Growth rate predicts mortality of *Abies concolor* in both burned and unburned stands

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Abstract: Tree mortality is often the result of both long-term and short-term stress. Growth rate, an indicator of long-term stress, is often used to estimate probability of death in unburned stands. In contrast, probability of death in burned stands is modeled as a function of short-term disturbance severity. We sought to narrow this conceptual gap by determining (*i*) whether growth rate, in addition to crown scorch, is a predictor of mortality in burned stands and (*ii*) whether a single, simple model could predict tree death in both burned and unburned stands. Observations of 2622 unburned and 688 burned *Abies concolor* (Gord. & Glend.) Lindl. (white fir) in the Sierra Nevada of California, U.S.A., indicated that growth rate was a significant predictor of mortality in the unburned stands, while both crown scorch and radial growth were significant predictors of mortality in the burned stands. Applying the burned stand model to unburned stands resulted in an overestimation of the unburned stand mortality rate. While failing to create a general model of tree death for *A. concolor*, our findings underscore the idea that similar processes may affect mortality in disturbed and undisturbed stands.

Résumé : Chez les arbres, la mortalité est souvent le résultat de stress à long et à court termes. Le taux de croissance, un indicateur de stress à long terme, est souvent utilisé pour estimer les risques de mortalité dans les peuplements qui n'ont pas été endommagés par le feu. Par contre, dans les peuplements endommagés par le feu, le risque de mortalité est modélisé en fonction de la sévérité d'une perturbation à court terme. Nous avons tenté de réconcilier cet écart conceptuel en déterminant (*i*) si le taux de croissance, en plus du roussissement de la cime, pouvait servir à prédire la mortalité dans les peuplements endommagés par le feu et (*ii*) si un modèle simple et unique pouvait prédire la mortalité tant dans les peuplements endommagés par le feu que non endommagés. Les observations faites sur 2622 tiges de *Abies concolor* (Gord. & Glend.) Lindl. (sapin argenté) non endommagées et 688 tiges endommagées par le feu dans la Sierra Nevada en Californie, aux États-Unis, montrent que le taux de croissance peut servir à prédire la mortalité dans les peuplements non endommagés par le feu alors que le roussissement de la cime et la croissance radiale peuvent servir à prédire la mortalité dans les peuplements endommagés par le feu. L'application du modèle conçu pour les peuplements endommagés par le feu aux peuplements non endommagés entraîne une surestimation du taux de mortalité dans les peuplements non endommagés. Bien que nous n'ayons pas réussi à élaborer un modèle général de mortalité des tiges de *A. concolor*, nos résultats soulignent la notion que des processus similaires peuvent affecter la mortalité dans les peuplements perturbés et non perturbés.

[Traduit par la Rédaction]

Introduction

Individual tree death often occurs as a result of the interacting effects of many different long-term and short-term stressors. The decline spiral model of tree death states that trees already suffering from long-term stress will be predisposed to die given an additional short-term stress (Manion 1981; Franklin et al. 1987; Pedersen 1998*a*, 1998*b*). Conversely, trees not experiencing long-term stress will be better able to resist the effects of short-term stress. Because tree mortality often arises from a complex, interacting set of stressors, ecologists have searched for simple risk factors that can be used to estimate probabilities of future mortality. In practice, the choice of variables used to predict mortality probabilities has taken place in the context of the particular stand in question.

Studies attempting to describe death in undisturbed stands have traditionally viewed suppression as a primary cause of mortality, at least among small trees (Peet and Christensen 1987; Kobe et al. 1995; Kobe and Coates 1997). Suppres-

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sion, brought about by the capture of resources by neighbors, is a long-term stress that affects the carbon balance of individual trees. Stress causes distinctive changes in photosynthate allocation patterns, and unusual morphological characteristics (e.g., reduced foliage growth, atypical root growth, or unusual amounts of stem taper) may indicate a tree is likely to die in the near future (Keen 1943; Waring 1987). Radial growth, indicative of whole plant carbon gain (Givnish 1988), may also be used to identify trees with high probabilities of mortality. Several studies have shown that death rates are inversely related to radial stem growth rates (Buchman et al. 1983; Kobe et al. 1995; Kobe and Coates 1997; Wyckoff and Clark 2000). A general finding of this work is that death rates decline as a power function of growth rates, although different model forms have been used to describe this relationship.

In contrast with undisturbed stands, models of disturbance-mediated tree mortality emphasize the results of short-term damage (wind damage: Hedden et al. 1995; Ruel 2000; herbivore outbreaks: Steinman and Maclean 1994; Volney 1998; Dobbertin and Brang 2001). Fire is a common disturbance in many forest types, and there is a large literature base concerning the effects of fire on tree mortality (Agee 1993). Crown damage is an obvious effect of fire, arising from direct foliage consumption or convective heat transfer (Van Wagner 1973). For conifers, there is a clear link between crown damage and fire-caused tree mortality (Wagener 1961; Peterson and Ryan 1985; Ryan et al. 1988; Ryan and Reinhardt 1988; Mutch and Parsons 1998; Stephens and Finney 2002). The severity of fire-caused root and cambial injuries may also be indicative of trees likely to die (Swezy and Agee 1991; Reggelbrugge and Conard 1993), although crown damage has been repeatedly found to be the single most important predictor of postfire mortality where damage to multiple organs was considered (Wyant et al. 1986; Peterson and Arbaugh 1989). Along with many other parameters, previous work has suggested that low vigor may be an additional risk factor for fire-caused mortality (Wagener 1961; Swezy and Agee 1991). Radial growth is clearly related to tree vigor, although to the best of our knowledge, it has yet to be incorporated into models of fire-caused mortality.

If tree death is the result of the combined effects of several types of stress, a more general description of tree death would include information from both long-term and short-term stressors. In this paper, we consider whether fire-caused damage (i.e., crown scorch) can be viewed as simply another type of short-term stress that, when combined with data measuring long-term stress (i.e., growth rate), provides improved models of tree mortality. We attempt to answer these questions using long-term plot data from white fir – mixed conifer forests of the Sierra Nevada of California. Our analyses required a large number of observations, so our investigation was restricted to the most common species in these stands, *Abies concolor* (Gord. & Glend.) Lindl. (white fir).

