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Modeling tree mortality in relation to climate, initial planting density, and competition in Chinese fir plantations using a Bayesian logistic multilevel method

Xiongqing Zhang, Quang V. Cao, Aiguo Duan, and Jianguo Zhang

Abstract: Tree mortality models are important tools for simulating forest dynamic processes, and logistic regression is widely used for modeling tree mortality. However, most of the mortality models that have been developed generally ignore the hierarchical structure. In this study, Bayesian logistic multilevel mortality models were developed with the independent variables of initial planting density, competition, site index, and climate factors in Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook.) plantations in southern China. The results showed that a Bayesian three-level model was best for describing tree mortality data with multiple sources of unobserved heterogeneity compared to fixed-effects and two-level models. The variance partition coefficient of tree mortality due to the tree level was much larger than that due to the plot level. The initial planting density and site index were positively correlated with mortality and symmetric competition was negatively correlated. For climate variables, the mortality probability decreased with the increasing mean annual temperature and previous summer mean temperature. By contrast, the mortality probability increased with the increasing previous winter mean minimum temperature and annual heat–moisture index. Identifying different sources of variation in tree mortality will help further our understanding of the factors that drive tree mortality during climate change.

Key words: Bayesian logistic multilevel model, climate, initial planting density and competition, tree mortality, variance partition coefficient.

Résumé : Les modèles de mortalité des arbres sont des outils importants pour simuler les processus dynamiques de la forêt, et la régression logistique est couramment utilisée pour modéliser la mortalité des arbres. Cependant, la plupart des modèles de mortalité qui ont été mis au point ignorent généralement la structure hiérarchique. Dans cette étude, des modèles de mortalité logistiques bayésiens multiniveaux ont été mis au point pour des plantations d'araucaria de Chine (*Cunninghamia lanceolata* (Lamb.) Hook.) du sud de la Chine avec, comme variables indépendantes la densité initiale de la plantation, la compétition, l'indice de qualité de station et des facteurs climatiques. Les résultats indiquent qu'un modèle bayésien à trois niveaux était le meilleur pour représenter les données de mortalité des arbres ayant plusieurs sources d'hétérogénéité non observées comparativement à des modèles à effets fixes et à deux niveaux. Le coefficient de répartition de la variance de la mortalité des arbres était beaucoup plus grand à l'échelle de l'arbre qu'à l'échelle de la placette. La densité initiale de la plantation et l'indice de qualité de station étaient positivement corrélés à la mortalité alors que la compétition symétrique y était négativement corrélée. Dans le cas des variables climatiques, la probabilité de mortalité diminuait avec la température annuelle moyenne et la température estivale moyenne de l'année précédente. En revanche, la probabilité de mortalité augmentait avec la température minimale moyenne de l'hiver précédent et l'indice humidex annuel. L'identification de différentes sources de variation de la mortalité des arbres contribuera à améliorer notre compréhension des facteurs qui déterminent la mortalité des arbres pendant les changements climatiques. [Traduit par la Rédaction]

Mots-clés : modèle logistique bayésien multiniveau, climat, densité initiale de la plantation et compétition, mortalité des arbres, coefficient de répartition de la variance.

Introduction

Tree mortality, one of the main components of forest succession, is important for the maintenance of biological and structural diversity in forest ecosystems (Bigler and Bugmann 2003; Zhang et al. 2011). A complex of endogenous and exogenous factors acting as induction agents lead to tree death during forest succession (van Mantgem et al. 2009). Among endogenous factors, perhaps the best known cause of increasing tree mortality probabilities is increasing competition for water, nutrients, and light within a stand, resulting from increasing stand density and stand basal area (Franklin et al. 2002). By manipulating the stand basal area and density, initial planting density has a significant effect on intertree competition, thereby affecting tree mortality. Lutz and Halpern (2006) reported that the initial planting density correlates strongly with suppression-induced mortality.

In addition to endogenous factors, the effect of climate on tree mortality was identified as an important exogenous factor (Breshears et al. 2005; Adams et al. 2009). Tree mortality studies were per-

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X. Zhang, A. Duan, and J. Zhang. State Key Laboratory of Tree Genetics and Breeding, Key Laboratory of Tree Breeding and Cultivation of the State Forestry Administration, Research Institute of Forestry, Chinese Academy of Forestry, Beijing 100091, P.R. China; Collaborative Innovation Center of Sustainable Forestry in Southern China, Nanjing Forestry University, No. 159 Lonpan Road, Nanjing, 210037, Jiangsu, China.
Q.V. Cao. School of Renewable Natural Resources, Louisiana State University, Agricultural Center, Baton Rouge, LA 70803, USA.
Corresponding author: Jianguo Zhang (email: zhangjg@caf.ac.cn).

Table 1. Summary statistics of stand and tree variables of Chinese fir (*Cunninghamia lanceolata*) plantations.

	Dg		*N*		*Ba*		*Hd*		*d*		Number of deaths	
Density	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Min.	max.
1	13.12	3.48	1663	8.07	24.00	11.47	10.65	3.16	12.93	4.07	0	1
2	10.55	2.62	3316	33.90	30.62	13.67	10.29	3.17	10.27	3.47	0	5
3	8.88	2.22	4893	170.16	31.76	13.72	9.81	2.76	8.55	3.08	1	18
4	7.78	1.97	6483	287.88	32.17	13.94	8.71	2.41	7.42	2.85	0	44
5	7.41	1.84	9225	989.16	40.34	14.95	9.37	2.67	6.96	2.69	9	55

Note: SD, standard deviation; *Dg*, stand quadratic mean of diameter (cm); *N*, live number of trees per hectare; *Ba*, stand basal area (m^2/ha); *Hd*, stand dominant height (m); *d*, diameter at breast height (cm).

formed primarily in established boreal or temperate areas where temperature is often a limiting factor. Additionally, temperature conditions associated with water availability are an important determining factor affecting tree mortality in these areas (Mueller et al. 2005; van Mantgem et al. 2009; Peng et al. 2011; Zhang et al. 2014). Phillips et al. (2009, 2010) reported that tropical forests also suffer increasing tree mortality probabilities in response to moisture stress. Allen et al. (2010) reviewed the research of drought-induced tree mortality and revealed emerging climate change risks for forests worldwide.

