

**MODELING MORTALITY OF SECOND-ROTATION LOBLOLLY
PINE PLANTATIONS IN THE PIEDMONT/UPPER COASTAL
PLAIN AND LOWER COASTAL PLAIN OF THE SOUTHERN
UNITED STATES**

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EXECUTIVE SUMMARY

Remeasurement data from permanent plots of six loblolly pine studies were used to develop mortality models for second-rotation loblolly pine plantations growing in the Piedmont/Upper Coastal Plain (PUCP) and Lower Coastal Plain (LCP) of the southern United States. The model consists of two complementary parts: a generalized logistic equation predicting the probability of survival for all trees over a period developed using all data with and without occurrence of mortality; and a difference equation predicting tree number reduction, given that some mortality has occurred.

In the PUCP, the survival probability is mainly affected by stand age, tree density, and site index, and the probability decreases with increasing values of each of these three variables. In the LCP, the survival probability is related to the stand basal area and site index, and the probability decreases with increasing stand basal area, but increases with increasing site index. The relative rates of instantaneous mortality for second-rotation loblolly pine plantations are proportional to stand density, age and site index, but with different functions of age and site index in the PUCP and LCP. Thus, two different forms of the best difference mortality equations were obtained for these two regions. Both survival probability equation and difference mortality equation indicate that site productivity affects mortality in an opposite way in the two regions: mortality increases with increasing productivity in the PUCP, but in the LCP higher mortality is related to lower productivity. The lower quality sites in the PUCP may support higher stocking than the same quality of sites in the LCP, while the higher quality sites in the PUCP may support lower stocking than the same quality of sites in the LCP.

Keywords: Loblolly pine plantation; Second rotation; Mortality; Generalized logistic regression; Difference mortality equation.

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1 INTRODUCTION

An important component of stand growth and yield models is a whole-stand mortality equation. Accurate prediction of mortality is essential to managing loblolly pine (*Pinus taeda* Engelm.) plantations, the most important sources of wood fiber and timber in the southern United States. Several predictive equations have been proposed for even-aged stands, most of them have been developed using the algebraic difference equation approach. This approach begins with an exploration of the relative rate of instantaneous mortality. Assuming the relative rate of mortality to be related to stand age, density and site index in some functions and integrating with the initial conditions yield the whole-stand mortality equations (see Clutter et al., 1983; Diéguez-Aranda et al, 2005). These whole-stand mortality equations possess the well known properties of consistency, path-invariance, and asymptotic limit of stocking approaching zero. For even-aged stands it is reasonable to assume that in-growth is negligible, thus tree number decreases monotonically as stand age increases (Clutter et al., 1983; Woollons, 1998).

The development of mortality equations generally requires data from the remeasurement of permanent plots. However, such longitudinal data often contain a large proportion of observations with no occurrence of mortality, even over periods of several years. In the current study, for example, there were 36.7% and 44.6% of measurement intervals over which no mortality was observed for the Piedmont/Upper Coastal Plain and Lower Coastal Plain, respectively). Mortality functions derived from differential equations are intrinsically nonlinear, and convergence in estimation is sometimes difficult to achieve. If all data are included in model development, then this convergence difficulty can frequently be exasperated and model selection could be also difficult (Woollons, 1998) and mortality rate may be underestimated. If only the subset of the data where mortality has happened is used, then mortality rate may be overestimated (Woollons, 1998; Eid and Øyen, 2003). A two-step modeling approach proposed by Woollons (1998) is one of the solutions to these problems, and has already been applied to modeling tree mortality (e.g. Eid and Øyen, 2003; Diéguez-Aranda et al, 2005; Zhao et al., 2006b). In the first step, a logistic model predicting the probability of mortality occurring in the subsequent measurement interval, given current stand condition, is developed using all the data with and without occurrence of mortality. Then a tree-number reduction equation is developed using only the subset of data with occurrence of mortality. Finally, the estimate derived from the tree-number reduction equation is modified by the estimated mortality probability from the logistic model, with deterministic or stochastic approaches (Woollons, 1998; Monserud and Sterba, 1999).

For first-rotation or conversion loblolly pine plantations in the southern U.S., some type of mechanical site preparation and planting was used, but little additional consideration was given to control of competing vegetation (herbaceous, woody brush or hardwood trees) and fertilization. Several sets of growth and yield models for these stands have

been developed (e.g., Harrison and Borders, 1996). For second-rotation loblolly pine plantations, the standard silvicultural practice is application of chemical treatment at site preparation, possibly in conjunction with a mechanical treatment. In addition to standard practice, starting in the mid to late 1980's, other silvicultural treatments such as post-plant herbaceous weed control, fertilization, and mid-rotation woody control have become common. Pienaar and Rheney (1995) proposed a modeling approach for second-rotation loblolly pine plantations, in which an adjustment term for competing vegetation control and fertilization treatments is added to the average growth and yield model for the stands under standard practice. Therefore, it is logical to develop the whole stand model first for second-rotation loblolly pine plantations under standard practice. A key component of the whole stand model is the mortality function.

The objectives of the present study are: (1) to develop generalized logistic models for predicting the probability of no mortality in the subsequent measurement interval, given current stand conditions; (2) to determine the "best" mortality function for predicting tree number reduction using the difference equation approach, if mortality happened, for second-rotation loblolly pine plantations without competing vegetation control (other than at site preparation) and fertilization treatments in the southern U.S..

2 MATERIALS AND METHODS

2.1 Data Description

Plantation Management Research Cooperative (PMRC) and Consortium for Accelerated Pine Productivity Studies (CAPPS) at the University of Georgia's Warnell School of Forestry and Natural Resources installed several large loblolly pine studies in the southern United States. In this study, data from control plots without fertilization or complete vegetation control treatments were used to develop and calibrate survival models (note however that a one time use of an herbicide may have been part of the site preparation method used on some plots). There were 447 control plots available for this study in the Piedmont/Upper Coastal Plain (PUCP). These plots were established in 1985 and later, and distributed throughout the PUCP of Alabama, Georgia, South Carolina and eastern Mississippi. The plots are comprised of all control treatment plots from a loblolly pine site preparation study (SAGSP85), loblolly pine growth and yield permanent plots (LOBGY94), a loblolly pine improved planting stock-vegetation control study (HGLOB87), an early mortality study (MORTL86), and plots from the CAPPS program. These plots were all relatively young and the initial measurement ranged from age 3 years to 11 years. Tree density at initial measurement point ranged from 200 to 1100 with an average of about 600 trees/acre.

In the Lower Coastal Plain (LCP), we have very limited data from stands established post-1985. For this region the difference in site preparation pre and post-1985 is not as

significant as in the PUCP. Thus data from 67 control plots selected from HGLOB87, CAPPs and the spacing and thinning study (MS33THN) were used to calibrate second rotation models for the LCP in this study. The initial measurement of these plots had an age range from 3 to 19 years. Trees per acre at the initial plot measurement ranged from approximately 170 to 800 with an average of about 660 trees/acre.

The CAPPs plots have been measured annually since planting, with a maximum of 15 remeasurements; while other plots have been measured every 3, 4 or 5 years with a maximum of 5 remeasurements. For each one of the inventories, the following stand variables were calculated: total stem number per acre (N), total basal area per acre (BA, ft²/acre), dominant height (H_D, ft), site index (S), and relative spacing (RS). The relative spacing (RS) was obtained as follows:

$$RS = \sqrt{\frac{43560}{N}} / H_D \quad (1)$$

Base age 25 years site index was estimated for each plot from the dominant height at the age of the most recent measurement using the site index equations developed by Borders et al. (2004) for second rotation loblolly pine plantations:

$$S = \alpha_0 \left\{ 1 - \left[1 - \left(\frac{H_D}{\alpha_0} \right)^{\frac{1}{\alpha_1}} \right]^{\frac{25}{A}} \right\}^{\alpha_1} \quad (2)$$

where $\alpha_0 = 117.6$ and $\alpha_1 = 1.336527$ in the PUCP; $\alpha_0 = 136.6$ and $\alpha_1 = 1.202941$ in the LCP. Site indices ranged from 48 to 95 feet in the PUCP, and from 30 to 105 feet in the LCP.