We initially address two basic issues to establish whether *A. concolor* in our forests behave as others have reported. First, we verify that radial growth predicts mortality for unburned *A. concolor* at our study sites. Second, we verify that crown scorch alone predicts postfire mortality for trees in our burned stands. We extend these results by taking into

account the potential improvements to our model of fire-induced mortality by introducing a term for radial growth. Finally, we determine whether we can use a single, simple model to predict mortality in both burned and unburned stands by applying our model of burned trees to a separate unburned forest stand, where the variable for crown scorch equals zero.

Materials and methods

Field site

We measured forest demographic rates in two burned and five unburned permanent plots in Sequoia National Park, California (36°34′N, 118°44′W). The primary difference among the plots is their recent fire history; two plots were prescribed burned in 1990, while the other nearby plots have not burned since the late 1800s (Swetnam et al. 1992). In other respects, the plots are comparable (Table 1). The plots are located at the headwaters of Tharp Creek, Log Creek, and Suwanee Creek watersheds within the Giant Forest region of the park. The climate of this area is mediterranean, with wet, snowy winters and long, dry summers. The mean annual precipitation of the Giant Forest area is 1255 mm at an elevation of 1950 m, with approximately half of this precipitation arriving as snow (Stephenson 1988). Average January and July air temperatures are 0 and 18°C, respectively. Soils are primarily Pachic Xerumbrepts, derived from grandodiorite (Huntington and Akeson 1987). Vegetation is typical for midelevation mixed conifer forests in the Sierra Nevada (Rundel et al. 1977). The forests are dominated by small *A. concolor*, with all plots initially showing an inverse J-shaped stem size distribution for this species. *Abies magnifica* A. Murr. (red fir), *Calocedrus decurrens* (Torrey) Florin (incense cedar), and *Pinus lambertiana* Douglas (sugar pine) are found in significant numbers in some of these plots (Table 1). *Pinus jeffreyi* Grev. & Balf. (jeffrey pine), *Quercus kelloggii* Newb. (black oak), and *Sequoiadendron giganteum* (Lindley) Buchh. (giant sequoia) also occur at low densities. Shrub and herbaceous cover is low, with litter and duff compromising the majority of the ground cover. Further details about the plots at the Tharp Creek and Log Creek watersheds can be found in Mutch and Parsons (1998).

The 14-ha Tharp Creek watershed containing two permanent plots was prescribed burned by a combination of strip headfires and backing fires in October 1990. The presence of the study plots did not influence ignition techniques. Total prefire fuel loads were relatively high (210 Mg/ha), composed primarily of large 7.6–20.3 cm diameter (1000-h) woody fuels (58%) and litter and duff (35%), with the remainder composed of smaller diameter woody fuels. Following the burn, the total fuel load was reduced to 15% of prefire levels, with the proportionally largest reduction in the litter and duff, giving postfire total fuels loads of 31 Mg/ha (Mutch and Parsons 1998). Backing fire flame lengths ranged from 0.05 to 0.15 m, while strip headfire flame lengths were observed from 0.6 to 2.4 m. There were scattered areas of high fuels accumulation and standing snags, which occasionally torched some of the nearby trees (Haggerty 1990).

Table 1. Characteristics of plots used to create mortality models.

Data type	Watershed and plot name	Establishment date	Size (ha)	Elevation (m)	No. of stems			
					ABCO	ABMA	CADE	PILA
Burned calibration	Tharp PILA	1984	1.1	2167	424			94
Burned validation	Tharp ABCO	1984	1.0	2202	338			
Unburned calibration	Log Meadow	1982	2.0	2128	474	133		15
	Log SEGI	1983	2.5	2170	804	160		
Unburned validation	Suwanee ABCO	1983	0.9	2035	403		191	
	Suwanee Creek	1983	1.4	2033	560		202	201
	Suwanee PILA	1983	1.1	2059	522			164

Note: Community composition at the time of plot establishment is given by the population size of species with >10% of stems. *Abies concolor* (ABCO), *Abies magnifica* (ABMA), *Calocedrus decurrens* (CADE), and *Pinus lambertiana* (PILA) dominated the plots.

Data collection

We compared demographic rates for all trees ≥1.37 m in height in our permanent plots. Mortality assessments were performed annually, starting at the time the plots were established. Trees were classified as dead only if they showed complete needle browning or loss. We took measurements of live tree stem diameter at breast height (DBH) (1.37 m) at five- or six-year intervals (Tharp Creek watershed plots measurement years: 1984, 1989, 1994; Log Creek watershed and Suwanee Creek watershed plot measurement years: 1982–1983, 1988, 1994). Breast height was marked with a nail for precise relocation. Radial growth rates were calculated from these sequential measurements. Because these stands are part of an ongoing long-term study, we chose not to core trees to determine growth rates. We calculated growth as radial (or diameter) increment (mm·year^{-1}) rather than basal area increment (mm^2·year^{-1}). Basal-area increment appears to increase continuously with tree size for many species (Stephenson and Demetry 1995; Clark and Clark 1999; Bragg 2001) and compounds the effect of tree size. Absolute ring widths are, therefore, more likely to reflect tree vigor, independent of tree size, than basal area increment. Severity of fire-caused injuries in the burned plots were measured by a field crew, who visually estimated percent crown volume scorch (PCVS) several months following the fire in the spring and summer of 1991. For a small number of trees (<4% of the sample population), postfire needle loss was too great to gauge prefire crown volume, so PCVS was not estimated.

