

The relationship between tree growth patterns and likelihood of mortality: a study of two tree species in the Sierra Nevada

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Abstract: We examined mortality of *Abies concolor* (Gord. & Glend.) Lindl. (white fir) and *Pinus lambertiana* Dougl. (sugar pine) by developing logistic models using three growth indices obtained from tree rings: average growth, growth trend, and count of abrupt growth declines. For *P. lambertiana*, models with average growth, growth trend, and count of abrupt declines improved overall prediction (78.6% dead trees correctly classified, 83.7% live trees correctly classified) compared with a model with average recent growth alone (69.6% dead trees correctly classified, 67.3% live trees correctly classified). For *A. concolor*, counts of abrupt declines and longer time intervals improved overall classification (trees with DBH ≥ 20 cm: 78.9% dead trees correctly classified and 76.7% live trees correctly classified vs. 64.9% dead trees correctly classified and 77.9% live trees correctly classified; trees with DBH < 20 cm: 71.6% dead trees correctly classified and 71.0% live trees correctly classified vs. 67.2% dead trees correctly classified and 66.7% live trees correctly classified). In general, count of abrupt declines improved live-tree classification. External validation of *A. concolor* models showed that they functioned well at stands not used in model development, and the development of size-specific models demonstrated important differences in mortality risk between understory and canopy trees. Population-level mortality-risk models were developed for *A. concolor* and generated realistic mortality rates at two sites. Our results support the contention that a more comprehensive use of the growth record yields a more robust assessment of mortality risk.

Résumé : Nous avons étudié la mortalité chez *Abies concolor* (Gord. & Glend.) Lindl. et *Pinus lambertiana* Dougl. en élaborant des modèles logistiques à l'aide de trois indices de croissance obtenus à partir des cernes annuels : la croissance moyenne, la tendance de la croissance et le dénombrement des diminutions abruptes de croissance. Dans le cas de *P. lambertiana*, les modèles qui incorporent la croissance moyenne, la tendance de la croissance et le dénombrement des diminutions abruptes de croissance ont globalement amélioré les prédictions (78,6 % des arbres morts et 83,7 % des arbres vivants ont été correctement classifiés) comparativement à la croissance moyenne récente seule (69,6 % des arbres morts et 67,3 % des arbres vivants ont été correctement classifiés). Dans le cas de *A. concolor*, le dénombrement des diminutions abruptes de croissance et l'utilisation d'intervalles de temps plus long ont globalement amélioré la classification des arbres avec un DHP ≥ 20 cm (78,9 % des arbres morts et 76,7 % des arbres vivants vs. 64,9 % des arbres morts et 77,9 % des arbres vivants ont été correctement classifiés) et des arbres avec un DHP < 20 cm (71,6 % des arbres morts et 71,0 % des arbres vivants vs 67,2 % des arbres morts et 66,7 % des arbres vivants ont été correctement classifiés). En général, les diminutions abruptes de croissance ont amélioré la classification des arbres vivants. Une validation externe des modèles pour *A. concolor* a montré qu'ils fonctionnent bien dans des peuplements qui n'ont pas été utilisés pour élaborer le modèle. L'élaboration de modèles propres à différentes dimensions a mis en évidence d'importantes différences dans le risque de mortalité entre les arbres de la canopée et ceux du sous-bois. Des modèles de risque de mortalité à l'échelle de la population ont été élaborés pour *A. concolor* et ces modèles ont généré des taux de mortalité réalistes dans deux stations. Nos résultats supportent l'assertion voulant qu'une utilisation plus poussée des données de croissance permette d'obtenir une évaluation plus robuste du risque de mortalité.

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Introduction

Forests today face a suite of novel stressors, including attack by exotic pests, fire suppression, land-use alteration, climate change, and air pollution (Liebhold et al. 1995;

Vitousek et al. 1997; Miller and Urban 2000; Lenihan et al. 2003). If we are to understand how forests will change, we must improve our understanding of how the trees within them die. Yet one of the most difficult challenges in the study of long-lived organisms is quantifying the process

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that leads to their mortality. In the case of tree death, typical approaches to modeling individual mortality have often focused on short-term measures such as average recent growth, usually taking into account no more than 5 years of growth (e.g., Pacala et al. 1996; Keane et al. 2001; Bigler and Bugmann 2004). Although several studies have documented a relationship between longer term growth characteristics and tree decline (Phipps and Whiton 1988; Leblanc 1990; Pedersen 1998b; Ogle et al. 2000; Cherubini et al. 2002; Duchesne et al. 2002, 2003; Suarez et al. 2004), relatively few attempts have been made to incorporate these characteristics when modeling the probability of mortality (Bigler and Bugmann 2003, 2004; Bigler et al. 2004).

The idea that tree death can be the result of a life-long accumulation of injuries (*sensu* Mangel and Bonsall 2004) was implicit in Franklin et al.'s (1987) landmark paper. They presented a conceptual model based on Manion's (1981) disease spiral to characterize the events that eventually lead to the demise of a tree. The key insight was that past events that reduce vigor increase future susceptibility to mortality agents. These mortality agents, which can include competition, biotic attack, and environmental stress, contribute either independently or synergistically to the death of a tree (Franklin et al. 1987; Keane et al. 2001).

In a broad sense, then, mortality can be conceptualized as a cumulative process (Anderson 2000) where the events that occur over the lifetime of an organism influence its likelihood of survival (Mangel and Bonsall 2004). Temperate-zone trees are particularly amenable to such an approach, as many species record a detailed history of these life events in their annual growth rings. A given tree's growth, then, can be understood as an integrated measure of the physiological realities that contribute to its likelihood of survival (Kyto et al. 1996).

Our goal in this study was to quantify aspects of the tree-ring record that provide reliable indicators of future mortality. We incorporated the concept of a cumulative mortality process by examining not only growth over time but also *changes* in growth over time. In this sense we defined the "cumulative" approach as one that takes into account additional aspects of the growth record to help specify the likelihood of mortality. We explicitly evaluated whether additional aspects of the growth record might give a more accurate assessment of a tree's health than a 5 year snapshot.

Several studies using average recent growth have demonstrated that slow growth is correlated with risk of mortality (e.g., Kobe et al. 1995; Yao et al. 2001). However, more information might be contained in the growth record. For example, Pedersen (1998b) showed that events leading to mortality often occur two decades before actual death and are characterized by abrupt growth decreases rather than just slow growth. Furthermore, Bigler and Bugmann (2003) demonstrated that the addition of a linear growth trend can significantly improve prediction.

In this study, we built general predictive models of tree mortality that combined measures of average growth, growth trend, and abrupt growth decreases to examine the relationship between a tree's growth history and probability of mortality. While Pedersen (1998b) was the first to demonstrate that the inclusion of terms that model abrupt decreases in

growth significantly improved mortality models for Mid-western oaks, his analysis only examined growth decreases in years that were identified as being more environmentally stressful than average. This approach detected stressful periods for all the trees in a stand but did not allow for nonclimatic or local stresses that a given tree might be experiencing. Bigler and Bugmann (2003) were specifically interested in trees that had died as a result of competition, so their study design intentionally avoided trees that showed obvious signs of attack by strong pathogens or insects. These exclusions limit the generality of their study, given the importance of insects and pathogens in many ecosystems (Waters et al. 1985; Schowalter and Filip 1993; Hansen and Goheen 2000; Maloney and Rizzo 2002).

In contrast, we did not screen the tree-ring record for stressful years, nor did we exclude certain causes of mortality. Instead, we evaluated the ability of a suite of growth measures, individually and in combination, to predict the probability of all forms of mortality. Moreover, we compared these models of mortality for two species of trees that share habitat but have different life-history characteristics. Our contention was that if tree death is a cumulative process, then the cumulative record of growth would be a superior predictor of mortality regardless of the specific circumstances of an individual population or species.

Materials and methods

We developed mortality models for two common conifer species in the Sierra Nevada of California: *Pinus lambertiana* Dougl. (sugar pine) and *Abies concolor* (Gord. & Glend.) Lindl. (white fir). *Pinus lambertiana* is a moderately tolerant gap-adapted species and *A. concolor* is a late-successional shade-tolerant species (Burns and Honkala 1990). These two species also provided different population trajectories in modern Sierran forests. With fire suppression, *A. concolor* has become an increasingly dominant species in the mixed-conifer forest, while *P. lambertiana*, because of a host of factors, has been declining in importance (Kinloch and Dulitz 1990; Ansley and Battles 1998; van Mantgem et al. 2004).

Site

The study sites were located in the mixed-conifer forest in Sequoia National Park (118°35'W, 36° 35'N) on the western slope of the Sierra Nevada at an elevation of approximately 2000 m. Soils are generally coarse loams derived from granitic parent material. Annual precipitation averages 1200 mm/year, with most falling between December and March (35%–65% as snow). Mean January temperature is 0 °C, while mean July temperature is 17 °C. The sites had never been logged, and had not experienced any stand-replacing disturbances in several centuries. Before Euro-American settlement, low- to moderate-intensity surface fires were common, with the mean fire-return interval at a nearby site reported at 7 years (Caprio and Swetnam 1993).

