RESEARCH ARTICLE

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silviculture

# Temporal Trends in Fusiform Rust Infections and Their Relationships with Stand Structure in Pine Plantations in East Texas

**Y.H. Weng, D.W. Coble, J. Grogan, and J.P. Stovall**

Fusiform rust is the most important disease affecting plantations of loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) in east Texas. Losses to fusiform rust on loblolly pine and slash pine in the South amount to 35 million dollars a year from the death of infected trees and from its degrading effect on products cut from the tree. This study, based on long-term measurements on permanent plots established on pine plantations across east Texas, assessed rust infection trends from 1984 to 2014 and the relationships between rust infections and common tree and stand variables for pine plantations in east Texas. Results showed that ratios of trees with rust-infected branches declined quickly from 1984 to early 1990s and thereafter leveled off. Ratios of stem-infection peaked in the period 1987–99 and then decreased over time. For both ratios, slash pine had higher values than loblolly pine at any given year. Multilevel logit models were developed to assess effects of tree variables (e.g., DBH, tree height, height to live crown, and crown class) and stand variables (e.g., age, site index, quadratic mean diameter, trees per acre, and basal area per acre) on the probabilities of fusiform rust infection levels (branch- and stem-infection). Results showed that height to live crown and site index were the most important variables; the branch- and stem-infection probabilities increased with increasing height to live crown and decreasing site index for both pines, although the changes were larger for slash pine than for loblolly pine. In addition, the larger DBH trees had a higher probability of branch- and stem-infection for loblolly pine. Older trees or trees growing in plantations of greater density (more trees per acre) had a higher probability of stem-infection for slash pine. Results should be incorporated into the regional pine plantation management planning to reduce loss due to fusiform rust infection.

**Keywords:** loblolly pine, slash pine, fusiform rust, tree variable, stand variable

Fusiform rust, caused by the fungus *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*, is the most prevalent disease affecting approximately 2.5 million acres of loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) plantations in east Texas (Adams 1989, Pye et al. 1995). The infection greatly increases mortality, in particular for trees less than 10 years old (Zhao et al. 2006). The resulting galls and cankers deform older trees, reducing growth and stem quality. Losses to fusiform rust on loblolly pine and slash pine in the South amount to 35 million dollars a year from the death of infected trees and from its degrading effect on products cut from the tree (Schmidt 1998). The substantial losses in growth underscore the need for monitoring and predicting the incidence of this disease so that prevention and control practices can be efficiently deployed as needed.

Fusiform rust incidence in pine plantations in the Southern United States, including east Texas, has been monitored over the past 40 years. During the period, the infection rate declined steadily for loblolly pine but relatively slowly for slash pine plantations (Starkey et al. 1997, Randolph et al. 2015). Similar trends were also confirmed in east Texas (Mason and Griffin 1970, Walterscheidt and van Arsdale 1976, Hunt and Lenhart 1986, Lenhart et al. 1988, 1994), where the rust infection rate declined slowly to 10 percent in loblolly pine plantations and declined by roughly 41 percent in slash pine plantations through 1990. Coble and Lee (2004) further extended the trends to 2002; by then, the fusiform rust infection rates decreased to about 5 percent and 15 percent in loblolly and slash pine plantations in east Texas, respectively.

Finding relationships between fusiform prevalence and biotic and abiotic factors is another topic of great interest. Optimal weather conditions for growth and spread of the fungus from the alternate hosts, oaks