Summary statistics for the primary stand characteristics at the beginning of each measurement interval were shown in Table 1. There were 1805 intervals in the PUCP and 280 intervals in the LCP. Of these there were 663 intervals (36.7%) in the PUCP and 125 intervals (44.6%) in the LCP over which no mortality was observed.

Table 1. Summary statistics for stand characteristics at the beginning of remeasurement intervals by the Piedmont/Upper Coastal Plain (PUCP) and Lower Coastal Plain (LCP), and mortality status (the occurrence of tree death over the remeasurement interval).

Region	Mortality	n	Variable	Mean	Minimum	Maximum	SD
PUCP	Occurrence (m = 1)	1142	Stand age (A)	10.6	3	18	3.4
			Dominant height (H_D , ft)	34.6	6.8	70.8	12.7
			Site index (S, ft)	73.9	48.5	93.2	7.2
			Basal area (BA, ft ² /acre)	86.8	0.4	198.9	45.5
			Trees per acre (N)	582	58	1089	146.2
			Relative spacing (RS)	3.1	0.1	1.9	1.2
	No Occurrence (m = 0)	663	Stand age (A)	9.0	3	18	3.4
			Dominant height (H_D , ft)	29.4	6.2	68.3	13.1
			Site index (S, ft)	75.2	51.8	93.2	8.1
			Basal area (BA, ft ² /acre)	64.7	0.2	180.0	44.9
			Trees per acre (N)	567	107	1089	139.7
			Relative spacing (RS)	2.3	0.1	2.0	1.2
LCP	Occurrence (m = 1)	155	Stand age (A)	12.6	4	31	4.8
			Dominant height (H_D , ft)	40.0	8.6	75.2	14.0
			Site index (S, ft)	73.1	30.0	107.0	14.0
			Basal area (BA ft ² /acre)	95.0	4.3	186.8	41.2
			Trees per acre (N)	632	148	804	118.5
			Relative spacing (RS)	0.2	0.1	1.0	0.1
	No Occurrence (m = 0)	125	Stand age (A)	9.8	3	25	4.2
			Dominant height (H_D , ft)	39.3	9.7	72.3	15.6
			Site index (S, ft)	85.5	49.4	107.0	11.4
			Basal area (BA ft ² /acre)	82.3	2.8	178.2	44.6
			Trees per acre (N)	628	152	731	65.0
			Relative spacing (RS)	0.3	0.1	0.9	0.2

2.2 Model Specification and Evaluation

A two-step modeling approach was applied to model observed mortality. In the first step, a model predicting the probability of survival of all trees in the stand over a measurement interval was fitted using all observations (i.e., with and without occurrence of mortality). In the second step, a mortality function estimating the reduction in tree number due to mortality was developed using only observations with occurrence of mortality.

2.2.1 Model for Predicting Survival Probability

Whether tree death happened or all trees survived in a plot over a remeasurement interval is a discrete event. In this study, the response variable (denoted as m) was coded as 0 for no occurrence of mortality (all trees survived) and 1 for occurrence of mortality (tree death happened) between two successive measurement occasions. The predicted probability of survival for all trees over the interval should be in the range $[0, 1]$ with 0 being occurrence of mortality and 1 being no occurrence of mortality. The logistic function appears to be the best equation for stand or individual mortality modeling and has been widely applied (e.g. Monserud, 1976; Hamilton, 1986; Woollons, 1998; Monserud and Sterba, 1999; Yao et al., 2001; Eid and Øyen, 2003; Zhao et al., 2004; Diéguez-Aranda et al., 2005; Zhao et al., 2006a, b). Since the remeasurement intervals of the data were irregular, a generalized logistic model proposed by Monserud (1976) was applied in the first step of the present study to predict the probability of survival. The generalized logistic model was formulated as:

$$\pi = (1 + e^{-\mathbf{X}\boldsymbol{\beta}})^{-L} \quad (3)$$

where π represents the probability of survival for all trees over a remeasurement interval L (i.e. the probability of tree death occurring over that interval is given by $1 - \pi$); \mathbf{X} is a vector of explanatory variables which characterize the stand competition state; $\boldsymbol{\beta}$ is the vector of parameters to be estimated, and e is the base of the natural logarithm.

In this model, L is an explanatory variable, thus the probability of survival for all trees can be projected by a variable time interval. For a specific stand, at the beginning of a growth interval, that is, when $L = 0$, there is no occurrence of tree mortality and $\pi = 1$, and when the time interval increases, the survival probability decreases and gradually approaches zero. The potential explanatory variables \mathbf{X} in the model include: number of trees per acre (N), age (A), basal area per acre (BA), site index (S), relative spacing (RS), and some combinations of these variables such as $A \times N$, $A \times BA$, and $S \times N$.

The log likelihood function of the generalized logistic model (Eq. 3) is:

$$\begin{aligned} l(m, \boldsymbol{\beta}) &= \sum_{i=1 \text{ \& } m_i=0}^n \log(\pi) + \sum_{i=1 \text{ \& } m_i=1}^n \log(1 - \pi) \\ &= - \sum_{i=1 \text{ \& } m_i=0}^n L_i \log(1 + e^{-\mathbf{X}_i \boldsymbol{\beta}}) + \sum_{i=1 \text{ \& } m_i=1}^n \log(1 - (1 + e^{-\mathbf{X}_i \boldsymbol{\beta}})^{-L_i}) \end{aligned} \quad (4)$$

where m_i is the response variable for the i th observation (i.e., $m_i = 0$ for no occurrence of mortality and $m_i = 1$ for occurrence of mortality over the remeasurement interval of L_i years), and \mathbf{X}_i is the vector of the explanatory variables for the i th observation. The

maximum likelihood estimates $\hat{\beta}$ for Eq. 3 can be obtained by directly maximizing this log likelihood function with the SAS/STAT NLMIXED procedure (SAS Institute, 2004b).

A set of variables for fitting the model for each region was selected based on the likelihood ratio test (Hosmer and Lemeshow, 2000) for assessing parameter significance combined with the ecological behaviors of the fitted models. Hosmer-Lemeshow goodness-of-fit (Hosmer and Lemeshow, 2000) was used to evaluate the model fit. In this study, the grouping method based on the percentiles of the predicted probabilities was used to create ten groups of roughly the same size. The discrepancies between the observed and expected number of observations in these groups are summarized by the Pearson chi-square statistic, which is then compared to the critical value from a chi-square. A small corresponding p -value suggests that the fitted model is not an adequate model. If a function fits the data well, the p -value associated with that function should be larger than 0.05, indicating no significant difference between the fitted function and the data at the 95% confidence level. The “best” model, based on the largest p -value, was selected from several potential functions.

2.2.2 Mortality Models for Predicting Tree Number Reduction

The algebraic difference equation approach was used to develop mortality models for predicting tree number reduction. In general, the relative rate of instantaneous mortality could be related to age, site index, and stand densities as the following differential equation forms:

$$\frac{dN / dA}{N} = \alpha N^{\beta} \cdot f_1(S) \cdot f_2(A), \quad (5)$$

or

$$\frac{dN / dA}{N} = \alpha N^{\beta} \cdot (f_1(S) + f_2(A)), \quad (6)$$

where N is the number of trees per acre at age A , dN / dA is instantaneous mortality rate operating at age A , $f_1(S)$ is a function of site index and $f_2(A)$ is a function of age; α and β are parameters.

The effect of site index on mortality could be represented as a general functional form $f_1(S) = \gamma_0 + \gamma_1 S^{\gamma_2}$. Based on our experience, keeping the parameter γ_2 produces little improvement in predictive ability of the corresponding difference equation model, and can sometimes cause difficulty in convergence. Thus, we set $\gamma_2 = 1$, that is,

$f_1(S) = \gamma_0 + \gamma_1 S$ was employed in the solutions of Eqs. 5 and 6. The effect of the age in

the differential equations may be expressed as $f_2(A) = A^\delta$, $f_2(A) = \delta^A$ or $f_2(A) = \delta / A$, from which many published whole stand mortality models can be derived.

