

# Improving estimates of tree mortality probability using potential growth rate

Adrian J. Das and Nathan L. Stephenson

**Abstract:** Tree growth rate is frequently used to estimate mortality probability. Yet, growth metrics can vary in form, and the justification for using one over another is rarely clear. We tested whether a growth index (GI) that scales the realized diameter growth rate against the potential diameter growth rate (PDGR) would give better estimates of mortality probability than other measures. We also tested whether PDGR, being a function of tree size, might better correlate with the baseline mortality probability than direct measurements of size such as diameter or basal area. Using a long-term dataset from the Sierra Nevada, California, U.S.A., as well as existing species-specific estimates of PDGR, we developed growth–mortality models for four common species. For three of the four species, models that included GI, PDGR, or a combination of GI and PDGR were substantially better than models without them. For the fourth species, the models including GI and PDGR performed roughly as well as a model that included only the diameter growth rate. Our results suggest that using PDGR can improve our ability to estimate tree survival probability. However, in the absence of PDGR estimates, the diameter growth rate was the best empirical predictor of mortality, in contrast to assumptions often made in the literature.

*Key words:* tree growth, tree mortality, potential growth, tree size, forest dynamics.

**Résumé :** Le taux de croissance des arbres est fréquemment utilisé pour estimer la probabilité de mortalité. Cependant, les mesures de croissance peuvent prendre des formes variées et la justification pour utiliser l'une plutôt que l'autre est rarement claire. Nous avons vérifié si un indice de croissance (IC) qui met en rapport le taux de croissance en diamètre réalisé et le taux de croissance en diamètre potentiel (ICDP) donnerait de meilleures estimations de la probabilité de mortalité que d'autres mesures. Nous avons également testé si l'ICDP, qui est fonction de la taille de l'arbre, pourrait être mieux corrélé avec une probabilité de mortalité de référence que des mesures directes de la taille, comme le diamètre ou la surface terrière. À l'aide d'un ensemble de données à long terme provenant de la Sierra Nevada en Californie, aux États-Unis, ainsi qu'avec des estimations existantes de l'ICDP, spécifiques aux espèces, nous avons développé des modèles de croissance et de mortalité pour quatre espèces communes. Pour trois des quatre espèces, les modèles qui incluaient l'IC, l'ICDP, ou une combinaison de l'IC et de l'ICDP étaient nettement meilleurs que les modèles n'incluant pas ces variables. Pour la quatrième espèce, le modèle comprenant l'IC et l'ICDP s'est comporté à peu près aussi bien qu'un modèle utilisant le taux de croissance en diamètre. Nos résultats indiquent que l'utilisation de la croissance potentielle peut améliorer notre capacité à estimer la probabilité de survie des arbres. Toutefois, en l'absence d'estimations de la croissance potentielle, le taux de croissance en diamètre est le meilleur prédicteur empirique de mortalité, contrairement aux hypothèses souvent mentionnées dans la littérature. [Traduit par la Rédaction]

*Mots-clés :* croissance des arbres, mortalité des arbres, croissance potentielle, taille des arbres, dynamique forestière.

## Introduction

As forests come under mounting pressure from climatic change and other anthropogenic stressors (Vitousek et al. 1997; Adams et al. 2010), the need to improve our tools for assessing forest health and vulnerability is becoming increasingly acute. Forests comprise an important component of the terrestrial biosphere, and changes to forests are likely to have significant feedbacks on the cycling of carbon, energy, and water (Bonan 2008; Adams et al. 2010). Tree mortality plays a crucial role in such changes, being a key process in any shifts in forest structure, composition, and function. Forest health and mortality may already be showing the effects of a changing climate, as evidenced by some documented regional increases in background mortality and potential increases in the incidence of large-scale, drought-related mortality events (van Mantgem et al. 2009; Allen et al. 2010). Yet, despite its importance, much remains to be learned about how best to predict tree mortality and quantify tree mortality probability (Hawkes 2000;

Bugmann 2001). Here, we consider an alternative method to the commonly used empirical measures for assessing tree mortality probability and test this method's efficacy against the more standard measures in forests experiencing noncatastrophic background mortality.

A tree's recent growth rate has frequently been used as a proxy for overall tree condition or health (defined for purposes of this manuscript as related to a tree's probability of mortality), marking an improvement and a complement to measures that rely solely on visual assessments of crown condition (e.g., Innes 1993; Mangold 1998; Zarnoch et al. 2004). For this purpose, growth rate is assumed to capture the effect of competition and other abiotic and biotic factors that might be affecting a given tree. A number of measures of growth rate have been tried, with diameter growth rate (e.g., Kobe et al. 1995; Yao et al. 2001), basal area growth rate (e.g., Pedersen 1998; Bigler and Bugmann 2003), and relative basal area growth rate (e.g., Bigler and Bugmann 2004) being commonly used measures. Although fast growth rates can sometimes indi-

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cate an increased vulnerability to breakage or pathogen attack (e.g., Bigler and Veblen 2009) and some very slow-growing species might be long lived, within a species and a site, slower growing trees usually have a higher probability of mortality than faster growing trees (Stephenson et al. 2011).

Importantly, recent work has shown that incorporating additional measures of growth into mortality models, including growth trend, abrupt changes in growth, and growth variability, can improve their performance over models that rely solely on an average of recent growth (Ogle et al. 2000; Bigler and Bugmann 2003, 2004; Das 2007; Kane and Kolb 2014). However, these more complex models require tree ring data, which are often not available and require additional collection effort beyond standard forest mensuration. In general, recent growth rate offers the most readily available information about tree vigor and probability of mortality at a given site, in part because of the relative ease with which it is obtained (i.e., successive diameter measurements). Broadly speaking, beyond crown assessments, much of our knowledge about forest condition and mortality probability comes from such data, and the value of the data is to a large extent dependent on our understanding of growth–mortality relationships. In short, in the absence of tree ring data, there is great potential value in improving our ability to use recent growth rate as a predictor of mortality probability.

