel, until only 0.5 cm of basal bark remained (including inner bark). We assumed this treatment would affect tree responses to fire because bark defenses would be most critical where they are in direct contact with burning fuels. The litter and duff were replaced following this treatment. The bark of ponderosa pine is extremely flaky and easy to work with, allowing us to reliably reduce the average basal bark thickness of any individual to 0.5 cm without damaging the cambium. This treatment does not appear to affect tree mortality in the absence of fire; in an adjacent unburned site, 15 trees that received the bark removal treatment exhibited no mortality over 2 years. The fuels removal treatment consisted of raking away all litter and duff, along with any woody fuels, within a radius of 0.5 m around the base of the tree. Because the fuels removal was only in the immediate neighborhood of the stem, roots and crowns of the trees receiving this treatment were still exposed to fire-related damage. Trees in the control treatment received no bark thinning or fuels removal, but the fuels around the base of the tree were disturbed and replaced as in the bark removal treatment. We expected trees in the bark removal treatment to have higher postfire mortality rates and to be more sensitive to stem damage than controls; and we anticipated that the trees in the fuels removal treatment would have lower mortality rates and be more sensitive to crown damage.

The area containing the study plot was subjected to a prescribed burn in June 1999. Flame lengths were estimated visually, with the use of marked reference stakes. Flame lengths were low (0.2–0.5 m), resulting in fireline intensities of 8–57 $kW \cdot m^{-1}$ (Agee 1993), within the typical range for surface fires. We measured fuels 2 weeks before and 1 month after the burn along four randomly placed 20-m transects within the plot, using standard methods (Brown et al. 1982). The average prefire fuel load was 6 $t \cdot ha^{-1}$. The fuels consisted primarily of duff (94%) with sparse woody fuels, accounting for the light fuel loads at this site. The burn reduced the total fuel load by approximately 70%, with a large proportion of the litter and duff layer being consumed.

Assessments of individual tree conditions were made before and after burning. Before the burning, we measured stem diameter at 1.37 m (DBH) and bark thickness at the stem base, using a standard bark gauge. One month after the fire a single observer visually estimated crown scorch class (percentage crown volume scorched; i.e., 0–5, 6–20, 21–50, 51–80, 81–95, 96–100) and measured maximum stem scorch height as an index of stem damage severity. We observed tree mortality for 2 years after the fire. The small trees used in this study do not exhibit delayed postfire mortality (Thomas and Agee 1986). Trees were noted as dead only if they showed complete needle browning or loss.

We used logistic regression to identify predictors of postfire mortality for ponderosa pine. The logistic regression model has the form

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

where P_m is the probability of mortality; X_1 through X_k are independent variables; and β_0 through β_k are regression coefficients estimated with the use of maximum likelihood (Hosmer and Lemeshow 2000). We modeled all appropriate variables (i.e., crown scorch class, stem scorch height, and bark thickness). We selected appropriate models for individual treatment groups using the Akaike information criterion corrected for small sample sizes (AIC_c), which is a ranking procedure defined as

$$AIC_c = -2 \log L + 2K + \frac{2K(K+1)}{n - K - 1}$$

where log L is the log of the likelihood of the model; K is the number of coefficients, including the constant; and n is the sample size (Burnham and Anderson 1998). The likelihood of a given model increases as more parameters are added, but the decreasing negative log likelihood is offset by increases in K. The best model has a relatively small AIC_c, as a result of the combination of a fairly large likelihood and a parsimoniously small number of parameters. Competing models are compared by scaling their AIC_c values against the best model with the lowest AIC_c value. The rescaled AIC_c values are written as ΔAIC_c. Models with $\Delta AIC_c \leq 2$ have substantial support and fit almost equally as well as the best model (Burnham and Anderson 1998). We looked for differences among treatment groups by combining the data across treatments and testing for the importance of a term

Table 1. Characteristics of trees used to develop models predicting postfire tree mortality for *Pinus ponderosa*.

			Crown scorch (%)			Stem scorch height (m)			DBH (cm)			Bark thickness (cm)		
Treatment	Status	*n*	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Bark removal	Live	38a	23a	32	0–100	0.55a	0.27	0.20–1.13	10.0a	2.3	6.3–15.4	0.5a	0.1	0.3–0.6
	Dead	15	48	45	0–100	0.86	0.40	0.25–1.51	8.3	1.2	5.2–9.8	0.5	0.1	0.3–0.6
Fuels removal	Live	51b	23a	32	0–100	0.00b	n.a.	n.a.	9.2a	2.2	5.2–14.3	1.6b	0.6	0.8–3.0
	Dead	2	50	68	0–100	0.00	n.a.	n.a	7.6	0.6	7.2–8.0	0.9	0.1	0.8–1.0
Control	Live	38a	21a	32	0–100	0.73a	0.38	0.18–1.66	9.7a	2.3	4.8–14.6	1.7b	0.5	0.7–2.7
	Dead	15	73	36	0–100	0.62	0.37	0.24–1.60	7.4	1.2	5.4–9.8	1.0	0.3	0.6–2.1