Data analysis

To assemble enough observations of unburned *A. concolor* deaths, we pooled the unburned plots by the watershed in which they were located (Table 1). We designated both burned and unburned plots for either model development (calibration) or external assessment of model fit (validation) (Table 1). We chose the Tharp PILA plot as the burned calibration stand, because it had the most even distribution of crown scorch severity. By default, we used the Tharp ABCO plot as the burned validation stand. We arbitrarily selected the Log Creek watershed plots as the unburned calibration stand and the Suwanee Creek watershed plots as the unburned validation stand. Hereafter, the plots will be referred
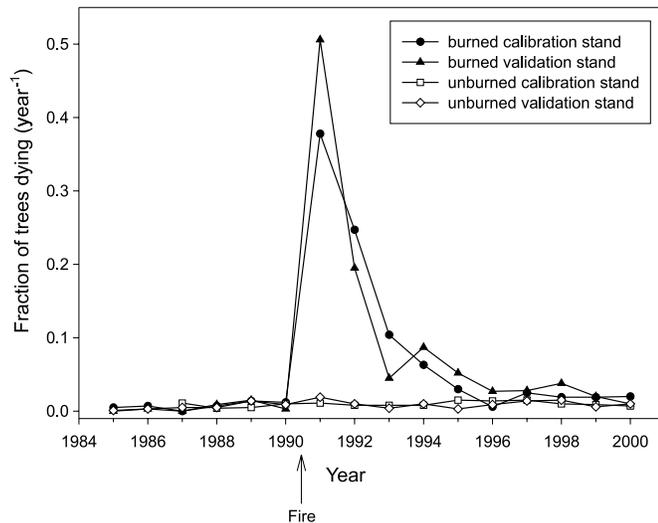
to as the burned calibration stand, burned validation stand, unburned calibration stand, and unburned validation stand.

Annual observations showed that *A. concolor* mortality rates were comparable among the stands during the prefire interval (Fig. 1). Mortality in the burned plots increased in the years immediately postburn, returning to prefire levels 6 years following the burn. After this date, mortalities in the burned stands were primarily related to factors other than fire-caused damage (e.g., suppression, pathogen attack). For this reason, we chose only to analyze mortalities that occurred up to 5 years postfire in the burned stands. For consistency, we also kept a 5-year mortality observation interval in the unburned stands.

For the unburned calibration stand, we used the averaged annual radial growth rate (GR) (derived from stem measurements of 1983–1988) and stem DBH (taken from stem measurements of 1988) as independent variables to predict the chance of dying in the following 5-year interval (1989–1993). We used several different models to predict mortality in the burned calibration stand. The first model used PCVS alone to predict mortality over the 5-year postfire interval with elevated mortality rates (1991–1995). Other models added preburn radial growth rate (derived from stem measurements of 1984–1989) and stem DBH (taken from stem measurements of 1989) as independent variables.

Somewhat problematic to our analysis is the presence of trees with negative growth rates. The amount of negative growth was typically small (<1.0 mm·year^{-1}), which could arise from bark sloughage or from slight differences in diameter tape alignment between the measurement years. We retained these data points in our analysis because we believed that our parameter estimates might become biased if we selectively removed one tail of the growth rate distribution (Clark 2002; Phillips et al. 2002). During initial model construction, graphical analysis of residuals showed that trees with extreme growth rates had a disproportionately large influence on parameter estimates and caused the models to fit the data poorly. We therefore removed trees with growth rates we deemed biologically implausible (<–2 and >10 mm·year^{-1}). Using this approach, we eliminated 14 *A. concolor* individuals from the burned calibration stand data set (4% of the sample population), 8 individuals from the burned validation data set (3% of the sample population),

Fig. 1. Annual mortality rates for *Abies concolor* in the burned calibration, burned validation, unburned calibration, and unburned validation stands. The arrow at the year 1990 indicates the prescribed fire in the burned stands.

10 individuals from the unburned calibration data set (1% of the sample population), and 14 individuals from the unburned validation data set (<1% of the sample population).

We used binary logistic regression to describe the relationship among stem diameter, growth, crown scorch, and mortality. The logistic model can be written as

$$[1] \qquad P(m) = \frac{1}{1 + \exp[-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_i X_i)]}$$

where $P(m)$ is the predicted probability of the dependent variable, β_0 is the constant, β_i represents model coefficients estimated from the data, and X_i represents independent variables.

In this case, $P(m)$ represents the probability of death during the 5-year mortality observation interval and is bounded between 0 and 1. The coefficients for the independent variables are estimated using maximum likelihood. We used graphical analysis of univariate models and tested a series of variable transformations (i.e., fractional polynomials) to check the assumption of linearity between the dependent variable and the logit of each independent variable (Hosmer and Lemeshow 2000). We first considered the model with all possible independent variables and tested interaction terms for significant main effects in subsequent model formulations. We dropped independent variables from the model if their coefficients were shown not to explain significant amounts of variation as determined by likelihood–ratio tests ($\alpha = 0.05$).

Upon arriving at a final model, we calculated multiple measures of goodness-of-fit. We checked the significance of each model by comparing it against a constants-only model using a likelihood–ratio test. Our data contained continuous variables, so Pearson χ^2 and deviance summary measures would give incorrect assessments of model fits. Instead, we used Hosmer–Lemeshow tests to evaluate overall model goodness-of-fit (Hosmer and Lemeshow 2000). This test partitions the sample into groups (typically 10) based on the

predicted probability of the observations. Observed and expected frequencies of these groups are compared, and a summary statistic of goodness-of-fit is then calculated. An important assumption of the Hosmer–Lemeshow test is that the expected frequencies for each group are sufficiently large (i.e., ≥5). Our burned calibration data required us to combine several groups to increase the size of the expected values, with a concomitant loss of degrees of freedom. In this case, we were able to create seven groups, so the sensitivity of the test was not significantly compromised. We also used graphical analyses of residuals to identify individual outliers (Hosmer and Lemeshow 2000).

We checked model discrimination using receiver operating characteristic (ROC) curve analysis. The area under the ROC curve is a measure of the proportion of the instances where 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). When the dependent variable is binary, the area under the ROC curve is closely related to the Mann–Whitney U statistic (Hosmer and Lemeshow 2000). As a general rule, an acceptable level of discrimination is given by a model if the area under the ROC curve is ≥0.70 (Hosmer and Lemeshow 2000). Higher proportions imply greater levels of discrimination. Several other authors have used this method to assess the fit of fire-caused tree mortality models (Saveland and Neuenschwander 1990; Regelbrugge and Connard 1993; Stephens and Finney 2002).