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(*Quercus* spp. L.), to the pine were reported by Siggers (1949). Most subsequent work has attempted to correlate infection levels to site quality or silvicultural treatments. Sites of higher productivity, such as better drained soils (Hollis and Schmidt 1977) and higher site index (Nance et al. 1981, Borders and Berry 1986), and silvicultural activities resulting in faster growth (Hollis et al. 1975, Forelich et al. 1983) were often associated with higher infection level. In contrast, plantation establishment density showed a weak relationship with rust incidence (Miller 1972). The improved understanding in relationships between fusiform prevalence and biotic and abiotic factors greatly facilitates modeling rust infection. Border and Berry (1986) found that stand variables such as stand geographic location, age, and site index were significant predictors of rust infection for site-prepared slash and loblolly pine plantations ranging from Virginia down to northern Florida and across the Gulf Coast to western Alabama. Similarly, Arabatzis et al. (1991) developed a stand model based on stand variables and geographic attributes to model rust infections for east Texas pine plantations. More recently, Choi et al. (2008) developed an individual tree model to predict trends in the incidence of all diseases and insects in unthinned loblolly pine plantations across 12 states in the US South. To account for the effects of fusiform rust on survival, separate equations for infected and uninfected trees in loblolly and slash pine plantations were developed (Clutter et al. 1984, Devine and Clutter 1985, Lee and Coble 2002b, Zhao et al. 2006). For all these models, the number of infected trees at the beginning of a designated projection period is needed.

Thus, some progress has been made both in monitoring temporal trends and in determining factors that contribute significantly to fusiform infection for both pines. However, trends in fusiform rust incidence in east Texas after year 2002 are lacking. Most often, data of fusiform rust infection, which are typically recorded as multiple-level, ordinal, and categorical type, are usually collected from sampling plots over time or in repeated measurement cycles. In determining key factors influencing rust incidence, previous studies utilized regression analysis but without considering data nature such as multinomial (Borders and Berry 1986), ordinal (Arabatzis et al. 1991), and clustering (Borders and Berry 1986, Arabatzis et al. 1991, Choi et al. 2008), or the analysis was based on rather limited data (Arabatzis et al. 1991). Ignoring the possible correlation of the categorical responses may lead, for example, to underestimated standard errors of the estimated regression coefficients (Agresti 2013). Current fusiform rust incidence is a complicated issue and may vary based on geographic location, stand structure, and stand origin (Schmidt et al. 1986). Therefore, effective rust management requires specific data on rust incidence through time and space on a regional scale. This is why guidelines to predict sites with a high hazard of fusiform rust have often been developed at the regional level (Schmidt et al. 1998). To our knowledge, for east Texas, information is still limited regarding how commonly available tree and stand characteristics, such as tree growth and stand structure, affect fusiform rust incidences of pine plantations. A better understanding of the role of common tree and stand variables on rust incidence is a prerequisite for rust management.

Based on long-term data collected from east Texas pine plantations, the first objective of this study was to update temporal trends in rust incidence in east Texas pine plantations, providing the most recent rust survey for this region. By "incidence," we mean the ratio of trees in a stand in each infection-level category and the change in these ratios over time. The second objective was to model the probabilities of fusiform rust in planted stands of loblolly and slash pine in east Texas. Our modeling effort was intended to determine tree and stand variables which significantly correlate with fusiform rust incidence. The overall goal is to provide information that can be used in forest management planning so that losses due to this disease can be reduced.

## Data and Methods

The East Texas Pine Plantation Research Project (ETPPRP) is a long-term research project initiated in 1982 by the Arthur Temple College of Forestry and Agriculture (ATCOFA) at Stephen F. Austin State University and participating forest industries (Lenhart et al. 1985). During the period of its Phase I study (1982 to 2015), 242 permanent plots (168 for 1oblolly and 74 for slash pine) were established in separate, extensively managed (refers to those sites treated with shearing, chopping, windrowing, and burning) plantations throughout 24 counties of east Texas (Lenhart et al. 1985). The counties are located within the rectangle from 30–35 north latitude and 93–96 west longitude. Most of these plantations were established between 1970 and 1985 and managed without any intermediate silvicultural treatments (no thinning, prescribed burning, pruning, fertilizer, or midrotation competition control). Plots were first installed between 1982 and 1990 (Tables 1 and 2). For example, of the 166 plots for loblolly pine, 70 were installed in 1982–84 (cycle one). An additional 52 (112 total) were installed in 1985–87 (cycle two), while the remaining 54 (166 total) were installed in 1988–90 (cycle three). The seed sources of these plantations are unknown, although they likely include provenances or the first generation orchard lots which were being operationally deployed by the industry (Fox et al. 2007). Measurement plots were 100 feet by 100 feet squares. Within each plot, the planted pines were tagged and numbered for remeasurement on a three-year cycle.

