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MODELING SURVIVAL FOR UNTHINNED SLASH PINE PLANTATIONS IN EAST TEXAS UNDER THE INFLUENCE OF NON-PLANTED TREE BASAL AREA AND INCIDENCE OF FUSIFORM RUST

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Abstract.—A stand level survival model for unthinned slash pine (*Pinus elliottii*) plantations in east Texas was developed that incorporates density of non-planted tree basal area per hectare competition and the incidence of fusiform rust (*Cronartium quercuum*). Survival data on planted slash pine trees were collected on 197 permanent research plots that represent a broad range of site, age, and competitive status combinations. A system of two equations was fit to the survival data using simultaneous nonlinear regression. All model parameters were significant at the 0.05 probability level. The model showed that the number of surviving planted slash pine trees decreased with increasing density (trees per hectare) of non-planted trees as well as increasing site quality (site index). The model further allowed the transition of the slash pine trees from being uninfected to being infected by fusiform rust.

Infection of pine plantations with fusiform rust (*Cronartium quercuum* [Berk.] Miyabe ex Shirai f. sp. *fusiforme*) causes serious problems for forest owners in the southern United States. An estimation of the annual financial loss from rust associated mortality in slash pine (*Pinus elliottii* Engelm.) and loblolly pine (*Pinus taeda* L.) plantations in the southern United States is 28 million dollars (Adams 1989). This includes death from girdling of the tree by the rust canker as well as incremental mortality from wind breakage, insect infestation, and other causes that exert additional stress on the already weakened condition of infected trees. Lenhart et al. (1994) reported that an average of 40% of east Texas slash pine trees had stem cankers caused by fusiform rust.

Competition for site resources from non-planted trees has also contributed to the mortality of planted pine trees (Stewart et al. 1984; Shiver et al. 1990; Haywood & Tiarks 1990; Glover & Zutter 1993; Fortson et al. 1996). These studies found significant negative growth effects of competing vegetation on the planted pine trees.

The incidence of fusiform rust and competition from non-planted trees must be considered in any prediction of future growth and yield for pine plantations. A primary component in the accurate prediction of future plantation growth and yield is the number of trees per unit area expected to survive to a harvestable age. Future yields are dependent on the number of trees per unit area in conjunction with other useful predictors, such as plantation age, tree height, site index, basal area, and average tree size.

Several approaches to predicting the surviving number of trees in pine plantations have been developed (Clutter & Jones 1980; Bailey et al. 1985; Clutter et al. 1984; Lenhart 1972; Somers et al. 1980), but none of these approaches directly considered non-planted tree competition or the incidence of fusiform rust. Burkhart & Sprinz (1984) and Burkhart et al. (1987) did include the effects of hardwood competition in estimating the surviving number of planted pines. They found significant negative effects of hardwood competition in estimating the surviving number of planted pines. However, they did not directly consider the effects of fusiform rust.

Devine & Clutter (1985) developed equations that predicted survival for slash pine trees that were either infected or not infected by fusiform rust. One survival equation was computed for uninfected trees, and another survival equation was computed for infected trees that included the additive effects of mortality associated with fusiform rust. Adams (1989) developed survival models for trees infected and uninfected with fusiform rust that allowed for the transition of trees from an uninfected stage to an infected stage. Multinomial logistic regression models were developed by Arabatzis et al. (1991) to predict the possible transition paths of planted loblolly pine trees from a live to dead status. Stem infection by fusiform rust was one of the stages along the transition paths. However, none of these studies directly incorporated the effects of non-planted tree competition on the survival of planted pine trees.

The objective of this study was to develop prediction equations to estimate the surviving number of planted slash pine trees growing under the influence of non-planted tree competition and fusiform rust. These equations are applicable to unthinned slash pine plantations located throughout east Texas.

MATERIALS AND METHODS

Slash pine plantation measurements.—Long-term data from 197 East Texas Pine Plantation Research Project (ETPPRP; Lenhart et al. 1985) permanent research plots located in slash pine plantations across east Texas were analyzed in this study. The ETPPRP study area covers 22 counties across east Texas. Generally, the counties are located within the rectangle from 30° - 35° north latitude and 93° - 96° west longitude. Each plot consists of two adjacent subplots separated by an 18.3-meter buffer. Within a subplot, the 15-year survival status (live or dead) was monitored for each planted slash pine tree. In addition, the numbers of non-planted trees (volunteer pine and hardwoods) within two embedded 0.002314 hectare circular plots (radius = 2.7 meters) in each subplot were monitored for 12 years.