Here, we suggest an alternative empirical method for assessing tree vigor using recent growth rate, which we hope will further enhance our ability to assess forest conditions. We posit that the closer a tree is to its maximum potential growth rate, the less likely it is to die. In other words, a completely healthy tree should, hypothetically, grow at its maximum rate, with any deviation from that rate being a sign of some stress. Therefore, a biologically informed index of tree vigor could be derived by simply dividing a given tree's realized diameter growth rate by its maximum potential diameter growth rate (hereafter we refer to this as the growth index (GI)). Indeed, this metric is currently used to estimate probability of mortality due to competition in the forest simulation model SORTIE-ND ([www.sortie-nd.org](http://www.sortie-nd.org)). In addition, many older forest models have used growth rate scaled against a maximum to define stress and assign probability of mortality (Bugmann 2001). However, we are unaware of any published studies that compare this metric with those metrics that are frequently used in empirical models of mortality (i.e., radial or diameter growth rate, basal area growth rate, and relative basal area growth rate).

Although the best estimates of a given tree's maximum potential growth rate would require a prohibitive degree of knowledge about a particular tree's genetics and various site factors, a number of recent studies have taken advantage of robust, spatially explicit datasets to estimate the potential diameter growth rate (PDGR) of trees in the absence of competition (Canham et al. 2004, 2006; Uriarte et al. 2004; Coates et al. 2009; Gomez-Aparicio et al. 2011; Das 2012). PDGR is an estimate of the expected mean potential growth rate without competition for a given species at a given set of sites for a given size tree and should, therefore, be a reasonable measure with which to calculate GI.

Notably, PDGR, an estimate of a hypothetical rate, is entirely a function of tree size. Therefore, PDGR itself might serve as an alternative to direct measures of tree size such as diameter or basal area when estimating probability of survival. There is much evidence to suggest that the baseline probability of mortality changes with tree size (e.g., Monserud and Sterba 1999; Yao et al. 2001; Yang et al. 2003), and one might speculate that a tree's growth potential correlates with its inherent probability of mortality (i.e., it might be an indicator of fundamental changes in a tree's probability of mortality as it grows larger).

In this study, we take advantage of a large, long-term dataset from the Sierra Nevada, California, to test our hypothesis that (i) GI, which scales realized growth against an estimate of PDGR, should be a better predictor of mortality than other commonly used measures and (ii) PDGR itself will better correlate with probability of mortality than other size-related measures. We present results for four common species in mixed-conifer and red fir forests: white fir, *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.; California red fir, *Abies magnifica* A. Murray; incense cedar, *Calocedrus decurrens* (Torr.) Florin; and sugar pine, *Pinus lambertiana* Douglas. For three of the four species (except for *P. lambertiana*), we show that the inclusion of GI and PDGR substantially improved our models of tree health.

## Methods

### Dataset and calculation of growth measures

Eighteen permanent study plots ranging in size from 0.9 ha to 2.5 ha were established between 1982 and 2001 in old-growth stands within the coniferous forests of Sequoia and Yosemite national parks, Sierra Nevada, California, U.S.A. (for plot characteristics, see Supplementary Table S1<sup>1</sup>). Other plots in the network were excluded either due to recent disturbances or because the plots did not contain our dominant study species. The plots are arranged along an elevational gradient from 1500 m to nearly 2600 m, including both mixed-conifer and red fir (Fites-Kaufman et al. 2007) forest types. The sites have never been logged. Frequent fires characterized many of the forest types prior to Euro-American settlement, but the areas containing the study plots mostly have not burned since the late 1800s (Caprio and Swetnam 1993). The climate is montane mediterranean, with hot, dry summers and cool, wet winters, in which ~25%–70% of annual precipitation (mean, 1100–1400 mm) falls as snow, depending on the elevation (Stephenson 1988). Mean annual temperature declines with elevation, ranging from roughly 11 °C at the lowest plots to 6 °C at the highest plots. Soils are relatively young (mostly inceptisols) and derived from granitic parent material.

Within each plot, all  $\geq 1.37$  m high trees were tagged, mapped, measured for diameter at breast height (dbh, 1.37 m), and identified to species. Each year, every tree in every plot was checked for mortality. Diameters of all trees were remeasured at intervals of ~5 years.

For this analysis, we used the two most recent diameter remeasurement intervals for each plot. The first interval was used to determine tree growth rate and the second interval was used to determine tree mortality, with mortality probability defined in our models as the probability of a tree dying over an interval of 5 years. In the case of one plot (YOHOPPO), only measurement intervals prior to a prescribed burn were used. All growth rate intervals for all the plots fell between the years of 1998 and 2007. All mortality intervals fell between 2004 and 2012, and all mortality intervals were 5 years in length.

We analyzed only those species for which potential growth curves had already been developed, as described in Das (2012), i.e., white fir, red fir, incense cedar, and sugar pine. Annual diameter growth rate was calculated by taking the difference between consecutive diameter measurements and dividing it by the length of the interval between measurements. Trees with annual diameter growth rates  $>4$  cm or  $<-0.2$  cm were excluded as likely errors. We allowed negative growth to avoid biasing the dataset toward positive growth, as undetectable overestimates of growth almost certainly occur as well. Basal area growth rate was calculated similarly except that the diameters were converted to basal areas (square of the radius multiplied by  $\pi$ ). Relative basal area growth rate and relative diameter growth rate were calculated by dividing

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2014-0368>.

**Table 1.** Description of predictor variables.

	Description
<b>Size-related variables</b>	
dbh	Diameter measured at breast height (1.37 m)
Basal area	$(dbh/2)^2(\pi)$
PDGR <sub>DI</sub>	Growth rate in the absence of competition as derived from the double-inflection model in Das (2012)
PDGR <sub>ME</sub>	Growth rate in the absence of competition as derived from the modified power function (exponential) in Das (2012)
<b>Growth-related variables</b>	
Diameter growth rate	Difference in dbh from first to second measurement divided by the time interval
Basal area growth rate	Difference in basal area from first to second measurement divided by the time interval
Relative diameter growth rate	Diameter growth rate/dbh
Relative basal area growth rate	Basal area growth rate/basal area
GI <sub>DI</sub>	Diameter growth rate/PDGR <sub>DI</sub>
GI <sub>ME</sub>	Diameter growth rate/PDGR <sub>ME</sub>

the basal area growth rate and diameter growth rate by the starting basal area of the tree and starting diameter of the tree, respectively.