The forests are dominated by a mix of *A. concolor*, *Abies magnifica* A. Murr. (California red fir), *Calocedrus decurrens* (Torr.) Florin (incense cedar), and *P. lambertiana*. In addition, some areas contain significant numbers of *Sequoiadendron giganteum* (Lindl.) Buchh. (giant sequoia). *Abies concolor* consitutes 30%–75% of stand density and

33%–56% of stand basal area. *Pinus lambertiana* constitutes 0.5%–7% of stand density and 2%–20% of stand basal area.

Model construction was based on data from a 3.375 ha permanent vegetation plot sited along Suwanee Creek that was established in 1982 and 1983 following the methods of Riegel et al. (1988). All living trees taller than 1.37 m were mapped and tagged and their diameters were measured at breast height (1.37 m). Trees were checked annually for mortality. At 5 year intervals, tree diameters were remeasured and newly established trees were mapped and measured.

Data from two other stands located in Sequoia National Park were used to validate the *A. concolor* models. We were unable to obtain an adequate second sample of *P. lambertiana*, owing to its relative scarcity. The first site contained plots totaling 6.625 ha located along Log Creek, ranging from 2100 to 2200 m in elevation. In terms of design and monitoring, these plots were identical with those at Suwanee Creek. This site was used for validation and for estimating mortality rates (see below). The second site was a true fir forest located near Clover Creek at an elevation of 2150 m. In 1992, a 1 ha plot was logged at the site to provide space for a new hotel. This site was used for estimating mortality rates (see below). All three sites were located between 4 and 7 km from one another.

Sampling design and data collection

Field assessments of newly dead *P. lambertiana* and *A. concolor* encountered during the annual censuses at the Suwanee Creek plot indicated that trees of both species died from a variety of proximate factors ranging from apparent competitive stress (i.e., no obvious biotic/mechanical factors) to mechanical mortality (e.g., windthrow, crushing) to attack by pathogens or insects. Given that the availability of recently dead trees was the limiting factor, we used a case-control research design for model development (Schleselman and Stolley 1982), where the dead trees served as cases and a matching set of live trees was collected as a control. This contrasts with a cohort study in which an entire population would be followed and the ratio of live and dead trees would be representative of actual mortality rates.

At the Suwanee Creek and Log Creek sites, we sampled dead trees and then matched them to live trees in terms of species and approximate size. Specifically, we collected increment cores for all dead trees with DBH over 20 cm that had died since plot establishment and for which an intact core could be obtained. For trees less than 20 cm, samples were collected from trees that had died in the last 5 years (2002–1998), as smaller trees were less likely to remain intact over time. Note that all trees that had reached 1.37 m in height before mortality were eligible for sampling. To avoid damaging live trees in the long-term vegetation plots, increment cores for the live tree sample were collected outside each plot. All live trees in a narrow band around the plot perimeter were sampled and then additional trees were collected in widening concentric bands until a given species and size class was adequately represented (i.e., enough live trees of each species and size were sampled to at least match the dead-tree sample). This procedure resulted in more live than dead trees in some size classes.

All cores were collected on the sides of the tree parallel to

the slope of the plot, generally below 1 m height and above any basal swell. For live trees greater than 60 cm DBH, two samples were collected from opposite sides of the tree. The two cores from the larger trees were used for developing the master chronology for the species at the site. For all other trees, we ensured that at least one good core was obtained.

At Clover Creek, basal stem sections of live trees were collected in conjunction with the logging operation. Samples were collected from all live trees with a DBH greater than 25 cm over the whole plot and from all live trees greater than 20 cm in height in nested subplots (the approximate total area subsampled was 0.4 ha). No dead-tree samples were available for this plot.

Cores were sanded until individual cells were visible under magnification. Tree rings were then measured to 0.01 mm using a dissecting microscope and a sliding-stage micrometer. Master chronologies were built for each species using all live trees greater than 60 cm DBH with the aid of the computer program COFECHA[®] (Grissino-Mayer 2001). Errors (missing or false rings) in the remaining cores were then identified by comparing them against the chronology using COFECHA[®] (Grissino-Mayer 2001). Corrections were made after errors were confirmed by visual inspection of the core. This check was done for all cores that could be cross-dated. The vast majority of corrections were for missing rings, and dead trees were far more prone to this problem. Thus, an inability to cross-date certain samples should generally have resulted in conservative errors, i.e., an overestimate of growth in the dead-tree sample. Therefore, cores were not excluded on the basis of an inability to cross-date, to avoid a bias against trees with strong ecological signals in their growth record.

We only used cores with at least 40 years of growth to enable comparison between models (see below). Our sampling design and data criteria produced 253 *P. lambertiana* (123 live, 130 dead) and 180 *A. concolor* (101 live, 79 dead) records for Suwanee Creek, 279 (155 live, 124 dead) *A. concolor* records for Log Creek, and 185 live *A. concolor* records for Clover Creek.

Growth index calculations

We calculated all growth indices using absolute annual radial increment. Other measures were considered and tested, including basal area increment and relative basal area increment (basal area increment/total initial tree basal area). For our data, however, we found radial growth to be the best metric (see Appendix A).

We identified three growth indices that have proven to be important for predicting mortality: average growth (Kobe et al. 1995; Yao et al. 2001), growth trend (Bigler and Bugmann 2003), and frequency of abrupt annual growth declines (Pedersen 1998b). For each sample, we calculated these indices at 5 year intervals from 5 to 40 years of age. Average growth was calculated as the mean ring width for the time interval (average growth for the last 5 years, 10 years, etc.); growth trend was calculated as the linear rate of increase or decrease in ring width for the given time interval; and abrupt growth declines were counted for a given time interval.

Based on the literature (Schweingruber 1985, 1986; Innes 1993; Pedersen 1998b) and preliminary analyses, we defined

abrupt growth declines as year-to-year growth rate decreases of more than 50% — a shift of about 1 standard deviation from the mean of all year-to-year growth rate changes (mean = 7%, SD = 46%, excluding large outliers). To avoid including large relative changes in an otherwise slow-growing tree, abrupt declines represented at least a 0.05 mm change in growth.

In addition to the growth indices calculated above, we also included one size-related design variable in our models. Although we did not see the typical negative exponential growth bias in the growth behavior of small versus large live trees for our data set (Appendix A), the possibility remained that mortality processes varied in nature across size classes (e.g., Pacala et al. 1996). We defined our size variable from the observed relationship between tree size and canopy position. For these plots, the vast majority of trees below 20 cm DBH were classified as subcanopy, while the vast majority above 20 cm DBH were classified as intermediate, codominant, or dominant. Therefore, we generated the size variable, where size = 1 for trees with DBH less than 20 cm and size = 0 for trees with DBH 20 cm or more. Ultimately, the size variable was only used for *P. lambertiana*, as separate *A. concolor* models were built for each size category (see below).

Model development

For *P. lambertiana* we randomly split the data from Suwanee Creek into parameterization ($n = 155$; 77 live, 78 dead) and internal-validation ($n = 105$; 49 live, 56 dead) sets. Only the parameterization set was used for model building. For *A. concolor* the Suwanee Creek data were used for model building and the Log Creek data for validation. Furthermore, as preliminary analysis showed that size was an important factor for *A. concolor* (see Appendix B), models were built separately for trees with DBH 20 cm or more (61 live, 45 dead in the model set; 86 live, 57 dead in the validation set) and for trees with DBH less than 20 cm (45 live and 36 dead in the model set; 69 live and 67 dead in the validation set). Tree-diameter distributions were consistent between model and validation (both external and internal) sets (Fig. 1).

Survival probability was modeled using the logistic function

$$[1] \quad \pi(x) = \frac{e^{g(x)}}{1 + e^{g(x)}}$$

where $\pi(x)$ is survival probability and $g(x)$ is a linear function of growth indices. Models were fit using the lrm function in the Splus[®] 6.2 (Insightful Corp., Seattle, Washington) design library.

For model development and selection we adopted an information theoretic approach using Akaike's Information Criterion (AIC) (Burnham and Anderson 1998). AIC values were calculated for each model as well as AIC difference values (ΔAIC , the difference in AIC values between a given model and the model with the lowest AIC value) and Akaike weights (w_i), a measure of the proportional likelihood that a model is the best model). Note that lower AIC values indicate better models and that AIC calculations penalize models with increased numbers of parameters.

Models were selected as follows. First, single-variable models were calculated for each growth index (with and without the size variable) in each category (e.g., average of 5 years of growth, average of 10 years of growth, ..., average of 40 years of growth) and compared using AIC values. The top two variables in each category were then selected, as well as any variables with a w_i value of 0.10 or greater. Models were then generated with all possible combinations of these selected variables (including the size variable) with the restriction that no model could have more than one variable from a given category. Single- and two-variable models were also included.

We assessed the five top-ranked models and any with ΔAIC less than 2 according to their ability to classify live and dead trees in validation sets. We also included three reference models: an average recent growth model (most recent 5 years of growth), the best abrupt-decline model, and the best average growth / growth trend model. The form of these reference models was based on published growth-mortality functions, and they provided a priori standards of performance.

