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Evaluation of mixed-effects models for predicting Douglas-fir mortality

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ABSTRACT

We examined the performance of several generalized linear fixed- and mixed-effects individual-tree mortality models for Douglas-fir stands in the Pacific Northwest. The mixed-effects models accounted for sampling and study design overdispersion. Inclusion of a random intercept term reduced model bias by 88% relative to the fixed-effects model; however, model discrimination did not substantially differ. An uninformed version of the mixed model that used only its fixed effects parameters produced predicted mortality values that exceeded the fixed-effects model bias by 31%. Overall, we did not find compelling evidence to suggest that the mixed models fit our data better than the fixed-effects model. In particular, the mixed models produced fixed-effects parameter estimates that predicted unreasonably high mortality rates for trees approaching 1 m in diameter at breast height.

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1. Introduction

Tree mortality is a critical component of stand growth and yield models. It is also highly variable and difficult to predict (Lee, 1971; Dobbertin and Biging, 1998). The nature of data collected to model and quantify mortality, however, may challenge the assumptions inherent in statistical tools used to estimate mortality. In this study we examine a generalized linear mixed-effects method to account for data structure and lack of independence.

Lee (1971) and Staebler (1953) described tree mortality as either regular or irregular. Irregular mortality includes death occurring from insects, disease, fire, snow damage, and wind. This type of mortality typically is episodic, brief, and difficult to predict. Regular mortality is more predictable, and includes influences such as competition for light, moisture, and nutrients. As stands become more crowded, a degree of mortality usually occurs. Trees may die for several possibly co-occurring reasons: suppression where stands are differentiating, weakening due to insects and disease, and buckling where stems become tall and thin (Oliver and Larson, 1996). Trees in stands characterized by regular mortality exhibit a preponderance of mortality amongst smaller-diameter individuals that are over-topped by neighbors (Peet and Christensen, 1987). Mortality rates become low for established trees until larger diameters are reached and the mortality rate increases again (Buchman et al., 1983; Harcombe, 1987; Monserud and Sterba, 1999).

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Although both classes of mortality may affect stands, only single-tree regular mortality models are routinely incorporated in most growth and yield simulators such as FVS (Dixon, 2011) and ORGA-NON (Hann, 2011).

Single-tree mortality models have been developed using a variety of data and approaches. Logistic models are common for data sets where revisit frequency consists of equal-length time periods (Hamilton, 1986; Bigler and Bugmann, 2003; Jutras et al., 2003; Moore et al., 2004; Adame et al., 2010). However, if the time periods differ, a common solution is to use the logistic model but insert time as a power upon survival probabilities or use a complementary log–log link function (e.g., Monserud, 1976; Eid and Tuhus, 2001; Moore et al., 2004; Temesgen and Mitchell, 2005; Fortin et al., 2008). For stands where remeasurement occurred multiple times, researchers either avoid pseudoreplication at the level of the tree by omitting all but the last remeasurement for each tree (Hamilton, 1986) or include the remeasurement information (Temesgen and Mitchell, 2005; Fortin et al., 2008).

Data used in these analyses are from nested samples, with the highest level referred to as installations. Each installation contains one or more plots; each plot contains many trees with repeated measurements. Analyses performed on individual tree mortality data has recently begun to account for the structured nature and non-independence by using generalized linear mixed-effects models. Logistic models by Adame et al. (2010) and Jutras et al. (2003) include random intercepts for study plots or stands. A complementary log–log model by Fortin et al. (2008) included an adjusted intercept with random effects for study plot and specific time interval nested within plot.

Prediction performance for nonlinear mixed-effects models may be improved (less bias and greater precision) when compared to corresponding fixed-effects models conditional on the availability

of previous information on the subject; however, in absence of random-effects information, predictions using just the fixed portions of the parameterization from the nonlinear mixed-effects model exhibit greater bias and less precision than even the original fixed-effects model (Monleon, 2003; Temesgen et al., 2008; Garber et al., 2009). Setting the random effect to zero follows from prediction theory only for linear mixed models, but it has a different meaning for nonlinear models. Consider a linear mixed model where X is a $(n \times p)$ design matrix where n is the number of observations and p is the number of fixed-effects parameters, β is a vector of linear slope values, Z is a $(n \times r)$ design matrix where r is the number of random effects parameters, γ represents G-sided random effects parameterization, and ε is the random error:

$$y = X\beta + Z\gamma + \varepsilon, \text{ where } E(\gamma) = E(\varepsilon) = 0$$

Then, conditional on the random effect, and because the expectation is a linear operator,

$$E(y|\gamma) = X\beta + Z\gamma$$

Unconditionally,

$$E(y) = E(X\beta + Z\gamma + \varepsilon) = X\beta + ZE(\gamma) = X\beta$$

Thus, in a linear model, the unconditional expectation can be calculated from the conditional expectation by setting the random effect to zero:

$$E(y) = E(y|\gamma = 0)$$

For a nonlinear model, this is not the case. The nonlinear mixed model can be written as:

$$Y = f(X, \beta, Z, \gamma) + \varepsilon, \text{ where } E(\gamma) = E(\varepsilon) = 0$$