If the proportional instantaneous mortality rate is found to be unrelated to site index, age, or stand density, we can set $f_1(S) = 1$, $f_2(A) = 1$ or $\beta = 0$, respectively. If we set $f_1(S) = 1$, $f_2(A) = 1$ and $\beta = 0$ simultaneously, then the proportional instantaneous mortality rate is constant for all site indexes, ages, and stand densities, that is,

$$\frac{dN / dA}{N} = \alpha . \quad (7)$$

Integrating Eq. 7 with the initial condition that $N = N_1$ when $A = A_1$ gives the difference equation model for predicting $N = N_2$ at remeasurement age $A = A_2$:

$$N_2 = N_1 e^{\alpha(A_2 - A_1)} . \quad (8)$$

The combination of $\beta = 0$ or $\beta \neq 0$ with different forms of age and site index functions gives several differential equations, and integrating over the initial condition specifying that $N = N_1$ at $A = A_1$ yields the corresponding difference equation models. Including Eq. 8, twenty eight difference equation models and their corresponding differential equations evaluated in the present study are listed in Table 2.

Several models in Table 2 have been used to predict the numbers of surviving trees for pine plantations. For example, Eq. 9 is similar to the survival functions of Pienaar and Shiver (1981) and Pienaar et al. (1990), in which the relative rate of instantaneous mortality is proportional to a power of age. Clutter and Jones (1980) presented a more flexible difference equation similar to Eq. 13 assuming that the relative rate of instantaneous mortality is proportional to age and tree density, which are also raised to a power. The model of Bailey et al. (1985) is similar to Eq. 18 including site index as an independent variable. This model has been used in several studies for slash pine plantations in the southeastern US. Diéguez-Aranda et al. (2005) also applied some of the models in Table 2 to model mortality of Scots pine plantations in the northwest of Spain.

Table 2. Mathematical expressions of some difference mortality models and the corresponding differential equations.

Conditions	Differential equation	Difference equation	Model
$\beta = 0$ $f(S) = 1$	$\frac{dN/dA}{N} = \alpha$	$N_2 = N_1 e^{b_1(A_2 - A_1)}$	(8)
	$\frac{dN/dA}{N} = \alpha A^\delta$	$N_2 = N_1 e^{b_1(A_2^{b_2} - A_1^{b_2})}$	(9)
	$\frac{dN/dA}{N} = \alpha + \frac{\delta}{A}$	$N_2 = N_1 e^{b_1(A_2 - A_1) \left(\frac{A_2}{A_1}\right)^{b_2}}$	(10)
	$\frac{dN/dA}{N} = \alpha \delta^A$	$N_2 = N_1 e^{b_1(b_2^{A_2} - b_2^{A_1})}$	(11)
$\beta \neq 0$ $f(S) = 1$	$\frac{dN/dA}{A} = \alpha N^\beta$	$N_2 = [N_1^{b_0} + b_1(A_2 - A_1)]^{(1/b_0)}$	(12)
	$\frac{dN/dA}{A} = \alpha N^\beta A^\delta$	$N_2 = [N_1^{b_0} + b_1(A_2^{b_2} - A_1^{b_2})]^{(1/b_0)}$	(13)
	$\frac{dN/dA}{A} = \alpha N^\beta \left(1 + \frac{\delta}{A}\right)$	$N_2 = [N_1^{b_0} + b_1(A_2 - A_1) + b_2 \ln\left(\frac{A_2}{A_1}\right)]^{(1/b_0)}$	(14)
	$\frac{dN/dA}{A} = \alpha N^\beta \delta^A$	$N_2 = [N_1^{b_0} + b_1(b_2^{A_2} - b_2^{A_1})]^{(1/b_0)}$	(15)
$\beta = 0$ $f(S) = \gamma_0 + \gamma_1 S$	$\frac{dN/dA}{N} = c_0 + c_1 S$	$N_2 = N_1 e^{(c_0 + c_1 S)(A_2 - A_1)}$	(16)
	$\frac{dN/dA}{N} = (c_0 + c_1 S) A^\delta$	$N_2 = N_1 e^{(c_0 + c_1 S)(A_2^{b_1} - A_1^{b_1})}$	(17)
	$\frac{dN/dA}{N} = c_0 + c_1 S + \frac{\delta}{A}$	$N_2 = N_1 e^{(c_0 + c_1 S)(A_2 - A_1) \left(\frac{A_2}{A_1}\right)^{b_1}}$	(18)
	$\frac{dN/dA}{N} = (c_0 + c_1 S) \delta^A$	$N_2 = N_1 e^{(c_0 + c_1 S)(b_1^{A_2} - b_1^{A_1})}$	(19)
$\beta \neq 0$ $f(S) = \gamma_0 + \gamma_1 S$	$\frac{dN/dA}{N} = (c_0 + c_1 S) N^\beta$	$N_2 = [N_1^{b_0} + (c_0 + c_1 S)(A_2 - A_1)]^{(1/b_0)}$	(20)
	$\frac{dN/dA}{N} = (c_0 + c_1 S) N^\beta A^\delta$	$N_2 = [N_1^{b_0} + (c_0 + c_1 S)(A_2^{b_1} - A_1^{b_1})]^{(1/b_0)}$	(21)
	$\frac{dN/dA}{N} = (c_0 + c_1 S + \frac{\delta}{A}) N^\beta$	$N_2 = [N_1^{b_0} + (c_0 + c_1 S)(A_2 - A_1) + b_1 \ln\left(\frac{A_2}{A_1}\right)]^{(1/b_0)}$	(22)
	$\frac{dN/dA}{N} = (c_0 + c_1 S) N^\beta \delta^A$	$N_2 = [N_1^{b_0} + (c_0 + c_1 S)(b_1^{A_2} - b_1^{A_1})]^{(1/b_0)}$	(23)

Table 2 (continued)

$\beta \neq 0$ $f(S) = \gamma_1 S$	$\frac{dN/dA}{N} = \alpha N^\beta S$	$N_2 = [N_1^{b_0} + b_1 S(A_2 - A_1)]^{(1/b_0)}$	(24)
	$\frac{dN/dA}{N} = \alpha N^\beta S A^\delta$	$N_2 = [N_1^{b_0} + b_1 S(A_2^{b_2} - A_1^{b_2})]^{(1/b_0)}$	(25)
	$\frac{dN/dA}{N} = \alpha N^\beta S \delta^A$	$N_2 = [N_1^{b_0} + b_1 S(b_2^{A_2} - b_2^{A_1})]^{(1/b_0)}$	(26)
	$\frac{dN/dA}{N} = N^\beta (\alpha S + \frac{\delta}{A})$	$N_2 = [N_1^{b_0} + b_1 S(A_2 - A_1) + b_2 \ln(\frac{A_2}{A_1})]^{(1/b_0)}$	(27)
$\beta \neq 0$ $f(S) = \frac{\gamma_1}{S}$	$\frac{dN/dA}{N} = \alpha N^\beta / S$	$N_2 = [N_1^{b_0} + \frac{b_1}{S}(A_2 - A_1)]^{(1/b_0)}$	(28)
	$\frac{dN/dA}{N} = \alpha N^\beta A^\delta / S$	$N_2 = [N_1^{b_0} + \frac{b_1}{S}(A_2^{b_2} - A_1^{b_2})]^{(1/b_0)}$	(29)
	$\frac{dN/dA}{N} = N^\beta (\frac{\alpha}{S} + \frac{\delta}{A})$	$N_2 = [N_1^{b_0} + \frac{b_1}{S}(A_2 - A_1) + b_2 \ln(\frac{A_2}{A_1})]^{(1/b_0)}$	(30)
	$\frac{dN/dA}{N} = \alpha N^\beta \delta^A / S$	$N_2 = [N_1^{b_0} + \frac{b_1}{S}(b_2^{A_2} - b_2^{A_1})]^{(1/b_0)}$	(31)
$\beta = 0$ $f(S) = \gamma_1 S$	$\frac{dN/dA}{N} = \alpha S$	$N_2 = N_1 e^{b_1 S(A_2 - A_1)}$	(32)
	$\frac{dN/dA}{N} = \alpha S A^\delta$	$N_2 = N_1 e^{b_1 S(A_2^{b_2} - A_1^{b_2})}$	(33)
	$\frac{dN/dA}{N} = \alpha S + \frac{\delta}{A}$	$N_2 = N_1 e^{b_1 S(A_2 - A_1) (\frac{A_2}{A_1})^{b_2}}$	(34)
	$\frac{dN/dA}{N} = \alpha S \delta^A$	$N_2 = N_1 e^{b_1 S(b_2^{A_2} - b_2^{A_1})}$	(35)