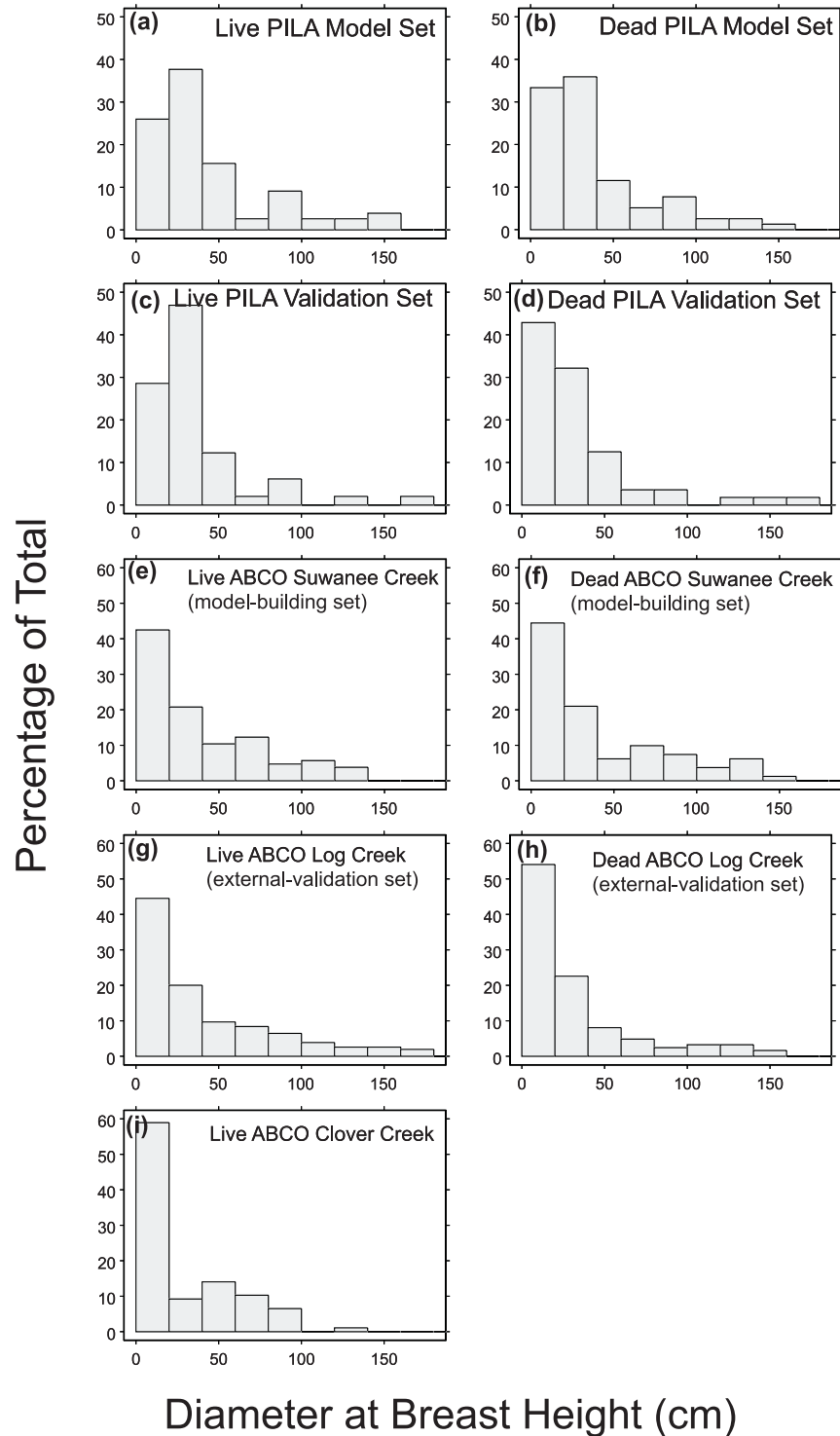
Model diagnostics

We calculated the area under the receiver operating characteristic (ROC) curve for each model — a fit criterion related to the classification technique we used for model comparison. The statistic is a threshold-independent measure of model discrimination where 0.5 suggests no discrimination, 0.7–0.8 suggests acceptable discrimination, and 0.8–0.9 suggests excellent discrimination (Hosmer and Lemeshow 2000). We also calculated variance inflation factors (VIF) for each model because of the sensitivity of logistic regression to multicollinearity among the predictor variables (Hosmer and Lemeshow 2000). VIFs above 10 are frequently taken as an indication that multicollinearity may be problematic for parameter estimation (Neter et al. 1996).

Model validation

For *P. lambertiana*, which lacked external validation data, an internal validation was done. For the size-specific *A. concolor* models we performed an external validation using models developed from the full Suwanee Creek data set to classify trees from the Log Creek data set. Trees in the validation sets were classified as live or dead based on whether the model-generated survival probability for a given tree was above a predetermined cut point (i.e., if the survival probability was greater than or equal to the cut point the tree was classified as live and otherwise classified as dead). An "optimal" cut point was determined for each model by plotting the sensitivity curve (proportion of live trees correctly classified in the model-development set over the range of cut points) and the specificity curve (proportion of dead trees correctly classified in the model-development set for the range of cut points) and choosing the cut point at which the specificity and sensitivity curves cross (Hosmer and Lemeshow 2000). The kappa coefficient, κ , — a measure of the proportional improvement by the classifier over a purely random assignment to classes — was also calculated for each model (Fleiss 1981).

Fig. 1. Size distributions of live and dead *Pinus lambertiana* (PILA) and *Abies concolor* (ABCO) for both model and validation sets. (a) Live *P. lambertiana* in the model set for Suwanee Creek ($n = 77$). (b) Dead *P. lambertiana* in the model set for Suwanee Creek ($n = 78$). (c) Live *P. lambertiana* in the validation set for Suwanee Creek ($n = 56$). (d) Dead *P. lambertiana* in the model set for Suwanee Creek ($n = 49$). (e) Live *A. concolor* in the Suwanee Creek (model-building) set ($n = 106$). (f) Dead *A. concolor* in the Suwanee Creek (model-building) set ($n = 81$). (g) Live *A. concolor* in the Log Creek (validation) set ($n = 155$). (h) Dead *A. concolor* in the Log Creek (validation) set ($n = 124$). (i) Live *A. concolor* in the Clover Creek set (no dead trees for this set; $n = 185$).



Model interpretation

The models generated above were developed from a matched sample of live and dead trees (i.e., a case-control

design), meaning that the data set did not represent the proportion of live and dead trees in the population. Thus, survival probabilities generated from these models were not

the true survival probabilities because the generated intercept was not the true intercept (Hosmer and Lemeshow 2000). However, using odds ratios to interpret and compare the model parameters was valid (Hosmer and Lemeshow 2000).

For a continuous variable, x , odds ratios approximate, all else being equal, how much more likely an outcome is at $x + a$ relative to x , where a is a meaningful increment (e.g., one additional abrupt decline). For example, an odds ratio of 2 suggests that the odds of survival at $x + a$ are twice those at x . For trees, where the likelihood of dying is quite small, this equates roughly to stating that the probability of dying at $x + a$ is half that at x (for a full explanation see Hosmer and Lemeshow 2000). Odds ratios were calculated for the best classifying models.

Estimating annual survival probabilities at the population level

To estimate survival at the population level we used a re-sampling technique similar to that used by Wyckoff and Clark (2002). The goal was to generate a sample population from our Suwanee Creek data set that represented the true population. Expected population values were based on plot data and annual mortality censuses from the Suwanee Creek plots. For each species we resampled to simulate the observed numbers of dead and live trees, the observed size distribution, and the observed size-specific mortality rates. Logistic-regression models based on the best classifying models from our case-control analysis were then estimated. The resampling process was repeated 1000 times. Final parameter values for the models were taken as the mean of each parameter for the 1000 trials, and 95% confidence intervals (CI) were taken as the interval bounded by the 25th and 975th values of each parameter when ranked from smallest to largest.

For *A. concolor* we tested whether these new models would reproduce realistic mortality rates by using data from the Log Creek and Clover Creek sites. We generated re-sampled populations from the live-tree samples taken from these sites, again matching the expected size distribution indicated by the plot data for each site. Survival probabilities were then estimated for each tree in the test populations using our population-level models. This process was repeated 1000 times each for the Log Creek and Clover Creek sites.

Mortality rates for these test populations were determined in a similar manner to that used by many individual-based forest simulation models (Bugmann 2001; Bigler and Bugmann 2004). For each tree a random number between 0 and 1 was picked. If the number chosen was greater than the survival probability for that tree, then the tree died; otherwise it survived. This procedure was repeated 1000 times for each test population, and an average mortality rate was then determined for that population. An average mortality rate and 95% CI for each site were then determined from the distribution of test-population mortality rates.