### Management and Policy Implications

Slash pine (Pinus elliottii) and loblolly pine (Pinus taeda) are the two most important commercial softwood timber species in east Texas (Edgar et al. 2015). Minimizing disease losses and thus increasing pine timber harvests are of great interest to forest management companies and landowners. Toward this goal, continuation of fusiform rust research and monitoring is imperative so that proper forest management plans can be developed. Even as fusiform rust incidence in planted loblolly and slash pine stands declined over the past 30 years, it was still high, particularly for slash pine stands. Our modeling efforts provide the tree and stand variables affecting fusiform incidence which should be considered when establishing slash and loblolly pine plantations and developing management plans. The results aid our understanding in fusiform rust prevalence and management in pine plantations in east Texas.

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**Table 1. Summary statistics. Mean, STD (standard deviation) and range (difference between minimum and maximum plot means) by cycle for loblolly pine plots. Abbreviations: SI, site index (ft); $D_Q$, quadratic mean diameter (in.); TPA, number of trees per acre; BAPA, basal area per acre (ft²/acre); DBH, diameter at breast height (in.); HT, total tree height (ft); HLC, tree height to live crown (ft).**

| Cycle | N | Statistic | Age | SI | $D_Q$ | TPA | BAPA | DBH | HT | HLC |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 72 | Mean | 10.4 | 66.5 | 5.0 | 476.8 | 66.8 | 5.5 | 31.4 | 11.8 |
| | | STD | 3.0 | 10.3 | 1.4 | 149.5 | 33.3 | 1.0 | 9.0 | 7.8 |
| | | Range | 13.0 | 58.7 | 7.5 | 657 | 167 | 4.9 | 46.6 | 33.5 |
| 2 | 114 | Mean | 10.2 | 67.0 | 4.9 | 458 | 65.1 | 5.5 | 31.3 | 10.9 |
| | | STD | 3.7 | 9.3 | 1.6 | 133 | 39.6 | 1.1 | 10.1 | 8.9 |
| | | Range | 14.0 | 53.8 | 6.4 | 602 | 174.5 | 4.3 | 39.2 | 35.9 |
| 3 | 168 | Mean | 11.2 | 66.4 | 5.3 | 473.5 | 72.2 | 5.7 | 33.5 | 12.4 |
| | | STD | 3.9 | 9.0 | 1.6 | 148.3 | 38.2 | 1.2 | 10.6 | 9.1 |
| | | Range | 15.0 | 53.8 | 6.9 | 911.0 | 183.6 | 5.3 | 45.0 | 40.4 |
| 4 | 162 | Mean | 13.7 | 65.5 | 6.2 | 461.0 | 96.0 | 6.4 | 41.1 | 18.7 |
| | | STD | 3.8 | 9.7 | 1.4 | 144.7 | 34.9 | 1.1 | 10.6 | 9.3 |
| | | Range | 15.0 | 59.1 | 7.6 | 841 | 172.3 | 5.6 | 59.1 | 41.6 |
| 5 | 153 | Mean | 16.5 | 65.2 | 7.0 | 447 | 116 | 7.1 | 47.1 | 25.6 |
| | | STD | 3.9 | 9.6 | 1.4 | 141.9 | 34.5 | 1.1 | 9.5 | 8.4 |
| | | Range | 15.0 | 56.4 | 8.3 | 819 | 184.1 | 6.4 | 53.8 | 45.4 |
| 6 | 150 | Mean | 19.6 | 65.2 | 7.7 | 421.8 | 129.1 | 7.6 | 53.0 | 31.0 |
| | | STD | 3.8 | 9.6 | 1.4 | 134.9 | 34.2 | 1.3 | 9.7 | 8.0 |
| | | Range | 15.0 | 56.4 | 10.1 | 758 | 191.2 | 8.3 | 57.1 | 44.1 |
| 7 | 130 | Mean | 22.6 | 65.4 | 8.2 | 395.3 | 138.2 | 8.1 | 59 | 36.8 |
| | | STD | 3.9 | 9.1 | 1.5 | 129.9 | 35.3 | 1.3 | 9.6 | 8.1 |
| | | Range | 15.0 | 52.9 | 10.5 | 702.0 | 208.2 | 8.6 | 57.2 | 49.0 |
| 8 | 97 | Mean | 25.5 | 66.2 | 8.8 | 368.7 | 146.8 | 8.6 | 63.4 | 42.3 |
| | | STD | 3.9 | 8.3 | 1.4 | 118.3 | 31.9 | 1.3 | 9.2 | 7.9 |
| | | Range | 16.0 | 46.0 | 7.0 | 649 | 163.1 | 6.5 | 49.2 | 38.3 |
| 9 | 69 | Mean | 29.1 | 66.7 | 9.4 | 316.8 | 144.9 | 9.2 | 69.7 | 48.5 |
| | | STD | 4.0 | 7.8 | 1.3 | 107.5 | 31.2 | 1.3 | 8.7 | 7.2 |
| | | Range | 16.0 | 39.6 | 7.0 | 588 | 174.5 | 6.8 | 49.8 | 40.0 |
| 10 | 42 | Mean | 31.6 | 66.3 | 10.1 | 275.8 | 146.2 | 9.8 | 72.2 | 52.0 |
| | | STD | 3.6 | 7.5 | 1.2 | 91.8 | 36.2 | 1.2 | 8.5 | 7.4 |
| | | Range | 14.0 | 39.6 | 6.6 | 427 | 177.1 | 6.4 | 51.7 | 39.7 |
| 11 | 31 | Mean | 35.2 | 66.4 | 10.2 | 266 | 146.1 | 10 | 75.6 | 51.4 |
| | | STD | 3.3 | 7.5 | 1.1 | 78.5 | 27.1 | 1.1 | 7.9 | 7.2 |
| | | Range | 14.0 | 38.0 | 5.7 | 387 | 122.1 | 5.6 | 38.6 | 34.4 |