Using only the subset of the data in which mortality had occurred over a measurement interval, all difference equations in Table 2 (Models 8 – 35) were fitted for the PUCP and LCP, respectively. Estimates of model parameters were obtained using the MODEL procedure in SAS/ETS (SAS Institute, 2004a). Four fit statistics obtained from tree number reduction models were used for model evaluation: mean residual (\bar{E}), root mean square error ($RMSE$), the coefficient of determination (R^2), and Akaike's information criterion (AIC). These fit statistics can be expressed as follows:

$$\bar{E} = \frac{\sum (N - \hat{N})}{n}, \quad (36)$$

$$RMSE = \sqrt{\frac{\sum (N - \hat{N})^2}{n}}, \quad (37)$$

$$R^2 = 1 - \frac{\sum (N - \hat{N})^2}{\sum (N - \bar{N})^2}, \quad (38)$$

$$AIC = n \left[\ln\left(\frac{\sum (N - \hat{N})}{n}\right) + \ln 2\pi + 1 \right] + 2p, \quad (39)$$

where N , \hat{N} and \bar{N} are the observed, predicted, and average number of surviving trees, respectively; n is the total number of observations used in the model; and p is number of fitted parameters. Leave-one-out (LOO) cross-validation was also performed for each model, and the summary statistics such as mean LOO error, root mean square LOO error, LOO cross-validation coefficient (R_{cv}^2 , equivalent to the R^2) and AIC were calculated using formulae 35 - 39, respectively. It is emphasized that determination of the “best” mortality function was the main aim of this research rather than methodology to modeling mortality.

2.2.3 Projection of Number of Surviving Trees

The estimated number of surviving trees at age A_2 can be calculated by stochastic or deterministic approaches (Monserud and Sterba, 1999). For this study, the most common deterministic approach based on decision theory is used. The predicted total number of trees (N_{adj}) is expressed as (Woollons, 1998):

$$N_{adj} = \hat{N}_2 + \hat{\pi}(N_1 - \hat{N}_2) \quad (40)$$

where $\hat{\pi}$ is the probability of survival for all trees over the period estimated by the final model 3, \hat{N}_2 is the number of trees at age A_2 estimated by a difference form survival model, and N_1 is the number of trees at the beginning of the period.

3 RESULTS AND DISCUSSION

3.1 Model for Predicting Survival Probability

The best set of explanatory variables obtained from the generalized logistic model (3) and their parameter estimates are listed in Tables 3 and 4 for second-rotation loblolly pine in the PUCP and in the LCP, respectively. All parameters were significant based on

the likelihood ratio test. The fitted models for the probability of survival of all trees over a time interval of L years were

$$\pi = (1 + e^{-(4.9891 - 0.1297A - 0.00095N - 0.03311S)})^{-L} \quad (41)$$

for the PUCP, and

$$\pi = (1 + e^{-(1.6100 - 0.00681BA + 0.03404S)})^{-L} \quad (42)$$

for the LCP. Based on the Hosmer-Lemeshow goodness-of-fit test, the observed and predicted numbers of plots without mortality occurrence, and the difference between them for each group are listed in Tables 3 and 4. At $\alpha = 0.05$, both models seem to fit quite well, and there was no evidence for a significant difference between the predicted and actual survival probability.

Table 3. (I) Parameter estimates of the model for the probability of survival for all trees and (II) Hosmer-Lemeshow goodness-of-fit test, for second rotation loblolly pine plantations in the Piedmont/Upper Coastal Plain region.

(I) Parameter estimates.					
Variable	Parameter estimate	Standard error	p-value		
Intercept	4.9891	0.4900	< 0.0001		
Age (A)	-0.1297	0.0120	< 0.0001		
Trees per acre (N)	-0.00095	0.000271	0.0005		
Site index (S)	-0.03311	0.005538	< 0.0001		

(II) Hosmer-Lemeshow goodness-of-fit test.					
Group	Total no. of plots	Probability ($\hat{\pi}$)	No. of plots without mortality occurrence		
			Observed	Expected	Difference
1	181	0.106	18	19.2	-1.2
2	181	0.158	23	28.6	-5.6
3	181	0.199	36	36.0	0.0
4	181	0.252	43	45.7	-2.7
5	181	0.314	58	56.8	1.2
6	180	0.379	75	68.1	6.9
7	180	0.439	75	79.0	-4.0
8	180	0.504	97	90.7	6.3
9	180	0.583	102	105.0	-3.0
10	180	0.718	136	129.2	6.8
Total	1805	0.365	663	658.3	4.7

Note: Hosmer-Lemeshow statistic $\hat{C} = 5.445$ and the corresponding p-value computed from the chi-square distribution with 8 degree of freedom is 0.709.

Table 4. (I) Parameter estimates of the model for the probability of survival for all trees and (II) Hosmer-Lemeshow goodness-of-fit test, for second rotation loblolly pine plantations in the Lower Coastal Plain region.

(I) Parameter estimates.					
Variable	Parameter estimate	Standard error	p-value		
Intercept	-1.6100	0.7177	0.0257		
Basal area (BA)	-0.00681	0.003069	0.0272		
Site index (S)	0.03404	0.009385	0.0003		

(II) Hosmer-Lemeshow goodness-of-fit test.					
Group	Total no. of plots	Probability ($\hat{\pi}$)	No. of plots without mortality occurrence		
			Observed	Expected	Difference
1	28	0.063	2	1.8	0.2
2	28	0.113	3	3.2	-0.2
3	28	0.147	3	4.1	-1.1
4	28	0.194	4	5.4	-1.4
5	28	0.346	6	9.7	-3.7
6	28	0.593	20	16.6	3.4
7	28	0.645	23	18.1	4.9
8	28	0.691	22	19.4	2.6
9	28	0.735	21	20.6	0.4
10	28	0.804	21	22.5	-1.5
Total	280	0.433	125	121.2	3.8

Note: Hosmer-Lemeshow statistic $\hat{C} = 10.280$ and the corresponding p-value computed from the chi-square distribution with 8 degree of freedom is 0.248.

For second rotation loblolly pine in the PUCP, stand age (A), tree density (N) and site index (S) were found to be highly significant in predicting the probability of survival of all the trees. The corresponding negative parameter estimates indicate that higher tree density, age and site index is associated with increased probabilities of mortality over the observation interval.

For second rotation loblolly pine in the LCP, stand basal area (BA) and site index were identified as key predictors of survival probability over the measurement interval. Basal area, as a measure of stand competition, reflects both tree size and tree density. It is biologically reasonable that the survival probability decreases with increasing stand basal area. The effect of site index on the survival probability in the LCP was different from that in the PUCP. In the PUCP, higher site index is associated with decreased survival probability. In the LCP, however, the survival probability increases with increasing site index.

3.2 Models for Tree Number Reduction

The difference equation, Models 8 – 35, were fitted for the PUCP and the LCP, respectively, using only data from sample plots with occurrence of mortality over the remeasurement interval. The fit statistics and LOO cross-validation statistics of these models are listed in Tables 5 and 6 separately for the two regions.

Table 5. Fit statistics and leave-one-out cross-validation statistics of the models for predicting the tree-number reduction fitted with only data from sampling plots with occurrence of mortality over a period in the Piedmont/Upper Coastal Plain.