Finally, we used classification tables as a supplemental measure of model fit. Mortality probabilities were extremely low for the unburned data sets, so it was not possible to use the traditional classification cutpoint of 0.5 (i.e., trees are classified as alive where $P(m) < 0.5$ and dead where $P(m) \geq 0.5$). For each calibration stand, we instead empirically established a cutpoint for classification that maximized both the proportion of correctly classified live trees (i.e., specificity) and the proportion of correctly classified dead trees (i.e., sensitivity). Classification table analysis should only be considered complementary to ROC curve analysis, which considers model discrimination over an entire range of possible cutpoints. We conducted all analyses using SYSTAT, version 9.01.

We performed model validation by applying the calibration models, with the coefficients held as fixed constants, to the data for their respective validation stands. From this, we calculated the Hosmer–Lemeshow goodness-of-fit statistic, area under the ROC curve, sensitivity, and specificity for the validation stands. We further checked the generality of the burned calibration model by testing against the unburned validation stand data, where the variable for crown scorch equals zero.

Results

The range of stem diameters and radial growth rates used to create the mortality models were roughly equivalent among the stands (Fig. 2). The distribution of crown scorch damage in the burned calibration and burned validation stands was bimodal, with the majority of trees experiencing either mild or severe amounts of crown damage (Fig. 3).

Fig. 2. Stem size and growth rate distributions for *Abies concolor* in the burned calibration, burned validation, unburned calibration, and unburned validation stands. Negative growth rates are likely due to measurement error or bark sloughage. Open circles are trees that survived; the filled circles are trees that died. The broken horizontal lines represent cutoff values used to exclude outliers with extreme growth rates (see text). DBH, diameter at breast height.
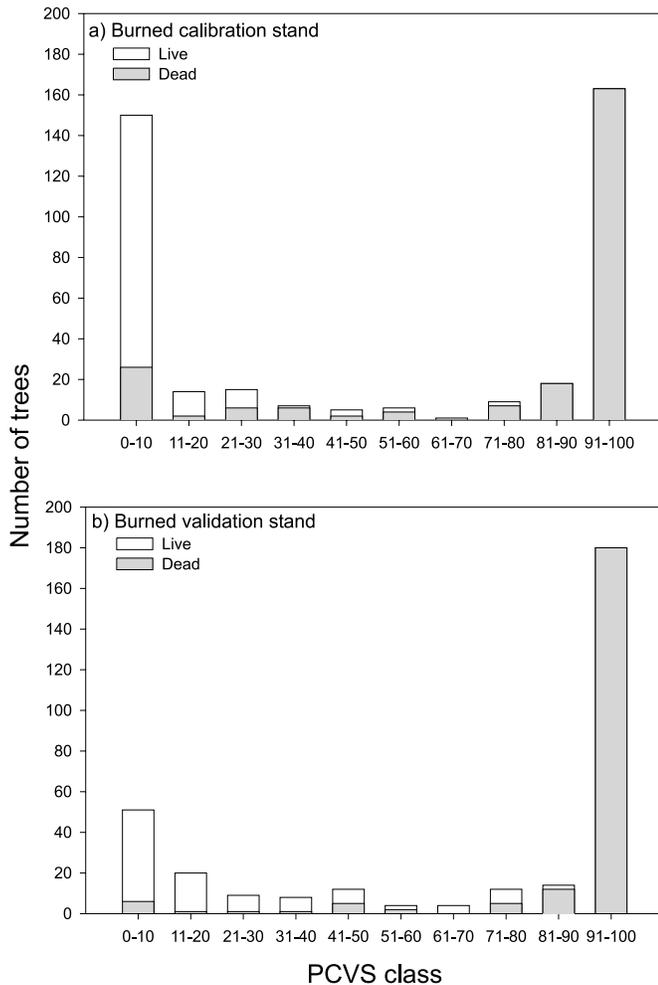