Conditional on installation:

$$E(y|\gamma) = f(X, \beta, Z, \gamma)$$

Unconditionally:

$$E(y) = E[E(y|\gamma)] = E[f(X, \beta, Z, \gamma)]$$

Unlike linear models, for nonlinear models, the unconditional model is not the same as the conditional model with the random effects set to zero:

$$E(y) \neq E(y|\gamma = 0) \text{ because } E[f(X, \beta, Z, \gamma)] = \int f(X, \beta, Z, \gamma) d\mu(\gamma) \neq f(X, \beta, Z, \gamma = 0), \text{ where } \mu(\gamma) \text{ is the distribution function of } \gamma.$$

The model for $E(y)$ is known as the population-average model and the model for $E(y|\gamma)$ is known as the subject-specific model. For nonlinear mixed models, those versions are different. Choosing which type of model and inference is appropriate for each objective is fundamental when dealing with nonlinear mixed models. For a tree from a completely new stand that does not have information to estimate the random effects and, therefore, condition on the stand effect, the proper model is a population average model. When using the subject-specific model with $\gamma = 0$ (i.e., the subject-specific model for the average stand), prediction performance is expected to decline. Again, in linear mixed models this is not an issue, because setting $\gamma = 0$ yields the population-average model.

Forest management requires models that are useful beyond their study areas. Generalized or nonlinear mixed-effects models can increase bias when applied to novel data (e.g., Robinson and Wykoff, 2004). Mixed models require estimated information about a hierarchical level that may be unknown for novel data sets. One technique to extend generalized linear or nonlinear mixed-effect model applicability is to utilize minimal data from new stands for estimating the random effects parameters. This allows the application of nonlinear mixed effects models beyond their original data frames (Monleon, 2003; Temesgen et al., 2008; Garber et al., 2009). However, this technique may be limited by the response variable type. In those studies it worked for tree height, a continuous static variable. Our

study's response variable, individual tree mortality, is rare, binomial, dynamic, and requires several years of data collection to observe. Thus, incorporating subsample information from new plots to inform mixed-effects model predictions is generally unfeasible.

The objectives of this study are to (1) determine whether a generalized linear mixed model fit to repeatedly remeasured Douglas-fir (*Pseudotsuga menziesii* [Mirb.] trees can improve mortality estimation over a previous nonlinear estimation approach (Hann et al., 2003, 2006), and (2) compare the predictive abilities of mixed-effects models to nonlinear least squares estimation in the presence and absence of random effects information. We expect biased predictions from the mixed model that lacks random effects information, but examine the degree by which those results are useful relative to the nonlinear least squares predictions. Taken together, our goal is to examine how well models met our objectives and whether we produce a model that is useful for current Douglas-fir growth and yield simulators.

2. Methods

2.1. Study area and data acquisition

Data used in this analysis were obtained from randomly located installations on nine land ownerships and represent a subset of data described in Hann et al. (2003, 2006). One of the uses of the overall data collection effort was to calibrate the ORGANON stand development model (Hann, 2011) for intensively managed Douglas-fir in the Pacific Northwest region of the USA and Canada. What follows is a description of the subsetted data. The data were from 304 permanent sample installations from Southwest British Columbia, Western Washington, and Northwestern Oregon. The 820 plots within those installations contained 195,795 revisit data collected from 70,720 Douglas-fir trees. Trees were revisited one to 18 times over the course of data collection. Time between revisits was not equal among trees or plots, and varied from 3 to 7 years (median = 5 years). The fixed-area plots varied in size from 0.041 to 0.486 ha (mean = 0.069). The average breast height age was 27.8 years and ranged from 3 to 108 years. Plots included in this study were not subject to thinning or fertilization experimental treatments.

We further reduced the data set according to two criteria. The first criterion only permitted data from installations that had two or more plots. This criterion was necessary for creating mixed-effects mortality predictions (described below), and it removed 12,616 trees, 38,314 observations, and 67 single-plot installations from the data set. The second criterion was that we retained only trees with DBH <101.6 cm. We removed larger-DBH trees to allay model convergence issues likely arising from a paucity of mortality information leading to a lack of fit at that extreme. This removed eight observations and five trees (<0.01% of data) and permitted model convergence. The resulting data set included 157,473 revisits of 58,099 trees in 753 plots located within 201 installations.

2.2. Mortality estimation

We based this analysis on a general equation of mortality given differing plot revisit schedules as described by Hann et al. (2006):

$$PM = 1.0 - [1.0 + e^{-(X/\beta)}]^{-PLEN} + \varepsilon_{PM} \quad (1)$$

where PLEN is the length of the growth period in 5-year increments (i.e., length of a growth period in years divided by 5), PM is the 5-year mortality rate, and ε_{PM} is the random error on PM. The response variable distribution is y – Bernoulli (π) where the observed response was y and π is the corresponding response probability.