In this study, one subplot per study plot was randomly selected for model fitting, and the other subplot was utilized for model evaluation. Minimum plantation age was set at 5 years because of inconsistent determination of main stem fusiform rust incidence in young (<5 years) plantations. As a result, the 197 slash pine subplots were used for model fitting and 194 slash pine subplots were used for model evaluation.

Mean plantation age and site index values (base age = 25 years; Lee 1998) are similar for both evaluation and development subplots. On the average, about 34% of the slash pines had stem cankers from fusiform rust (Table 1).

Survival models.—Adams (1989) developed survival models for fusiform rust infected and uninfected pine trees that allow for the transition of trees from an uninfected stage to an infected stage. His work was based on Shapiro's (1946) differential equations, which are used to describe the growth of two different bacteria types (X, Y). These two populations increase not only by cell divisions resulting in the same type (e.g., X dividing to yield X), but also by mutation (e.g., X mutation to Y). Shapiro's (1946) equations are:

$$\frac{dx}{dt} = ax + by$$

$$\frac{dy}{dt} = mx + cy, \tag{1}$$

where:

a, c = population growth rates, and

b, m = mutation rates.

Table 1. Observed stand characteristics for east Texas unthinned slash pine plantations data sets. AGE = plantation age (years), S = site index (meters), TPH = total trees per hectare, N_u = number of trees per hectare without a fusiform rust stem gall, N_i = number of trees per hectare with a fusiform rust stem gall, PBA = planted slash pine basal area (m^2/ha), NPTB = non-planted tree basal area (m^2/ha), and RNTB = ratio of the non-planted tree basal area to total basal area per hectare.

	Model development subplots (n = 197)				Model evaluation subplots (n = 194)			
Variables	Mean	Std Dev.	Min.	Max.	Mean	Std Dev.	Min.	Max.
AGE	13.5	3.9	7	26	13.5	3.9	7	26
S	22.9	3.4	6.7	29.3	23.0	2.5	14.3	29
TPH	910	419.6	193	2,283	935	400	225	2,249
N_U	598	355.3	42	1,638	621	353	86	1,618
N_i	312.3	161.5	7.4	775.9	314	149	49	714
PBA	16	7.2	0.2	38.1	16.6	6.6	2.3	34.4
NPTB	2.2	2.7	0	23.6	2.3	3.3	0	34.7
RNTB	0.14	0.11	0	0.60	0.09	0.11	0	0.70

Adams (1989) modified Shapiro's equations (1) to consist of two components: surviving trees infected with fusiform rust (N_i) and surviving trees uninfected with fusiform rust (N_u):

$$\frac{dN_i}{dA} = -(\rho_i + \gamma)N_i + \phi N_u$$

$$\frac{dN_u}{dA} = \gamma N_i - (\rho_u + \phi)N_u, \qquad (2)$$

where:

ρ_i = instantaneous mortality rate for infected trees,

ρ_u = instantaneous mortality for uninfected trees and,

ϕ = instantaneous rate of uninfected trees becoming infected, and

γ = instantaneous rate of infected trees becoming uninfected = 0.

After a period of time (dA), the numbers in each group will change (dN_i and dN_u). The number of trees in the infected group will decrease due to mortality at the rate ρ_i, but will gain the number of uninfected trees that become infected during this time at the rate ϕ. Mortality and a change in uninfected status at the rates ρ_u and ϕ, respectively, will both decrease the number in the uninfected component. The parameter $\gamma = 0$ because there is no possibility of infected trees becoming uninfected.