DBH (cm)
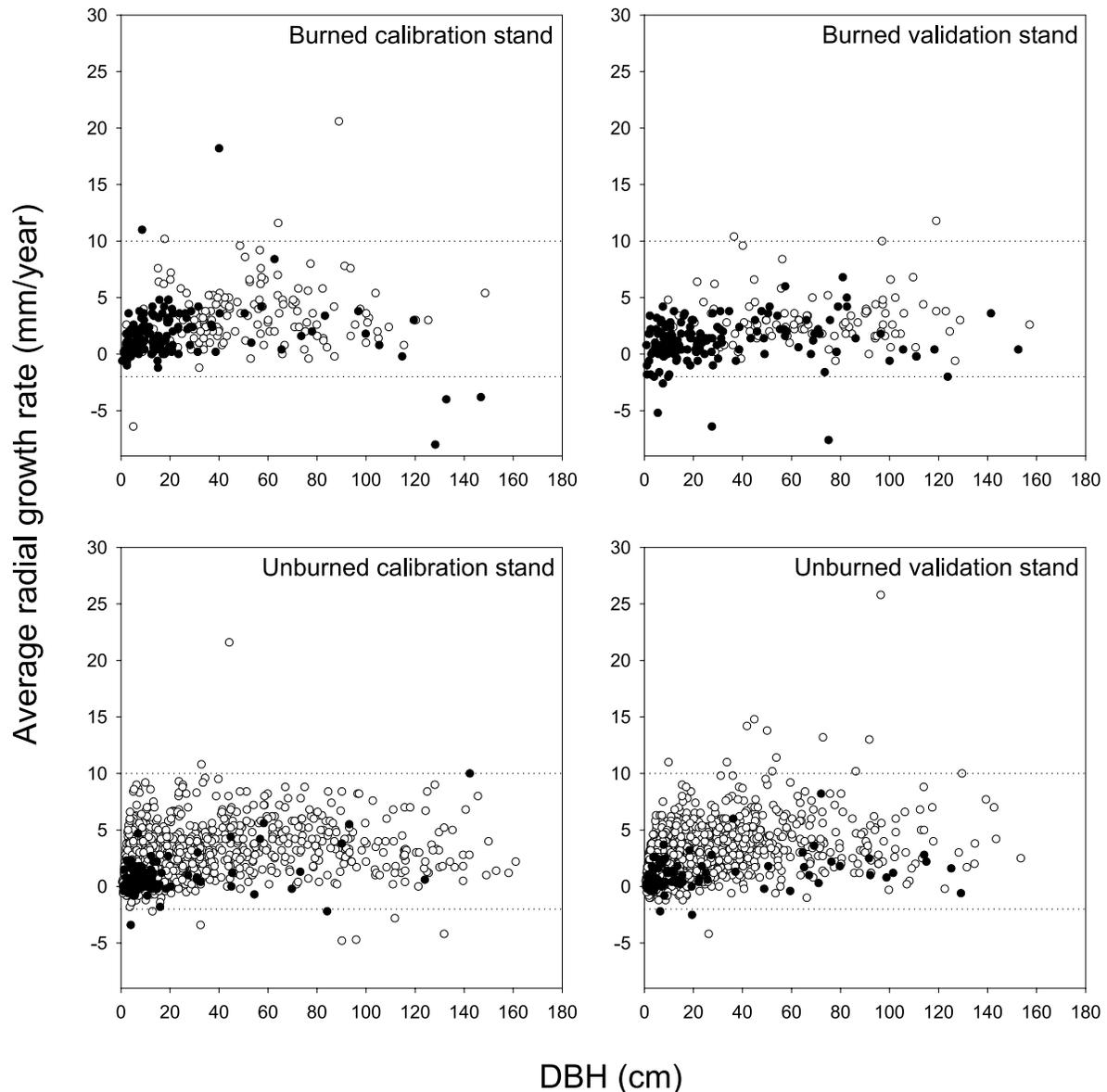
High probabilities of mortality were clearly associated with low radial growth rates for *A. concolor* in the unburned calibration stand (Table 2). We found that the logits of each of the independent variables were linear in relation to the predicted probability of mortality. The best fit model for the unburned calibration stand was a univariate model using growth rate as the single predictor variable (log likelihood of constants only model = –316.8; log likelihood of univariate DBH model = –310.7; log likelihood of univariate GR model = –282.6). We used parameters for both GR and DBH during our initial model formulation, but the term for DBH did not explain sufficient amounts of additional variation ($G = 0.6$, df = 1, $p = 0.44$) and was dropped from our final model. The univariate model using GR appeared to fit the data reasonably well, as indicated by a nonsignificant result

for the Hosmer–Lemeshow test (Table 2). This model also had a satisfactory level of discrimination (Table 2). We found the cutpoint of 0.11 (i.e., trees are classified as live or dead when $P(m) < 0.11$ and $P(m) \geq 0.11$, respectively) to maximize specificity and sensitivity when comparing the results against the data used to create the model (specificity = 0.73; sensitivity = 0.66).

High probabilities of mortality in the burned calibration stand were strongly associated with high levels of crown scorch (Table 2). The logit of crown scorch parameter appeared to be linear with respect to the predicted probability of mortality. We also found the logits of GR and DBH to be linear. The univariate model of PCVS explained far more variation compared with univariate models using GR or DBH (log likelihood of constants only model = –316.8; log

Fig. 3. Percent crown volume scorched (PCVS), an index of fire-caused crown damage, for *Abies concolor* in the (*a*) burned calibration stand and (*b*) burned validation stand.

vided an adequate fit to the data (Table 2). Model discrimination was extremely high, with an area under the ROC curve of 0.96. We found the optimal cutpoint for model classification to be 0.40 (i.e., trees are classified as live or dead when $P(m) < 0.40$ and $P(m) \geq 0.40$, respectively), which resulted in a specificity of 0.92 and a sensitivity of 0.88. Although both predictor variables are significant, crown scorch was a superior predictor of postfire mortality (Table 2).

Figure 4 graphically summarizes the best-fit models for both the burned and unburned calibration stands. In the unburned stand, there is a steep decline in the probability of mortality with increasing growth rates, essentially reaching zero at average growth rates of approximately 6.0 mm·year^{-1}. The response of trees in the burned calibration stand roughly follows the same pattern, although there is generally a lower tolerance of slow growth, and the response to declining growth is less steep. Postfire mortality rates increase sharply with increasing levels of crown scorch, but this response is modified by differences in growth rate. Trees growing faster than 5.0 mm·year^{-1} appear to be relatively resistant to losing over half of their crown volume, while slowly growing trees (<5.0 mm·year^{-1}) generally die when challenged with this level of fire-caused damage.

In spite of the visual similarities, the following exercise illustrates that the burned and unburned models predict different responses to growth rate. The data sets for the burned and unburned calibration stands were combined and analyzed as described above, but with the inclusion of a dummy variable to indicate stand identity (0 = unburned, 1 = burned). The coefficients for PCVS and GR were statistically significant ($p < 0.0001$), as was the interaction term for GR and stand identity ($p = 0.025$). No other main effects or interaction terms were significant. Thus, the growth–mortality relationship appears to change for *A. concolor* when burned.

The high frequency of extremely severe crown scorch in our data set may have biased our model against finding a more important role for growth rate as a predictor of postfire mortality. For this reason, we reanalyzed the data, removing trees that had extreme levels of crown scorch (>90 PCVS) or exceeded the average amount of crown scorch (>50 PCVS). The significance of radial growth rate as a predictor of mortality became relatively greater as the number of heavily scorched trees in the data set was progressively restricted (Table 3).

Assessments of model fit using validation data sets show the models to be accurate. The unburned calibration model supplied a reasonable fit to the unburned validation data. A Hosmer–Lemeshow test revealed a good overall fit, and ROC curve analysis showed an acceptable level of discrimination (Table 4). Classifications using a cutpoint of 0.11 resulted in a relatively poor ability to predict tree death. The model for the burned calibration stand was also generally correct when applied to the burned validation stand. The high frequency of extreme values for crown scorch in the burned validation data set prevented us from creating more than five groups with a sufficient number of expected observations for both live and dead trees. We were therefore unable to meet the assumptions for the Hosmer–Lemeshow goodness-of-fit test, and this statistic was not calculated. The burned calibration model, however, was able to correctly discriminate between live and dead trees in the burned valida-

likelihood of univariate PCVS model = –98.2; log likelihood of univariate GR model = –222.3; log likelihood of univariate DBH model = –192.9). The univariate PCVS model was statistically significant ($G = 305.9$, df = 1, $p < 0.0001$); however, the Hosmer–Lemeshow test showed that this model did not fit the data at an acceptable level (H–L = 11.9, df = 5, $p = 0.036$). Regression diagnostics showed cases with the largest residuals to be (*i*) live trees with high levels of crown scorch and high growth rates or (*ii*) dead trees with low crown scorch and low growth rates.