At each remeasurement of a plot, tree age of the plot was recorded, and each monumented tree was evaluated for tree growth (diameter at breast height [DBH]) in inches, total height (HT) in feet, crown class (CC), and tree height to live crown (HLC) in feet, and fusiform rust infection. Records of tree growth data allow us to calculate the following stand variables: trees per acre (TPA), basal area per acre (BAPA in ft²/acre), quadratic mean diameter ($D_Q$ in inches), and site index (SI in feet). Base age 25 years site index was estimated for each plot from the dominant height at the age of the most recent measurement. Summary statistics by cycle can be found in Tables 1 and 2 for loblolly and slash pine, respectively. The overall averages for slash pine plots were 65.9 feet for SI, 17.0 years for age, 6.8 inches for $D_Q$, 432 trees for TPA, and 80.2 ft² for BAPA. The overall averages for loblolly pine plots were 68.0 feet, 15.9 years for age, 6.5 inches for $D_Q$, 341 trees for TPA, and 72.7 ft² for BAPA. For both species, all stands were five years or older when the measurement plots were established. Individual tree fusiform rust infection was recorded in three ordinal scale categories: 1 (free-infection, no gall observed), 2 (branch-infection, gall on a live branch more than 12 inches from the stem only), and 3 (stem-infection, gall on a stem or a live branch within 12 inches of the stem or both).

Data from all available plots and cycles were used to investigate the temporal trend of rust incidence. The rust incidence ratios by category were calculated for each plot and cycle first and then across plots by cycle to examine rust incidence trends for consecutive three-year periods. The incidence rate was simply calculated as the ratio of infected trees over the total living trees.