Adams' equations can be solved (Lee & Coble 2002) via the Method of Determinants (Grossman & Derrick 1988). The resulting equations are expressed as the change in numbers of slash pine trees between two time periods, A_1 and A_2:

$$N_{i2} = \beta N_{u1}\, e^{-\alpha(A_2 - A_1)} + (N_{i1} - \beta N_{u1}) e^{-\rho_i(A_2 - A_1)} \tag{3}$$

$$N_{u2} = N_{u1}\, e^{-\alpha(A_2 - A_1)},$$

where:

A_2 = projection age (years),

A_1 = initial age (years),

N_{i2} = number of surviving infected trees per hectare at A_2,

N_{i1} = number of surviving infected trees per hectare at A_1,

N_{u2} = number of surviving uninfected trees per hectare at A_2,

N_{u1} = number of surviving uninfected trees per hectare at A_1, and

α, β, ρ_i = parameters to be estimated.

Equations (3) provide for separate estimates of mortality rates for infected and uninfected slash pine trees, as well as the possible transition from an uninfected to infected status. The parameter $\alpha = (\rho_u + \phi)$ is the rate at which trees are lost from the uninfected class. The parameter $\beta = \frac{\phi}{\rho_i - \alpha}$ represents the proportion of unifected trees that become infected, some of which are lost at the rate, α. Behavior of this model is consistent with the desired properties of path invariance and convergence; the number surviving planted pine trees converge to zero as age goes to positive infinity.

Adams (1989) and Adams et al. (1996) reported that pine survival in their studies decreased as site productivity (as measured by site index) increased. The faster rate of stand development in plantations (and natural forests) of higher site productivity triggers competition-induced mortality at earlier ages than in plantations of lower site productivity (Oliver and Larson 1996). Thus, the number of surviving trees at any plantation age will be lower in plantations of higher site productivity versus plantations of lower site productivity.

As mentioned earlier, the competitive effects of non-planted trees may also influence pine survival. So, a combined variable for the ratio of non-planted tree basal area to total basal area per hectare (RNTB) and site index (S) in meters (base age = 25 years) was incorporated into the differential equations (2) of Adams (1989) and solved in a similar manner as before (subject to the assumption that RNTB is constant with respect to age; see discussion below):

$$N_{i2}=\beta N_{u1}\, e^{-\alpha(S^{*}RNTB)(A_2-A_1)}+(N_{i1}-\beta N_{u1})e^{-\rho i(S^{*}RNTB)(A_2-A_1)}$$

$$N_{u2}=N_{u1}\, e^{-\alpha(S^{*}RNTB)(A_2-A_1)}, \qquad (4)$$

where all other variables and parameters defined as before.

The introduction of the two variables, S and RNTB, had the potential to alter the solution of equations (2) if they were not constant terms; i.e., if S and/or RNTB were functions of plantation age, then the solutions in equations (4) do not follow from the differential equations. The following hypotheses were tested via simple linear regression to determine if S and RNTB were constant terms before the equations (4) were fit to the data:

Ho1: S is constant across plantation age,

Ho2: RNTB is constant across plantation age, and

Ho3: S*RNTB is constant across plantation age.

None of the three hypotheses were rejected at the $\alpha = 0.01$ probability level ($P = 0.6393$, $P = 0.0117$, $P = 0.0706$, respectively), so S and RNTB were assumed to be constant across the range of plantation ages in this study.

After S and RNTB were found to be constants, equations (4) were fit to the data. Preliminary analyses (not presented) showed that survival, site index, and RNTB were significantly correlated ($P < 0.05$). A fitting procedure described by Borders (1989) was used to account for the presence of this cross-equation error correlation. As a result, equations (4) were fit to the 197 observations in a simultaneous manner using the SYSNLIN procedure in SAS (1985).

Model evaluation.—The statistical measures used in this study for model evaluation were the coefficient of determination (R^2), root mean square error (RMSE), mean percent bias (described below), and a simple linear regression analysis of observed versus predicted total surviving trees per hectare (described next).

Simple linear regression (Zar 1999) was used to compare observed and predicted total surviving trees per hectare. Observed and predicted values were related according to the following simple linear model: Predicted TPH = $b_0 + b_1$ * Observed TPH. If the survival prediction models correctly estimated the number of surviving trees per hectare, then the intercept (b_o) would not be significantly different from zero and the slope (b_1) would be not be significantly different from one. A simultaneous *f*-test (Neter et al. 1985:p. 147) was used to evaluate the hypothesis: Ho: $(\beta_0, \beta_1) = (0,1)$, Ha: $(\beta_0, \beta_1) \neq (0,1)$.