Multiple logistic regression models showed growth rate to explain a significant additional amount of variation (univariate PCVS model vs. PCVS and GR models: $G = 10.6$, df = 1, $p = 0.001$). Including an interaction term for these variables did not improve the explanatory power of the model. Stem diameter failed to explain sizeable amounts of variation when modeled with crown scorch (univariate PCVS model vs. PCVS and DBH models: $G = 0.1$, df = 1, $p = 0.75$) or when modeled in conjunction with crown scorch and growth rate (PCVS and GR models vs. PCVS, GR, and DBH models: $G = 0.0001$, df = 1, $p = 0.99$). According to the Hosmer–Lemeshow test, our best fit model, which contained only crown scorch and growth rate, pro-

Table 2. Best fit logistic regression models predicting *Abies concolor* mortality in the unburned calibration and burned calibration stands.

Data type	n		Estimated coefficients				G^a	H–L^b	ROC area
	Live	Dead	β_0 (constant)	β_1 (GR)	β_2 (PCVS)	β_3 (DBH)			
Unburned calibration	1107	89	−1.52 (0.15)	−0.60 (0.09)	na	ns	<0.0001	0.26	0.77
Burned calibration	150	224	−1.18 (0.33)	−0.31 (0.10)	0.06 (0.01)	ns	<0.0001	0.70	0.96

Note: Parameter estimates are presented with standard errors in parentheses. β_0, the constant; β_i, model coefficients estimated from the data; GR, growth rate; PCVS, percent crown volume scorch; DBH, diameter at breast height; ROC area, area under the receiver operating characteristic curve; na, not applicable; ns, not significant at $p < 0.05$.

[a]p values for the G statistic of the likelihood ratio test. Unburned calibration model: df = 1; burned calibration model: df = 2.

[b]p values for the Hosmer–Lemeshow goodness-of-fit statistic (see text). Unburned calibration model: df = 8; burned calibration model: df = 5.

Fig. 4. *Abies concolor* postfire mortality as predicted by both percent crown volume scorched (PCVS) and preburn average radial growth rate (GR) in the burned calibration stand. The solid line represents mortality predicted by growth rate in the unburned calibration stand.
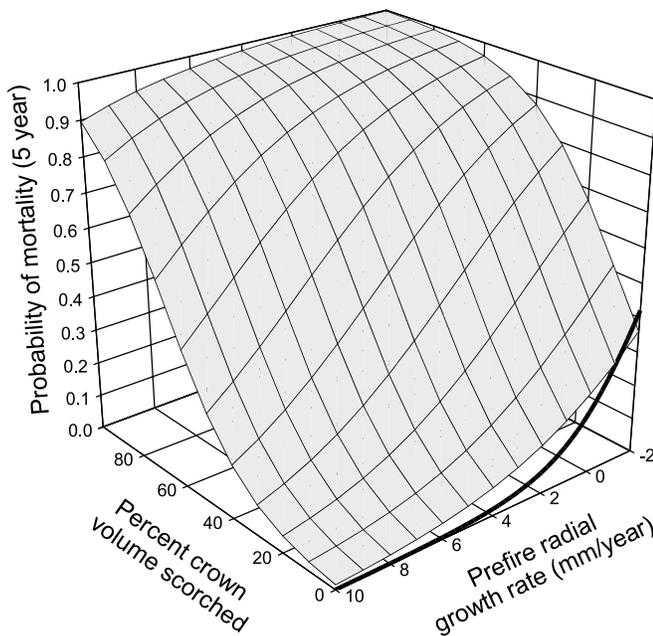
tion stand for the majority of cases (area under the ROC curve = 0.94; classifications with a cutpoint of 0.40: number of false positives = 36; number of false negatives = 7; number of correct classifications = 271).

The burned calibration model did not provide a reasonably accurate prediction of *A. concolor* mortality in the unburned validation stand (Table 4). The burned model overpredicted mortality, resulting in a poor overall model fit and high rates of false positive responses (type I errors). There were enough data from the burned calibration stand to create an additional model using only lightly scorched trees (0–15 PCVS), using both crown scorch and radial growth to predict mortality. When applied to the unburned calibration stand data, this model still did not fit the data adequately but did produce a much reduced level of type I errors (Table 4).

Discussion

Our key finding is that growth rate can be used to predict mortality of *A. concolor* in both burned and unburned stands. This result is significant because it provides an un-

derstanding of the tree mortality process regardless of the recent history of disturbance. Mortality in unburned stands is often viewed as related to long-term stress, typically predicted by some index of tree vigor. In contrast, mortality in disturbed stands is usually understood in terms of short-term damage directly caused by the disturbance. Our data suggest that the mortality processes in both disturbed and undisturbed stands are not fundamentally different but can be conceptually unified under the "decline spiral" model. Our demonstration that prefire growth rate supplies information useful for predicting postfire mortality is simply an application of the decline spiral model in a novel context. Specifically, our results imply that trees already experiencing long-term stress, as measured by low radial growth rates, have higher mortality probabilities when challenged with additional fire-related damage. Although the decline spiral model of tree death is intuitive, empirical demonstrations of it are rare (see Pedersen 1998*b*). An interesting implication of our findings is that various stressors could lead to de facto increases in fire severity without corresponding increases in fire intensity. For example, if air pollution caused a decline in growth rate in a significant proportion of a population of susceptible trees (Peterson and Arbaugh 1992), any given fire can be expected to kill more trees than it would in the absence of air pollution. In other words, the stressors may interact, with air pollution predisposing trees to being killed by fire.