Note: Trees are grouped by treatment (see text for details). Different letters within a column denote significant differences between treatment means for both live and dead trees at $p < 0.05$. We collected crown scorch data by classes, but data are shown here as percentages. DBH, diameter at breast height; n.a., not applicable (there is no variation in this measure).

for treatment group identity, using AIC_c. We chose the final model for each treatment group by comparing competing models with AIC_c.

We subjected the models to diagnostic tests to determine whether the data met the assumptions of logistic regression and to assess the influence of potential outliers (Hosmer and Lemeshow 2000). We used the Pearson χ^2 to measure model fit. The number of mortalities was sparse, and we could not reliably use Hosmer–Lemeshow tests as an additional measure of model fit. We assessed model discrimination, using receiver operating characteristic (ROC) curve analysis. The area under the ROC curve is a measure of the proportion of the instances in which pairwise comparisons of the predicted response variable (i.e., P_m) is greater for trees with a positive score for the observed response variable (dead trees) than for trees with a negative score for the observed response variable (live trees). Models show acceptable levels of discrimination if the area under the ROC curve is ≥0.7 (Hosmer and Lemeshow 2000). Higher proportions imply greater levels of discrimination. We used SYSTAT version 10.2 (SYSTAT 2002) to conduct all analyses.

Table 2. Logistic regression model selection for *Pinus ponderosa* postfire mortality by treatment group.

Treatment	Model	log L^a	K^b	$AIC_c{}^c$	$\Delta AIC_c{}^d$
Bark removal	CSC, SSH, BT	–24.3	4	57.5	1.2
	CSC, SSH	–24.9	3	56.3	0
	CSC, BT	–29.3	3	65.0	8.7
	SSH, BT	–26.3	3	59.0	2.7
	CSC	–29.5	2	63.2	6.9
	SSH	–27.1	2	58.4	2.1
	BT	–31.1	2	66.4	10.1
Fuels removal	n.a.				
Control	CSC, SSH, BT	–14.2	4	37.3	1.5
	CSC, SSH	–21.8	3	50.1	14.4
	CSC, BT	–14.6	3	35.8	0
	SSH, BT	–19.7	3	45.9	10.1
	CSC	–21.9	2	48.0	12.3
	SSH	–31.1	2	66.5	30.7
	BT	–19.8	2	43.9	8.1

Note: The models include a constant and terms for bark thickness (BT); crown scorch class (CSC); and stem scorch height (SSH). n.a., not applicable, no acceptable model could be created.

[a]Log likelihood of the model.

[b]Number of parameters in the model.

[c]Corrected Akaike information criterion.

[d]Corrected Akaike information criterion relative to the best model.

Results

Table 1 presents summary statistics used to assess differences among treatments. The trees in the fuels removal treatment exhibited fewer deaths than either the bark removal group or the control group (Krusal–Wallis test statistic = 13.1, df = 2, p = 0.001). Differences in tree diameters and crown scorch severity among the treatment groups were not significant (DBH: F = 0.5, df = 2, p = 0.601; crown scorch class: F = 1.1, df = 2, p = 0.321) and therefore do not explain the difference in mortality among groups. In contrast, stem scorch heights differed among groups (F = 92.0, df = 2, p < 0.001), with stem scorch in the fuels removal treatment being entirely absent. Pretreatment differences in basal bark thickness were not significant (F = 0.3, df = 2, p = 0.731), although following treatment the bark removal group had significantly thinner basal bark than the other treatment groups (F = 83.1, df = 2, p < 0.001).

Logistic regression successfully provided models of postfire mortality for the bark removal and control groups but not for the fuels removal group, which had too few deaths to create a model. AIC_c supported separating the bark removal and control groups when we combined the data for these groups and modeled mortality using crown scorch class, stem scorch height, and bark thickness (log L, including term for treatment group identity = –40.2, K = 5, AIC_c = 90.9, ΔAIC_c = 0.0; log L, excluding term for treatment group identity = –46.8, K = 4, AIC_c = 102.1, ΔAIC_c = 11.1). The best model for the bark removal group included crown scorch class and stem scorch height, although including a term for bark thickness also had support (Table 2). The best model for the control group included crown scorch class and bark thickness, although there was support for including a term for stem scorch height (Table 2).