Reynolds (1984) developed estimation procedures to test the accuracy of models. His procedures test both bias and precision rather than overall prediction accuracy. These procedures were converted to a BASIC program (Rauscher 1986), then later to a SAS program (SASATEST; Gribko & Wiant 1992). SASATEST was used in this study to further examine the performance of the survival prediction models. SASATEST examines both bias and precision on an absolute or percentage basis. In SASATEST, percent bias is calculated as a percentage of the observed surviving trees per hectare:

$$\text{BIAS} = 100\ \frac{\hat{Y} - Y}{Y},$$

where:

$\hat{Y}$ = predicted surviving trees per hectare and Y = observed surviving trees per hectare. In this study, precision is expressed as the standard deviation of percent bias, which is also calculated by SASATEST. SASATEST then uses the mean percent bias (measure of bias) and the standard deviation (measure of precision) to calculate a 95% confidence interval. If this confidence interval does not contain zero, then the bias is significant at the $\alpha = 0.05$ level. SASATEST also checks the errors between predicted and observed values for departures from normality. If non-normality is detected, a 10% trimmed mean and jackknife standard deviation were used to provide more robust confidence intervals.

Results and Discussion

Survival prediction models.—The following model developed from the slash pine plantation survival data provides separate estimates of the surviving number of slash pine trees:

$$\begin{aligned} N_{i2} &= (N_{i1} - 0.424429 N_{u1}) e^{(-0.021002((S*RNTB)(A_2 - A_1))} \\ &\quad + 0.424429 N_{u1}\, e^{(-0.00541647(S*RNTB)(A_2 - A_1))} \\ N_{u2} &= N_{u1}\, e^{(-0.00541647(S*RNTB)(A_2 - A_1))}, \end{aligned} \tag{5}$$

where, all variables are defined as before.

The asymptotic standard errors for coefficients $\hat{\rho}_i$, $\hat{\alpha}$, $\hat{\beta}$ are 0.0030458, 0.0012421 and 0.12514, respectively. All parameters were significantly different from zero ($P < 0.05$). The uninfected component in equation (5) explained about 92% of the variation in the surviving number of trees per hectare, while the infected component in equation (5) explained about 56% of the variation in the surviving number of trees per hectare (Table 2). Thus, the uninfected component was more accurately predicted than the number of surviving infected trees. Residual plots (not shown) revealed a random pattern around zero with no detectable trends. Fit statistics for equation (5) based on the data from 194 evaluation subplots are presented in Table 2.

The survival prediction model (5) for uninfected slash pine trees over-estimated the number of surviving trees per hectare by 2.42%, though this value was not significant ($P > 0.05$; Table 2). The survival prediction model (5) for infected slash pine trees significantly ($P < 0.05$) over-estimated the number of surviving trees per hectare by 7.46% (Table 2). This large value can be explained by the large amount of variability in the percent bias values (note the large confidence interval

Table 2. Fit statistics for performance evaluation of east Texas unthinned slash pine plantation survival model. N_{u2} = number of surviving trees per hectare without a fusiform rust stem gall at Age 2, N_{i2} = number of surviving trees per hectare with a fusiform rust stem gall at Age 2, and ** = significant ($P < 0.05$).

Equation	R^2	Root Mean SquareError	Mean Percent Bias	95% Confidence Interval for Percent Bias
N_{u2}	0.92	100.82	2.42	2.42 ± 3.12
N_{i2}	0.56	106.23	7.46**	7.46 ± 5.59

in Table 2). This result was not unexpected since less variability in the predicted number of surviving trees was explained by the model for infected trees (R^2 = 56%; Table 2) versus uninfected trees (R^2 = 92%; Table 2). Adams (1989) and Adams et al. (1996) also found a larger variability in predicting infected fusiform rust incidence versus an uninfected incidence.