Mutch and Parsons (1998) and Stephens and Finney (2002) have proposed models for fire-caused mortality for *A. concolor* that conform to the general findings about fire-related mortality for other conifers (e.g., Ryan and Reinhardt 1988). Mortality probabilities were found to increase sharply with greater amounts of crown scorch, with the mortality response becoming attenuated in large-diameter trees. Our findings confirm the earlier results concerning the relationship between crown scorch and mortality but do not find a significant role for stem diameter. Our data appear to indicate that growth rate, instead of stem diameter, is better able to account for unexplained variation when predicting mortality using crown scorch severity. This result was surprising, because stem diameter is correlated to important fire defenses such as bark thickness and crown height. *Abies concolor* has characteristically thin bark (van Mantgem and Schwartz 2003), perhaps making it difficult to find an important role for stem diameter. The relationship between growth rate and probability of postfire death may be at least partly mediated through the absolute amount of tree crown remaining after a fire, and hence, the tree's capacity to fix carbon. For a given size of tree, slowly growing trees are

Table 3. Models predicting postfire *Abies concolor* mortality using data with pro-
gressively restricted amounts of crown scorch severity.

PCVS range	Predictor variable	Estimate	SE	Estimate/SE
0–100	β_0 (constant)	–1.18	0.33	–3.60
	β_1 (GR)	–0.31	0.10	–3.08
	β_2 (PCVS)	0.06	0.01	9.18
0–90	β_0 (constant)	–1.15	0.32	–3.54
	β_1 (GR)	–0.28	0.10	–2.84
	β_2 (PCVS)	0.05	0.01	6.62
0–50	β_0 (constant)	–1.31	0.36	–3.67
	β_1 (GR)	–0.27	0.11	–2.50
	β_2 (PCVS)	0.07	0.02	4.76

Note: The models use average annual prefire radial growth rate (GR) and percent crown
volume scorch (PCVS) to predict mortality probabilities. The value of each parameter divided by
its standard error (Estimate/SE) gives an approximate *t* statistic used to determine the
significance of the individual coefficients. All coefficients are significant at $p < 0.05$.

Table 4. Logistic model classifications for *Abies concolor* when applying the calibration models to the unburned validation stand data.

Model	PCVS data range	H–L	Live Correct	Live Errors	Dead Correct	Dead Errors	Correct live	Correct dead	ROC area
Unburned calibration	na	8.14[a]	1101	234	54	37	0.825	0.593	0.75
Burned calibration	0–100	83.49[b]	474	861	85	6	0.355	0.934	0.65
Burned calibration	0–15	37.09[c]	729	606	74	17	0.546	0.813	0.76

Note: We performed a second iteration of the model for the burned stand using only lightly scorched trees (0–15 PCVS). All classifications were based
on a cutoff point found to be optimal for the unburned calibration model; trees were therefore classified as alive if $P(m) < 0.11$, and dead if $P(m) \geq 0.11$
(see text). Correct responses are agreements between the observed data and the model classifications. PCVS, percentage crown volume scorch; H–L,
Hosmer–Lemeshow goodness-of-fit statistic; ROC area, area under the receiver operating characteristic curve; na, not applicable.
[a]df = 8, $p = 0.42$.
[b]df = 8, $p < 0.001$.
[c]df = 8, $p < 0.001$.

more likely to have a sparser crown and lower total leaf area
than rapidly growing trees. Thus, 50% crown scorch on a
slowly growing tree would leave that tree with much less
total photosynthetic leaf area than the same percentage of
crown scorch on a rapidly growing tree. Unfortunately, we
had no estimates of absolute prefire crown volume, and thus,
could not test this possibility.

Forest "gap" models exploit the relationship between
growth and death to drive stand-level changes, although it is
becoming increasingly clear that the simple algorithm used
by these models is unrealistic (Keane et al. 2001). Variation
among species in shade tolerance and differences in the
causal agent of death have been shown to alter the shape of
the growth–mortality function in undisturbed stands (Kobe
et al. 1995; Kobe and Coates 1997; Wyckoff and Clark
2000; N.L. Stephenson, unpublished data). Our results also
suggest that for *A. concolor*, fire can alter the association be-
tween growth and mortality. Specifically, we were able to
detect significant differences in the way that growth is re-
lated to mortality between burned and unburned stands. We
were also able to detect some differences in the relative im-
portance of growth rate as a predictor of postfire mortality
with varying levels of fire-caused damage. Additional differ-
ences in the relationship between growth and postfire mor-
tality will also likely arise when considering other species.
Abies concolor is shade tolerant (Laake 1990) and may not
reflect stress in terms of slow growth as dramatically as
other species. We suspect that slow growth rates may be a

more sensitive predictor of postfire mortality for shade-
intolerant species. Assessing how mortality predictors vary
across disturbance severities, sites, and species is an impor-
tant avenue for future research.

The complex relationships among growth, fire-caused
damage, and mortality highlight the difficulties in creating a
general model of tree death. Indeed, when we applied our
model of burned *A. concolor* to an unburned stand, we con-
sistently overpredicted mortality rates and failed to repro-
duce the steep drop in mortality probabilities with increasing
growth rates. As discussed above, fire may have altered the
association between growth and mortality. Trees became in-
creasingly sensitive to low growth when further challenged
with fire-caused injuries, which could imply a requirement
for superior carbon balances when faced with the need to
recover from crown loss. Alternately, other stressors (e.g.,
cambial damage, increased postfire pathogen load) may have
supplied additional stress to the trees beyond what was mea-
sured by radial growth and crown scorch severity.

On a practical level, the collection of growth rate data
may be of particular interest when trying to anticipate the ef-
fects of accelerated mortality rates in a postfire environment
(e.g., protecting old-growth trees in a prescribed burn). In-
formation concerning tree vigor may also be useful in the
context of salvage logging operations, where a high degree
of precision is desired. It has been difficult, however, to gen-
eralize the results of these models, because there have been
few attempts to describe the process of postfire mortality in

a comprehensive manner. A more mechanistic description of fire-caused mortality would include measures of the prefire physiological status of a tree, severity of fire-caused damage, and an account of the effects of the damage on postfire carbon gain.