Results

Pinus lambertiana

For *P. lambertiana*, 9 of the top 12 models (Table 1) con-

tained all three growth indices. The combination of short-term growth (5 or 10 years), long-term trend (35 or 40 years) and short-term counts of abrupt decline (5 or 10 years) more fully captured survival probability than any one measure alone. Differences in mortality indicators between large and small trees appeared to be marginal, as only two models contained the size variable. All the top models provided excellent or near-excellent discrimination, and multicollinearity was not apparent ($VIF < 1.15$).

In addition to ranking far higher than the average recent-growth model (P45), the more complex models also classified the internal-validation set more effectively. (Note that “P” in the model names refers to *P. lambertiana* and the accompanying number denotes the model rank.) For example, the best classifying model (P1) had 9.0% fewer dead-tree misclassifications, 16.4% fewer live-tree misclassifications, and 12.4% fewer misclassifications overall.

In general, counting abrupt declines in growth improved our ability to classify live trees (see model P49), suggesting that the lack of such declines was indicative of survival. This improvement was illustrated by comparing models P25 and P8, where the abrupt-decline term improved live-tree classification by 6.1%. In addition, removal of the abrupt-decline term from model P1 (not shown) caused a 7.2% increase in live-tree misclassification.

Models with a 5 year count of abrupt declines were consistently better classifiers than those with a 10 year count. Apparently, the increase in mortality risk indicated by an abrupt decline was relatively short-lived. In contrast, as can be seen comparing models P45 and P25, the addition of a long-term trend tended to improve overall classification, indicating that long-term changes in growth had strong implications for tree health.

Abies concolor, DBH 20 cm or greater

All of the top models for large *A. concolor* (Table 2) contained both a long-term average growth index (20 or 25 years) and a short-term count of abrupt declines. Again, a combination of measures, as well as longer term measures, improved our ability to assess mortality risk. Though the top two models (which accounted for most of the AIC weight) contained a short-term trend index, neither offered an improvement in classification over their two-variable counterparts ($A_{\text{large}3}$ and $A_{\text{large}4}$). All the top models provided excellent discrimination, and none showed indications of multicollinearity ($VIF < 1.5$).

More complex models outperformed all of the reference models in the classification of the external-validation set (Table 2). For example, the best classifying model ($A_{\text{large}4}$) yielded 4.9% fewer misclassifications overall, 1.2% more live-tree misclassifications, and 14.0% fewer dead-tree misclassifications than a model with average recent growth alone ($A_{\text{large}26}$). Overall, the models suggested that a longer record of growth provided a better estimate of the health of large *A. concolor* and that abrupt declines in growth indicated a short period of high mortality risk (or at least the lack of them indicated improved prospects for survival). Count of abrupt declines again effectively classified live trees (see $A_{\text{large}27}$), and the addition of this term in the more complex models improved live-tree classification (compare $A_{\text{large}1}$ with $A_{\text{large}20}$).

Table 1. AIC and internal-validation results for *Pinus lambertiana*.

Model	ΔAIC^a	w_i^b	Area under ROC curve ^c	Dead trees correctly classified (%)	Live trees correctly classified (%)	Total trees correctly classified (%)	κ	Cut-point
P1: avg10 + trend40 + abrupt5	0	0.104	0.800	78.6	83.7	81.0	0.619	0.49
P2: avg5 + trend40 + abrupt5	0.42	0.084	0.800	76.8	81.6	79.0	0.581	0.49
P3: trend40 + abrupt10	0.85	0.068	0.792	66.1	75.5	70.5	0.412	0.50
P4: avg10 + trend35 + abrupt5	1.05	0.061	0.802	76.8	83.7	80.0	0.601	0.48
P5: avg10 + trend40 + abrupt10	1.24	0.056	0.802	67.9	77.6	72.4	0.450	0.46
P6: avg5 + trend40 + abrupt10	1.32	0.053	0.802	67.9	77.6	72.4	0.450	0.46
P7: trend35 + abrupt10	1.40	0.051	0.792	69.6	77.6	73.3	0.468	0.48
P8: avg5 + trend35 + abrupt5	1.61	0.046	0.801	75.0	81.6	78.1	0.562	0.48
P9: avg10 + trend35 + abrupt10	1.70	0.044	0.802	69.6	79.6	74.3	0.487	0.47
P10: avg10 + trend40 + abrupt10 + size	1.78	0.043	0.802	69.6	75.5	72.4	0.449	0.49
P11: trend4 + abrupt5 + size	1.79	0.042	0.794	76.7	83.7	80.0	0.601	0.51
P12: avg5 + trend35 + abrupt10	1.92	0.040	0.802	71.4	75.5	73.3	0.467	0.48
Best growth and growth trend								
P25: avg5 + trend35	5.78	0.006	0.786	78.6	75.5	77.1	0.540	0.45
Average recent growth								
P45: avg5	14.45	0.000	0.747	69.6	67.3	68.6	0.369	0.44
Best abrupt decline								
P49: abrupt10	21.59	0.000	0.689	55.4	79.6	66.7	0.342	0.52 ^d

Note: Models were developed from the parameterization subset of the Suwanee Creek data ($n = 155$; $n = 77$ live and $n = 78$ dead) by combining variables from the best single-variable models. Internal validation was based on a comparison of classification rates for the validation subset of the Suwanee Creek data ($n = 105$; $n = 49$ dead and $n = 56$ live). Model names are derived from the species and the model rank; "p" specifies *Pinus lambertiana*; "avg" denotes average growth; "trend" refers to the linear slope of growth and "abrupt" to a count of abrupt growth declines; the number suffix indicates the number of years of growth over which the index was calculated. The total number of models was 52.

^aDifference in AIC relative to the best model (P1).

^bAIC weights, which are a measure of the proportional likelihood that a given model is the best model. A weight of 0.10, for example, indicates that a given model is 10% likely to be the best model of those being considered.

^cROC, receiver operating characteristic.

^dOptimization for abrupt10 was not at the sensitivity/specificity intersection because of the stepwise nature of the curve. There was a threshold at which sensitivity went to 0 and specificity to 100%. Instead we chose the midpoint at which the curves are parallel before the threshold.

Table 2. AIC results and external validation for large *A. concolor*.

Model	Δ AIC	w_i	Area under ROC curve	Dead trees correctly classified (%)	Live trees correctly classified (%)	Total trees correctly classified (%)	K	Cut-point
<i>A</i> _{large1} : avg25 + trend5 + abrupt5	0	0.485	0.874	71.9	77.9	75.5	0.494	0.56
<i>A</i> _{large2} : avg20 + trend5 + abrupt5	0.45	0.387	0.873	73.7	77.9	76.2	0.510	0.57
<i>A</i> _{large3} : avg25 + abrupt5	4.87	0.043	0.848	82.5	73.3	76.9	0.525	0.61
<i>A</i> _{large4} : avg20 + abrupt5	5.77	0.027	0.846	78.9	76.7	77.6	0.544	0.59
<i>A</i> _{large5} : avg25 + trend15 + abrupt5	6.80	0.016	0.850	77.2	75.6	76.2	0.516	0.61
Best growth and growth trend								
<i>A</i> _{large20} : avg25 + trend5	13.19	0.001	0.809	66.7	70.9	69.2	0.369	0.54
Average recent growth								
<i>A</i> _{large26} : avg5	20.07	0.000	0.801	64.9	77.9	72.7	0.429	0.49
Best abrupt decline								
<i>A</i> _{large27} : abrupt5	20.77	0.000	0.709	36.8	89.5	68.5	0.287	0.46 ^a

Note: Models were developed from Suwanee Creek data by combining variables from the best single-variable models for trees with DBH greater than 20 cm ($n = 106$; $n = 61$ live and $n = 45$ dead). External validation was based on a comparison of classification rates for the Log Creek data set ($n = 143$; $n = 86$ live and $n = 57$ dead). For growth index nomenclature see Table 1. Here, *A*_{large} specifies *A. concolor* with DBH 20 cm or greater. The total number of models was 36.

^aOptimization for abrupt10 was not at the sensitivity/specificity intersection because of the stepwise nature of the curve. There was a threshold at which sensitivity went to 0 and specificity went to 100%. Instead we chose the midpoint at which the curves are parallel before the threshold.

***Abies concolor*, DBH less than 20 cm**

Many of the top-ranked models for small *A. concolor* were able to correctly classify trees in the validation set at a rate of about 70% (Table 3). These classification rates were 5–10 percentage points worse than for the best *P. lambertiana* (Table 1) and large *A. concolor* models (Table 2). This relatively poor performance occurred despite the excellent discrimination indicated by the ROC curves and the lack of multicollinearity ($VIF < 1.9$). Nonetheless, models with long-term average growth indices (20–30 years) out-ranked and generally out-performed the model with only average recent growth (*A*_{small56}). One of the best classifying models (*A*_{small3}) yielded 4.4% fewer misclassifications overall, 4.3% fewer live-tree misclassifications, and 4.4% fewer dead-tree misclassifications. In essence, longer records of growth were more indicative of tree health. Also, count of abrupt declines, despite classifying poorly in a single-variable model (*A*_{small46}), still tended to improve live-tree classification (compare *A*_{small2} with *A*_{small1} and *A*_{small3}), and in combination with long-term average growth resulted in the best classifying models overall (*A*_{small3} and *A*_{small11}).