The survival prediction equations (5) significantly ($P < 0.05$) over-estimated the total number of surviving trees by 3.25% (95% confidence interval for overall model bias = 3.25% (1.19%) across the range of observed stand densities. The simultaneous f-test also revealed that the total estimated number of surviving trees per hectare was significantly different ($P < 0.0001$; f-statistic = 33) from the total observed number of surviving trees per hectare (Figure 1). The total number of surviving trees per hectare is over-estimated to a greater magnitude for densities >1000 trees per hectare than at densities <1000 trees per hectare (Figure 1). This result is not unexpected considering that fewer, high-density plots were available for model fitting. However, this bias is not a practical concern because tree densities in operational east Texas slash pine plantations typically do not exceed 1000 trees per hectare.

In this study, the null hypothesis, Ho2: RNTB is constant across plantation age, would have been rejected at the $\alpha = 0.05$ probability level ($P = 0.0117$). This implies that RNTB is not strongly disassociated from plantation age, which may be a problem because the solution to the differential equation does not follow as stated in this study if RNTB is a function of age (note that S*RNTB was used in [5], and it was not significantly [$P = 0.0706$] associated with age). We did not find a similar result when this survival model was fit to data for loblolly pine plantations in east Texas (Lee & Coble 2002). No clear explanation can be provided as to the different results. One possible explanation could be that slash pine was more likely to become infected and die

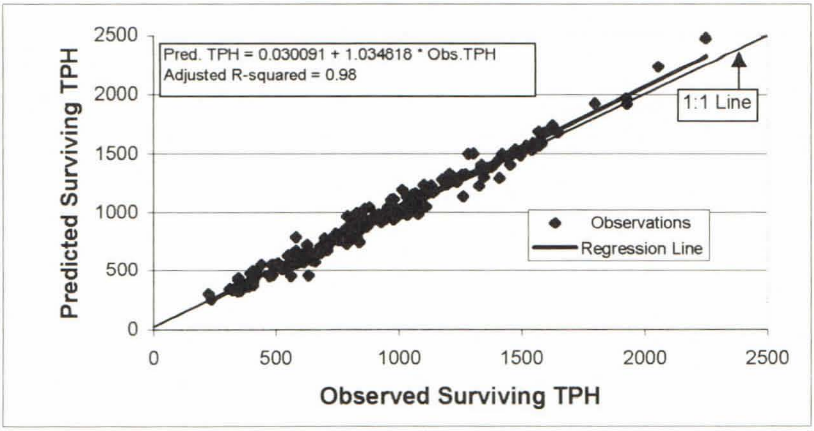

Figure 1. Comparison between observed and predicted total surviving slash pine trees per hectare (TPH).

than loblolly pine. So, more growing space might have been available to the non-planted trees as the plantation aged, thereby increasing RNTB as time increased. Another possible explanation could be that a larger dataset was available to fit the loblolly survival equations, thereby better capturing the effects of non-planted tree competition on planted pine survival. In any case, a survival model that incorporates non-planted tree competition as a function of age would be ideal.

ILLUSTRATIONS OF SURVIVAL PROJECTIONS

The predicted numbers of surviving slash pine trees (both infected and uninfected) decreases as the percent of non-planted tree basal area increases (Figure 2). In Figure 2, the percent of non-planted tree basal area to total basal area per hectare ranges from 10% to 60%, site index = 21 meters, and stem fusiform rust incidence at year 5 = 10%.

The total number of survivors can also be divided into the number of slash pine trees infected or uninfected by fusiform rust (Figure 3). In Figure 3, the numbers of uninfected and infected slash pine trees are displayed for the 15% of non-planted tree basal area to total basal area per hectare (RNTB = 0.15), site index = 21 meters, and stem fusiform rust incidence at year 5 = 10%.