Our modeling effort focused on identifying significant relationships between various rust infection levels and tree and stand variables. Due to clearcutting, natural disturbances, land sales, or other reasons, few plots remained at the end of the study (cycle 11). Any plots that were measured only once were removed. Also, because all the plots at the ninth measurement were beyond the typical rotation age, we restricted our modelling analysis to data from cycles one through nine, encompassing a 24-year period from 1984 to 2008. The ordinal and multinomial nature of the rust infection data complicates the modeling (Stroup 2012). Furthermore, the data include several nested levels (e.g., county, plot within cycle, and tree within plot) on which the multinomial response may be correlated to some level. Therefore, generalized linear mixed models (GLMMs) were used to model relationships between tree or stand characteristics and fusiform rust infections. We used the individual tree infection as the response variable, with a multinomial error distribution. The following GLMM model was used to model the data:

$$logit(P) = log\left(\frac{P(Y \le k)}{1 - P(Y \le k)}\right) = \gamma_k + \beta_j x + Zu + e$$

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**Table 2. Summary statistics. Mean, STD (standard deviation) and range (difference between minimum and maximum plot means) by cycle for slash pine plots. Abbreviations: SI, site index (ft); $D_Q$, quadratic mean diameter (in.); TPA, number of trees per acre; BAPA, basal area per acre (ft²/acre); DBH, diameter at breast height (in.); HT, total tree height (ft); HLC, tree height to live crown (ft).**

| Cycle | Var | N | Age | SI | $D_Q$ | TPA | BAPA | DBH | HT | HLC |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Mean | 35 | 9.9 | 69.3 | 4.7 | 360.9 | 46.2 | 5.3 | 29.8 | 9.5 |
| | STD | | 3.9 | 8.0 | 1.6 | 151.5 | 29.4 | 1.1 | 10.5 | 9.2 |
| | Range | | 15.0 | 31.4 | 6.2 | 867.0 | 97.6 | 4.2 | 41.8 | 35.1 |
| 2 | Mean | 63 | 9.5 | 70 | 4.6 | 393.0 | 44.0 | 5.2 | 29.4 | 9.1 |
| | STD | | 3.7 | 7.4 | 1.6 | 181.1 | 27.4 | 1.1 | 9.5 | 7.4 |
| | Range | | 13.0 | 44.5 | 6.2 | 876.0 | 123.7 | 3.5 | 40.8 | 26.8 |
| 3 | Mean | 74 | 11.0 | 68.3 | 5.3 | 387.1 | 55.4 | 5.6 | 33 | 12.0 |
| | STD | | 3.5 | 8.1 | 1.5 | 177 | 26.9 | 1.2 | 9.6 | 6.5 |
| | Range | | 14.0 | 46.5 | 6.3 | 810 | 133.3 | 4.3 | 40.1 | 26.4 |
| 4 | Mean | 68 | 13.6 | 67.8 | 6.1 | 376.2 | 71.6 | 6.3 | 39.8 | 19.0 |
| | STD | | 3.2 | 8.1 | 1.4 | 174.1 | 28.9 | 1.1 | 8.9 | 6.4 |
| | Range | | 15.0 | 43.9 | 6.2 | 806 | 150.4 | 4.8 | 42.5 | 29.1 |
| 5 | Mean | 67 | 16.4 | 67.9 | 7.0 | 344.3 | 85.6 | 7.1 | 47.3 | 25.1 |
| | STD | | 3.1 | 8.1 | 1.5 | 161.8 | 31.5 | 1.3 | 9.4 | 6.8 |
| | Range | | 14.0 | 43.9 | 6.5 | 680 | 119.4 | 5.3 | 50.4 | 40.3 |
| 6 | Mean | 67 | 19.5 | 67.9 | 7.7 | 311.2 | 93.2 | 7.7 | 54.3 | 31.0 |
| | STD | | 3.1 | 8.1 | 1.5 | 154.6 | 35.3 | 1.3 | 9.1 | 6.4 |
| | Range | | 14.0 | 43.9 | 6.9 | 623 | 130.5 | 5.9 | 46.6 | 33.6 |
| 7 | Mean | 61 | 22.4 | 67.9 | 8.4 | 285.3 | 100.1 | 8.3 | 60.2 | 35.9 |
| | STD | | 3.1 | 8.3 | 1.6 | 151 | 39.7 | 1.4 | 9 | 6.5 |
| | Range | | 15.0 | 43.9 | 7.0 | 601 | 154.2 | 6.0 | 44.6 | 31.2 |
| 8 | Mean | 43 | 25.1 | 67.1 | 8.8 | 269.5 | 106.2 | 8.7 | 64 | 41.2 |
| | STD | | 3.0 | 9.2 | 1.6 | 141.2 | 42.3 | 1.5 | 8.9 | 7.4 |
| | Range | | 14.0 | 43.9 | 6.9 | 553 | 149.6 | 6.4 | 38.7 | 32.7 |
| 9 | Mean | 22 | 29.1 | 66 | 9.7 | 182.5 | 85.1 | 9.6 | 70.2 | 48.6 |
| | STD | | 3.1 | 9.9 | 1.8 | 115.6 | 39.0 | 1.7 | 10.8 | 8.5 |
| | Range | | 12.0 | 32.7 | 6.8 | 496 | 142.2 | 6.3 | 34.5 | 27.3 |
| 10 | Mean | 9 | 32.3 | 64 | 9.9 | 200.2 | 91.7 | 9.8 | 72.1 | 51.3 |
| | STD | | 4.0 | 8.8 | 2.2 | 135.7 | 45.5 | 2.1 | 11.4 | 9.7 |
| | Range | | 12.0 | 25.7 | 6.9 | 471 | 153.2 | 6.2 | 29.8 | 29.6 |
| 11 | Mean | 5 | 34.4 | 59.5 | 9.7 | 214.2 | 86.0 | 9.6 | 69.1 | 45.6 |
| | STD | | 2.2 | 9.0 | 2.9 | 175.5 | 56.9 | 2.8 | 12.2 | 8.4 |
| | Range | | 6.0 | 21.7 | 7.3 | 431.0 | 127.1 | 7.0 | 29.5 | 18.7 |