The importance of trend in estimating the health of small *A. concolor* was more equivocal. The short-term trend (10 years) tended to improve dead-tree classification at the expense of live-tree classification (compare *A*_{small4} with *A*_{small15}), and long-term trend (30–40 years), as part of three-variable models, tended to improve classification overall (compare *A*_{small1} with *A*_{small13}, *A*_{small14}, and *A*_{small16}). However, none of these models classified better than a simpler two-variable model with a count of abrupt declines (*A*_{small3}). In summary, although one model with only trend and average growth (*A*_{small18}) classified quite well, the evidence for the importance of trend was certainly weaker for small *A. concolor* than for *P. lambertiana*.

Comparison of model parameters

Odds ratios (Table 4) and probability surfaces (Fig. 2) were used to compare models between size classes and species. We show only probability surfaces generated from the population-level models, as parameter estimates for these models did not differ markedly from those for the case-control models (see below). Odds ratios are shown for two average growth increments, a moderate increase (0.1 mm/year) and a large increase (0.5 mm/year); for a trend increase of 0.01 mm/year; and for one more or less abrupt decline. These changes are well within the range of observed values for these growth indices (Table 4).

These results indicated that *P. lambertiana* were more sensitive to growth trend than to average growth, as the odds ratio for a moderate change in trend was larger than that for a moderate change in growth (Table 4). Trend also had a stronger effect on survival probability across its range than did average growth (Figs. 2a and 2b). Large *A. concolor* were more sensitive to abrupt declines and less sensitive to average growth than small ones (Table 4; Figs. 2c and 2d), and based on odds ratios, *A. concolor* were more sensitive to changes in average growth than *P. lambertiana*, though, overall, small *A. concolor* were less likely to die (Fig. 2d).

Table 3. AIC results and external validation for small *A. concolor*.

Model	ΔAIC	w_i	Area under ROC curve	Dead trees correctly classified (%)	Live trees correctly classified (%)	Total trees correctly classified (%)	κ	Cut-point
A_{small1} : avg25 + abrupt30	0	0.057	0.809	65.7	69.6	67.6	0.353	0.47
A_{small2} : avg25	0.19	0.052	0.802	71.6	65.2	68.4	0.368	0.46
A_{small3} : avg25 + abrupt25	0.49	0.045	0.812	71.6	71.0	71.3	0.426	0.46
A_{small4} : avg20 + abrupt30	0.65	0.041	0.813	62.7	71.0	66.9	0.337	0.47
A_{small5} : avg30 + abrupt30	0.92	0.036	0.802	59.7	69.6	64.7	0.293	0.48
A_{small6} : avg20 + abrupt25	1.33	0.030	0.813	65.6	72.5	69.1	0.381	0.46
A_{small7} : avg20	1.38	0.029	0.802	71.6	65.2	68.4	0.368	0.48
A_{small8} : (see below)								
A_{small9} : avg25+trend10 + abrupt30	1.42	0.028	0.808	73.1	65.2	69.1	0.383	0.48
$A_{small10}$: avg30 + abrupt25	1.59	0.026	0.805	70.1	68.1	69.1	0.382	0.49
$A_{small11}$: avg25 + trend10 + abrupt25	1.73	0.024	0.805	73.3	69.6	71.3	0.426	0.45
$A_{small12}$: avg30	1.75	0.024	0.784	73.1	68.1	70.6	0.412	0.47
$A_{small13}$: avg25 + trend30 + abrupt30	1.81	0.023	0.808	67.2	72.4	69.9	0.396	0.47
$A_{small14}$: avg25 + trend40 + abrupt30	1.83	0.023	0.812	68.6	71.0	69.9	0.396	0.47
$A_{small15}$: avg20 + trend10 + abrupt30	1.87	0.023	0.806	74.6	66.7	70.5	0.412	0.49
$A_{small16}$: avg25 + trend35 + abrupt30	1.88	0.023	0.809	67.2	71.0	69.1	0.382	0.47
$A_{small17}$: avg25 + trend40	1.91	0.022	0.806	71.6	65.2	68.4	0.368	0.47
$A_{small18}$: avg25 + trend30	1.99	0.021	0.803	70.1	71.0	70.6	0.412	0.46
Best growth and growth trend								
A_{small8} : avg25 + trend10	1.39	0.029	0.798	76.1	65.2	70.6	0.412	0.47
Best abrupt decline								
$A_{small46}$: abrupt30	5.36	0.004	0.777	64.2	63.8	64.0	0.279	0.52
Average recent growth								
$A_{small56}$: avg5	9.19	0.001	0.756	67.2	66.7	66.9	0.338	0.48

Note: Models were developed from Suwanee Creek data by combining variables from the best single-variable models for trees with a DBH < 20 cm ($n = 81$; $n = 45$ live and $n = 36$ dead). External validation was based on a comparison of classification rates for the Log Creek data set ($n = 136$; $n = 69$ live and $n = 67$ dead). For growth index nomenclature see Table 1. Here A_{small} denotes *A. concolor* with DBH less than 20 cm. The total number of models was 60.

Table 4. Odds ratios for the best classifying models listed in Tables 1–3 (the case-control models and simulated population-level models).

	Average growth		Trend, 0.01 mm/year increase	Abrupt	
	0.1 mm increase	0.5 mm increase		One more decline	One less decline
Case-control models					
<i>Pinus lambertiana</i>					
P1: avg10 + trend40 + abrupt 5	1.05	1.27	1.34	0.37	2.71
<i>Abies concolor</i>					
A _{large} 4: avg20 + abrupt5	1.16	2.17	—	0.22	4.50
A _{small} 3: avg25 + abrupt 25	1.46	6.81	—	0.80	1.25
Population-level models					
<i>Pinus lambertiana</i>					
P1: avg10 + trend40 + abrupt 5	1.10	1.64	1.43	0.36	2.74
<i>Abies concolor</i>					
A _{large} 4: avg20 + abrupt5	1.09	1.58	—	0.14	7.32
A _{small} 3: avg25 + abrupt 25	1.62	11.13	—	0.84	1.19

Note: “Average growth” refers to an annual average increase in radial growth, “trend” refers to a rate increase in the radial growth trend, and “abrupt” refers to a change in the number of abrupt growth declines. The results represent a multiplicative change in the odds of survival with the listed change in the growth index. For example, the odds of survival in P1 increase 1.05 times for each increase in average growth of 0.1 mm. For reference, median average-growth values for the relevant indices for *P. lambertiana* and large and small *A. concolor* were 0.81, 0.97, and 0.33 mm/year, respectively, and ranged between 0.04 and 5.69 mm/year. The trend for *P. lambertiana* had a median value of 0.00 mm/year and ranged between –0.09 and 0.10 mm/year. The median 5 year count of abrupt declines for both species regardless of size was 0 (range 0–2), and the median 25 year count of abrupt declines for small *A. concolor* was 3 (range 0–8).

Estimation of annual survival probabilities at the population level

The models that best classified the internal validation set for *P. lambertiana*, P1, and the external validation sets for *A. concolor*, A_{large}4 and A_{small}3, were chosen for building the population-level mortality models via resampling. The parameter results from the original models (directly from the case-control set) all fell within the confidence intervals of the parameters generated for the population-level models (Table 5), except for the intercept, as expected. Odds ratios were consistent with those found in the original models (Table 4). For *A. concolor* models, the parameters demonstrated that, all else being equal, for most of the range of growth, small trees had a higher survival probability than large trees for the same growth rate. This relationship was consistent with results found for the non-size-specific models (Appendix B) and was evident in the probability surfaces (Figs. 2c and 2d). These surfaces also demonstrated the predictive power of abrupt declines, even for trees with very slow growth.

Mortality rates predicted for *A. concolor* by the population-level models were 1.25%/year (95% CI, 1.05–1.51%/year) at the Log Creek site and 1.35%/year (95% CI, 1.10–1.72%/year) at the Clover Creek site. CIs for these predictions overlapped that of the observed mortality rate of 1.2%/year (95% CI, 1.0% and 1.4%/year) determined from plot data for Log Creek. Since Clover Creek is located at a similar elevation, a similar mortality rate would be expected for this site (Stephenson and van Mantgem 2005). In short, our population-level models were capable of producing realistic survival probabilities and mortality rates at sites not used in model development and, in the case of Clover Creek, in a different forest type.