The accurate prediction of tree mortality is an essential feature in any individual tree forest growth and yield system. Hamilton (1974) introduced logistic regression to modeling tree mortality and found that logistic regression is a good choice for modeling tree mortality. Since then, logistic regression has been used to model tree mortality for a variety of tree species (e.g., Avila and Burkhart 1992; Yang et al. 2003; Boeck et al. 2014) due to the ease of parameter interpretation (Rose et al. 2006). Although logistic regression is the most widely used for modeling tree mortality, other statistical methods have been used for describing and modeling tree mortality, such as the exponential function (Moser 1972), Weibull function (Somers et al. 1980), Richard function (Buford and Hafley 1985), gamma function (Kobe and Coates 1997), lognormal distribution (Preisler and Slaughter 1997), and hazards model (Woodall et al. 2005). Vanclay (1995) recommended that logistic regression for tree mortality in tropical forests is appropriate because of its biologically meaningful interpretation, mathematic flexibility, and ease of use.

However, most of the tree mortality models developed generally ignore the heterogeneity that may occur due to repeated measurements nested within a tree and trees nesting within a plot. Multiple sources of heterogeneity occur naturally for most permanent plots used in forestry experiments. Recently, Bayesian multilevel models have been widely used in forestry to account for multiple sources of heterogeneity and to consider prior knowledge of the parameters (e.g., Dietze et al. 2008; Vieilledent et al. 2010; X. Zhang et al. 2015*b*; Chen et al. 2016).

Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook.), a fast-growing evergreen coniferous tree, is one of the most important tree species for timber production in southern China. As a native species, Chinese fir has been widely planted for over 1000 years (X. Zhang et al. 2015*b*). The objectives of this study were as follows: (1) develop an individual-tree mortality model using a Bayesian logistic multilevel method considering the full multiple sources of variability of data, (2) examine the effects of climate, initial planting density, and competition on tree mortality, and (3) calculate the variance partition coefficient (VPC) for reporting the variation associated with multiple levels in tree mortality models.

Materials and methods

Data

The Chinese fir stands were established in 1981 using bare-root seedlings in Fenyi County (27°30′N, 114°33′E), Jiangxi Province, in southern China, which has a middle-subtropical climate. A total of 15 plots were planted in a random block arrangement with the following tree spacing: 2 m × 3 m (1667 trees/ha), 2 m × 1.5 m (3333 trees/ha), 2 m × 1 m (5000 trees/ha), 1 m × 1.5 m (6667 trees/ha), and 1 m × 1 m (10 000 trees/ha). Each spacing level was replicated three times. Each plot comprised an area of 20 m × 30 m, and a buffer zone (two lines) consisting of similarly treated trees surrounded each plot. Tree diameter measurements in all plots were conducted after the tree height reached 1.3 m. More than 50 trees, including dominant trees in each plot, were tagged and measured for total height. Measurements were performed each winter from 1983 to 1989 and then every other year from 1989 to 1999. Summary statistics are shown in Table 1.

Methods

Candidate variables

Endogenous variables

The selection of appropriate independent variables should not only be based on *t* test statistics but also on a basic understanding of how forest ecosystems function and how factors contributing to death are expressed (Pedersen 2007; Adame et al. 2010). Hamilton (1986) classified the endogenous factors contributing to mortality into three groups: (*i*) measures of individual tree size, such as diameter at breast height (*d*) or tree height, (*ii*) measures of tree competition, such as stand basal area (*Ba*), stand density (*N*), the ratio of the diameter of the subject tree to the stand quadratic mean diameter (*d*/*Dg*), and the ratio of the height of the subject tree to the stand dominant height (however, the height of each tree in a plot was not recorded for the present data, nor was it possible to appropriately calculate this value), and (*iii*) other growth-related variables at the stand level, such as site fertility. For most tree species, the mortality probability for the smallest tree in a plot is quite high and declines rapidly as small trees survive to larger diameter classes (Adame et al. 2010), which can be captured with a hyperbolic d^{-1} transformation of the diameter (Monserud and Sterba 1999). In addition, Yao et al. (2001) reported that tree size is also used as a proxy of tree age (*A*). Earlier studies found that trees exhibited different mortalities at different site quality levels (Eid and Tuhus 2001; Yao et al. 2001). In the present study, we examined initial planting density (IPD) effects, etc. Moreover, we normalized the initial planting densities (1667, 3333, 5000, 6667, anf 10 000 trees/ha) before modeling. In summary, the following endogenous variables were tested for inclusion in the mortality model: IPD, tree size index (*A*, d^{-1}), tree competition (*d*/*Dg*, *Ba*), and site quality (dominant height, log(*Hd*)).

Climate variables

ClimateAP (T. Wang et al., unpublished data) was used to generate climate data across the study region. ClimateAP is a climate data downscaling tool that produces directly calculated seasonal and annual climate variables and derives climate variables for specific locations (scale-free) based on longitude, latitude, and elevation. The climatic variables tested in this study are shown in Table 2 and are widely used in tree mortality modeling

Table 2. Summary statistics of climate variables.

Climate variable	Description	Mean	Min.	Max.
MAT (°C)	Mean annual temperature	18.18	17.3	19.2
MAP (mm)	Mean annual precipitation	1697.29	1334	1975
MCMT (°C)	Mean coldest month temperature	6.96	4.1	9.1
AHM	Annual heat–moisture index (Wang et al. 2006)	16.82	14.4	21.1
DD_0	Degree-days below 0 °C, chilling degree-days	3	2	9
NFFD	Number of frost-free days	349	334	355
SMMT (°C)	Summer mean maximum temperature	32.02	30.7	33.3
WMMT (°C)	Winter mean minimum temperature	4.28	2.3	6
SMT (°C)	Summer (June–August) mean temperature	27.27	26.4	28

(van Mantgem and Stephenson 2007; van Mantgem et al. 2009; Peng et al. 2011; Zhang et al. 2014). In addition, the annual heat–moisture index (AHM) (Wang et al. 2006) was used to indicate the annual climatic water deficit because it integrates the mean annual temperature (MAT) and annual precipitation (MAP) into a single parameter: AHM = (MAT + 10)/(MAP/1000), which better reflects evapotranspiration and soil moisture content than precipitation and temperature alone (Zhang et al. 2014). Large values of AHM indicate dry conditions due to high evaporative demand relative to the available moisture, whereas low values of AHM represent relatively wet conditions.

Independent variables included in the function were selected as variables through forward stepwise regressions. The set of variables is a combination of different groups (tree size, initial planting density, competition, site quality, and climate), avoiding correlations between the groups.

Bayesian logistic multilevel models

For a given single tree, survival or death can be represented as a binary that has a value of 1 if the tree survives or 0 if it dies over a given time interval. The most widely used link function for binary data is the logit link function, also named the logistic regression model (Vanclay 1995; Zhang et al. 2014). The traditional logistic mortality model is given by

$$\ln\left(\frac{p}{1-p}\right) = \alpha_1 + \boldsymbol{\beta x} \tag{1}$$

where $\boldsymbol{x}$ is a vector of explanatory variables, including nonclimatic candidate variables, IPD and climatic variables. α_1 is the intercept, and $\boldsymbol{\beta}$ is a vector of parameters including the intercept.