Several different parameterizations have been examined for $X\beta$. Hann et al. (2006) modeled $X\beta$ as:

$$X\beta = \beta_0 + \beta_1\text{DBH} + \beta_2\text{CR} + \beta_3\text{BAL} + \beta_4\text{DFSI} \quad (2)$$

The variable DBH is diameter at breast height (cm) at 1.3 m, CR is tree crown ratio, BAL (m²/ha) is basal area per ha in trees with diameters larger than that of the subject tree on the plot, and DFSI is the Douglas-fir site index (Hann and Scrivani, 1987) in meters. We examined the predictive ability of this model in three ways. We wished to investigate whether the mixed-effects approach would provide a reasonable mortality prediction for older trees, so we included the square of DBH (DBH²) as a predictor variable (e.g., Monserud and Sterba, 1999; Hann and Hanus, 2001). CR was subsampled on many of the plots in the modeling data set and would require the imputation of the missing values if used in a mortality equation. This would introduce prediction error issues which we decided to avoid by removing CR from the analysis. We retained BAL to represent competition experienced by an individual tree (Wykoff et al., 1982; Wykoff, 1986; Temesgen and Mitchell, 2005). The parameterization we used in this analysis was:

$$X\beta = \beta_0 + \beta_1\text{DBH} + \beta_2\text{DBH}^2 + \beta_3\text{BAL} + \beta_4\text{DFSI} \quad (3)$$

We present a generalized linear fit of this model, fit via a maximum likelihood estimator (PROC GLIMMIX, SAS Inc. 2008). This model produced results identical to those from the nonlinear approach employed by Hann et al. (2006) to estimate tree mortality. We refer to this model as NLS given its equality to the original procedure. We also examined two generalized linear models with the same parameterization as (3). One corrected for model overdispersion by altering the model variance. The other corrected for overdispersion and included a random effect term for the model intercept grouped by installation. We selected installation as a grouping level instead of plot due to our desire to validate models using a leave-one-out approach (described below). We refer to these models as GXR and GXME, respectively.

We constructed GXR and GXME using the generalized linear mixed-model procedure Proc GLIMMIX (SAS Institute Inc., 2008). The procedure made use of a pseudo-likelihood estimator instead of a maximum likelihood estimator due to the presence of R-sided mixed effects (Schabenberger, 2007). The advantages of GLIMMIX over other SAS procedures (e.g., Proc NLMIXED) included the ability to incorporate more than one random effect into the model (G-sided random effect) and to include a multiplicative overdispersion parameter (R-sided random effects). A disadvantage of GLIMMIX is that its pseudo-likelihood estimator may produce biased estimates in certain contexts (Breslow and Lin, 1995). The main structural difference between the marginal (fixed-effects or population-averaged; i.e., NLS, GXR) and the mixed-effects model GXME is the incorporation of the G-sided random effects terms $Z\gamma$ into the mixed-effects model structure:

$$\text{PM} = 1.0 - [1.0 + e^{-(X\beta + Z\gamma)}]^{-\text{PLEN}} + \varepsilon_{\text{PM}} \quad (4)$$

The $Z\gamma$ term alters the model linear predictors. We created a model with an installation grouped random intercept by structuring the linear predictors of our model as:

$$\begin{aligned} \eta &= X\beta + Z\gamma \\ &= \beta_0 + b_i + \beta_1\text{DBH}_{ij} + \beta_2\text{DBH}_{ij}^2 + \beta_3\text{BAL}_{ij} + \beta_4\text{DFSI}_{ij} \end{aligned} \quad (5)$$

The linear predictors included a population-level intercept β_0 , a deviation from that intercept of amount b for installation i , and the remaining parameter estimates for observations j in installations i . The modified logit function is:

$$\pi_{ij} = f(\eta) = 1 - \{1 + \exp(-[\eta])\}^{-\text{PLEN}}$$

$$b_i \sim N(0, \theta_b^2)$$

$$\text{Var}(y_{ij} | \pi_{ij}) = \pi_{ij}(1 - \pi_{ij}) \quad (6)$$

In GLIMMIX, the variance of observations, conditional on the random effects, is:

$$\text{Var}[Y|\gamma] = A^{1/2}RA^{1/2}$$

The diagonal matrix A contains the variance functions of the model (i.e., Eq. (6)) and expresses the variance function for the i th observation (Littell et al., 2006, p. 535). G-sided random effects will therefore affect the values for A . The random effects matrix $R = \phi I$ where I is an identity matrix and ϕ is a dispersion scale parameter. In binomial models where there is no overdispersion, $\phi = 1$. However, if data are overdispersed, the variances can be accordingly increased by changing this parameter. We tested for model overdispersion using the Pearson's statistic (Littell et al., 2006). We additionally weighted our tree remeasurement data by their respective plot sizes (Flewelling and Monserud, 2002). Model weighting is accomplished by calculating ϕ/w_i , where w is the weight associated with observation i . To summarize, GXME was constructed in PROC GLIMMIX with linear mixed- and fixed-effects predictors from (5) used in the nonlinear Eq. (4). A random intercept was estimated by installation and we included an R-sided random effect to account for overdispersion. Observations for the model were weighted by plot size.