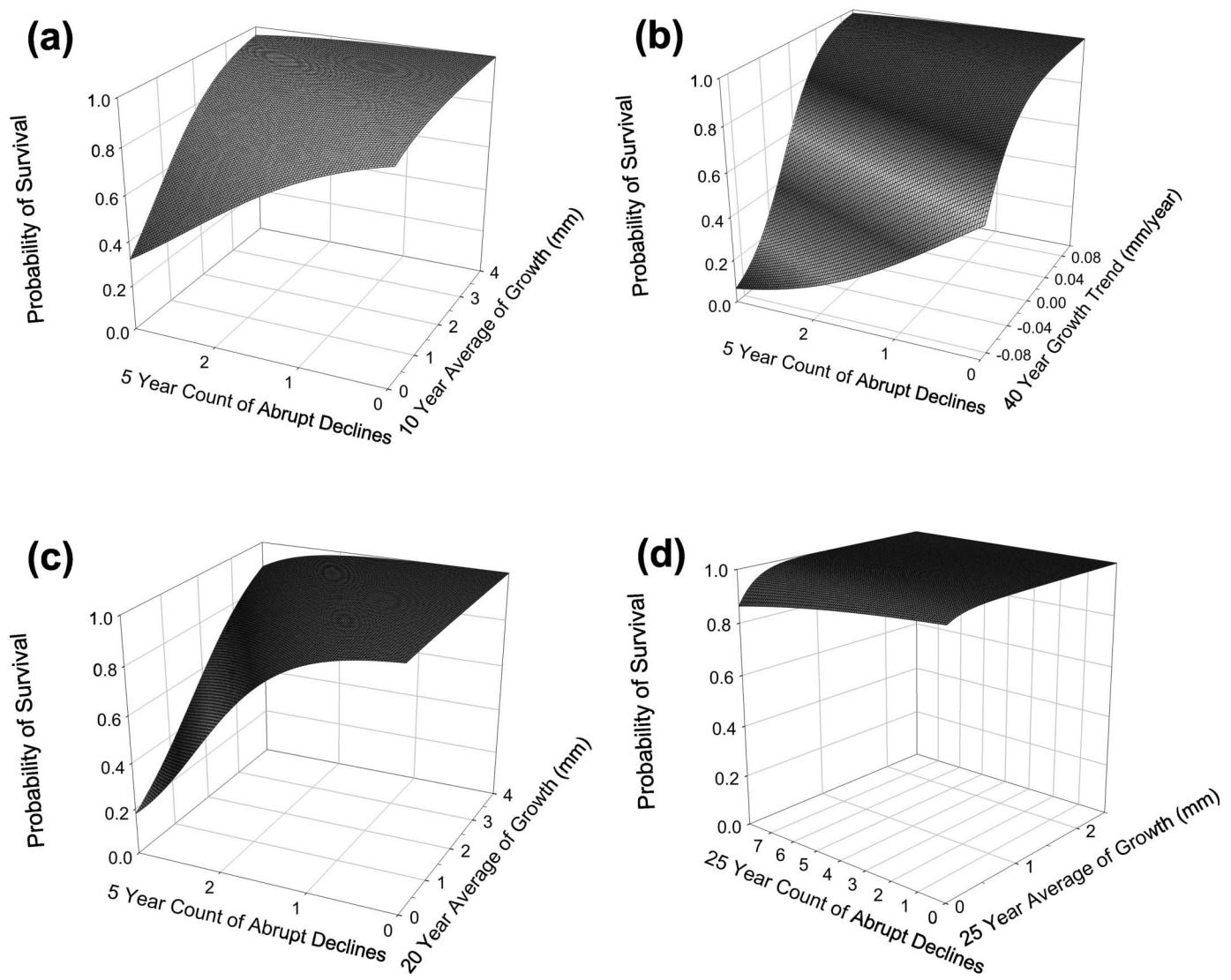
Discussion

Our results supported the contention that a cumulative record of tree growth would provide a better estimate of mortality probability than average recent growth alone. Moreover our models applied to the general case where no effort was made to screen for type of mortality or to correlate growth changes with specific events (i.e., droughts). The best models included more than one growth index and considered more than the last 5 years of growth (Table 5). Not only did such models have higher AIC rankings, they were consistently more effective at classifying validation sets. Finally, we demonstrated that for *A. concolor* our best models were able to reproduce realistic mortality rates at stands not used in model development.

These results were also consistent with the expectation that tree growth is a reliable predictor of mortality (e.g., Kobe et al. 1995; Yao et al. 2001). More specifically, the importance of abrupt declines was in keeping with Pedersen’s (1998b) finding of better fits for time-series regressions that contained an abrupt decline term. In addition, the inclusion of the long-term growth trend in the best *P. lambertiana* model was in line with Bigler and Bugmann’s (2003) finding that a 25 year growth trend was a good predictor of *Picea abies* (L.) Karst. (Norway spruce) mortality. Our classification results were also on par with those of Bigler and Bugmann (2003), who achieved between 70% and 80% accuracy in their validation sets. Although they did not use abrupt declines in their models, they excluded dead trees that showed signs of pathogen or insect attack. This exclusion may account for the effectiveness of their models without an abrupt-decline term, as they noted that misclassified trees were often characterized by abrupt declines.

As with any tree-mortality study, our work had its attend-

Fig. 2. Conditional probabilities of survival generated by the population-level models shown in Table 5. (a) Population-level *P. lambertiana* model holding the slope at its average value for the data set (-0.004 mm/year). (b) Population-level *P. lambertiana* model holding average 10 years of growth at its average value for the data set (1.13 mm). (c) Population-level model for *A. concolor* with DBH 20 cm or greater. (d) Population-level model for *A. concolor* with DBH less than 20 cm.



ant limitations. Because of the nature of our case-control design, in which we matched the size distributions of live and dead trees, we were unable to fully explore the effect of tree size on mortality risk. Clearly, size is an important correlate of tree mortality rate (e.g., Eid and Tuhus 2001; Fridman and Stahl 2001; Bravo-Oviedo et al. 2006), and even our two-category analysis showed size-specific differences for at least one species (see Appendix B). We also did not account for the spatial circumstances of a given tree that might not be reflected in its growth but still might influence its survival. For example, the proximity of conspecific neighbors could influence the likelihood of infection by root pathogens (e.g., Garbelotto et al. 1999; Hansen and Goheen 2000). In addition, the definition of abrupt decline was necessarily arbitrary, though we defined it in the context of previous work (Schweingruber 1985, 1986). Moreover, our results were not particularly sensitive to the exact definition

of abrupt decline. Sensitivity analyses showed that while using a 60% drop in growth to define abrupt declines resulted in somewhat poorer mortality classification (i.e., too strict a definition), a 40% decline gave roughly the same results as a 50% decline. Finally, there were also unavoidable biases that came with the sampling of dead trees. Trees that died of rot, for instance, may have been underrepresented, owing to a potentially lower frequency of such trees from which readable cores could be obtained. We also decided not to exclude trees that could not be confidently cross-dated, resulting in the inclusion of samples with uncorrected errors. As noted in the Methods, we considered these errors to be conservative, and we were more concerned with the potential bias caused by excluding trees with a strong ecological signal, an especially frequent occurrence in very unhealthy trees.

Nonetheless, despite their limitations, we believe that our

Table 5. Model parameters for estimating annual survival probability generated by the resampling procedure described in the Methods.

Model	Parameter estimate	95% CI
<i>Pinus lambertiana</i> model (P1)		
Intercept	2.43	2.25 to 2.61
Avg10	0.99	0.78 to 1.24
Trend40	35.53	31.25 to 39.84
Abrupt5	-1.01	-1.16 to -0.84
<i>Abies concolor</i> models		
Large-tree model $A_{\text{large}4}$		
Intercept	4.47	3.69 to 5.36
Avg20	0.91	0.37 to 1.53
Abrupt5	-1.99	-2.78 to -1.18
Small-tree model $A_{\text{small}3}$		
Intercept	3.24	2.37 to 4.10
Avg25	4.82	3.08 to 6.94
Abrupt25	-0.17	-0.29 to -0.06

Note: Model forms were chosen on the basis of the best classifiers from Tables 1–3.

best models captured more of the biological processes involved in mortality than their simpler counterparts. As is assumed in many studies (e.g., Pacala et al. 1996; Yao et al. 2001; Wyckoff and Clark 2002), average diameter growth was an indicator of a given tree's health. It was included in all three of our best models (Table 4). However, without any context for how that rate was reached, the information was incomplete. Abrupt declines and growth trend, which measure changes in growth, helped provide that context. For example, for both *P. lambertiana* and large *A. concolor*, our best models suggested that for two trees growing at the same rate, the one that had reached that rate through a recent abrupt decline in growth was more likely to die. Also, in the case of *P. lambertiana*, a tree that had declined over a long period was more likely to die than one that had grown steadily.

While we cannot pinpoint the exact biological mechanisms that underlie the predictive power of these changes in growth, there are plausible explanations. For example, Pedersen (1998b), Schweingruber et al. (1990), and Schweingruber (1985, 1986) have directly linked abrupt declines in growth to droughts, climate fluctuations, and pollution. Such declines could also be caused by biotic agents, such as root-rot infection (e.g., Cherubini et al. 2002), or even by physical damage. Decreasing trends are likewise probably related to an accumulation of biological or physical stressors that gradually lead to tree mortality, as described by Franklin et al. (1987). Alternatively, these declining growth trends could result from the imposition of a single stressor from which the tree does not recover. For instance, Pedersen (1998a) demonstrated theoretically how exposure to a stress could trigger a positive feedback mechanism that results in a long-term slide toward death.