Two-level models

In this study, we developed two two-level models: measurement occasions (level 1) and trees (level 2) called two-level1 and measurement occasions (level 1) and plots (level 2) called two-level2. Let i ($I = 1, \ldots, N$) denote the level-2 units (trees or plots) and j ($j = 1, \ldots, m_i$) denote the level-1 units (measurement occasions); therefore, a two-level random intercept logistic model is expressed as

$$\begin{aligned} &\ln\left(\frac{p}{1-p}\right) = \alpha_1 + \boldsymbol{\beta x}_{ij} + \mu_i \\ &\mu_i \sim N(0, \sigma^2) \end{aligned} \tag{2}$$

where μ_i is a level-2 random effect assumed to have a normal distribution with mean 0 and variance σ^2.

Three-level model

The simple two-level model (eq. 2) may be adequate for analyzing data from the permanent plots because the trees that are measured repeatedly are also nested within plots. Therefore, a three-level random intercept logistic model is needed:

$$\begin{aligned} &\ln\left(\frac{p}{1-p}\right) = \alpha_1 + \boldsymbol{\beta x}_{ijk} + \mu_i + \nu_k \\ &\mu_i \sim N\left(0, \sigma_\mu^2\right) \qquad \nu_k \sim N\left(0, \sigma_\nu^2\right) \end{aligned} \tag{3}$$

where μ_i and ν_k represent the random effects of the ith tree and kth plot, respectively.

In the Bayesian models, we used "noninformative" priors for all parameters, i.e., a normal distribution with zero mean and a large variance (10^4). Such priors typically arise in the form of a parametric distribution with large or infinite variance. Notably, the word "noninformative" prior used here is the classical expression but does not necessarily mean that the prior is truly noninformative (Li et al. 2011). The random effect in the intercept is assumed to follow a normal distribution with a mean 0, and the variance of the random effects is given a prior distribution by the inverse gamma (0.001,0.001). The Bayesian method is performed through Markov chain Monte Carlo (MCMC) simulation using the SAS procedure PROC MCMC (SAS Institute Inc. 2011), which uses a random walk Metropolis algorithm to obtain posterior samples (Lindsey 2011). The total number of iterations for tree mortality models was 250 000 with a burn-in of 30 000. Additionally, the thinning parameters were all set to 50 to reduce autocorrelation.

Bayesian model evaluation

The Bayesian three-level model was compared with Bayesian fixed-effects (nonhierarchical), two-level1, and two-level2 models using the deviance information criterion (DIC). This is very useful in Bayesian model selection (Spiegelhalter et al. 2002), which is given by

$$\mathrm{DIC} = \mathrm{Dbar} + \mathrm{pD} \tag{4}$$

where Dbar refers to the posterior mean of the deviance and pD is the effective number of parameters in the model. The posterior mean of the deviance is Dbar = $E_\theta(-2\log(p(y|\theta)))$ and pD = Dbar − Dhat. Dhat is a point estimate of deviance given by Dhat $= -2\log\,(p(y|\bar{\theta}))$. The advantage of DIC over other criteria in Bayesian model selection is that DIC is easily calculated from samples generated by a MCMC simulation. Models with lower DIC values indicate a better fit to the data in which differences ≥5 are regarded as substantial evidence and differences ≥10 are regarded as very strong evidence in favor of the model with the lowest DIC (Hurst et al. 2011).

The value of the area under the receiver operating curve (AUC) is widely used for evaluating tree mortality models (Saveland and Neuenschwander 1990; Zhang et al. 2011) and was also used in this study. The larger the value of the AUC, the better the model performs (Fielding and Bell 1997). A rough guideline for the AUC follows the traditional academic point system as follows: 0.9–1 = excellent (A), 0.8–0.9 = good (B), 0.7–0.8 = fair (C), 0.6–0.7 = poor (D), and 0.5–0.6 = fail (F) (Zhang et al. 2011).

Table 3. Parameter estimates (standard deviation) of tree survival models from fixed-effects (nonhierarchical), two-level, and three-level random effects models using the Bayesian method.

Parameter	Fixed-effects	Two-level1	Two-level2	Three-level
x_1: (intercept)	−106.9 (10.2526)*	−119.6 (12.2375)*	−105.9 (10.6529)*	−114.2 (12.2388)*
x_2: d/Dg	8.9948 (0.2374)*	9.6711 (0.3080)*	9.2175 (0.2478)*	9.7465 (0.2846)*
x_3: IPD	−5.1925 (0.2519)*	−5.7857 (0.3070)*	−6.7770 (0.8996)*	−7.0934 (0.9994)*
x_4: log(Hd)	−6.8546 (0.3522)*	−7.4654 (0.4070)*	−7.8437 (0.4385)*	−7.1610 (0.4773)*
x_5: MAT	5.7495 (0.5022)*	6.3514 (0.5983)*	5.9990 (0.5320)*	6.3809 (0.6018)*
x_6: AHM	−0.3482 (0.0378)*	−0.3845 (0.0455)*	−0.3826 (0.0405)*	−0.4038 (0.0456)*
x_7: WMMT	−1.3833 (0.1515)*	−1.4721 (0.1745)*	−1.3162 (0.1562)*	−1.3802 (0.1728)*
x_8: SMT	1.1672 (0.1150)*	1.3346 (0.1360)*	1.0929 (0.1175)*	1.2009 (0.1377)*
Variance component				
Tree level		0.9659 (0.1495)*		0.6253 (0.2267)*
Plot level			0.3380 (0.1782)*	0.3581 (0.1961)*
Measurement level		3.29	3.29	3.29
DIC	4700.3890	4560.6140	4603.9500	4536.8260
AUC	0.9543	0.9668	0.9554	0.9736

Note: DIC, deviance information criterion; AUC, area under the receiver operating curve.
*$p < 0.05$.