We developed our GIs by dividing the diameter growth rate for each tree by the PDGR for a tree of that size, as determined by the potential growth models developed in Das (2012). Note that our estimate of potential growth is simply the mean growth expected at the study sites in the absence of competition and is not a measure of the absolute maximum growth that might be achieved if different and potentially more productive sites were included. Furthermore, a given tree's maximum growth might be faster or slower than this mean, depending on various factors particular to that tree (e.g., genetics or microsite conditions). Note that PDGR is entirely a function of tree diameter and does not incorporate the realized growth of a given tree.

We created two different indices using the top two model forms from Das (2012), including the following double-inflection model:

$$PDGR = adbh^{(b_1e^{-c_1dbh} - b_2e^{-c_2dbh})}$$

where dbh is diameter at breast height, and  $b_1$ ,  $b_2$ ,  $c_1$ , and  $c_2$  are fitted parameters. The modified power function (exponent) model is

$$PDGR = adbh^{be^{-cdbh}}$$

where  $b$  and  $c$  are fitted parameters. (Further model details are provided in Das (2012).) We included the second model because the additional predictive power of the double-inflection model was due to its ability to capture an apparent initial sharp decline in PDGR for the smallest trees in the dataset. As it was not clear if this initial decline would be important for predicting mortality, we opted to include the simpler, but functionally related, model as well.

### Model fitting and comparison

We fit survival probability using a generalized linear mixed effects model with a logit link (i.e., assuming a binomial distribution) — effectively, a mixed effects logistic regression. The dependent variable was survival over the 5-year mortality interval, and the predictors were combinations of size-related variables (variables that are either measures of tree size or solely a function of tree size) and growth variables (variables that incorporate the realized growth rate of a given tree). Plot was included as a random variable that modified the intercept. We tried models with interactions between the variables to test whether those terms would obviate the need for PDGR and GI but in only one case did the interaction models provide improvement — in that case, they simply strengthened a GI-PDGR model.

In total, we used four size-related variables and six growth variables (Table 1). The size-related variables were dbh, basal area, and two measures of PDGR (as quantified by the aforementioned equations from Das (2012)). The growth variables were diameter growth rate, basal area growth rate, relative diameter growth rate, relative basal area growth rate, and the two GI metrics described above. Each model included either a size or a growth variable or a combination of the two, for a total of 32 models. All models were fit using the glmer function from the lme4 package in the R statistical software (R Development Core Team 2013).

Models were compared using an information-theoretic approach (Burnham and Anderson 1998), including differences in Akaike's information criteria (AIC), Akaike weights, and evidence ratios. Models within two AIC units were considered to have a roughly equal weight of evidence, and differences of more than four AIC units between models was considered as strong evidence favoring one model over another. Model fit was characterized by both discrimination (ability of the model to distinguish between live and dead trees) and calibration (how well the model fit actual survival probabilities). Discrimination was quantified using the area under the receiver operating characteristic curve (ROC), with values greater than 0.7 indicating good discrimination (Hosmer and Lemeshow 2000). Calibration was assessed using linear logistic calibration plots (from val.prob function in the rms R package). We considered Nakagawa and Schielzeth's (2012)  $R^2$  for mixed models (r.squaredGLMM function in the MuMIn R package), but that measure proved to be highly sensitive to extreme values. Models were also checked for multicollinearity between predictor variables using variance inflation factors (VIF).

### Results

All of the best models for *A. concolor* included PDGR and GI metrics as predictors (Table 2). The weight of evidence for these models far exceeds that of any models with dbh, basal area, or any other growth variable. The discrimination of these models is good, and calibration (shown in Fig. 1 for the best model) is excellent for most of the trees, although there is a tendency to mildly overestimate the survival probability of the small proportion of trees with a survival probability of <0.80 (i.e., very unhealthy trees) (Fig. 1). Parameters behaved as expected, with survival probability increasing with GI and PDGR (Fig. 2a; Supplementary Table S2<sup>1</sup>), and VIF indicated no problems with multicollinearity, with all values being less than 2.

All of the best models for *A. magnifica* included a GI metric (Table 3). However, PDGR does not appear to offer any advantage over dbh. As with *A. concolor*, the discrimination of the best models is good, and calibration is also good, except for a mild overestimation of survival probability for the unhealthiest trees (Fig. 1). Parameters behave as expected (Fig. 2b; Supplementary Table S2<sup>1</sup>),