Table 3 presents the best models for the bark removal and control groups. Crown scorch class was a predictor of postfire mortality for both the bark removal and the control groups. The best model for the bark removal group did not include a term for bark thickness, whereas the best model for the control group did not include a term for stem scorch height. Both models fit the data reasonably well (bark removal group: Pearson χ^2 = 54.535, df = 49, p = 0.272; control group: Pearson χ^2 = 34.476, df = 49, p = 0.942). The ROC curve analysis showed that both models discriminate between live and dead trees at an acceptable level (Table 3). We found no evidence of interactions among the predictor

Table 3. Best logistic regression models predicting postfire *Pinus ponderosa* mortality for the prefire treatment groups.

		Estimated coefficients				
Treatment	*n*	β_0 (constant)	β_1 (CSC)	β_2 (SSH)	β_3 (BT)	ROC
Bark removal	53	–4.017 (1.089)	0.382 (0.190)	0.030 (0.011)	n.a.	0.784
Fuels removal	53	n.a.	n.a.	n.a.	n.a.	n.a.
Control	53	2.554 (1.897)	0.663 (0.237)	n.a.	–4.582 (1.681)	0.943

Note: The independent variables included crown scorch class (CSC), stem scorch height (SSH), and bark thickness (BT); n.a., not applicable (term not used in model, or no acceptable model could be created); ROC, area under the receiver operating characteristic curve. Standard errors of the estimated coefficients are presented in parentheses.

variables for either model using AIC_c. When all predictor variables were used to model mortality, as supported by AIC_c, the bark removal group had high standard errors for the bark thickness term, whereas the control group had high standard errors for the stem scorch height term.

Discussion

Our results experimentally demonstrate that stem damage is an important determinant of postfire mortality for small ponderosa pine, although this relationship may not be readily apparent from observational data alone. Trees that lacked stem damage essentially escaped postfire mortality, although this would not have been predicted from observations of untreated trees. The low mortality rate of trees that did not receive stem damage implies that it is the additive effects of damage to different tree organs that actually results in tree death. Tree death in the absence of fire is often the result of many stressors interacting in concert (Manion 1981); our results suggest that the process of fire-mediated tree mortality is also complicated and likely involves the integration of damage to different tree organs. Bark removal did not cause an increase in postfire mortality as expected, perhaps because fuel loading and fire intensities were low. This treatment, however, altered the usefulness of the postfire mortality predictor variables. Mortality for the control trees was strongly related to both crown scorch severity and bark thickness. In contrast, when bark defenses were artificially weakened, mortality was predicted by crown scorch and stem scorch severity, suggesting an increased sensitivity to stem damage. Heavier fuel loading or higher fire intensities may have resulted in increased mortality for the bark removal group.

Data from additional fires and species are needed to determine the general importance of stem damage as a predictor of postfire mortality. It seems logical, however, that the importance of stem damage depends on both tree defenses and the severity of fire-related stress. Many models consider only stem defenses, although it is easy to imagine situations in which thick-barked trees would be susceptible to stem damage (e.g., thick duff layers producing long-lasting smoldering fires) or in which a high variation in fire severity would obscure the relationship between bark thickness and fire-induced mortality. Additional measures would also increase predictive abilities of mortality models, so long as these measures are biologically meaningful. For example, prefire tree vigor (van Mantgem et al. 2003), postfire root necrosis (Swezy and Agee 1991), and pathogen load (Peterson and Arbaugh 1986) would allow greater model precision. Stem diameter, although easy to measure and commonly used, is biologically ambiguous, compared with direct measures of bark thickness and crown height.

Understanding the process of fire-caused death, particularly for small trees, is important in the context of forest management. In the American Southwest researchers have found low-intensity prescribed fire to be relatively ineffective for selectively removing small trees (Sackett et al. 1996; Fulé et al. 2002), which has translated into recommendations for forest restoration that emphasize mechanical thinning (Covington 2000). In contrast, prescription burning in the Sierra Nevada has been successful at reducing small-tree densities (Keifer 1998), and prescribed fire without mechanical treatments remains a feasible forest-thinning tool (Stephenson 1999). Our results suggest that systematic differences in stem damage, perhaps mediated by differences in fuels characteristics, could provide a partial explanation of the variable mortality responses between these regions.

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References

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

Brown, J.K., Oberhue, R.D., and Johnson, C.M. 1982. Inventorying surface fuels and biomass in the Interior West. USDA For. Serv. Gen. Tech. Rep. INT-129.

Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag New York Inc., New York.

Covington, W.W. 2000. Helping western forests heal: the prognosis is poor for United States forest ecosystems. Nature (London), **408**: 135–136.