where $k$ = 1, 2, 3 representing the three categories. For each cut-point (boundary), representing the boundary of the multinomial scales, there is a separate "intercept" ($\gamma$) to reflect cumulative odds, with the constraint that ($\gamma_1 < \gamma_2$). $\beta_j$ are coefficients for vector of predictors, $x$ (tree variables and stand variables); $u$ is the vector of random effects (plot and trees within a plot). Separate random effects in $u$ were assumed to be uncorrelated. **Z** is the incidence matrix corresponding to random effects in $u$. The term **e** is the vector of random residuals. Since the analysis used the logit link, the term **e** should be close to 3.29 (Stroup 2012). The significance of a random effect was tested using a likelihood ratio test method. Our model selection was done using a top-down strategy (Zuur et al. 2009). We started with a full model (i.e., including all predictors and random factors) to select the variations which were significant ($\alpha$ = 0.05). Variation among counties was negligible, and thus it was not included to the model. The nonsignificant predictors were then removed one-by-one, until all predictors in the model were statistically significant ($\alpha$ = 0.05). Probability estimates for each category were calculated as,

$$\text{For category 1 (Free} - \text{infection)}:$$

$$P_1 = \frac{exp[\gamma_1 + \beta_j x]}{1 + \exp[\gamma_1 + \beta_j x]}$$

$$\text{For category 2 (Branch} - \text{infection)}:$$

$$P_2 = \frac{exp[\gamma_2 + \beta_j x]}{1 + \exp[\gamma_2 + \beta_j x]} - P_1, \text{ and}$$