**Table 2.** *Abies concolor*,  $n = 6231$  (5852 survivors and 379 dead).

Model	$\Delta$ AIC	Akaike weight	Evidence ratio	ROC
PDGR <sub>ME</sub> + GI <sub>ME</sub>	0.00	0.75	1.00	0.770
PDGR <sub>DI</sub> + GI <sub>DI</sub>	2.17	0.25	2.96	0.769
GI <sub>ME</sub>	22.56	0.00	$7.90 \times 10^4$	0.764
PDGR <sub>DI</sub> + diameter growth rate	23.71	0.00	$1.41 \times 10^5$	0.767
dbh + GI <sub>ME</sub>	24.21	0.00	$1.81 \times 10^5$	0.764
dbh + diameter growth rate	24.32	0.00	$1.91 \times 10^5$	0.767
Diameter growth rate	24.94	0.00	$2.60 \times 10^5$	0.766
GI <sub>DI</sub>	25.00	0.00	$2.69 \times 10^5$	0.763
PDGR <sub>ME</sub> + diameter growth rate	25.19	0.00	$2.96 \times 10^5$	0.767
dbh + GI <sub>DI</sub>	26.97	0.00	$7.17 \times 10^5$	0.763
Basal area + GI <sub>ME</sub>	59.09	0.00	$6.80 \times 10^{12}$	0.753
Basal area + diameter growth rate	60.23	0.00	$1.20 \times 10^{13}$	0.760
Basal area + GI <sub>DI</sub>	60.86	0.00	$1.64 \times 10^{13}$	0.752
PDGR <sub>ME</sub> + relative diameter growth rate	75.33	0.00	$2.28 \times 10^{16}$	0.741
PDGR <sub>DI</sub> + relative diameter growth rate	81.13	0.00	$4.15 \times 10^{17}$	0.740
PDGR <sub>ME</sub> + relative basal area growth rate	98.91	0.00	$3.00 \times 10^{21}$	0.734
PDGR <sub>DI</sub> + relative basal area growth rate	105.18	0.00	$6.92 \times 10^{22}$	0.733
dbh + relative diameter growth rate	138.64	0.00	$1.27 \times 10^{30}$	0.720
PDGR <sub>DI</sub> + basal area growth rate	156.01	0.00	$7.55 \times 10^{33}$	0.705
Relative diameter growth rate	158.62	0.00	$2.78 \times 10^{34}$	0.711
dbh + basal area growth rate	159.96	0.00	$5.43 \times 10^{34}$	0.714
dbh + relative basal area growth rate	160.84	0.00	$8.42 \times 10^{34}$	0.711
PDGR <sub>ME</sub> + basal area growth rate	161.13	0.00	$9.75 \times 10^{34}$	0.703
Basal area growth rate	167.38	0.00	$2.22 \times 10^{36}$	0.713
PDGR <sub>DI</sub>	170.79	0.00	$1.22 \times 10^{37}$	0.689
PDGR <sub>ME</sub>	176.81	0.00	$2.48 \times 10^{38}$	0.685
Relative basal area growth rate	177.62	0.00	$3.71 \times 10^{38}$	0.703
Basal area + basal area growth rate	206.28	0.00	$6.21 \times 10^{44}$	0.733
Basal area + relative diameter growth rate	206.43	0.00	$6.70 \times 10^{44}$	0.715
dbh	215.88	0.00	$7.55 \times 10^{46}$	0.666
Basal area + relative basal area growth rate	227.73	0.00	$2.83 \times 10^{49}$	0.712
Basal area	277.31	0.00	$1.64 \times 10^{60}$	0.654

**Notes:** PDGR<sub>DI</sub> and PDGR<sub>ME</sub> are potential growth rate for the double-inflection and modified exponent models, respectively. GI<sub>ME</sub> and GI<sub>DI</sub> are the growth indices calculated using the double-inflection and modified exponent models, respectively.  $\Delta$ AIC represents differences in model performance relative to the best model, with values less than 2 indicating essentially no difference. The Akaike weight and evidence ratio represent the relative strength of the model compared with the others. ROC is the receiver operating characteristic curve, a measure of model discrimination (see Methods for more detail).

and VIF indicated no problems with multicollinearity, with all values being less than 2.

The best models for *C. decurrens* included a combination of a PDGR metric and a GI metric (Table 4). Models with PDGR far exceed those with other size-related measures in terms of weight of evidence. However, the best GI model is only modestly better than the best model that included the diameter growth rate ( $\Delta$ AIC = 2.53). Discrimination for the top models is excellent. Calibration appears to be good, except for, again, the slight over-estimation of survival probability for the unhealthiest trees. Parameters behave as expected (Fig. 2c; Supplementary Table S2<sup>1</sup>), and VIF indicated no problems with multicollinearity, with all values being less than 2.

Finally, the top-ranked model for *P. lambertiana* was a simple combination of dbh and diameter growth rate (Table 5). Models with PDGR and GI were essentially indistinguishable ( $\Delta$ AIC < 2) but, being more complex measures to calculate, did not appear to offer any advantage. Discrimination was excellent for the models. Calibration showed the same pattern as for the other three spe-

cies, with excellent calibration for most trees and a modest over-estimation of survival probability for the unhealthiest trees. Parameters behave as expected (Fig. 2d; Supplementary Table S2<sup>1</sup>), and VIF indicated no problems with multicollinearity, with all values being less than 2.

## Discussion

Forest researchers have long known that, within a species for trees of similar size and growing under similar conditions, a rapidly growing tree is usually more likely to survive than a slowly growing tree. This basic observation is at the root of attempts to develop indices of tree health based on simple metrics of growth rate. However, the creation of such indices is complicated by the fact that, in addition to varying with tree health, the most widely used metrics of tree growth rate also vary systematically (i.e., regardless of tree health) with tree size. For example, after an initial increase, diameter (or radial) growth rate often declines with increasing size, a trend that is routinely removed in dendro-chronological analyses (e.g., Diaz et al. 2001). As a result, a simple index based solely on absolute diameter growth would systematically underestimate the survival probability of big trees relative to small trees. Relative diameter growth rate (diameter growth rate divided by diameter) decreases even more rapidly with tree size. Conversely, in spite of some early assertions that basal area growth rate remains effectively constant across tree sizes (Baker 1934; Spurr 1951; Hartesveldt et al. 1975), basal area growth rate instead usually increases with tree size (e.g., Phipps and Whiton 1988; Clark and Clark 1999; Duchesne et al. 2002, 2003; Johnson and Abrams 2009; Di Filippo et al. 2012), meaning that an index based on absolute basal area growth would systematically overestimate the survival probability of big trees relative to small trees. Finally, relative basal area growth rate (basal area growth rate divided by basal area), like relative diameter growth, decreases rapidly with tree size.

We tested whether we could remove the complicating effects of tree size by creating a GI that expresses a tree's actual diameter growth rate as a fraction of the PDGR of a tree of that size and whether PDGR by itself also had explanatory value.