Mode	Fit				Leave-one-out cross-validation			
	\bar{E}	RMSE	R^2	AIC	\bar{E}	RMSE	R_{cv}^2	AIC
8	-3.25	24.70	0.971	10567.63	-3.25	24.74	0.971	10570.68
9	-3.02	24.34	0.972	10535.98	-3.02	24.42	0.972	10543.37
10	-3.19	24.51	0.971	10551.43	-3.19	24.57	0.971	10556.68
11	-2.88	24.25	0.972	10527.63	-2.94	24.39	0.972	10540.73
12	-2.02	24.35	0.972	10536.88	-2.00	24.41	0.972	10542.18
13	-1.98	24.10	0.972	10515.08	-1.98	24.20	0.972	10524.48
14	-2.04	24.21	0.972	10525.45	-2.04	24.29	0.972	10532.96
15	-1.91	24.03	0.973	10508.65	-1.91	24.13	0.972	10518.20
16	-2.69	24.12	0.972	10514.48	-2.70	24.23	0.972	10525.60
17	-2.37	23.77	0.973	10483.33	-2.57	23.99	0.973	10504.65
18	-2.58	23.83	0.973	10489.54	-2.60	23.97	0.973	10502.71
19	-22.62	33.13	0.948	11241.99	-22.62	33.21	0.948	11247.13
20	-1.73	23.90	0.973	10496.25	-1.74	24.05	0.973	10510.21
21	-1.69	23.65	0.973	10474.39	-1.70	23.86	0.973	10494.21
22	-1.80	23.70	0.973	10478.37	-1.81	23.87	0.973	10495.01
23	-1.61	23.60	0.974	10468.71	-1.63	23.81	0.973	10489.13
24	-1.68	24.05	0.973	10508.54	-1.68	24.11	0.972	10514.00
25	-1.64	23.80	0.973	10486.40	-1.64	23.90	0.973	10495.72
26	-1.73	23.78	0.973	10484.36	-1.74	23.86	0.973	10492.41
27	-1.55	23.74	0.973	10480.23	-1.55	23.84	0.973	10489.91
28	-2.61	24.74	0.971	10572.55	-2.61	24.79	0.971	10577.66
29	-2.60	24.48	0.972	10550.77	-2.59	24.58	0.971	10560.29
30	-2.64	24.73	0.971	10573.99	-2.63	24.82	0.971	10582.42
31	-2.50	24.41	0.972	10544.04	-2.50	24.51	0.971	10553.80
32	-2.79	24.36	0.972	10535.08	-2.79	24.39	0.972	10538.15
33	-2.52	23.99	0.973	10502.59	-2.62	24.07	0.972	10510.41
34	-2.64	23.96	0.973	10500.15	-2.64	24.02	0.973	10505.09
35	-22.68	33.14	0.948	11240.53	-22.69	33.15	0.948	11241.34

Table 6. Fit statistics and leave-one-out cross-validation statistics of the models for predicting the tree-number reduction fitted with only data from sampling plots with occurrence of mortality over a period in the Lower Coastal Plain.

Mode	Fit				Leave-one-out cross-validation			
	\bar{E}	<i>RMSE</i>	R^2	AIC	\bar{E}	<i>RMSE</i>	R_{cv}^2	AIC
8	-0.93	35.46	0.912	1548.04	-0.92	35.75	0.910	1550.63
9	-0.94	35.14	0.913	1547.23	-1.02	35.85	0.910	1553.48
10	-1.06	35.34	0.912	1549.06	-1.10	35.89	0.909	1553.83
11	-0.69	35.00	0.914	1546.03	-0.71	35.61	0.911	1551.37
12	-0.37	35.32	0.912	1548.86	-0.32	35.70	0.910	1552.18
13	-0.90	35.14	0.913	1549.23	-1.05	36.12	0.908	1557.76
14	-0.54	35.28	0.912	1550.47	-0.61	36.00	0.909	1556.76
15	-1.13	34.97	0.914	1547.77	-2.50	36.74	0.905	1563.03
16	-1.63	33.29	0.922	1530.46	-1.69	34.25	0.917	1539.28
17	-1.44	33.25	0.922	1532.17	-1.61	34.89	0.914	1547.02
18	-1.67	33.25	0.922	1532.17	-1.80	34.52	0.916	1543.72
19	-20.72	41.69	0.878	1602.24	-21.30	43.03	0.870	1612.05
20	-1.30	33.23	0.922	1531.90	-1.32	34.32	0.917	1541.96
21	-1.31	33.23	0.922	1533.90	-1.61	35.60	0.911	1555.32
22	-1.38	33.22	0.922	1533.82	-1.49	34.68	0.915	1547.21
23	-1.33	33.23	0.922	1533.90	-1.53	35.16	0.913	1551.41
24	-2.48	37.14	0.903	1564.39	-2.43	37.42	0.901	1566.71
25	-3.58	36.57	0.906	1561.61	-3.29	37.24	0.902	1567.23
26	-1.62	36.27	0.907	1559.06	-1.76	37.66	0.900	1570.77
27	-3.69	36.25	0.908	1558.89	-3.85	37.02	0.904	1565.42
28	0.92	33.18	0.923	1529.48	0.95	33.77	0.920	1534.96
29	0.90	33.18	0.923	1531.48	0.71	34.95	0.914	1547.55
30	-0.55	32.53	0.926	1525.32	-0.57	33.46	0.921	1534.12
31	0.84	33.17	0.923	1531.34	0.37	34.13	0.918	1540.19
32	-3.07	37.25	0.902	1563.32	-3.04	37.48	0.901	1565.21
33	-3.18	36.59	0.906	1559.78	-3.26	37.18	0.903	1564.75
34	-2.59	36.71	0.905	1560.78	-2.70	37.66	0.900	1568.70
35	-2.65	36.39	0.907	1558.09	-2.64	36.87	0.904	1562.18

3.2.1 Piedmont/Upper Coastal Plain (PUCP)

Models 19 and 35 showed the worst results both in the fit and LOO cross-validation statistics (Table 5), in which the relative rate of change in the number of trees ($\frac{dN/dA}{N}$) is proportional to an exponential function of age and constrained for $\beta = 0$. For each combination of initial conditions, β and the function of site index, it can be observed that equations with a larger bias and a lower precision are those in which $\frac{dN/dA}{N}$ is not related to stand age. This seems to indicate that $\frac{dN/dA}{N}$ is directly proportional to the initial stand density, some function of age, and some function of site index.

Models 21–23, in which $\frac{dN/dA}{N}$ is proportional to stand density (N^β), a linear function of site index ($f_1(S) = \gamma_0 + \gamma_1 S$) and some functions of age, provided the more accurate estimates with better LOO cross-validation statistics. Model 23 had the smallest values of AIC and $RMSE$, the biggest value of R^2 , and the second smallest bias (Table 5). Thus the proposed equation for predicting the reduction of the tree number between ages (A_1 and A_2) for second-rotation loblolly pine plantations in the PUCP is:

$$N_2 = \left[N_1^{0.47404} + (1.04804 - 0.02566S)(1.06602^{A_2} - 1.06602^{A_1}) \right]^{0.47404}. \quad (43)$$

3.2.2 Lower Coastal Plain (LCP)

Model 19 also showed the worst results both in the fit and LOO cross-validation statistics with the largest values of AIC and $RMSE$, the smallest value of R^2 , and the largest bias (Table 6). In general, those models in which $\frac{dN/dA}{N}$ is not related to site index (i.e. Models 8–15), or directly proportional to a site index function ($\gamma_1 S$) without an intercept (i.e. Models 24–27, 32–35) showed poorer results, no matter whether $\frac{dN/dA}{N}$ is related to a function of age or not (Tables 2 and 6).

Unlike for the PUCP those models with a linear site index function ($f_1(S) = \gamma_0 + \gamma_1 S$) performed better, for the LCP those models in which $\frac{dN/dA}{N}$ is inversely proportional to site index ($f_1(S) = \gamma_1 / S$) got better results (Models 28 – 31, Table 6). Model 30, in which $\frac{dN/dA}{N}$ is proportional to initial stand density (N^β), site index function $f_1(S) = \gamma_1 / S$ and an exponential function of age, had the smallest values of AIC and $RMSE$, the largest value of R^2 , and a smaller bias (Table 6). Thus the proposed equation for predicting the reduction of the tree number between ages (A_1 and A_2) for second-rotation loblolly pine plantations in the LCP is:

$$N_2 = \left[N_1^{0.10665} - \frac{0.44226}{S} (A_2 - A_1) + 0.03405 \ln\left(\frac{A_2}{A_1}\right) \right]^{0.10665} \quad (44)$$

In previous PMRC studies on the whole stand models for second-rotation loblolly pine plantations in the southeastern U.S., the same survival equation was used for both the PUCP and the LCP, while dominant height and stand basal area equations were developed separately for the PUCP and LCP (Borders et al., 2004). The form of their survival equation is:

$$N_2 = S^\alpha + \left[(N_1 - S^\alpha)^\lambda + \beta S (A_2^\theta - A_1^\theta) \right]^{1/2} \quad (45)$$

where N_i = number of trees/acre at age A_i , S = base age 25 site index, $\alpha = 0.85$, $\lambda = -0.7$, $\theta = 2.3$, and $\beta = 0.4 \times 10^{-7}$. This equation could be seen as a modified form of Model 25, in which the relative rate of mortality is proportional to site index, a power of initial tree density and age. Predictive performance of equations (43), (44) and (45) is examined below in more detail.