$$\text{For category 3 (Stem} - \text{infection)}:$$

$$P_3 = 1 - P_2$$

## Results

For loblolly pine, tree ratio with branch-infection declined quickly from around 7 percent at the 1st cycle (1984) to about 1 percent at the 4th cycle (1993) and thereafter continually decreased at a smaller rate, while the stem-infection proportion increased from less than 2 percent at the 1st cycle to over 7 percent at the 5th cycle and then declined to about 2~3 percent at the 11th cycle (Figure 1a, c). Similar cycle trends were found for slash pine (Figure 1b, d). The overall ratio of trees infected by rust (branch- plus stem-infection) was relatively stable from cycles one to six, around 8 percent, and thereafter reduced to 3–4 percent in 2014 for loblolly pine. Fusiform rust infection rates remained higher for slash versus loblolly pine for all years; the overall rust incidence rate remained around 31 percent for the first six cycles and then decreased to 12 percent at the 11th cycle (2014). For both species, the biggest change was observed between cycles six and seven (1999~2002), and more infection occurred on stem than on branches across cycles except the 1st cycle.

When multicategorical logit models were developed with tree and stand variables, the random variations among plots within a cycle and trees within a plot were

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significant for both species. The effects of plot (cycle) and trees within a plot explained more than 16.5 percent and 5.5 percent for loblolly pine and 14.7 percent and 5.2 percent for slash pine of their respective total variation. Tree variable HLC and stand variable SI were selected as regressor variables for both pines, while tree DBH for loblolly pine and stand variables stand age and TPA for slash pine were also respective useful predictors. Table 3 lists the parameter estimates and their statistical significance by species. The *t*-tests showed that the parameter estimates for both models were significant ($P < 0.01$).

Figure 2 presents the effects of each selected model variable on the rust infection probability while keeping the other model variables as constants (the averages across plots and measurement cycles) for loblolly pine. Probabilities of rust infections increased either linearly or exponentially with increasing site index or tree DBH, and this was slightly more obvious on stem-infection than on branch-infection. For example, because of a change in site index from 50 to 80 feet, the stem-infection probability increased from 2.43 percent to 3.39 percent, compared with the increase in the branch-infection from 0.98 percent to 1.23 percent. Relatively, tree DBH effect was stronger; when it increased from 4 to 12 inches, the branch- and stem-infection probabilities increased from 0.98 percent to 1.49 percent and from 2.58 percent to 3.98 percent, respectively. In contrast, HLC showed a negative impact on the rust infection probabilities, which decreased with increasing HLC. For a tree with an HLC increasing from 18 to 26 feet, the probabilities for branch- and stem-infection decreased from 1.19 percent to 1.02 percent and from 3.16 percent to 2.69 percent, respectively. Overall, the probabilities of rust infection remained low, especially for smaller trees growing at poor sites. Therefore, the practical impact of all the selected factors might not be as important as statistical significance.

Site index and HLC acted on the rust infection probabilities for slash pine the same direction as those for loblolly pine (Figures 2 and 3). Regardless of the similar direction in effects, slash pine trees were more susceptible to changes of these variables than loblolly pine and thus were more likely to exhibit increased infections. Unlike loblolly pine, stem-infection increased significantly with age, with probability changing from less than 20 percent at age 10 years to about 80 percent at age 45 years(Figure 3). Impacts of age on branch-infection were small and curvilinear in nature (Figure 3). In addition, trees per acre affected rust infections negatively; when it increased from 350 to 650 TPA, the accompanied probabilities changed from 7.8 percent to 9.4 percent for branch-infection and from 20.8 percent to 29.0 percent for stem-infection. Overall, model calculations showed that the probabilities of rust infections always remained high, especially for plantations of higher initial density, better growing quality, or of older age.