## Value of potential growth

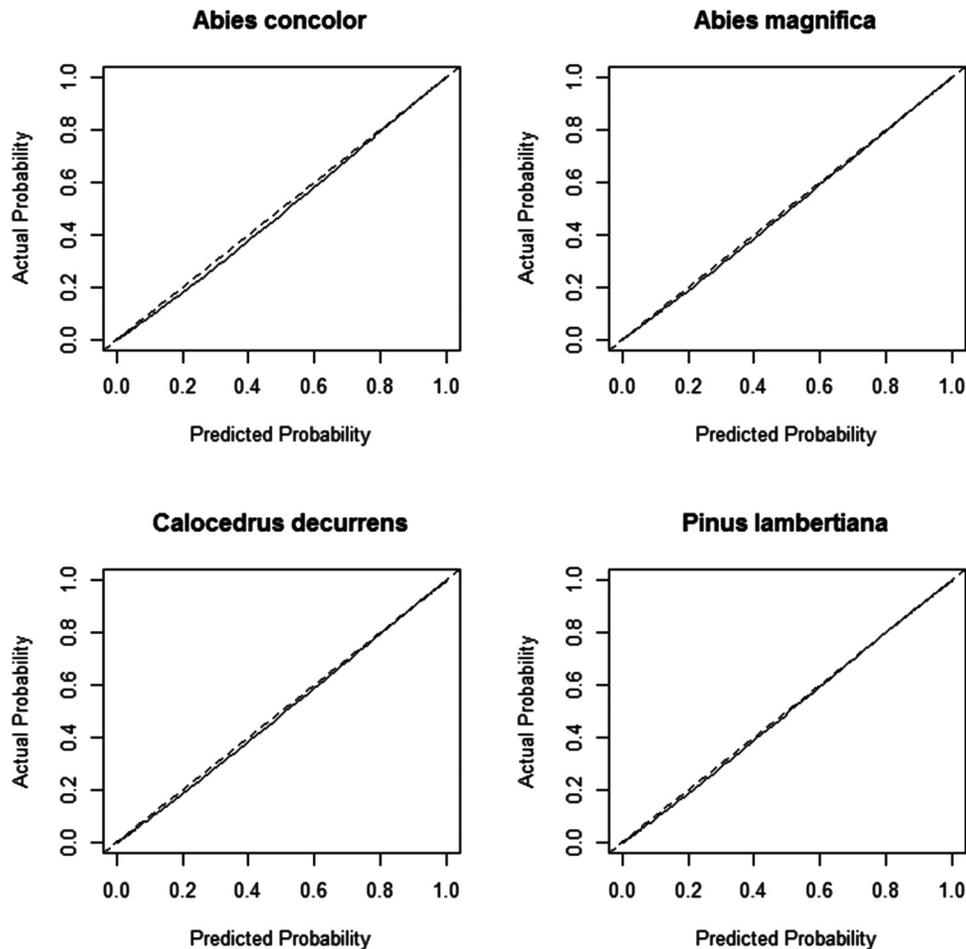
For *A. concolor*, *A. magnifica*, and *C. decurrens*, models that included GI or a combination of GI and PDGR were substantially better than models that included only standard measures. This suggests that for many species, potential growth — both directly and as part of an index — may hold information important to understanding tree mortality and that our ability to assess tree health as a whole might be improved through its use.

For GI, the explanation is straightforward. Scaling realized growth against its potential (i.e., PDGR) should plausibly provide a better estimate of tree vigor. The index represents how far a given tree is from its maximum potential vigor, and because PDGR is a function of tree diameter, GI should perform consistently across the full range of tree sizes.

## Size-related measures

An ideal measure of tree health would be one in which a given value of the metric indicates the same survival probability regardless of the diameter of the tree; this was our motivation for creating and testing GI. Interestingly, however, the best models for all species also included either a direct measure of tree size or a metric related to size (i.e., PDGR), upending the hope that the GI metric alone might offer the best prediction. The most obvious explanation is that there is a fundamental change in the baseline survival probability of a tree with size. Such changes could be caused by, for example, differences in the insects and pathogens that attack trees of different sizes or changes in resource availability (e.g., a bigger tree might have more reserves and better access to light, water, and nutrients).

Fig. 1. Logistic calibration curves for the top models for each species comparing actual and predicted 5-year probabilities of survival. The solid line is the calibration curve, and the dashed line is the one-to-one line representing perfect calibration.



### PDGR versus dbh and basal area

In two cases, PDGR proved to be a stronger size-related predictor than dbh or basal area in our models, although the mechanism for this is not clear. It may be that the growth potential of some tree species corresponds with developmental changes in a tree's ability to survive. In other words, a tree has the capacity to achieve its largest diameter growth rate when it is at its maximum vigor and most resistant to the agents of mortality. An alternative explanation is that the shape of the PDGR curve for some species roughly corresponds to the shape of a hypothetical potential survival curve (i.e., the change in survival probability with size in the absence of competition) and that this correspondence is by chance.

Other studies have found that the relationship between probability of mortality and tree size is U-shaped (e.g., Monserud and Sterba 1999; Yao et al. 2001; Yang et al. 2003) and the estimated PDGR curves for many but not all species roughly mimic the inverse of that shape (e.g., Canham et al. 2006; Das 2012). However, if the connection between PDGR and mortality is simply an otherwise meaningless correspondence of curve shapes, one might expect that just using a polynomial fit for dbh might work better than PDGR for estimating mortality probability, as the curve could be fit more directly. However, no polynomial models (up to the third degree) of dbh offered any improvement over the models shown in Tables 1–4, and in fact, all were notably poorer (analysis not shown). Such an analysis does not definitively rule out the “coincidence” hypothesis, as it is possible that a polynomial form

is simply a poor model, but it does point to a need for further investigation.