VPC in multilevel logistic models

Multilevel models, also known as hierarchical models, assume multiple sources of unobserved heterogeneity and recognize units at one level as grouped (nested) in the next higher level. In multilevel models, the residual variance is split up into components that are attributed to the various levels in the data (Goldstein 1995). Partitioning the variance in binary models is complex because the level-1 variance (Bernoulli) is measured on a different scale compared to the level-2 variance. Rodríguez and Goldman (2001) said that if the relationship between the dependent and independent variables is nonlinear (e.g., logit link function), then ignoring grouping (nested) structures can result in large biases in estimating parameters. Additionally, note that for the logistic multilevel model, the level-1 variance is not identifiable from the likelihood. The classically reported fixed variance pertains to the latent continuous scale and is the variance of $\pi^2/3$ (3.29), a standard logistic density for logit (Goldstein et al. 2002; Rodríguez and Elo 2003). Goldstein et al. (2002) defined VPC as the percentage of the variation due to higher levels of the model and also showed the method to calculate the VPC at each level. A large VPC value (close to 1) indicates maximally segregated clusters and a low VPC value (close to zero) suggests homogeneous risk of tree mortality among clusters. Here, we adopt the nomenclature in which the random error term is recognized as the lowest level. Therefore, we have measurement occasions nested within trees (level 1), trees nested within plots (level 2), and plots (level 3). VPCs due to tree level and plot level are given by

$$\text{VPC}_{\text{tree}} = \frac{\text{Var(level2)}}{\text{Var(level2)} + \text{Var(level3)} + \text{Var(level1)}} \tag{5}$$

$$\text{VPC}_{\text{plot}} = \frac{\text{Var(level2)}}{\text{Var(level2)} + \text{Var(level3)} + \text{Var(level1)}} \tag{6}$$

where Var(level1) is $\pi^2/3 \approx 3.29$.

Results

Tree mortality models and VPC

According to the stepwise analysis, the endogenous variables of IPD, d/Dg, and log(Hd) were reserved. Additionally, the climate variables of MAT, AHM, winter mean minimum temperature (WMMT), and summer (June–August) mean temperature (SMT) are reserved in basic models and used for modeling tree mortality with Bayesian methods.

Parameter estimates, associated standard deviation, DIC, and AUC for Bayesian fixed-effects (nonhierarchical), two-level, and three-level models are presented in Table 3. The fixed-effects parameter estimates in multilevel models were larger for most than in the fixed-effects model; therefore, ignoring random effects underestimated most of the fixed-effects parameters. DIC and AUC value outputs from both Bayesian two-level models and three-level models were much smaller than the fixed-effects model, which indicates that multilevel models are superior to the fixed-effects model (Table 3). For the Bayesian multilevel models, the DIC from the three-level model was approximately 24 less than the two-level1 and nearly 67 of the two-level2 (Table 3). These DIC values provide a measure of model fit and allow the researcher to compare how different models perform in their ability to model the mortality data satisfactorily. The lower DIC value indicates which model fits the data best. The AUC value was 0.9736 for the Bayesian three-level model versus 0.9668 and 0.9554 for the two-level models and 0.9543 for the fixed-effects model (Table 3). All four models were considered excellent. The AUC test has advantages in assessing model performance in a threshold-independent fashion and comparing several different models (e.g., Wunder et al. 2007; Zhang et al. 2011). Thus, the Bayesian three-level model was the best model for fitting the tree mortality of Chinese fir plantations.

The VPC due to tree level was calculated as 0.1463, which indicates that 14.63% of the variation in mortality is attributed to tree variability, and the VPC due to the plot level was 0.0838. These results suggest significantly more variation in mortality data at the tree level than at the plot level.

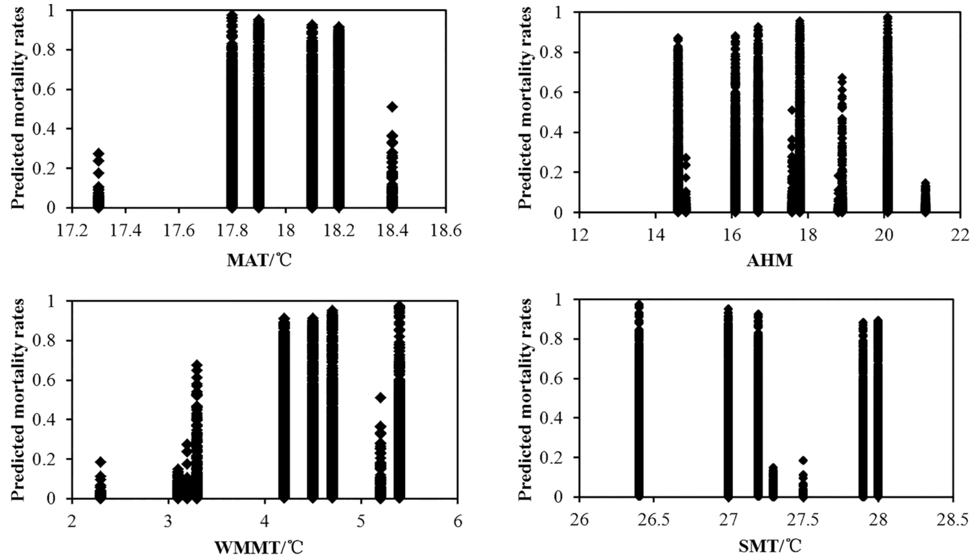
Effects of initial planting density and competition on tree mortality

In the Bayesian multilevel mortality model, the IPD was significantly positive with tree morality (Table 3). Because the mortality probability of a tree is influenced by its relative position (competitive status) within the stand, we calculated the competition index using the ratio of d to Dg. For a given Dg, a tree with a larger diameter has lower mortality probability (Table 3). The positive estimated coefficient for dominant height in the mortality model indicates that mortality is higher on better sites.

Climate effects on tree mortality

A summary of the parameter estimates obtained in the climate sensitive mortality models is provided in Table 3. Four climatic variables, including MAT, AHM, WMMT, and SMT, are significantly correlated with tree mortality. In the mortality models, MAT had a negative effect on the mortality of Chinese fir. A negative significant correlation with SMT was also found. By contrast, the tree mortality probability had a positive significant correlation with WMMT. Additionally, AHM was significantly positively

Fig. 1. Effects of climate variables on the predicted probabilities of mortality in Chinese fir (*Cunninghamia lanceolata*) plantations.



correlated with mortality probabilities (Table 3), which suggests that climate change induced drought increases tree mortality. Although the climate effects, including MAT, AHM, WMMT, and SMT, on mortality were significant (Table 3), the effects were relatively small (Fig. 1).

Discussion

Bayesian multilevel methods in tree mortality

A Bayesian multilevel model is an alternative method that accounts for variation at multiple clustering levels of data, such as the tree or plot level in the tree mortality analysis. An advantage of Bayesian methods over classical methods when fitting models is that independent, prior information, if available, can be incorporated into the model through prior distributions of unknown parameters (Masuda and Stone 2015). In this paper, we do not intend to argue that the Bayesian multilevel model is superior to the classical mixed-effects model. We believe that both classical and Bayesian methods have their own features. In particular, when the Bayesian prior is uninformative, the results would be very close to those obtained with classical mixed-effect models (Pinheiro and Bates 2000; McCarthy 2007).