The predicted numbers of surviving slash pine trees (both infected and uninfected) also decrease as site index increases (Figure 4). In Figure 4, site index ranges from 15 to 30 meters, the ratio of non-planted tree

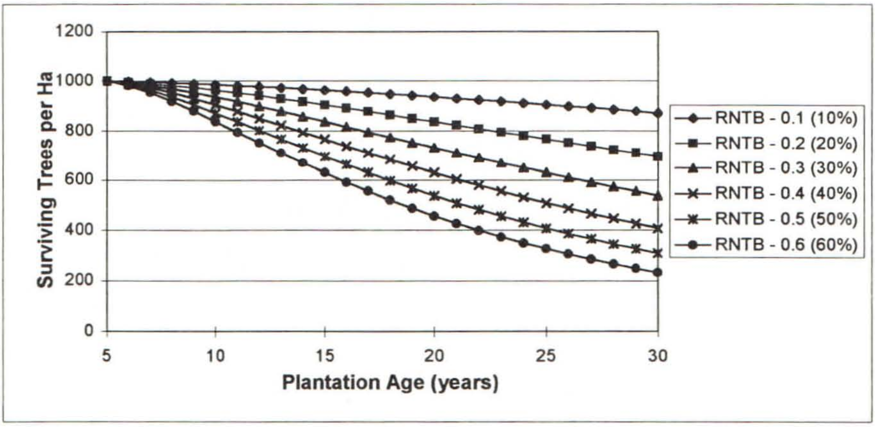

Figure 2. Predicted surviving planted slash pine trees by plantation age and the percent of non-planted tree basal area to total basal area per hectare classes. Site index = 21 meters (base age = 25 years); stem fusiform rust incidence = 10% at 5 years.

Figure 3. Numbers of surviving slash pine trees infected and not infected by fusiform rust by plantation age. The ratio of non-planted tree basal area to total basal area per hectare = 15%; site index = 21 meters (base age = 25 years); stem fusiform rust incidence = 10% at 5 years.

basal area to total basal area per hectare was 15% (RNTB = 0.15), and stem fusiform rust incidence at year 5 was 10%. These results corroborate those of Adams (1989) and Adams et al. (1996). As explained

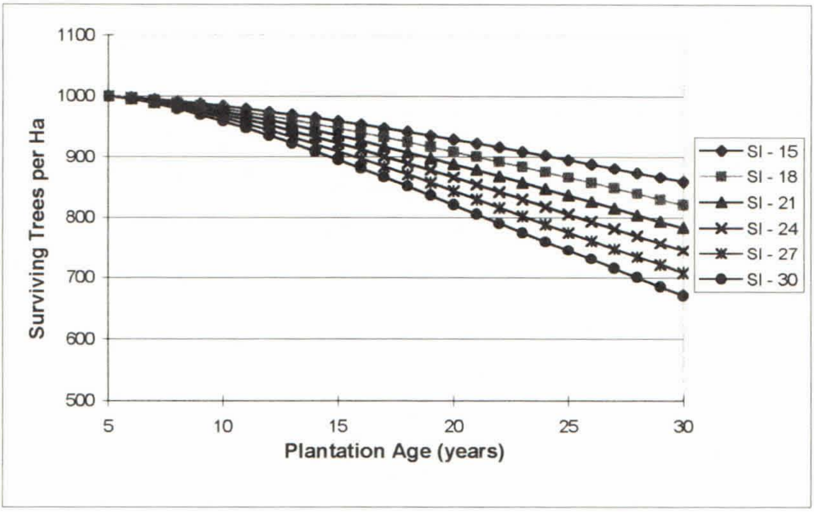

Figure 4. Number of surviving slash pine trees, infected and not infected by fusiform rust, by plantation age and site index in meters (base age = 25 years). The ratio of non-planted tree basal area to total basal area per hectare = 15%; stem fusiform rust incidence = 10% at 5 years.

earlier, mortality occurs at a faster rate on more productive sites. Thus, more productive sites have fewer trees at a given age than less productive sites.

CONCLUSIONS

The results of this study show that the number of surviving slash pine trees both infected and uninfected by fusiform rust can be accurately predicted for a range of site qualities and levels of non-planted tree competition. The survival model (equation 5) depicts the decreasing number of surviving slash pine as non-planted tree competition and fusiform rust incidence increases. Though the model significantly over-estimates the total number of surviving trees at densities >1000 trees per hectare, this is of no practical concern since operational slash plantations in east Texas typically do not exceed 1000 trees per hectare. Management activities that reduce the number of non-planted trees early in the life of the plantation are beneficial to increasing the survival of the planted slash pine trees. This reduction is also an important consideration on the sites with higher productivity since the total number of surviving trees decreases as site index increases.

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