A difficulty with using the estimates for GXME to predict mortality for trees that are not part of a current installation is that no hierarchical parameter values for that installation would be available. The random effects parameters remain uninformed. We explored the utility of applying the uninformed mixed model by examining the predictive ability of an additional model, GXFE. This model incorporates the fixed-effects parameter estimates from GXME but discards its random effects parameterization.

We validated models NLS, GXME, and GXFE using a leave-one-out approach. GXR was excluded as model validation relies on parameter point estimates and its parameter point estimates (not error) should be identical to those for NLS. In this instance we repeatedly fit models to subsets of the data. Each subset included all but one of the plots (model set). The resulting model was used to predict the response of each of the excluded sites' observations (prediction set). In order to facilitate inclusion of models that relied on random effects at the level of installations, we reduced the data set to include only installations with two or more plots. With one plot excluded, the model was still able to estimate a random effect for that installation.

We used model estimates from the model data set to produce residual values for the validation set. We used the Hosmer–Lemeshow test to determine model goodness-of-fit (Hosmer and Lemeshow, 2000) and compared model discrimination by using receiver operating characteristic (ROC) curve analysis and examining the area under the ROC curves. We examined model and bias for the overall validation data set and for different values of BAL, DFSI, and DBH. We calculated mean bias using the following equation:

$$\text{Bias} = \frac{\sum(y_j - \hat{\pi}_{ij})}{n} \quad (7)$$

The symbol y_j is a single mortality observation (1 or 0), $\hat{\pi}_{ij}$ is the fitted value, and n is the number of observations.

3. Results

The data set included the mortality of 9982 trees (6.3% of total). Deaths appeared to be skewed towards smaller DBH categories while mortality appeared to increase at higher BAL volumes,

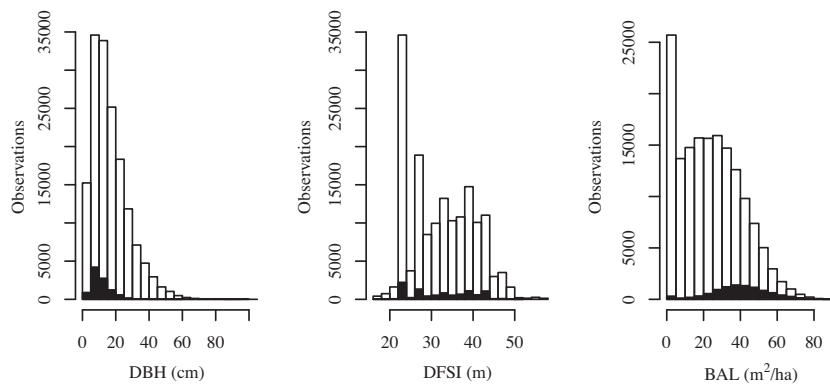


Fig. 1. Histograms of observations (live + dead) by variable name. The clear bars represent all data of a particular category; black bars represent the number of dead observations.

indicating that trees may have been more likely to perish if the stand typically had more trees with basal area greater than the tree in question (Fig. 1).

Model coefficients for the three models were estimated from the full sample data set (Table 1). The inclusion of R-sided random effects variables reduced overdispersion. The Pearson's statistic for the condition distribution for the NLS model was 10.88, substantially different from a value of 1. The Pearson's statistics for GXR and GXME were 1.00 indicating that the inclusion of the R-sided or R- and G-sided random effects corrected for the overdispersion. As a consequence, GXR fixed-effects parameter standard errors were greater than NLS standard errors. A difference among models was the parameter values for DBH^2 , which increased by 60% when comparing NLS to GXME.

Predicted values generated from the mixed-effects model with random variables improved bias compared to the nonlinear model. However, the mixed model's bias suffered when only its fixed effects were considered (Table 2). On average, GXME, with random effects and overdispersion terms, exhibited a bias that was 22% the values of model NLS. Model GXFE's bias was four times greater than the value of NLS.

The area under the ROC curve was 2.3% higher for GXME than for NLS or GXFE, indicating that the mixed model exhibited a slightly greater degree of model discrimination. The values for NLS and GXFE were nearly identical. The Hosmer–Lemeshow goodness-of-fit test statistics were significant ($df = 8, p < 0.001$) for all models considered, indicating that no models fit data at an acceptable level (e.g., $\chi^2 \leq 15.5$). Pearson's residuals increased with $DBH > 20$ cm and $BAL < 40$ m²/ha; a pattern did not appear evident between residuals and DFSI. Among the models, GXFE's score was substantially higher than either NLS or GXME, and NLS had the lowest score of the three. Pearson's correlations among variables was highest between DBH and DBH^2 (0.935), the next highest was between DBH^2 and DFSI (0.191).