Bayesian logistic models with fixed effects only and with multilevel random effects added to the intercept were fitted, including both endogenous and exogenous variables. One two-level model (two-level1) was fitted to account for the correlation in measurement occasions (level 1) from a tree (level 2). The other two-level model (two-level2) was also fitted to account for the correlation in measurement occasions (level 1) of a tree in a plot (level 2) as well as the three-level logistic model accounting for the correlation in repeated measurements (level 1) from trees (level 2) nested in a plot (level 3). The multilevel models were much better than the fixed-effects only model according to DIC, and the three-level model also performed best compared to the two-level models (Table 3). Ma et al. (2013) reported that the multilevel logistic model incorporating both the plot and measurement random effects performed the best compared to standard logistic and marginal logistic models based on the generalized estimating equations. Thapa (2014) modeled loblolly pine (*Pinus taeda* L.) mortality using multilevel mixed-effects logistic regression and found that the model accounting for measurement, tree, and plot three levels compared to the two levels of measurement and plot was consistent with our study. Groom et al. (2012) observed that inclusion of a random intercept in multilevel tree mortality models for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands significantly reduced model bias compared to the fixed-effects model.

The VPC attributed to tree level was 74.58% larger than that due to plot level. This may be because a large part of the variance is due to the direct environment of the tree, which cannot be fully described with the symmetric competition index. Some researches reported that the variation of seeds used for seedlings also resulted in different mortality probabilities (Bonfil 1998; Khan and Shankar 2001; Westoby et al. 2002).

Endogenous factors affecting tree mortality

A major mortality agent is intertree competition, which can be either symmetric or asymmetric (Yang et al. 2003; Adame et al. 2010). In symmetric competition, larger trees in a plot have competitive advantages over smaller trees and neighbors do not affect the growth (Cannel et al. 1984). Hamilton (1986) reported that the variable d/Dg was a good symmetric competition index (Avila and Burkhart 1992; Zhang et al. 1997). A positive effect of d/Dg on tree survival is shown in Table 3, indicating that tree death tended to occur in strong symmetric competition stands, which was consistent with the result obtained by Laarmann et al. (2009). For long-term competition, if a given tree size was small compared with a mean tree size, the tree must have strong competition in the stand. In an undisturbed stand, intense competition for nutrients, water, and light particularly affects small trees and induces a higher mortality probability (Coomes and Allen 2007). In asymmetric competition, all trees in a plot impose some competition on their neighboring trees, regardless of their size (Cannel et al. 1984), and this can be described by stand density and basal area. Yang et al. (2003) found that the stand basal area is a good measure of stand crowding and could adequately capture asymmetric competition because it combines both tree size and density. However, here, the two variables were excluded in the mortality model according to the stepwise analysis.

Stand density management, using different initial planting densities, was a key factor driving the mortality process. For a given age and site index, competition-induced mortality was higher at higher planting density (Williams 1994; Zhao et al. 2007), which was consistent with the result of this case (Table 3). The increase in crown ratio and crown length led to a reduction in the relative risk of death among the surviving trees (Thapa 2014). The live crown length and crown ratio decreased with increasing planting density due to competition from neighbors (McClain et al. 1994; Akers et al. 2013).

Site index has frequently been introduced into mortality models. For a given age and initial planting density, the mortality probability of Chinese fir increased with the site index (Table 3). Our finding is consistent with the conclusion of Eid and Tuhus (2001), Yao et al. (2001), and X. Zhang et al. (2015*a*) that higher mortality was related to better productivity. Empirical evidence suggests that density-dependent mortality in plantations becomes apparent earlier in better sites and increases with site productivity (Diéguez-Aranda et al. 2005). However, opposite results were obtained in some studies. Woollons (1998) reported that mortality decreased with increasing site index. Jutras et al. (2003) found that site index had a significant effect on mortality, with a higher mortality probability for Scots pine (*Pinus sylvestris* L.) but lower mortality probability for pubescent birch (*Betula pubescens* Ehrh.). Zhao et al. (2007) also found that site productivity affects mortality in an opposite way in the Piedmont/Upper Coastal Plain and Lower Coastal Plain of the southern United States as follows: mortality increases with increasing productivity in the Piedmont/ Upper Coastal Plain, but in the Lower Coastal Plain, higher mortality is related to lower productivity. The different effects of site index on mortality may be related to the availability of certain key nutrients (Jutras et al. 2003).

Climate variables affecting tree mortality

In addition to endogenous variables, climate variables were also directly related to tree mortality and may be helpful for exploring the effects of climate change on forest dynamics under future climate scenarios. However, the effects of these four climate variables were relatively small (Fig. 1). This may be because the forest stand structure and age mediated the climate effects on tree mortality (Ruiz-Benito et al. 2013; Bell et al. 2014). In general, an increasing mean annual temperature decreases tree mortality probabilities physiologically, when water availability is not limiting. Temperature exerts effects on tree growth and mortality by altering rates of photosynthesis, respiration, cell division and elongation, chlorophyll synthesis, enzymatic activity, water uptake, and transpiration (Ricker et al. 2007). Additionally, an increasing mean annual temperature prolongs the nonfrost growing season during the entire year and increases the CO_2 sequestration rate (Bergh et al. 2003). The tree mortality of Chinese fir decreased with increasing MAT (Table 3; Fig. 1). However, our finding was different from other studies showing that temperature was positively related to tree mortality (van Mantgem et al. 2009; Ruiz-Benito et al. 2013; Zhang et al. 2014). Chinese fir is a shade-intolerant tree species, the growth of which tends to increase with high temperature, thus decreasing the mortality probability (Wu 1984). In addition, a warm late summer can extend the growing season, increasing radial growth and consequently affecting tree mortality in the following year, which is supported by the negative relationship between the late-summer mean temperature and tree mortality probabilities observed in this study.

For the AHM, higher mortality was related to a higher AHM (Table 3). This result confirmed the findings of Breshears et al. (2005), Peng et al. (2011), Zhou et al. (2013), and Zhang et al. (2014), who showed that climate change induced drought stress increased tree mortality. Zhang et al. (2014) reported that drought-induced mortality may be primarily caused by three factors: (*i*) carbon starvation, which halts most photosynthesis, thus failing to support metabolism and carbon balance, (*ii*) hydraulic failure, which increases water deficits and drought stress on trees, and (*iii*) outbreaks of biotic agents, such as the growth and reproduction of insects and pathogens that attack trees (van Mantgem et al. 2009). Generally, climate change induced drought was an inciting tree mortality factor (Bigler et al. 2006; Allen et al. 2010).

Conclusions

This study investigated tree mortality models with the inclusion of initial planting density, competition, and climate variables in Chinese fir plantations in southern China using Bayesian logistic multilevel methods. The Bayesian three-level model was the best to describe tree mortality data with multiple sources of unobserved heterogeneity. The VPC attributed to the tree level was much larger than that due to the plot level.