Acknowledgements

References

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

Bragg, D.C. 2001. Potential relative increment (PRI): a new method to empirically derive optimal tree diameter growth. Ecol. Model. **137**: 77–92.

Buchman, R.G., Pederson, S.P., and Walters, N.R. 1983. A tree survival model with application to species of the Great Lakes region. Can. J. For. Res. **13**: 601–608.

Clark, D.A. 2002. Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. Ecol. Appl. **12**: 3–7.

Clark, D.A., and Clark, D.B. 1999. Assessing the growth of tropical rain forest trees: issues for forest modeling and management. Ecol. Appl. **9**: 981–997.

Dobbertin, M., and Brang, P. 2001. Crown defoliation improves tree mortality models. For. Ecol. Manage. **141**: 271–284.

Franklin, J.F., Shugart, H.H., and Harmon, M.E. 1987. Tree death as an ecological process. BioScience, **37**: 550–556.

Givnish, T.J. 1988. Adaptation to sun and shade: a whole plant perspective. Aust. J. Plant Physiol. **15**: 63–92.

Haggerty, P. 1990. Final report on the Tharp's research burn. Unpublished report to Sequoia and Kings Canyon national parks, California.

Hedden, R.L., Fredericksen, T.S., and Williams, S.A. 1995. Modeling the effect of crown shedding and streamlining on the survival of loblolly pine exposed to acute wind. Can. J. For. Res. **25**: 704–712.

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

Huntington, G.L., and Akeson, M.A. 1987. Soil resource inventory of Sequoia National Park, Central Part, California. Final contract report to the National Park Service.

Keane, R.E., Austin, M., Field, C., Huth, A., Lexer, M.J., Peters, D., Solomon, A., and Wyckoff, P. 2001. Tree mortality in gap models: application to climate change. Clim. Change, **51**: 509–540.

Keen, F.P. 1943. Ponderosa pine tree classes redefined. J. For. **41**: 249–253.

Kobe, R.K., and Coates, K.D. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. Can. J. For. Res. **27**: 227–236.

Kobe, R.K., Pacala, S.W., Silander, J.A., and Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol. Appl. **5**: 517–532.

Laake, R.J. 1990. *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. White fir. *In* Silvics of North America. *Edited by* R.M. Burns and B.H. Honkala. U.S. Dep. Agric. Agric. Handb. 654. pp. 36–46.

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.

Pedersen, B.S. 1998*a*. Modeling tree mortality in response to short- and long-term environmental stresses. Ecol. Model. **105**: 347–351.

Pedersen, B.S. 1998*b*. The role of stress in the mortality of Midwestern oaks as indicated by growth prior to death. Ecology, **79**: 79–93.

Peet, R.K., and Christensen, N.L. 1987. Competition and tree death. BioScience, **37**: 586–594.

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 Arbaugh, M.J. 1992. Mixed conifer forests of the Sierra Nevada. *In* The response of western forests to air pollution. Ecol. Stud. 97. pp. 433–459.

Peterson, D.L., and Ryan, K.C. 1985. Modeling post-fire conifer mortality for long-range planning. Environ. Manage. **10**: 797–808.

Phillips, O.L., Malhi, Y., Vinceti, B., Baker, T., Lewis, S.L., Higuchi, N., Laurance, W.F., Núñez Vargas, P., Vásquez Martinez, R., Laurance, S., Ferreira, L.V., Stern, M., Brown, S., and Grace, J. 2002. Changes in growth of tropical forests: evaluating potential biases. Ecol. Appl. **12**: 576–587.

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

Ruel, J. 2000. Factors influencing windthrow in balsam fir forests: from landscape studies to individual tree studies. For. Ecol. Manage. **135**: 169–178.

Rundel, P.W., Parsons, D.J., and Gordon, D.T. 1977. Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. *In* Terrestrial vegetation of California. *Edited by* M.G. Barbour and J. Major. John Wiley & Sons, New York. pp. 559–600.

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.

Saveland, J.M., and Neuenschwander, L.F. 1990. A signal detection framework to evaluate models of tree mortality following fire damage. For. Sci. **36**: 66–76.

Steinman, J.R., and Maclean, D.A. 1994. Predicting effects of defoliation on spruce–fir stand development: a management-oriented growth and yield model. For. Ecol. Manage. **69**: 283–298.

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. 1988. Climatic control of vegetation distribution: the role of the water-balance with examples from North America and Sequoia National Park, California. Ph.D. dissertation, Cornell University, Ithaca, New York.

Stephenson, N.L., and Demetry, A. 1995. Estimating ages of giant sequoias. Can. J. For. Res. **25**: 223–233.

Swetnam, T.W., Baisan, C.H., Caprio, A.C., Touchan, R., and Brown, P.M. 1992. Tree-ring reconstruction of giant sequoia fire regimes. Final report on Cooperative Agreement 8018-1-0002 to USDI National Park Service, Sequoia and Kings Canyon national parks, California, U.S.A.

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.

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**(3). In press.

Van Wagner, C.E. 1973. Height of crown scorch in forest fires. Can. J. For. Res. **3**: 373–378.

Volney, W.J. 1998. Ten-year tree mortality following a jack pine budworm outbreak in Saskatchewan. Can. J. For. Res. **28**: 1784–1793.

Wagener, W.W. 1961. Guidelines for estimating the survival of fire-damaged trees in California. USDA Forest Service, California Range and Experiment Station, Berkeley, California. Misc. Pap. 60.

Waring, R.H. 1987. Characteristics of trees predisposed to die. BioScience, **37**: 569–574.

Wyant, J.G., Omi, P.N., and Laven, R.D. 1986. Fire induced tree mortality in a Colorado (U.S.A.) ponderosa pine [*Pinus ponderosa*] and Douglas-fir [*Pseudotsuga menziesii*] stand. For. Sci. **32**: 49–59.

Wyckoff, P.H., and Clark, J.S. 2000. Predicting tree mortality from diameter growth: a comparison of maximum likelihood and Bayesian approaches. Can. J. For. Res. **30**: 156–167.