Table 1
Fixed and random effects estimates and standard errors (SE) for the generalized linear least squares models NLS, GXR, and GXME. The overdispersion parameter (residual) indicates the size of the underlying residual effect's variance and the standard error of that effect.

	NLS		GXR		GXME	
	Estimate	StdError	Estimate	StdError	Estimate	StdError
<i>Fixed effects</i>						
Intercept	-4.5118	0.02807	-4.5118	0.09267	-5.0958	0.2891
DBH	-0.2105	0.00251	-0.2105	0.00829	-0.2719	0.00677
DBHSQ	0.00168	7.8E-05	0.00168	0.00026	0.00279	0.00017
BAL	0.00421	1.8E-05	0.00421	6.1E-05	0.00495	8.3E-05
DFSI	0.04897	0.00068	0.04897	0.00224	0.05996	0.00804
<i>Random effects</i>						
Residual (Subject = tree)			10.884	0.03879	10.275	0.03665
Intercept (Subject = installation)					0.6353	0.07953

Table 2
Comparisons of model performance at predicting the probability of tree mortality over a five-year period (PM_5). Comparisons include model bias, area under the ROC curve (AUC), a and the Hosmer–Lemeshow goodness-of-fit test statistic (H–L Test). Number of observations = 157,473.

Models	Bias ($P_{5\text{-year mort}}$)	AUC	H–L test
NLS	0.002643908	0.845	366.8
GXME	-0.000604775	0.864	388.8
GXFE	0.0110345	0.844	1505.6

Bias was generally lowest for model GXME across all values of all predictor variables with a few close exceptions (Fig. 2). Values and patterns of bias were similar for NLS and GXFE across variables, although the bias values for GXFE were generally but not always more extreme. In particular, bias for GXFE was more than twice as great as other models at $DBH < 20$ cm. Comparisons of observed and predicted values of mortality (Fig. 3) demonstrate the generally closer fit of the mixed model predicted values to observed mortality. Relative to GXFE, NLS better predicts tree mortality at DBH values < 20 cm and is fairly equivalent at other DBH values. NLS mortality predictions were closer to observed values at all BAL categories except 50–59 m. NLS also outperformed GXFE at four of the six DFSI categories (not including 30–34 and > 45 m).

We compared predicted model performance to observed values to determine where model shortcomings were (Fig. 4). Of note, GXME appeared to best match observed mortality at DBH values < 20 cm while the other models generally underpredicted tree mortality. However, all models except for NLS predicted a dramatic increase in mortality beyond 90 cm DBH. The 20% observed mortality at 97 cm DBH represented one of five trees of that size class perishing. We examined fixed-effects parameter values for GXME for trees with $DBH < 90$ cm to determine if this mortality

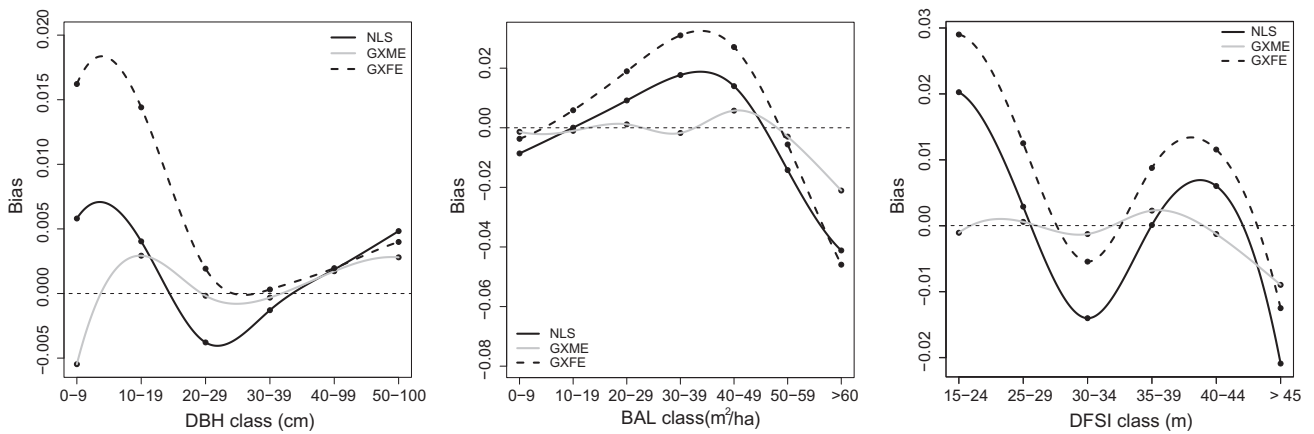


Fig. 2. Prediction bias associated with models NLS, GXME, and GXFE across the range of data values for DBH, BAL, and DFSI.