The differences between our two species in the mortality models were also consistent with known life-history characteristics. The fact that *A. concolor* were better modeled by a long-term average growth index (20 or 25 years) and *P. lambertiana* by a short-term index (5 or 10 years) is con-

sistent with the expectation that a more shade-tolerant species, such as *A. concolor* (Burns and Honkala 1990), would be more tolerant of slow growth. It makes sense that a shade-tolerant species could sustain a longer period of slow growth before being considered at risk of death. Further, also in keeping with relative shade tolerance, the intercept and growth coefficients for the population-level models (Table 5) demonstrated that *A. concolor* were more likely to survive at a given annual growth rate than *P. lambertiana* in the absence of a declining growth trend or abrupt declines, although these models are admittedly not directly comparable, owing to the different time periods over which average growth rates were determined.

Relative shade tolerance might also explain why trend was a more powerful predictor for *P. lambertiana* than for *A. concolor*. As a shade-tolerant species, *A. concolor* would be more likely to persist at low growth rates for extended periods rather than dying immediately after a gradual declining trend in growth. In contrast, *P. lambertiana*, being less shade-tolerant, would be more likely to suffer mortality just after such a declining trend. The lesser importance of average growth compared with trend for *P. lambertiana* (Table 4) can be explained by the same argument (i.e., *P. lambertiana* would not frequently persist at low growth rates but would instead show a declining trend just prior to mortality).

As a final example of the potential biological relevance of these models, we note that *A. concolor* model results showed distinct differences between small and large trees, with small *A. concolor* having a higher survival probability at most growth rates (see the coefficients in Table 5 and size variable in Appendix B). Woody plants are known to go through various life stages (Greenwood 1995), and trees undergo numerous physiological changes as they age and grow taller, including some that may affect shade tolerance (Niinemets 1998; Fraga et al. 2003; Lusk 2004). Kneeshaw et al. (2006), for instance, found that trees became less shade-tolerant with increasing size. We suggest that our model differences were also due to some loss of shade tolerance by larger *A. concolor*, perhaps because the ability to persist at low growth rates becomes less relevant as trees grow into the canopy. In contrast, as *P. lambertiana* do not have the same survival strategy (i.e., persisting in the understory), one would not necessarily expect differences in how large and small trees respond to slow growth.

Given, then, that a more comprehensive use of the growth record appears to better capture mortality probability, what are the implications for mortality prediction? In general, we suggest that the use of average recent growth alone may not be adequate for reliable mortality prediction for all species. In particular, such models may be overly sensitive to short-term changes in growth rate and miss factors that indicate survival. We know, for example, that the inclusion of abrupt-decline terms tends to improve live-tree classification, apparently increasing the ability of models to distinguish between slow-growing trees that die and those that survive.

The ability to correctly classify live trees is especially important for predicting mortality, given the predominance of live trees in the population. One might argue that the improvement in classification by our models, particularly in the case of *A. concolor*, was fairly modest. In our sample,

however, live and dead trees were artificially close in number, giving roughly equal weights to misclassifications. In natural populations, live trees greatly outnumber dead trees in a given year, so errors that result in underestimation of the number of trees that survive could have far more impact on mortality prediction. For example, a stand of 1000 trees with 1% annual mortality would have 990 live trees and 10 dead trees after the first year. Underestimating the number of dead trees by 5% (9.5 dead trees / 1000 trees in total) would result in a mortality rate of 0.95%. In contrast, underestimating the number of live trees by 5% would result in a mortality rate of 4.95% ((990-0.95(990)) / 1000 trees in total). Therefore, capturing mechanisms — as abrupt declines appear to do — that indicate increased survival becomes a great deal more important.

However, incremental improvements in classification are less critical than our confidence that a given mortality model adequately captures realistic mortality processes. For example, we have shown that our more complex models can reproduce realistic mortality rates, but an average recent growth model can be calibrated to do the same. In fact, an intercept-only model could effectively mimic current mortality rates but not the mortality process, thereby limiting the model's application to novel conditions.

In developing our models, we have been informed by the fact that, for trees, mortality processes can operate over decades and by the idea that indices that account for an accumulation of injuries should yield a better picture of a given tree's survival probability. We have also demonstrated that our model results dovetail nicely with what we know about the life history of each species. Therefore, we argue that these types of models, despite being more complex, are more likely to be robust to changing conditions. As our AIC and external-validation results indicate, we have not "overfit" our particular data set.

Such considerations are important, as model choice can have large implications for understanding the effect of novel events (e.g., climate change) on forests. Forest-gap models, for instance, frequently use mortality functions based on the premise that probability of mortality increases when average growth drops below some threshold (Keane et al. 2001; Bigler and Bugmann 2004). Many such models predict rapid, large-scale forest dieback with changing climate (Loehle 1996). Loehle and LeBlanc (1996) argued that the mechanisms underlying these mortality functions are unrealistic and that such diebacks are unlikely. Bigler and Bugmann (2004) further demonstrated that these mortality functions performed relatively poorly when confronted with actual growth data.

Even in empirically parameterized models such as SORTIE® (Pacala et al. 1996), the mortality function does not capture a generalized mechanism of mortality. All trees are given a baseline mortality probability of 0.01 so as to mimic a "natural low-disturbance stand", then additional mortality risk is assessed on the basis of a growth–mortality relationship parameterized from sapling data. This procedure essentially sets a 1% annual mortality rate to which the growth–mortality risk is added, and because of the nature of the growth functions of SORTIE®, the growth–mortality portion of the mortality submodel acts almost exclusively on saplings.

In addition to demonstrating the potential for overestimating the sensitivity of many species to changes in growth (Loehle and LeBlanc 1996), our research also suggests that mortality functions based only on average recent growth may fail to account for the importance of other aspects of growth history in determining mortality probability. Given the sensitivity of gap models to the mortality function (Bugmann 2001), it is crucial to improve our understanding of tree mortality and to try to capture the underlying biological processes that drive it.

In this pursuit we do need to recognize the dangers of increasing the complexity of models. As Pacala et al. (1996) pointed out, increasing their complexity risks introducing errors that can swamp biological signals. In addition, calculation of long-term growth indices, as we have advocated here, is not always possible or relevant, as when studying young saplings or seedlings (e.g., Kobe et al. 2002). Nonetheless, we must balance a desire for simplicity with the need to account for biological complexity. For long-lived organisms like trees, looking further back in history and at the character of that history may prove important.

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- increment. If this is true, as a tree grows, its ring width will decrease in proportion to the square of its radius, thereby making basal area increment a better indicator of individual tree health across size classes.
- This is clearly not true in all cases, such as white oaks in Connecticut (Phipps and Whiton 1988) and the more extreme case of giant sequoia in the Sierra Nevada (Stephenson and Demetry 1995). In fact, deviations from an *increasing* trend in basal area increment have been used to indicate declining stand health (Phipps and Whiton 1988; Leblanc 1990; Duchesne et al. 2002, 2003). In addition, in a preliminary analysis of tree samples from California, Yoo and Wright (2000) found that the growth trend in ring width with age is often nearly flat.
- In our live-tree sample, basal area increment increases markedly with size, while radial increment shows no obvious trend (Fig. A1). Furthermore, preliminary analyses were done using both absolute and relative basal area increments (basal area increment/total initial tree basal area) and compared with the results reported in this article. Neither measure provided any improvement with regard to fit or classification and in many cases performed more poorly. We therefore opted to use radial increment rather than a transformed version of it (i.e., basal area increment).
- A separate, although related, concern when using ring widths as an indicator of tree health across size classes is the commonly observed negative exponential pattern in ring widths for a given tree, which would result in small trees growing faster than large trees and exhibiting a strong decreasing trend regardless of health. We have not observed the negative exponential pattern with any consistency in our data set, at least for the 40 year span that was used in data analysis. In fact, large *A. concolor* from our live tree data set grew, on average, faster than small trees (by 0.6731 mm/year (95% CI = 0.3031 mm/year), $p = 0.000$) and had a slightly decreasing trend (–0.009 mm/year (95% CI = 0.006 mm/year), $p = 0.002$). The average trend for small *A. concolor*, on the other hand, did not differ significantly from 0 (0.004 mm/year (95% CI = 0.006 mm/year), $p = 0.295$). For *P. lambertiana*, large trees again grew faster than small trees (by 1.08 mm/year (95% CI = 0.47 mm/year), $p = 0.000$), while the slopes did not differ significantly from one another (the difference was 0.001 mm/year (95% CI = 0.01 mm/year), $p = 0.8192$). In addition, rather than decreasing, the slopes for both categories of trees increased slightly (large trees: 0.011 mm/year (95% CI = 0.007 mm/year); small trees: 0.009 mm/year (95% CI = 0.006 mm/year)).
- Although these results contradict those typically expected, the difference in average growth rates between large and small trees is marked. It is difficult to say a priori whether such differences are simply an indication of the fact that subcanopy trees are less likely to survive (and therefore should behave similarly in our models) or if there is some intrinsic difference in the relationship between growth and mortality. For this reason we have included a size-specific variable, as discussed in the Methods and Results sections.