The endogenous factors of IPD, *d*/*Dg*, and log(*Hd*) were significantly related to mortality. Tree mortality increased with increasing IPD and *Hd* and with a decreasing symmetric competition index *d*/*Dg*. Four climate variables were also related to tree mortality. In the mortality model, MAT and SMT had negative effects on the mortality of Chinese fir. By contrast, the tree mortality probability was positively significantly correlated with WMMT and AHM.

The effect of the initial planting density has implications for forest management because high planting density results in high mortality. Inclusion of climate variables in mortality models can facilitate the projection of tree mortality under future climate change conditions. The Bayesian multilevel model accounting for the uncertainty in parameter estimates shown by the posterior distribution and the heterogeneity that may occur due to the measurement occasions nesting within a tree (i.e., repeated measurements) and trees nesting within a plot was a good method for modeling the tree mortality of Chinese fir plantations.

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References

Adame, P., del Río, M., and Cañellas, I. 2010. Modeling individual-tree mortality in Pyrenean oak (*Quercus pyrenaica* Willd.) stands. Ann. For. Sci. **67**(8): 810–810. doi:10.1051/forest/2010046.

Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., Villegas, J.C., Breshears, D.D., Zou, C.B., Troch, P.A., and Huxman, T.E. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global change-type drought. Proc. Natl. Acad. Sci. U.S.A. **106**: 7063–7066. doi:10.1073/pnas.0901438106. PMID:19365070.

Akers, M.K., Kane, M., Zhao, D., Teskey, R.O., and Daniels, R.F. 2013. Effects of planting density and cultural intensity on stand and crown attributes of mid-rotation loblolly pine plantations. For. Ecol. Manage. **310**: 468–475. doi: 10.1016/j.foreco.2013.07.062.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J., Allard, G., Running, S.W., Semerci, A., and Cobb, N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. **259**: 660–684. doi:10.1016/j.foreco.2009.09.001.

Avila, O.B., and Burkhart, H.E. 1992. Modeling survival of loblolly pine trees in thinned and unthinned plantations. Can. J. For. Res. **22**: 1878–1882. doi:10.1139/x92-245.

Bell, D.M., Bradford, J.B., and Lauenroth, W.K. 2014. Forest stand structure, productivity, and age mediate climatic effects on aspen decline. Ecology, **95**: 2040–2046. doi:10.1890/14-0093.1. PMID:25230455.

Bergh, J., Freeman, M., Sigurdsson, B., Kellomäki, S., Laitinen, K., Niinistö, S., Peltola, H., and Linder, S. 2003. Modelling the short-term effects of climate change on the productivity of selected tree species in Nordic countries. For. Ecol. Manage. **183**: 327–340. doi:10.1016/S0378-1127(03)00117-8.

Bigler, C., and Bugmann, H. 2003. Growth-dependent tree mortality models based on tree rings. Can. J. For. Res. **33**: 210–221. doi:10.1139/x02-180.

Bigler, C., Bräker, O.U., Bugmann, H., Dobbertin, M., and Rigling, A. 2006. Drought as an inciting mortality factor in scots pine stands of the valais, switzerland. Ecosystems, **9**(3): 330–343. doi:10.1007/s10021-005-0126-2.

Boeck, A., Dieler, J., Biber, P., Pretzsch, H., and Ankerst, D.P. 2014. Predicting tree mortality for European beech in southern Germany using spatially explicit competition indices. For. Sci. **60**(4): 613–622. doi:10.5849/forsci.12-133.

Bonfil, C. 1998. The effects of seed size, cotyledon reserves, and herbivory on seedling survival and growth in *Quercus rugosa* and *Q. laurina* (Fagaceae). Am. J. Bot. **85**(1): 79–79. doi:10.2307/2446557. PMID:21684882.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., and Meyer, C.W. 2005. Regional vegetation die-off in response to global-change-type drought. Proc. Natl. Acad. Sci. U.S.A. **102**: 15144–15148. doi:10.1073/pnas.0505734102. PMID:16217022.

Buford, M.A., and Hafley, W.L. 1985. Modeling the probability of individual tree mortality. For. Sci. **31**: 331–341.

Cannel, M.G.R., Rothery, P., and Ford, E.D. 1984. Competition within stands of *Picea sitchensis* and *Pinus contorta*. Ann. Bot. **53**: 349–362. doi:10.1093/oxfordjournals.aob.a086699.

Chen, D., Huang, X., Sun, X., Ma, W., and Zhang, S. 2016. A comparison of hierarchical and non-hierarchical Bayesian approaches for fitting allometric larch (*Larix*. spp.) biomass equations. Forests, **7**(1): 18. doi:10.3390/f7010018.

Coomes, D.A., and Allen, R.B. 2007. Effects of size, competition and altitude on tree growth.. J. Ecol. **95**(5): 1084–1097. doi:10.1111/j.1365-2745.2007.01280.x.

Diéguez-Aranda, U., Castedo-Dorado, F., Álvarez-González, J.G., and Rodríguez-Soalleiro, R. 2005. Modelling mortality of Scots pine (*Pinus sylvestris* L.) plantations in the northwest of Spain. Eur. J. For. Res. **124**(2): 143–153. doi:10.1007/s10342-004-0043-5.

Dietze, M.C., Wolosin, M.S., and Clark, J.S. 2008. Capturing diversity and interspecific variability in allometries: a hierarchical approach. For. Ecol. Manage. **256**: 1939–1948. doi:10.1016/j.foreco.2008.07.034.

Eid, T., and Tuhus, E. 2001. Models for individual tree mortality in Norway. For. Ecol. Manage. **154**: 69–84. doi:10.1016/S0378-1127(00)00634-4.

Fielding, A.H., and Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. **24**(1): 38–49. doi:10.1017/S0376892997000088.

Franklin, J.F., Spies, T.A., van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., and Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. **155**(1–3): 399–423. doi:10.1016/S0378-1127(01)00575-8.

Goldstein, H. 1995. Multilevel statistical models. Edward Arnold, London, UK.

Goldstein, H., Browne, W., and Rasbash, J. 2002. Partitioning variation in multilevel models. Understanding Stat. **1**: 223–231. doi:10.1207/S15328031US0104_02.

Groom, J.D., Hann, D.W., and Temesgen, H. 2012. Evaluation of mixed-effects models for predicting Douglas-fir mortality. For. Ecol. Manage. **276**: 139–145. doi:10.1016/j.foreco.2012.03.029.

Hamilton, D.A. 1974. Event probabilities estimated by regression. USDA For. Serv. Res. Pap. INT-152.