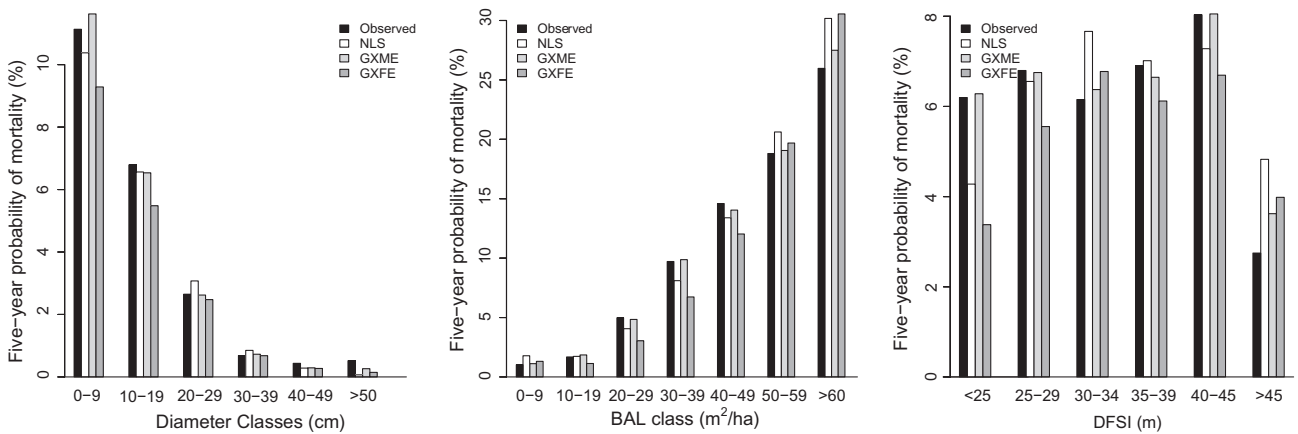


Fig. 3. Five-year predicted and observed probability of mortality. Mortality probabilities are presented by diameter, BAL, and DFSI classes.

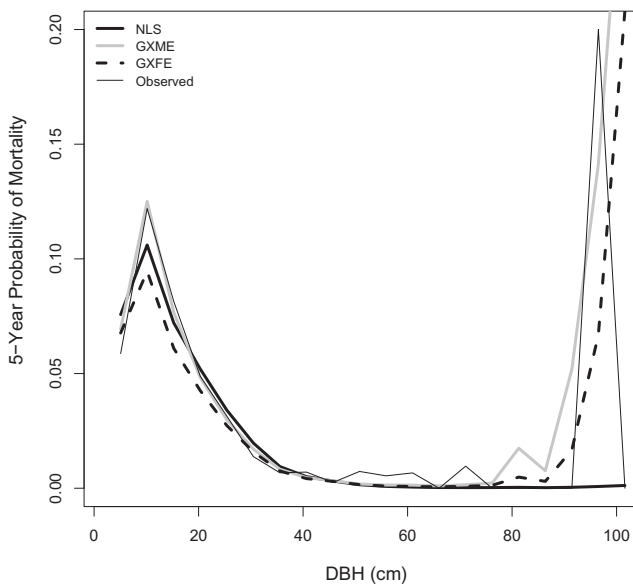


Fig. 4. Predicted mortality rates by DBH and average parameter values at specific DBH values.

was exhibiting a strong influence on DBH^2 and found that results were virtually unchanged.

4. Discussion

We report partial success at meeting our study objectives. The mixed-effect models accounted for overdispersion in the data and accordingly increased parameter standard errors. The mixed-effects model GXME additionally reduced prediction bias relative to NLS. However, the predicted fits at observed parameter values were of concern; the DBH^2 parameter of the mixed-effects model GXME and its related models predicted an unreasonably high mortality rate for trees with $DBH > 90$ cm. The larger-DBH predictions for NLS were more reasonable. The GXME model appeared to best fit the data at $DBH < 40$ cm, a range that included the bulk of our data.

The inclusion of R-sided random effects assisted in reducing model overdispersion. Although unreported, the estimated standard errors of parameter estimates resulting from earlier analyses such as Temesgen and Mitchell (2005) and Hann et al. (2003, 2006) would have been too small. For those authors the models were used in validation trials so the means, not standard errors, affected validation outcomes. The increase in error terms could indicate that previously-supported parameters were not contributing to the model, although all of our parameters remained supported in all models.

Once we included a random intercept in the model along with an R-sided random effect, the term for DBH^2 increased markedly. Bias for the mixed-effects model was improved relative to the marginal model. However, when we examined predicted fits for the

mixed model's fixed-effects parameters without taking into account the individual installation information (random intercept) the bias increased to an amount four times greater than the marginal model. Clearly, it would be difficult to justify this model's use. This finding is similar to results reported by several other authors (Monleon, 2003; Temesgen et al., 2008; Garber et al., 2009), and confirms our expectation that this would be the case.

Other authors provide examples of studies in which mixed models produce an improvement in predictive ability, and minimal data collection allowed for an application of the mixed models to novel stands (Monleon, 2003; Temesgen et al., 2008; Garber et al., 2009). Obtaining ancillary mortality data to estimate random effects is prohibitively difficult. Given the modest improvements in prediction from the G-sided mixed model, the anticipated poor performance of the uninformed mixed model, and our lack of ability to apply the mixed model to novel stands, we find no advantage here with utilizing the generalized linear mixed-effects models for predicting Douglas-fir mortality.