4. SURVIVAL PROJECTIONS

Given the initial stand conditions (i.e. A , N and S) for second-rotation loblolly pine in the PUCP, the survival probability and number of surviving trees throughout the development of the plantation can be projected directly with equations (41), (43) and (40).

For second-rotation loblolly pine in the LCP, stand basal area (BA) is used to predict survival probability (Eq. 42). To project the survival probability and the number of surviving trees, stand basal area in the future has to be projected using the dominant height (H_D) model, BA prediction and projection equations developed by Borders et al. (2004) for second-rotation loblolly pine plantations in the LCP:

$$H_D = 136.6 \left\{ 1 - \left[1 - \left(\frac{S}{136.6} \right)^{1/1.202941} \right]^{A/25} \right\}^{1.202941} \quad (46)$$

$$\ln(B) = b_0 + b_1 / A + b_2 \ln(N) + b_3 \ln(H_D) + b_4 \ln(N) / A + b_5 \ln(H_D) / A \quad (47)$$

$$\begin{aligned} \ln(B_2) = b_0 + \frac{A_1}{A_2} \left[\ln(B_1) - b_0 - b_2 \ln(N_1) - b_3 \ln(H_{D1}) - b_4 \frac{\ln(N_1)}{A_1} - b_5 \frac{\ln(H_{D1})}{A_1} \right] \\ + b_2 \ln(N_2) + b_3 \ln(H_{D2}) + b_4 \frac{\ln(N_2)}{A_2} + b_5 \frac{\ln(H_{D2})}{A_2} \end{aligned} \quad (48)$$

where $b_0 = -1.96561$, $b_1 = -31.6234$, $b_2 = 0.408805$, $b_3 = 1.038358$, $b_4 = 2.59909$, $b_5 = 4.304848$. Given the initial stand conditions (i.e. A , N and S) for second-rotation loblolly pine in the LCP, the initial basal area can be estimated using H_D and BA prediction models (Eqs. 46 and 47). Then, the survival probability and the number of surviving trees throughout the development of plantations can be jointly and iteratively projected using equations (42), (44), (40), (46) and (48).

Assume loblolly pine plantation stands with three levels of site index (60, 70 and 80 ft at base age 25 years) have three levels of tree density (400, 600 and 800 trees per acre at age 5 years). The predicted probabilities of survival for all trees over 2-year periods and numbers of surviving trees between 5 and 25 years were calculated for the plantations in the PUCP and LCP, respectively, using the equations developed in the current study. The surviving trees were also predicted with equation (45) developed by Borders et al. (2004). Predicted survival probabilities and survival patterns are presented in Figures 1-6.

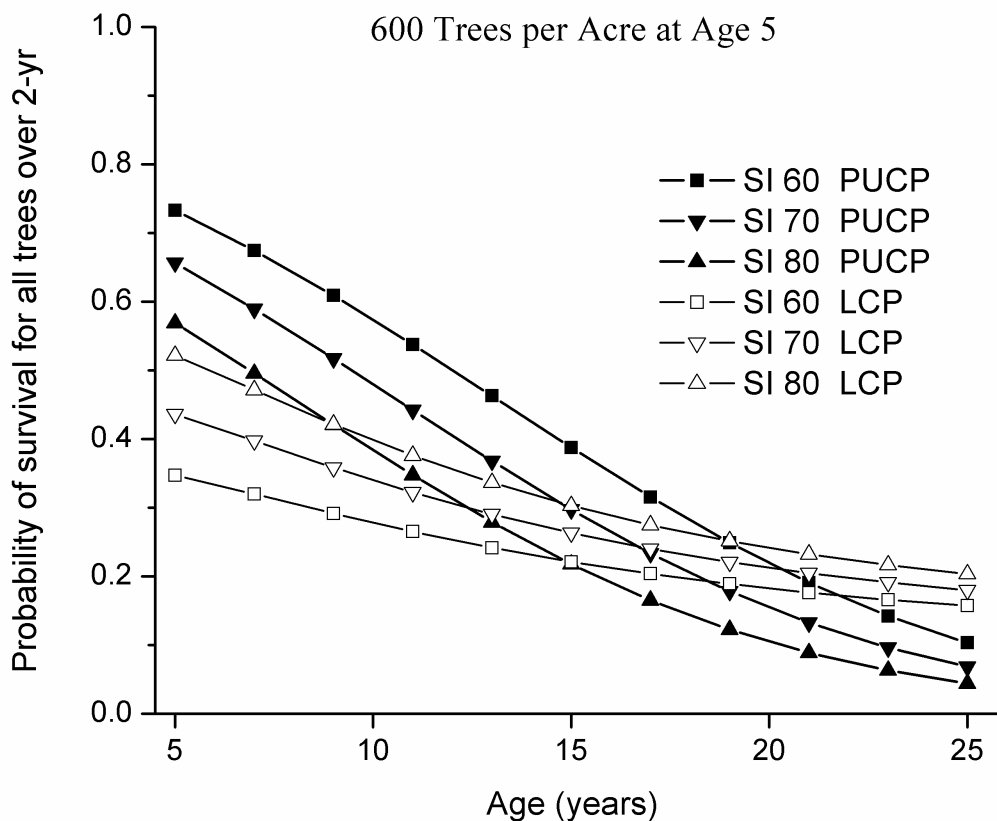


Figure 1. Predicted survival probability over age for 600 trees per acre at age 5 and three site index values. Predictions are for second-rotation loblolly pine plantations in the Piedmont/Upper Coastal Plain (PUCP) and the Lower Coastal Plain (LCP).

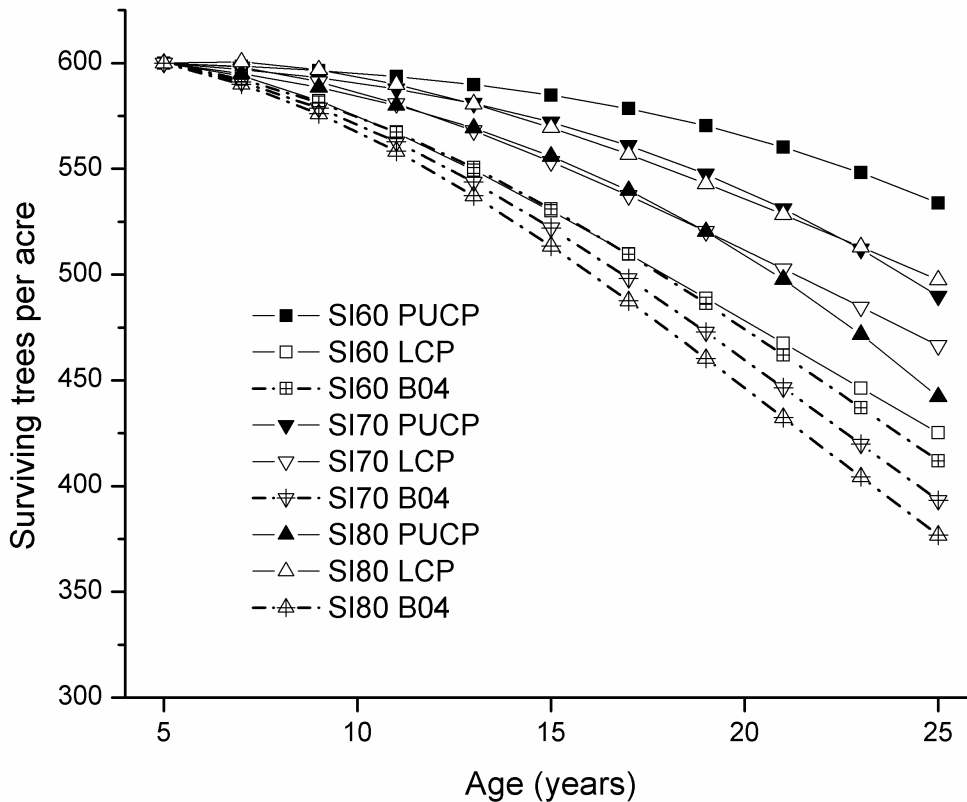


Figure 2. Survival pattern for an age five density of 600 trees per acre and three site indices. Projections are for the Piedmont/Upper Coastal Plain (PUCP) and Lower Coastal Plain (LCP) with the new models, and for all physiographic regions with the survival function of Borders et al. (2004) (B04).