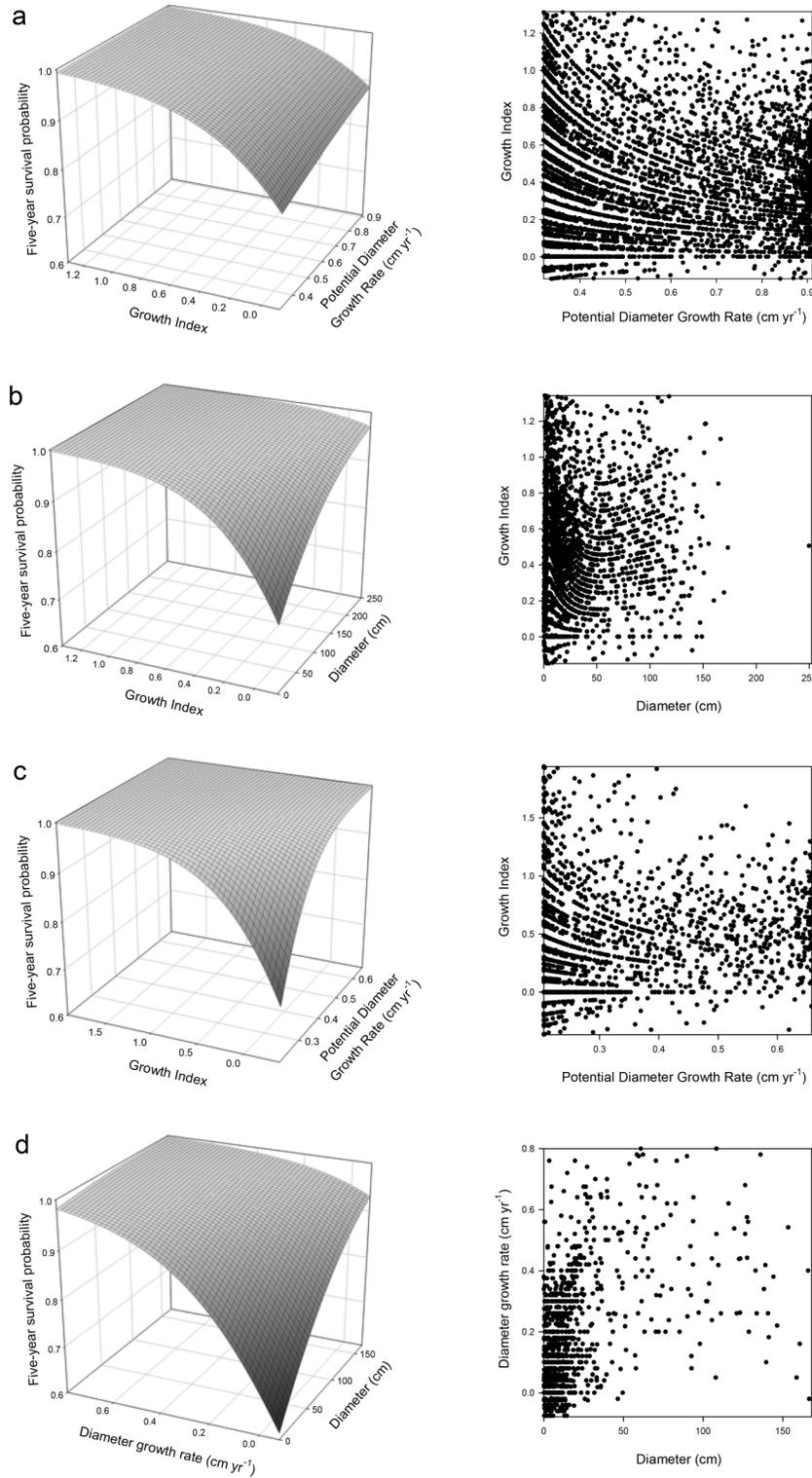
Indeed, our results suggest that we need a better grasp of the baseline survival probability of a tree (i.e., in the absence of competition) and how it changes with tree size. Such an analysis would be conceptually equivalent to estimating PDGR curves in the absence of competition. In the meantime, as a practical matter, including PDGR as a candidate for predicting mortality seems prudent. If one has the needed information to calculate the growth indices, then including the PDGR itself requires no additional effort.

### Examining the exception

For *P. lambertiana*, GI and PDGR models offered no improvement over a simple model that included dbh and diameter growth rate, although the models are essentially indistinguishable ( $\Delta AIC = 0.06$ ). This suggests some fundamental difference in the growth–mortality relationship for this species.

*Pinus lambertiana* differs in several ways from the other species in this study. The PDGR curve for *P. lambertiana* is notably flatter, especially for trees with a >50 cm dbh (Das 2012). This would diminish any relative differences between GI and absolute diameter growth rate, at least for larger trees. In addition, smaller *P. lambertiana* trees are under severe pressure from an exotic pathogen, i.e., *Cronartium ribicola* A. Dietr. (van Mantgem et al. 2004). Perhaps probability of mortality for small *P. lambertiana* trees is thus at least partly decoupled from vigor.

**Fig. 2.** Survival probability surfaces and distributions of data points for the top model for each of the following species: (a) *Abies concolor*, (b) *Abies magnifica*, (c) *Calocedrus decurrens*, and (d) *Pinus lambertiana*. For each species, the left frame shows the survival probability surface, and the right frame shows the distribution of data points used to derive the surface. For each species, values of growth index or diameter growth rate had a few large outliers, and the survival probability surfaces have thus been trimmed at the 2.5% and 97.5% quantiles for these metrics.



Finally, *P. lambertiana* is less shade tolerant than the other species (Burns and Honkala 1990) and relies on gaps to establish rather than persisting under the canopy. Perhaps species that are less shade tolerant have an absolute threshold for growth that is

not tightly related to growth potential when determining survival. This hypothesis could be tested using a suite of species that crosses a broader range of shade tolerance than was available for this study.