Fulé, P.Z., Covington, W.W., Smith, H.H., Springer, J.D., Heinlein, T.A., Huisinga, K.D., and Moore, M.M. 2002. Comparing ecological restoration alternatives: Grand Canyon, Arizona. For. Ecol. Manage. **170**: 19–41.

Hengst, G.E., and Dawson, J.O. 1994. Bark properties and fire resistance of selected tree species from the central hardwood region of North America. Can. J. For. Res. **24**: 688–696.

Hosmer, D.W., and Lemeshow, S. 2000. Applied logistic regression. 2nd ed. John Wiley & Sons Inc., New York.

Keifer, M. 1998. Fuel load and tree density changes following prescribed fire in the giant sequoia – mixed conifer forest: the first 14 years of fire effects monitoring. *In* Proceedings of the 20th Tall Timbers Fire Ecology Conference: Fire in Ecosystem Management: Shifting Paradigms from Suppression to Prescription, Boise, Idaho, 7–10 May 1996. *Edited by* T.L. Pruden and L.A. Brennan. Tall Timbers Research, Inc., Tallahassee, Fla. pp. 306–309.

Major, J. 1977. California climate in relation to vegetation. *In* Terrestrial vegetation of California. *Edited by* M.G. Barbour and J. Major. John Wiley & Sons Inc., New York. pp. 11–74.

Manion, P.D. 1981. Tree disease concepts. Prentice-Hall, Englewood Cliffs, N.J.

Mutch, L.S., and Parsons, D.J. 1998. Mixed conifer forest mortality and establishment before and after prescribed fire in Sequoia National Park, California. For. Sci. **44**: 341–355.

Peterson, D.L. 1985. Crown scorch volume and scorch height: estimates of postfire tree condition. Can. J. For. Res. **15**: 596–598.

Peterson, D.L., and Arbaugh, M.J. 1986. Postfire survival in Douglas-fir and lodgepole pine: comparing the effects of crown and stem damage. Can. J. For. Res. **16**: 1175–1179.

Peterson, D.L., and Arbaugh, M.J. 1989. Estimating postfire survival of Douglas-fir in the Cascade Range. Can. J. For. Res. **19**: 530–533.

Peterson, D.L., and Ryan, K.C. 1986. Modeling post-fire conifer mortality for long-range planning. Environ. Manage. **10**: 797–808.

Regelbrugge, J.C., and Conard, S.G. 1993. Modeling tree mortality following wildfire in *Pinus ponderosa* forests in the Central Sierra Nevada of California. Int. J. Wildl. Fire **3:** 139–148.

Ryan, K.C., and Reinhardt, E.D. 1988. Predicting postfire mortality of seven western conifers. Can. J. For. Res. **18**: 1291–1297.

Ryan, K.C., Peterson, D.L., and Reinhardt, E.D. 1988. Modeling long-term fire-caused mortality of Douglas-fir. For. Sci. **34**: 190–199.

Sackett, S.S., Haase, S.M., and Harrington, M.G. 1996. Lessons learned from fire use for restoring southwestern ponderosa pine ecosystems. USDA For. Serv. Gen. Tech. Rep. RM-GTR-278.

Stephens, S.L., and Finney, M.A. 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. For. Ecol. Manage. **162**: 261–271.

Stephenson, N.L. 1999. Reference conditions for giant sequoia forest restoration: structure, process, and precision. Ecol. Appl. **9**: 1253–1265.

Swezy, M.D., and Agee, J.K. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Can. J. For. Res. **21**: 626–634.

SYSTAT. 2002. SYSTAT version 10.2 [computer program]. SYSTAT Software Inc., Richmond, Calif.

Thomas, T.L., and Agee, J.K. 1986. Prescribed fire effects on mixed conifer forest structure at Crater Lake, Oregon. Can. J. For. Res. **16**: 1082–1087.

van Mantgem, P.J., and Schwartz, M.W. 2003. Bark heat resistance of small trees in Californian mixed conifer forests: testing some model assumptions. For. Ecol. Manage. **178**: 341–352.

van Mantgem, P.J., Stephenson, N.L., Mutch, L.S., Johnson, V.G., Esperanza, A.E., and Parsons, D.J. 2003. Growth rate predicts mortality of *Abies concolor* in both burned and unburned stands. Can. J. For. Res. **33**: 1029–1038.

Wyant, J.G., Omi, P.N., and Laven, R.D. 1986. Fire induced tree mortality in a Colorado ponderosa pine/Douglas-fir stand. For. Sci. **32**: 49–59.

Yuancai, L., and Parresol, B.R. 2001. Remarks on height–diameter modeling. USDA For. Serv. Res. Note SRS-IO.