4.1 Effects of Site Index

Figs. 1-2 indicate strong effects of site index and age on the probability of survival for all trees and number of surviving trees over age for loblolly pine plantations in both the PUCP and LCP. As discussed for equations (41) and (42), however, site productivity affects mortality in an opposite way in the two regions. In the PUCP both the predicted survival probability and number of surviving trees decrease as the site index increases (Figs. 1 and 2). Our finding coincides with the conclusion of Bailey et al. (1985), Adams et al. (1996) and Zhao et al. (2006b) that higher mortality was related to better productivity. In the LCP the predicted survival probability and number of surviving trees increases with increasing site index (Figs. 1 and 2). Woollons (1998) also found that higher mortality was related to lower productivity for *Pinus radiata* in New Zealand.

Jutras et al. (2003) found that site productivity had a significant effect on mortality, giving higher mortality rate for Scots pine but lower mortality rate for pubescent birch in more productive sites. The higher rate of mortality on good sites may be partly an effect of higher local competition (Jutras et al., 2003), but better sites may also support higher stocking than lower productivity sites (Vanclay, 1994). The different effects of site productivity on mortality may be also related to the availability of certain key nutrients (Jutras et al., 2003).

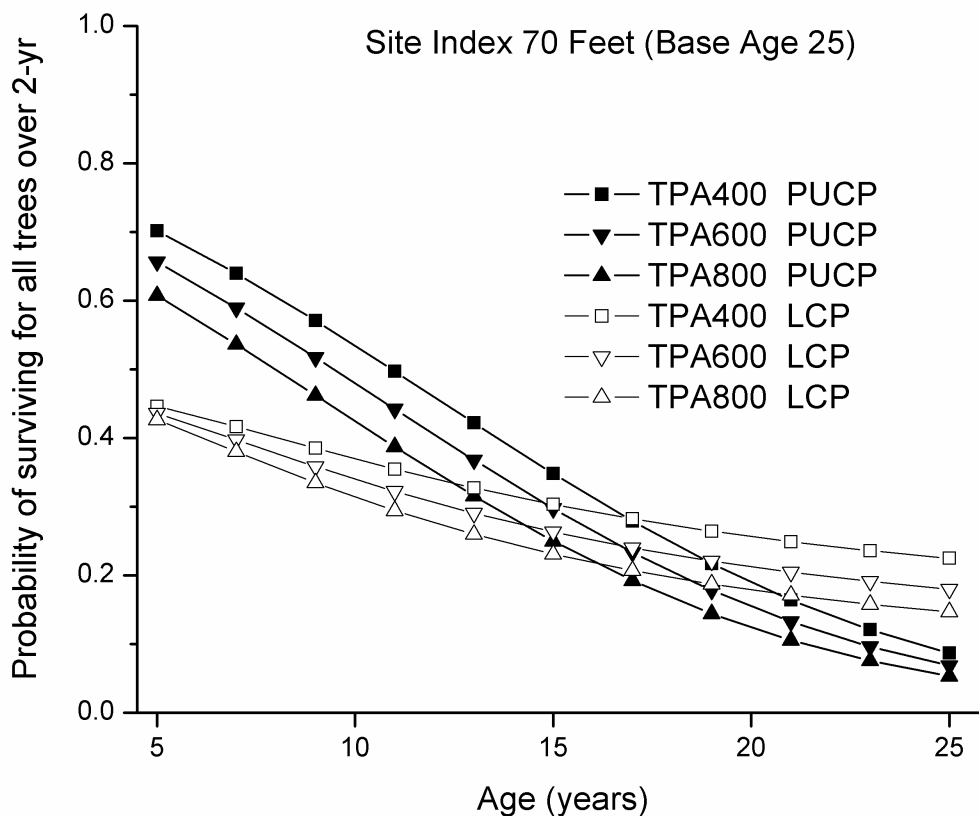


Figure 3. Predicted survival probability over age for site index 70 ft and three levels of initial density at age 5. Predictions are for second-rotation loblolly pine plantations in the Piedmont/Upper Coastal Plain (PUCP) and the Lower Coastal Plain (LCP).

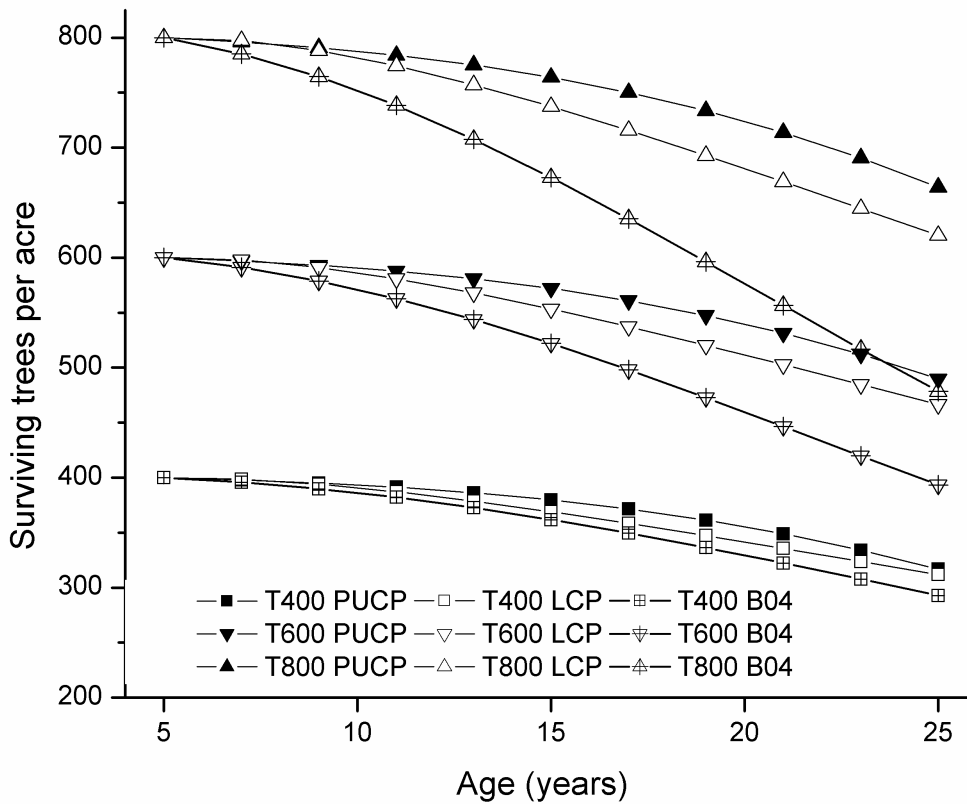


Figure 4. Survival pattern for site index 70 ft and three age five densities. Predictions are for the Piedmont/Upper Coastal Plain (PUCP) and the Lower Coastal Plain (LCP) using the new models, and for all physiographic regions using the survival function of Borders et al. (2004) (B04).