**Table 3.** *Abies magnifica*,  $n = 3399$  (3149 survivors and 250 dead).

Model	$\Delta$ AIC	Akaike weight	Evidence ratio	ROC
dbh + $GI_{DI}$	0.00	0.87	1.00	0.782
PDGR <sub>DI</sub> + $GI_{DI}$	6.11	0.04	21.17	0.776
dbh + $GI_{ME}$	6.98	0.03	32.79	0.778
$GI_{DI}$	7.09	0.03	34.61	0.777
PDGR <sub>ME</sub> + $GI_{ME}$	7.11	0.02	35.03	0.775
Basal area + $GI_{DI}$	7.91	0.02	52.17	0.776
Basal area + $GI_{ME}$	16.85	0.00	$4.56 \times 10^3$	0.771
$GI_{ME}$	19.53	0.00	$1.75 \times 10^4$	0.770
Diameter growth rate	24.85	0.00	$2.48 \times 10^5$	0.774
PDGR <sub>DI</sub> + diameter growth rate	25.49	0.00	$3.42 \times 10^5$	0.776
dbh + diameter growth rate	25.89	0.00	$4.19 \times 10^5$	0.777
PDGR <sub>ME</sub> + diameter growth rate	26.73	0.00	$6.36 \times 10^5$	0.776
Basal area + diameter growth rate	29.10	0.00	$2.09 \times 10^6$	0.775
PDGR <sub>ME</sub> + relative diameter growth rate	121.91	0.00	$2.97 \times 10^{26}$	0.714
dbh + relative diameter growth rate	125.22	0.00	$1.55 \times 10^{27}$	0.717
PDGR <sub>ME</sub> + relative basal area growth rate	135.26	0.00	$2.35 \times 10^{29}$	0.710
dbh + relative basal area growth rate	138.21	0.00	$1.03 \times 10^{30}$	0.710
Basal area growth rate	145.97	0.00	$4.99 \times 10^{31}$	0.713
PDGR <sub>ME</sub> + basal area growth rate	146.47	0.00	$6.39 \times 10^{31}$	0.707
dbh + basal area growth rate	147.66	0.00	$1.16 \times 10^{32}$	0.712
PDGR <sub>DI</sub> + basal area growth rate	147.90	0.00	$1.30 \times 10^{32}$	0.711
Basal area + relative diameter growth rate	155.14	0.00	$4.87 \times 10^{33}$	0.705
PDGR <sub>DI</sub> + relative diameter growth rate	155.20	0.00	$5.02 \times 10^{33}$	0.680
Basal area + basal area growth rate	155.30	0.00	$5.28 \times 10^{33}$	0.727
PDGR <sub>ME</sub>	158.07	0.00	$2.11 \times 10^{34}$	0.680
dbh	159.19	0.00	$3.69 \times 10^{34}$	0.677
PDGR <sub>DI</sub> + relative basal area growth rate	165.68	0.00	$9.48 \times 10^{35}$	0.665
Basal area + relative basal area growth rate	167.11	0.00	$1.94 \times 10^{36}$	0.697
Relative diameter growth rate	173.77	0.00	$5.41 \times 10^{37}$	0.662
PDGR <sub>DI</sub>	174.82	0.00	$9.16 \times 10^{37}$	0.636
Relative basal area growth rate	181.40	0.00	$2.46 \times 10^{39}$	0.657
Basal area	184.68	0.00	$1.26 \times 10^{40}$	0.668

Notes: See Note under Table 2 for the definitions of variables.

### The performance of models without PDGR and GI

If we ignore the PDGR and GI models (which may not always be available), dbh and diameter growth rate far outperformed all other measures for all four species, indicating little advantage in transforming data to basal area growth rate or other relative measures for these species at these sites — a result in keeping with a previous study from some of the same sites (Das et al. 2007). This belies the implicit assumption sometimes made in the literature that basal area growth rate will always be a better measure of tree health than diameter growth rate (e.g., Pedersen 1998; Ireland et al. 2014). Although it is true that basal area growth rate more closely represents tree mass growth, our results demonstrate that this does not always translate into a more accurate representation of tree mortality probability.

Note that our results are in contrast to work with *Picea abies* (L.) Karst (Norway spruce) in Switzerland (Bigler and Bugmann 2004) in which a relative basal area growth rate model outperformed absolute radial growth rate in distinguishing between live and dead trees (model 4 and model 5 in that paper). In part, the differences might be due to the analytical approach, as the authors of that study were able to perform a longitudinal analysis using tree rings, but they might also be explained by species differences and stand history. In our old-growth forests, for example, ring widths do not always follow the expected negative exponential pattern when comparing small and large trees (see appendix A in Das et al.

**Table 4.** *Calocedrus decurrens*,  $n = 3363$  (3096 survivors and 267 dead).

Model	$\Delta$ AIC	Akaike weight	Evidence ratio	ROC
PDGR <sub>ME</sub> + $GI_{ME}$	0.00	0.65	1.00	0.831
PDGR <sub>ME</sub> + diameter growth rate	2.53	0.18	3.54	0.830
PDGR <sub>DI</sub> + $GI_{DI}$	3.29	0.13	5.17	0.830
PDGR <sub>DI</sub> + diameter growth rate	5.72	0.04	17.45	0.829
dbh + diameter growth rate	13.83	0.00	$1.01 \times 10^3$	0.826
dbh + $GI_{ME}$	18.68	0.00	$1.14 \times 10^4$	0.827
dbh + $GI_{DI}$	18.82	0.00	$1.22 \times 10^4$	0.827
Diameter growth rate	45.14	0.00	$6.35 \times 10^8$	0.814
Basal area + diameter growth rate	51.51	0.00	$1.53 \times 10^{11}$	0.813
Basal area + $GI_{ME}$	70.15	0.00	$1.71 \times 10^{15}$	0.813
Basal area + $GI_{DI}$	70.35	0.00	$1.89 \times 10^{15}$	0.813
$GI_{ME}$	78.24	0.00	$9.76 \times 10^{16}$	0.802
$GI_{DI}$	78.31	0.00	$1.01 \times 10^{17}$	0.802
PDGR <sub>ME</sub> + basal area growth rate	137.99	0.00	$9.19 \times 10^{29}$	0.785
PDGR <sub>DI</sub> + basal area growth rate	138.84	0.00	$1.41 \times 10^{30}$	0.786
dbh + basal area growth rate	141.91	0.00	$6.54 \times 10^{30}$	0.772
Basal area growth rate	157.23	0.00	$1.39 \times 10^{34}$	0.781
Basal area + basal area growth rate	157.88	0.00	$1.92 \times 10^{34}$	0.798
PDGR <sub>ME</sub> + relative diameter growth rate	166.86	0.00	$1.71 \times 10^{36}$	0.762
PDGR <sub>DI</sub> + relative diameter growth rate	172.18	0.00	$2.44 \times 10^{37}$	0.760
dbh + relative diameter growth rate	182.66	0.00	$4.61 \times 10^{39}$	0.763
PDGR <sub>ME</sub> + relative basal area growth rate	199.56	0.00	$2.16 \times 10^{43}$	0.741
PDGR <sub>DI</sub> + relative basal area growth rate	202.94	0.00	$1.17 \times 10^{44}$	0.740
PDGR <sub>ME</sub>	205.43	0.00	$4.05 \times 10^{44}$	0.706
PDGR <sub>DI</sub>	208.04	0.00	$1.50 \times 10^{45}$	0.698
dbh + relative basal area growth rate	226.22	0.00	$1.33 \times 10^{49}$	0.723
dbh	236.80	0.00	$2.63 \times 10^{51}$	0.696
Basal area + relative diameter growth rate	247.07	0.00	$4.47 \times 10^{53}$	0.761
Basal area + relative basal area growth rate	272.82	0.00	$1.74 \times 10^{59}$	0.718
Basal area	276.13	0.00	$9.13 \times 10^{59}$	0.694
Relative diameter growth rate	292.45	0.00	$3.19 \times 10^{63}$	0.684
Relative basal area growth rate	308.79	0.00	$1.13 \times 10^{67}$	0.646

Notes: See Note under Table 2 for the definitions of variables.