Hamilton, D.A. 1986. A logistic model of mortality in thinned and unthinned mixed conifer stands of northern Idaho. For. Sci. **32**: 989–1000.

Hurst, J.M., Allen, R.B., Coomes, D.A., and Duncan, R.P. 2011. Size-specific tree mortality varies with neighbourhood crowding and disturbance in a montane *Nothofagus* forest. PLoS One, **6**(10): e26670. doi:10.1371/journal.pone.0026670. PMID:22046327.

Jutras, S., Hökkä, H., Alenius, V., and Salminen, H. 2003. Modeling mortality of individual trees in drained peatland sites in Finland. Silva Fenn. **37**(2): 235–251. doi:10.14214/sf.504.

Khan, M.L., and Shankar, U. 2001. Effect of seed weight, light regime and substratum microsite on germination and seedling growth of *Quercus semiserrata* Roxb. Trop. Ecol. **42**(1): 117–126.

Kobe, R.K., and Coates, K.D. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. Can. J. For. Res. **27**(2): 227–236. doi:10.1139/x96-182.

Laarmann, D., Korjus, H., Sims, A., Stanturf, J.A., Kiviste, A., and Köster, K. 2009. Analysis of forest naturalness and tree mortality patterns in Estonia. For. Ecol. Manage. **258**: S187–S195. doi:10.1016/j.foreco.2009.07.014.

Li, B., Lingsma, H.F., Steyerberg, E.W., and Lesaffre, E. 2011. Logistic random effects regression models: a comparison of statistical packages for binary and ordinal outcomes. BMC Med. Res. Methodol. **11**: 77. doi:10.1186/1471-2288-11-77. PMID:21605357.

Lindsey, H.L. 2011. An introduction to Bayesian methodology via WinBUGS and PROC MCMC [online]. Brigham Young University ScholarsArchive. Available from http://scholarsarchive.byu.edu/cgi/viewcontent.cgi?article=3783&context=etd.

Lutz, J.A., and Halpern, C.B. 2006. Tree mortality during early forest development: a long-term study of rates, causes, and consequences. Ecol. Monogr. **76**(2): 257–275. doi:10.1890/0012-9615(2006)076[0257:TMDEFD]2.0.CO;2.

Ma, Z., Peng, C., Li, W., Zhu, Q., Wang, W., Song, X., and Liu, J. 2013. Modeling individual tree mortality rates using marginal and random effects regression models. Nat. Resour. Model. **26**(2): 131–153. doi:10.1111/j.1939-7445.2012.00124.x.

Masuda, M.M., and Stone, R.P. 2015. Bayesian logistic mixed-effects modelling of transect data: relating red tree coral presence to habitat characteristics. ICES J. Mar. Sci. **72**(9): 2674–2683. doi:10.1093/icesjms/fsv163.

McCarthy, M.A. 2007. Bayesian methods for ecology. Cambridge University Press, Cambridge, UK.

McClain, K.M., Morris, D.M., Hills, S.C., and Buse, L.J. 1994. The effects of initial spacing on growth and crown development for planted northern conifers: 37-year results. For. Chron. **70**(2): 174–182. doi:10.5558/tfc70174-2.

Monserud, R.A., and Sterba, H. 1999. Modeling individual tree mortality for Austrian forest species. For. Ecol. Manage. **113**: 109–123. doi:10.1016/S0378-1127(98)00419-8.

Moser, J.W. 1972. Dynamics of an uneven-aged forest stand. For. Sci. **18**(3): 184–191.

Mueller, R.C., Scudder, C.M., Porter, M.E., Trotter, R.T., III, Gehring, C.A., and Whitham, T.G. 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. J. Ecol. **93**: 1085–1093. doi:10.1111/j.1365-2745.2005.01042.x.

Pedersen, S.M. 2007. Models of individual tree mortality for trembling aspen, lodgepole pine, hybrid spruce and subalpine fir in northwestern British Columbia. Examensarbeten, Institutionen för skongens ekologi och skötsel, Umea.

Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W., Liu, S., Li, W., Fang, X., and Zhou, X. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. Nat. Clim. Change, **1**: 467–471. doi:10.1038/nclimate1293.

Phillips, O.L., Aragão, L.E., Lewis, S.L., Fisher, J.B., Lloyd, J., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Bánki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., de Oliveira, A.C., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jiménez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patiño, S., Peñuela, M.C., Prieto, A., Ramírez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., Steege, H.T., Stropp, J., Vásquez, R., Zelazowski, P., Alvarez Dávila, E., Andelman, S., Andrade, A., Chao, K.J., Erwin, T., Di Fiore, A., Honorio, C.E., Keeling, H., Killeen, T.J., Laurance, W.F., Peña Cruz, A., Pitman, N.C., Núñez Vargas, P., Ramírez-Angulo, H., Rudas, A., Salamão, R., Silva, N., Terborgh, J., and Torres-Lezama, A. 2009. Drought sensitivity of the Amazon rainforest. Science, **323**: 1344–1347. doi:10.1126/science.1164033. PMID:19265020.

Phillips, O.L., van der Heijden, G., Lewis, S.L., López-González, G., Aragão, L.E., Lloyd, J., Malhi, Y., Monteagudo, A., Almeida, S., Dávila, E.A., Amaral, I., Andelman, S., Andrade, A., Arroyo, L., Aymard, G., Baker, T.R., Blanc, L., Bonal, D., de Oliveira, A.C., Chao, K.J., Cardozo, N.D., da Costa, L., Feldpausch, T.R., Fisher, J.B., Fyllas, N.M., Freitas, M.A., Galbraith, D., Gloor, E., Higuchi, N., Honorio, E., Jiménez, E., Keeling, H., Killeen, T.J., Lovett, J.C., Meir, P., Mendoza, C., Morel, A., Vargas, P.N., Patiño, S., Peh, K.S., Cruz, A.P., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez, H., Rudas, A., Salamão, R., Schwarz, M., Silva, J., Silveira, M., Slik, J.W., Sonké, B., Thomas, A.S., Stropp, J., Taplin, J.R., Vásquez, R., and Vilanova, E. 2010. Drought–mortality relationships for tropical forests. New Phytol. **187**: 631–646. doi:10.1111/j.1469-8137.2010.03359.x. PMID:20659252.

Pinheiro, J.C., and Bates, D.M. 2000. Mixed-effects models in S and S-PLUS. Springer, New York. doi:10.1007/b98882.

Preisler, H.K., and Slaughter, G.W. 1997. A stochastic model for tree survival in stands affected by annosum root disease. For. Sci. **43**(1): 78–85.