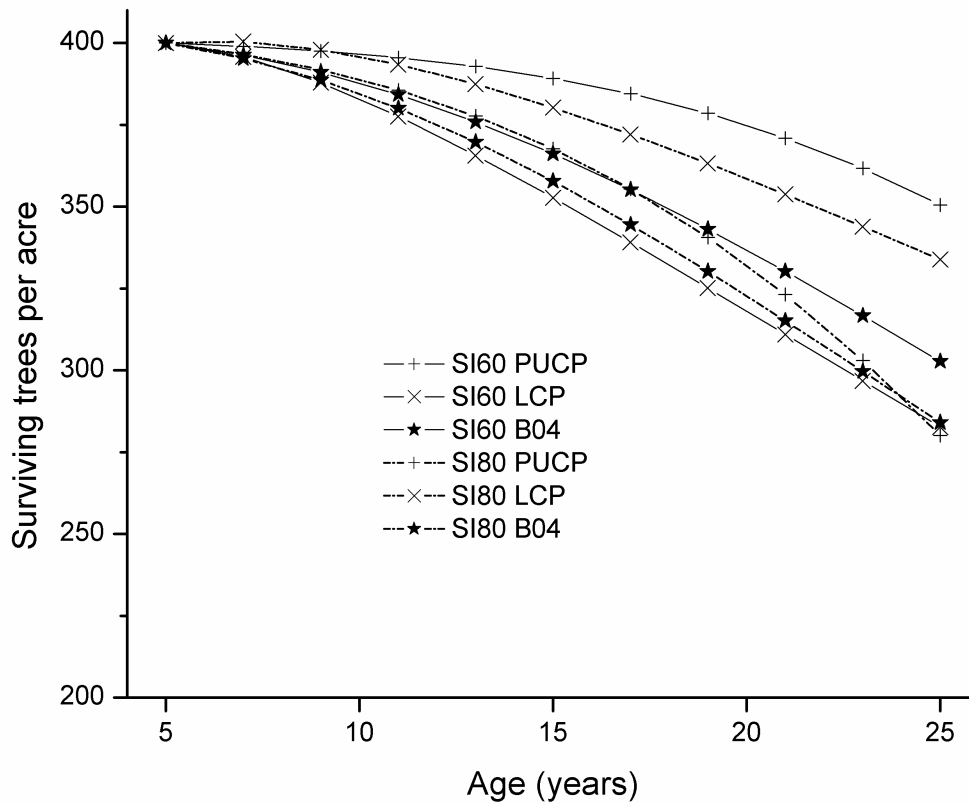


Figure 5. Survival pattern for an age five density of 400 trees per acre and two levels of site index (60 and 80 ft). Predictions are for the Piedmont/Upper Coastal Plain (PUCP) and the Lower Coastal Plain (LCP) with the new models, and for all physiographic regions using the survival function of Borders et al. (2004) (B04).

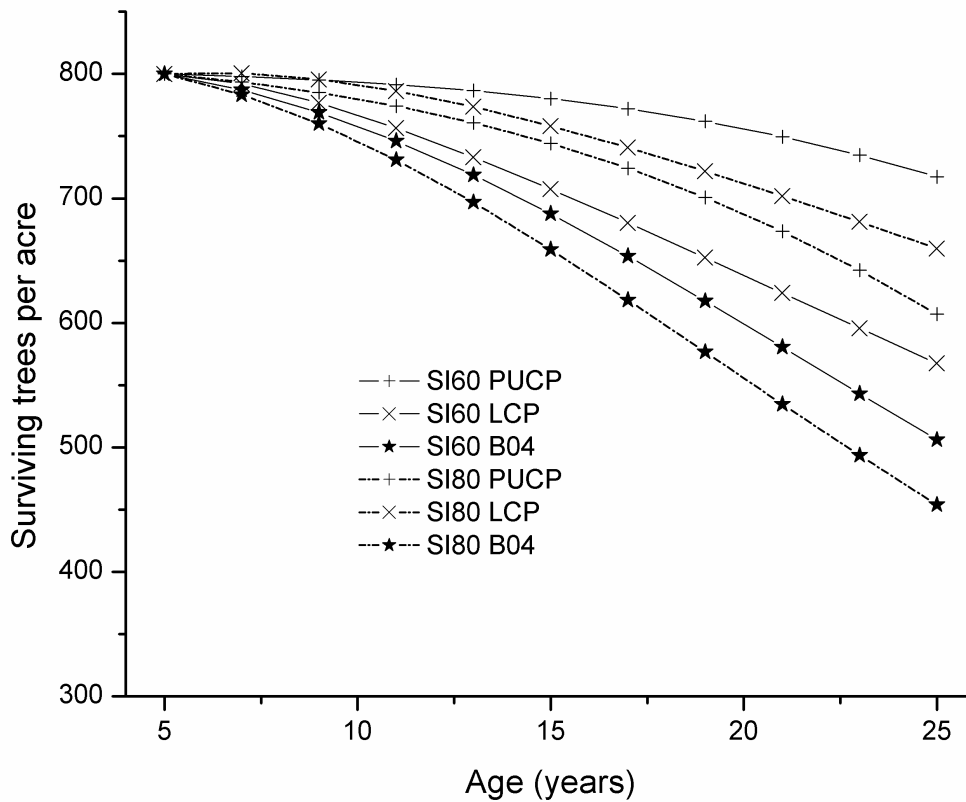


Figure 6. Survival pattern for an age five density of 800 trees per acre and two levels of site index (60 and 80 ft). Predictions are for the Piedmont/Upper Coastal Plain (PUCP) and the Lower Coastal Plain (LCP) with the new models, and for all physiographic regions using the survival function of Borders et al. (2004) (B04).

For a given initial density and site index, second-rotation loblolly pine plantations in the LCP initially show lower survival probability than those in the PUCP, but subsequently survival probability in the LCP is higher than that in the PUCP. The intersection age, at which the survival probability curves in the PUCP and the LCP intersect for given initial density and site index, decreases with increasing site index (Fig. 1). Fig. 2 and 4-6 also show higher mortality rate in the LCP than in the PUCP, for a given age, site index and initial density. This mortality difference may be due to the availability of certain limiting nutrients (Shen et al., 2001; Jutras et al., 2003). Nitrogen and phosphorus tend to be the most limiting nutrients for loblolly pine in the PUCP, and the soils in the LCP tend to be deficient in both N and P. But we propose that the difference in drainage may be related to the higher mortality rates in the LCP. The soils in the PUCP plots range

from moderately well-drained to well-drained, while the soils in the LCP plots range from poorly to moderately well-drained. Further investigation of this explanation remains.

The survival function of Borders et al. (2004) (Eq. 45, denoted as B04 in figures) did not distinguish this physiographic region difference in mortality behavior. For a given initial density and site index, their function implied that higher mortality was related to higher site index (Figs. 2, 5 and 6). For a given site index and higher initial density, or for a given initial density and higher site index, the predicted mortality with Eq. (45) is higher than that with the new models developed separately for the PUCP and LCP (Figs. 2, 4 and 6). For a given lower initial density and lower site index, the predicted number of surviving trees per acre with Eq. 45 is smaller than that predicted with the new model for the PUCP, but may be larger than that predicted with the new model for the LCP (Fig. 5). Generally speaking, the survival function of Borders et al. may overestimate the mortality rate, compared with the new models.

4.2 Effects of Initial Density

For a given age and site index, the survival probability is generally lower at higher initial density, although the shapes of survival probability in the UPCP and LCP are different (Fig. 3). For a given age, site index and initial density, survival probability in the LCP is lower than that in the UPCP during early ages, subsequently survival probability in the LCP is higher than that in the UPCP (Fig. 3). In terms of mortality rate, mortality is higher at higher initial density, for a given age and site index (Fig. 4).

5 CONCLUSIONS

Mortality models for second-rotation loblolly pine plantations are developed separately for the PUCP and LCP physiographic regions of the southern United States. There are different mortality patterns in the PUCP and LCP. In the PUCP, the survival probability is mainly influenced by the stand age, density, and site index. The survival probability decreases with increasing stand age, site index, and tree density. The best difference mortality function was derived from a differential equation where the relative rate of mortality is proportional to an exponential function of age, a power function of the initial stand density, and a function of site index. In the LCP, survival probability is related to stand basal area and site index, and the probability decreases with increasing basal area, but increases with increasing site index. The best difference mortality equation was derived from a differential equation where the relative rate of mortality is proportional to a power function of the initial stand density, and inversely proportional to site index and stand age.

It is clear that site productivity affects mortality in an opposite way in the two regions. In the PUCP both the predicted survival probability and number of surviving trees decreases as the site index increases; in the LCP, however, both the predicted survival probability and number of surviving trees increases with increasing site index. For a given initial density and lower site index, second-rotation loblolly pine in the LCP has higher mortality than in the PUCP, which implying that sites in the PUCP may support higher stocking than the same lower quality of sites in the LCP. For a given initial density and higher site index, second-rotation loblolly pine in the LCP has lower mortality than in the PUCP, which implying that sites in the PUCP may support lower stocking than the same higher quality of sites in the LCP.

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