Our issues with model bias when fixed-effects parameter estimates were extracted from the generalized mixed model indicate a problem with our application, not a problem with the model. We wished to obtain a finding we could generalize between subjects when the mixed models were best able to generalize results within subjects. We imagine that if we desired inference to additional plots within installations, our mixed model would have proven more useful than the marginal model.

All of our models examined failed the goodness-of-fit test; it appears this may be in part due to results for larger-diameter trees that were among the largest trees in a stand. We interpret this to indicate that our model did not fit mortality data well at these larger ranges where we had a relative paucity of data. Other possible contributing issues include overfitting the model or providing insufficient fixed-effects parameters. Among models, the goodness-of-fit scores were lowest for GXME with GXFE a distant third.

Across models, bias was highest at low DBH and high BAL values (both well-represented in the data set). With DFSI, bias was high for the smallest category which corresponded with few data relative to other categories. Bias patterns differed across models as well. GXME tended to exhibit a different and reduced pattern of bias across all three predictor variable categories. The models that were not incorporating installation-specific effects into their estimates tended to behave similarly with model GXFE frequently providing the most extreme bias per variable category.

The intensity of the effect DBH^2 had on mortality prediction at greater DBH values surprised us. Although our predicted U-shaped mortality curve is in spirit similar to that discussed by Harcombe (1987) and found by Monserud and Sterba (1999) for Norway Spruce and Hann and Hanus (2001) for Douglas-fir, grand fir, white fir, incense-cedar, ponderosa pine, and California black oak, only the predicted mortality for large DBH values from the model NLS appeared reasonable. The mixed-effects based models predicted mortality rates at 95 cm DBH that are simply too extreme; if those estimates were real, old-growth (>180 year) Douglas fir stands would not exist. However, the models, particularly GXME, did appear to predict observed mortality for trees <80 cm DBH. GXFE appeared to most severely underpredict the 5-year mortality rate.

5. Conclusion

Our generalized linear mixed model of Douglas-fir mortality did not outperform a similar model lacking mixed effects. In particular, the incorporation of mixed effects resulted in alterations to fixed effects that produced unreasonably high mortality rates for trees approaching 1 m in diameter. The practical application of predicting mortality rates for novel stands did not improve with the

utilization of a mixed model. We believe this will generally be the case for tree mortality estimation when random effects information is unavailable, a condition that should be common. The correction for model overdispersion was appropriate and represented an improvement in parameter variance estimation, but overall we cannot recommend the mixed model as a suitable replacement for the original model form.