Ricker, M., Gutiérrez-García, G., and Daly, D.C. 2007. Modeling long-term tree growth curves in response to warming climate: test cases from a subtropical mountain forest and a tropical rainforest in Mexico. Can. J. For. Res. **37**(5): 977–989. doi:10.1139/X06-304.

Rodríguez, G., and Elo, I. 2003. Intra-class correlation in random-effects models for binary data. Stata J. **3**: 32–46.

Rodríguez, G., and Goldman, N. 2001. Improved estimation procedures for multilevel models with binary response: a case study. J. R. Stat. Soc. A, **164**: 339–355. doi:10.1111/1467-985X.00206.

Rose, C.E., Jr., Hall, D.B., Shiver, B.D., Clutter, M.L., and Borders, B. 2006. A multilevel approach to individual tree survival prediction. For. Sci. **52**(1): 31–43.

Ruiz-Benito, P., Lines, E.R., Gómez-Aparicio, L., Zavala, M.A., and Coomes, D.A. 2013. Patterns and drivers of tree mortality in Iberian forests: climatic effects are modified by competition. PLoS One, **8**(2): e56843. doi:10.1371/journal.pone.0056843. PMID:23451096.

SAS Institute, Inc. 2011. SAS/STAT 9.3 user's guide. SAS Institute, Inc., Cary, N.C.

Saveland, J.M., and Neuenschwander, L.F. 1990. A signal detection framework to evaluate models of tree mortality following fire damage. For. Sci. **36**(1): 66–76.

Somers, G.L., Oderwald, R.C., Harris, W.R., and Lamgdon, O.G. 1980. Predicting mortality with a Weibull function. For. Sci. **26**(2): 291–300.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P., and van der Linde, A. 2002. Bayesian measures of model complexity and fit. J. R. Stat. Soc. B, **64**(4): 583–639. doi:10.1111/1467-9868.00353.

Thapa, R. 2014. Modeling mortality of loblolly pine (*Pinus taeda* L.) plantations. Virginia Polytechnic Institute and State University, Blacksburg, Va.

van Mantgem, P.J., and Stephenson, N.L. 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. Ecol. Lett. **10**: 909–916. doi:10.1111/j.1461-0248.2007.01080.x. PMID:17845291.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., and Veblen, T.T. 2009. Widespread increase of tree mortality rates in the western United States. Science, **323**: 521–524. doi:10.1126/science.1165000. PMID:19164752.

Vanclay, J.K. 1995. Growth models for tropical forests: a synthesis of models and methods. For. Sci. **41**(1): 7–42.

Vieilledent, G., Courbaud, B., Kunstler, G., Dhôte, J.F., and Clark, J.S. 2010. Individual variability in tree allometry determines light resource allocation in forest ecosystems: a hierarchical Bayesian approach. Oecologia, **163**: 759–773. doi:10.1007/s00442-010-1581-9. PMID:20169451.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., and Wright, I.J. 2002. Plant ecological strategies: some leading dimensions of variation between species. Annu. Rev. Ecol. Syst. **33**: 125–159. doi:10.1146/annurev.ecolsys.33.010802.150452.

Wang, T., Hamann, A., Yanchuk, A., Nell, G.A.Ó., and Aitken, S.N. 2006. Use of response functions in selecting lodgepole pine populations for future climates. Glob. Chang. Biol. **12**: 2404–2416. doi:10.1111/j.1365-2486.2006.01271.x.

Williams, R.A. 1994. Stand density management diagram for loblolly pine plantations in north Louisiana. South. J. Appl. For. **18**(1): 40–45.

Woodall, C.W., Grambsch, P.L., and Thomas, W. 2005. Applying survival analysis to a large-scale forest inventory for assessment of tree mortality in Minnesota. Ecol. Modell. **189**: 199–208. doi:10.1016/j.ecolmodel.2005.04.011.

Woollons, R.C. 1998. Even-aged stand mortality estimation through a two-step regression process. For. Ecol. Manage. **105**: 189–195. doi:10.1016/S0378-1127(97)00279-X.

Wu, Z. 1984. Chinese fir. China Forestry Publishing House, Beijing, China. [In Chinese.]

Wunder, J., Reineking, B., Matter, J.-F., Bigler, C., and Bugmann, H. 2007. Predicting tree death for *Fagus sylvatica* and *Abies alba* using permanent plot data. J. Veg. Sci. **18**(4): 525–534. doi:10.1111/j.1654-1103.2007.tb02567.x.

Yang, Y., Titus, S.J., and Huang, S. 2003. Modeling individual tree mortality for white spruce in Alberta. Ecol. Modell. **163**(3): 209–222. doi:10.1016/S0304-3800(03)00008-5.

Yao, X., Titus, S.J., and MacDonald, S.E. 2001. A generalized logistic model of individual tree mortality for aspen, white spruce, and lodgepole pine in Alberta mixedwood forests. Can. J. For. Res. **31**: 283–291. doi:10.1139/x00-162.

Zhang, S., Amateis, R.L., and Burkhart, H. 1997. Constraining individual tree diameter increment and survival models for loblolly pine plantations. For. Sci. **43**: 414–423.

Zhang, X., Lei, Y., Cao, Q.V., Chen, X., and Liu, X. 2011. Improving tree survival prediction with forecast combination and disaggregation. Can. J. For. Res. **41**(10): 1928–1935. doi:10.1139/x11-109.

Zhang, X., Lei, Y., Pang, Y., Liu, X., and Wang, J. 2014. Tree mortality in response to climate change induced drought across Beijing, China. Clim. Change, **124**(1–2): 179–190. doi:10.1007/s10584-014-1089-0.

Zhang, X., Lei, Y., and Liu, X. 2015*a*. Modeling stand mortality using Poisson mixture models with mixed-effects. iForest, **8**: 333–338. doi:10.3832/ifor1022-008.

Zhang, X., Zhang, J., and Duan, A. 2015*b*. A hierarchical Bayesian model to predict self-thinning line for Chinese fir in southern China. PLoS One, **10**(10): e0139788. doi:10.1371/journal.pone.0139788. PMID:26440942.

Zhao, D., Borders, B., Wang, M., and Kane, M. 2007. Modeling mortality of second-rotation loblolly pine plantations in the Piedmont/Upper Coastal Plain and Lower Coastal Plain of the southern United States. For. Ecol. Manage. **251**(1): 132–143. doi:10.1016/j.foreco.2007.06.030.

Zhou, G., Peng, C., Li, Y., Liu, S., Zhang, Q., Tang, X., Liu, J., Yan, J., Zhang, D., and Chu, G. 2013. A climate change-induced threat to the ecological resilience of a subtropical monsoon evergreen broad-leaved forest in Southern China. Global Change Biol. **19**(4): 1197–1210. doi:10.1111/gcb.12128.