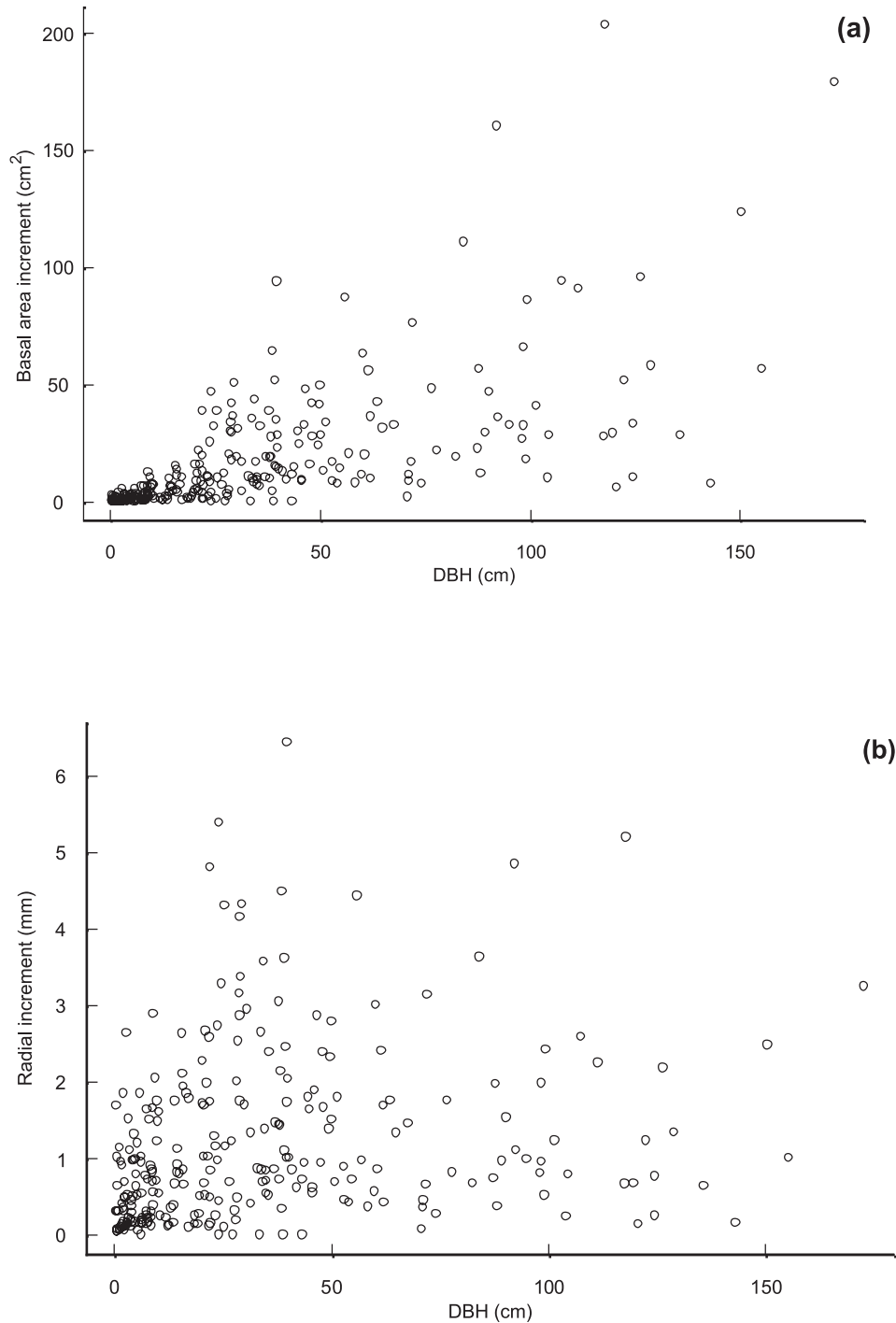
Appendix A. Use of radial increment

All growth indices were calculated using radial increment. We wished to use a measure that was as size-independent as possible. Some researchers have preferred to use basal area increment for this purpose (e.g., Pedersen 1998; Bigler and Bugmann 2003). The attraction of using basal area increment lies in the assumption that once a tree reaches a certain minimum size, all else being equal, it will add a constant amount of basal area each year, at least relative to growth

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Fig. A1. (a) Relationship between most recent basal area increment and diameter at breast height (1.37 m (DBH)) for all live trees in the data ($n = 433$). (b) Relationship between most recent radial increment and DBH for all live trees in the data ($n = 433$).



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Appendix B. Model results for *A. concolor* using all tree sizes

For preliminary analysis, *A. concolor* models were built using all *A. concolor* samples from the Suwanee Creek site. This was done following the procedure given in the Methods for the size-specific models except that the size variable was included to account for the differences between large and small trees (size = 1 for DBH less than 20 cm; size = 0 for DBH 20 cm or greater). External validation was performed using the *A. concolor* data set from Log Creek.

All of the five top-ranked models (Table B1) include both an average-growth term as well as an abrupt-decline term, with 20 or 25 years of average growth and 25 or 30 year counts of abrupt declines providing the best fits. Two of the five have a trend term, with 5 or 35 year trends providing the best fits. The reference models (A17, A50, A52) are ranked more poorly in comparison, although the best growth and growth trend model is ranked in the top 20.

All of the best models contained the size variable, suggesting a difference in the growth-related mortality risk for small trees. The coefficient for this term is always positive, indicating that smaller trees have a higher survival rate for the same growth characteristics (i.e., smaller trees have a higher capacity to survive slow growth).

The area under the ROC curve indicates excellent discrimination for the top five models as well as the best growth and growth trend model (A17). The average recent growth model (A50) and the best abrupt-decline model (A52) provided acceptable discrimination.

Variance inflation factors were below 1.4 for all average growth and growth trend indices. However, they rose as high as 3.5 for the abrupt-decline indices and the size variable. This is still well below the “warning” value, 10, but it does suggest a potentially problematic correlation between the number of abrupt declines and size. This result provided a further incentive for us to develop size-specific models for this species.

External validation of these models on the Log Creek data (Table B1) shows that the top five models consistently classified better than the reference models. The best classifying model, A1, performed better in all categories, with 4.1% fewer dead-tree misclassifications, 5.2% fewer live-tree classifications, and 4.7% fewer misclassifications overall.

The best average growth and growth trend model, A17, though performing more poorly than the five top-ranked models, yielded only 1.5% more misclassifications than the best model (A1). It is worth noting that in this case, A1, A2, and the best growth and growth trend model (A17) are closely related: A2 is simply A17 with the addition of an abrupt-decline term and A1 simply A2 without a trend term. The addition of trend to A1 actually increases misclassifications, while the addition of abrupt declines to A17 decreases them. In light of this result, if one is forced to choose between a trend and

Table B1. AIC and external-validation results for the Suwanee Creek *A. concolor* models generated by combining variables from the best single-variable models.

Model	Δ AIC	w_i	Area under ROC curve				Trees correctly classified (%)			
			Dead	Live	Total	κ	Dead	Live	Total	Cut-point
A1: avg25 + abrupt25.5 + size	0	0.268	0.823	71.0	73.5	0.463	71.0	75.5	73.5	0.53
A2: avg25 + trend35 + abrupt25 + size	0.831665	0.177	0.826	71.8	73.5	0.451	71.8	73.5	72.8	0.53
A3: avg20 + abrupt25 + size	1.186044	0.148	0.821	71.0	73.5	0.443	71.0	73.5	72.4	0.54
A4: avg25 + abrupt30 + size	1.373839	0.135	0.821	72.6	72.3	0.443	72.6	72.3	72.4	0.54
A5: avg25 + trend5 + abrupt25 + size	1.446252	0.130	0.823	72.6	72.3	0.445	72.6	72.3	72.4	0.54
Best growth and growth trend										
A17: avg25 + trend35 + size	5.887655	0.014	0.804	68.5	72.9	0.414	68.5	72.9	71.0	0.48
Average recent growth										
A49: avg5 + size	19.00633	0.000	0.787	66.9	70.3	0.371	66.9	70.3	68.8	0.49
Best abrupt decline										
A52: abrupt25 + size	21.20023	0.000	0.764	60.5	78.1	0.391	60.5	78.1	70.3	0.57

Note: AIC results were generated using all trees in the Suwanee Creek sample ($n = 187$; $n = 106$ live and $n = 81$ dead). In the model names, “A” refers to *A. concolor* and the number refers to the model rank. Seventy-two models were used in this case, although only 36 of these are unique when the dichotomous size variable is ignored. External-validation results are from the Log Creek *A. concolor* validation set ($n = 279$; $n = 155$ live and $n = 124$ dead), using the Suwanee Creek *A. concolor* models for classification.

Table B2. Odds ratios for the best classifying all-tree *A. concolor* model.

Model	Odds ratio			
	0.1 mm increase in average growth	0.5 mm increase in average growth	One more abrupt decline	One less abrupt decline
A1: avg25 + abrupt25 + size	1.19	2.43	0.70	1.43

The best abrupt-decline term again showed a pattern of accurate classification of live trees and relatively poor classification of dead trees.

Odds ratios (Table B2) show that *A. concolor* is quite sensitive to average growth relative to *P. lambertiana* (Table 4).

abrupt-decline term, the latter will probably prove to be a more powerful classifier.