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References

- Adame, P., del Río, M., Cañellas, I., 2010. Modeling individual-tree mortality in Pyrenean oak (*Quercus pyrenaica* Willd.) stands. *Ann. For. Sci.* 67, 810.
- Bigler, C., Bugmann, H., 2003. Growth-dependent tree mortality models based on tree rings. *Can. J. For. Res.* 33, 210–221. <http://dx.doi.org/10.1139/X02-180>.
- Breslow, N.E., Lin, X., 1995. Bias correction in generalised linear mixed models with a single component of dispersion. *Biometrika* 82, 81–91.
- Buchman, R.G., Pederson, S.P., Walters, N.R., 1983. A tree survival model with application to species of the Great Lakes region. *Can. J. For. Res.* 13, 601–608.
- Dixon, G.E., 2011. Essential FVS: A user's guide to the Forest Vegetation Simulator. United States Department of Agriculture Forest Service, Forest Management Service Center, Fort Collins, CO. Available from: <<http://www.fs.fed.us/fmcs/ftp/fvs/docs/gtr/EssentialFVS.pdf>> (accessed 10.03.2012).
- Dobbertin, M., Biging, G.S., 1998. Using the non-parametric classifier CART to model forest tree mortality. *For. Sci.* 44 (4), 507–516.
- Eid, T., Tuhus, E., 2001. Models for individual tree mortality in Norway. *For. Ecol. Manage.* 154, 69–84.
- Flewelling, J.A., Monserud, R.A., 2002. Comparing methods for modeling tree mortality. *USDA For. Serv. Proc. RMRS-P-25*, 168–177.
- Fortin, M., Bédard, S., DeBlois, J., Meunier, S., 2008. Predicting individual tree mortality in northern hardwood stands under uneven-aged management in southern Québec, Canada. *Ann. For. Sci.* 65, 205–217.
- Garber, S.M., Temesgen, H., Monleon, V.J., Hann, D.W., 2009. Effects of height imputation strategies on stand volume estimation. *Can. J. For. Res.* 39, 681–690. <http://dx.doi.org/10.1139/X08-188>.
- Harcombe, P.A., 1987. Tree life tables: simple birth, growth, and death data encapsulate life histories and ecological roles. *Bioscience* 37 (8), 557–568.
- Hamilton Jr., D.A., 1986. A logistic model of mortality in thinned and unthinned mixed conifer stands of Northern Idaho. *For. Sci.* 32 (4), 989–1000.
- Hann, D.W., 2011. ORGANON User's Manual, Edition 9.1. Department of Forest Resources, Oregon State University, Oregon. Available from <<http://www.cof.orst.edu/cof/fr/research/organon/download.htm#man>> (accessed 10.03.2012).
- Hann, D.W., Hanus, M.L., 2001. Enhanced mortality equations for trees in the mixed conifer one of southwest Oregon. Research Contribution 34, Forest Research Laboratory, Oregon State University, Corvallis, p. 34.
- Hann, D.W., Scriverani, J.A., 1987. Dominant height-growth and site-index equations for Douglas-fir and ponderosa pine in southwest Oregon. Research Bulletin 59, Forest Research Laboratory, Oregon State University, Corvallis.
- Hann, D.W., Marshall, D.D., Hanus, M.L., 2003. Equations for predicting height-to-crown-base, 5-year diameter-growth rate, 5-year height-growth rate, 5-year mortality rate, and maximum size-density trajectory for Douglas-fir and western hemlock in the coastal region of the Pacific Northwest. Research Contribution 40, Forest Research Laboratory, Oregon State University, Corvallis, p. 53.
- Hann, D.W., Marshall, D.D., Hanus, M.L., 2006. Reanalysis of the SMC-ORGANON equations for diameter-growth rate, height-growth rate, and mortality rate of Douglas-fir. Research Contribution 49, Forest Research Laboratory, Oregon State University, Corvallis.
- Hosmer, D.W., Lemeshow, S., 2000. Applied Logistic Regression, second ed. John Wiley & Sons, Inc., pp. 392.
- Jutras, S., Hökkä, H., Alenius, V., Salminen, H., 2003. Modeling mortality of individual trees in drained peatland sites in Finland. *Silva Fenn.* 37 (2), 235–251.
- Lee, Y., 1971. Predicting mortality for even-aged stands of lodgepole pine. *For. Chronicle* 47, 29–32.
- Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., Schabenberger, O., 2006. SAS® for Mixed Models, second ed. SAS Institute Inc. Cary, NC, pp. 840.
- Monleon, V.J., 2003. A hierarchical linear model for tree height prediction. Joint Statistical Meetings – Section on Statistics & the Environment, pp. 2865–2869.
- Monserud, R.A., 1976. Simulation of forest tree mortality. *For. Sci.* 22 (4), 438–444.
- Monserud, R.A., Sterba, H., 1999. Modeling individual tree mortality for Austrian forest species. *For. Ecol. Manage.* 113, 109–123.

- Moore, J.A., Hamilton Jr., D.A., Xiao, Y., Byrne, J., 2004. Bedrock type significantly affects individual tree mortality for various conifers in the inland Northwest, USA. *Can. J. For. Res.* 34, 31–42. <http://dx.doi.org/10.1139/X03-196>.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*, updated ed. John Wiley and Sons, pp. 520.
- Peet, R.K., Christensen, N.L., 1987. Competition and tree death: most trees die young in the struggle for the forest's scarce resources. *Bioscience* 37 (8), 586–594.
- Robinson, A.P., Wykoff, W.R., 2004. Imputing missing height measures using a mixed-effects modeling strategy. *Can. J. For. Res.* 34, 2492–2500. <http://dx.doi.org/10.1139/X04-137>.
- SAS Institute Inc., 2008. *SAS/STAT® 9.2 User's Guide*. SAS Institute Inc., Cary, NC.
- Schabenberger, O., 2007. Growing up fast: SAS® 9.2 enhancements to the GLIMMIX procedure. *SAS Global Forum 2007: Statistics and Data Analysis*. Paper 177, 2007.
- Staabler, G.R., 1953. Mortality estimation in fully stocked stands of young-growth Douglas-fir. U.S. Forest Service, Pacific Northwest Forest and Range Experiment Station. Research Paper 4, pp. 8.
- Temesgen, H., Mitchell, S.J., 2005. An individual-tree mortality model for complex stands of southeastern British Columbia. *West. J. Appl. For.* 20 (2), 101–109.
- Temesgen, H., Monleon, V.J., Hann, D.W., 2008. Analysis and comparison of nonlinear tree height prediction strategies for Douglas-fir forests. *Can. J. For. Res.* 38, 553–565. <http://dx.doi.org/10.1139/X07-104>.
- Wykoff, W.R., 1986. Supplement to the User's Guide for the Stand Prognosis Model—Version 5.0. Gen. Tech. Rpt. INT-208. USDA For. Serv., Ogden, UT, p. 36.
- Wykoff, W.R., Crookston, N.L., Stage, A.R., 1982. User's guide to the Stand Prognosis Model. Gen. Tech. Rpt. INT-133. USDA For. Serv., Ogden, UT, p. 112.