(2007)). In fact, preliminary work at other locations in the Sierra Nevada suggests that the best predictors among standard measures may well vary depending on the history of the stand.

Whatever the reason, we argue that one should not assume that diameter growth rate will be an inferior predictor to other transformations for predicting mortality (e.g., Pedersen 1998; Ireland et al. 2014). None of the standard measures would seem to have an inherent advantage over the others, and until some more mechanistic picture emerges, we should not prefer one over another without first testing them all.

Ultimately, the best tree mortality models will also likely include metrics that are more directly related to a tree's probability of mortality than to its growth rate or size such as growth efficiency (e.g., Waring and Pitman 1985), allocations to defenses, and nonstructural carbohydrate reserves. However, until these metrics become easier to obtain, it remains likely that simple measurements of growth rate and size will continue to be the most practical information that we can obtain for large numbers of trees.

### Looking beyond the Sierra Nevada

An obvious next step would be to extend this work to other species for which PDGR curves are available to assess the generality of our results. Although developing PDGR models is both data and computationally intensive, a number of such growth-competition studies have already been completed in a variety of forested eco-

**Table 5.** *Pinus lambertiana*,  $n = 1418$  (1045 survivors and 373 dead).

Model	$\Delta$ AIC	Akaike weight	Evidence ratio	ROC
dbh + diameter growth rate	0.00	0.35	1.00	0.798
PDGR <sub>ME</sub> + diameter growth rate	0.06	0.34	1.03	0.799
PDGR <sub>ME</sub> + GI <sub>ME</sub>	1.27	0.19	1.89	0.797
dbh + GI <sub>ME</sub>	4.13	0.05	7.87	0.796
Diameter growth rate	4.28	0.04	8.50	0.795
PDGR <sub>DI</sub> + diameter growth rate	6.05	0.02	20.58	0.796
dbh + GI <sub>DI</sub>	7.03	0.01	33.66	0.794
PDGR <sub>DI</sub> + GI <sub>DI</sub>	19.78	0.00	1.97×10 <sup>4</sup>	0.792
GI <sub>DI</sub>	20.38	0.00	2.66×10 <sup>4</sup>	0.789
GI <sub>ME</sub>	26.57	0.00	5.89×10 <sup>5</sup>	0.786
Basal area growth rate	30.56	0.00	4.33×10 <sup>6</sup>	0.794
dbh + basal area growth rate	32.22	0.00	9.93×10 <sup>6</sup>	0.790
PDGR <sub>ME</sub> + basal area growth rate	32.28	0.00	1.02×10 <sup>7</sup>	0.793
PDGR <sub>DI</sub> + basal area growth rate	32.46	0.00	1.12×10 <sup>7</sup>	0.797
PDGR <sub>ME</sub> + relative diameter growth rate	38.29	0.00	2.07×10 <sup>8</sup>	0.784
PDGR <sub>ME</sub> + relative basal area growth rate	41.90	0.00	1.25×10 <sup>9</sup>	0.783
dbh + relative diameter growth rate	42.61	0.00	1.78×10 <sup>9</sup>	0.784
dbh + relative basal area growth rate	46.43	0.00	1.21×10 <sup>10</sup>	0.782
Basal area + diameter growth rate	49.70	0.00	6.20×10 <sup>10</sup>	0.788
PDGR <sub>ME</sub>	49.78	0.00	6.45×10 <sup>10</sup>	0.774
dbh	55.45	0.00	1.10×10 <sup>12</sup>	0.772
Basal area + GI <sub>DI</sub>	57.69	0.00	3.36×10 <sup>12</sup>	0.785
Basal area + GI <sub>ME</sub>	60.50	0.00	1.37×10 <sup>13</sup>	0.785
Basal area + basal area growth rate	87.99	0.00	1.28×10 <sup>19</sup>	0.792
Relative diameter growth rate	101.90	0.00	1.34×10 <sup>22</sup>	0.750
PDGR <sub>DI</sub> + relative diameter growth rate	102.16	0.00	1.53×10 <sup>22</sup>	0.748
Relative basal area growth rate	103.97	0.00	3.77×10 <sup>22</sup>	0.750
PDGR <sub>DI</sub> + relative basal area growth rate	104.59	0.00	5.14×10 <sup>22</sup>	0.745
PDGR <sub>DI</sub>	108.76	0.00	4.15×10 <sup>23</sup>	0.735
Basal area + relative diameter growth rate	130.58	0.00	2.27×10 <sup>28</sup>	0.776
Basal area + relative basal area growth rate	133.33	0.00	8.95×10 <sup>28</sup>	0.775
Basal area	139.08	0.00	1.59×10 <sup>30</sup>	0.767

Notes: See Note under Table 2 for the definitions of variables.

systems, including a number of studies on species in the United States, Canada, Spain, and Panama (Canham et al. 2004, 2006; Uriarte et al. 2004; Coates et al. 2009; Gomez-Aparicio et al. 2011; Das 2012; van Mantgem and Das 2014). Indeed, barriers to further analyses continue to decrease as computational power increases and the computational software for developing complex growth-competition models becomes increasingly available.

## Conclusions

Relating a tree's health to its potential for growth has a strong intuitive appeal and a sensible biological underpinning. Recent advances in the development of growth-competition relationships have begun to make available empirically derived estimates of how a tree's potential growth changes with tree size. We have shown that the metrics calculated from those PDGR curves were effective at estimating tree survival probability and, in most cases, substantially improved our ability to assess tree health. Hopefully, as we move forward, the details of these growth-mortality relationships — particularly when they do not behave as expected — will lead us to a clearer understanding of the mechanisms that lead to a tree's death and ultimately a better understanding of forest health as a whole.

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