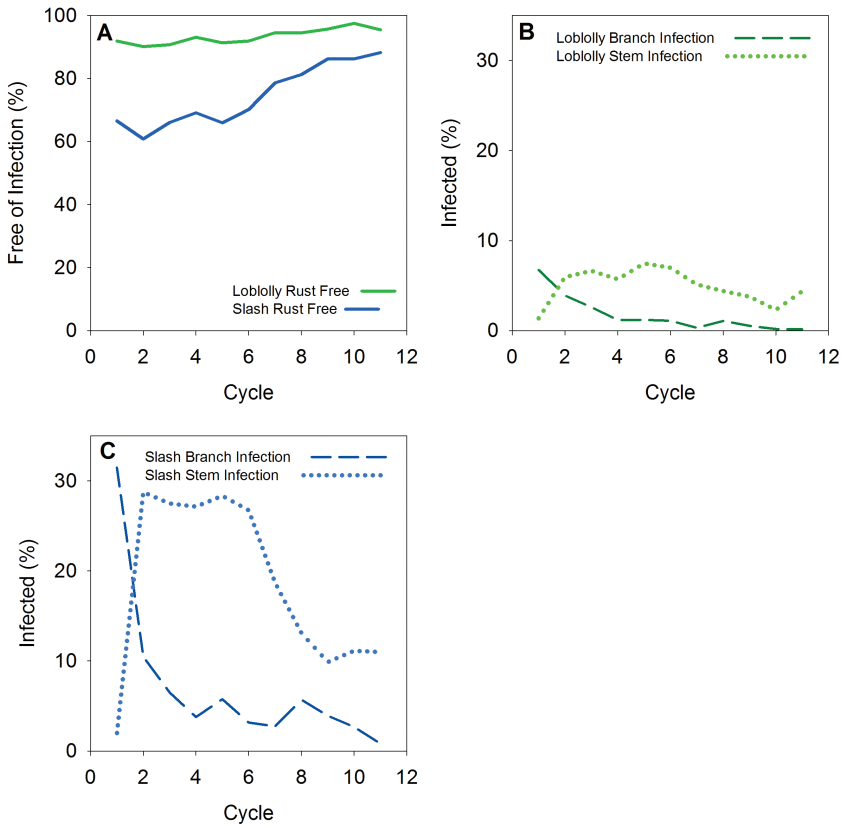


**Figure 1. Temporal trend in rust infection for loblolly pine and slash pine plantations in east Texas. Cycle one was in1984, and thereafter, every three years would be the next cycle.**

**Table 3. Model parameters for predicting fusiform rust incidence in east Texas. Abbreviations: SI, site index (ft); TPA, number of trees per acre; DBH, diameter at breast height (in.); HLC, tree height under tree crown (ft).**

| Species | Effect | Infection | Estimate | SE | t Value | Pr > \|t\| |
|---|---|---|---|---|---|---|
| LP | Intercept | 1 | 3.8016 | 0.1469 | 25.87 | <.0001 |
| | Intercept | 2 | 4.1347 | 0.1473 | 28.07 | <.0001 |
| | DBH | | -0.0560 | 0.0086 | -6.53 | <.0001 |
| | HLC | | 0.0209 | 0.0012 | 17.52 | <.0001 |
| | SI | | -0.0115 | 0.0021 | -5.45 | <.0001 |
| SP | Intercept | 1 | 5.7931 | 0.8640 | 6.71 | <.0001 |
| | Intercept | 2 | 6.2170 | 0.8642 | 7.19 | <.0001 |
| | HLC | | 0.0403 | 0.0023 | 17.8 | <.0001 |
| | SI | | -0.0630 | 0.0122 | -5.15 | <.0001 |
| | TPA | | -0.0010 | 0.0004 | -2.77 | 0.0056 |
| | AGE | | -0.0764 | 0.0062 | -12.39 | <.0001 |

## Discussion

The inventory data in this study—lasting almost 30 years for both pines, paired with previous studies—provide valuable insights into temporal patterns in fusiform rust infections in east Texas. Planted loblolly and slash pine had rust infection ratios of approximately 6 percent and 8 percent, respectively, in the early 1970s (Mason and Griffin

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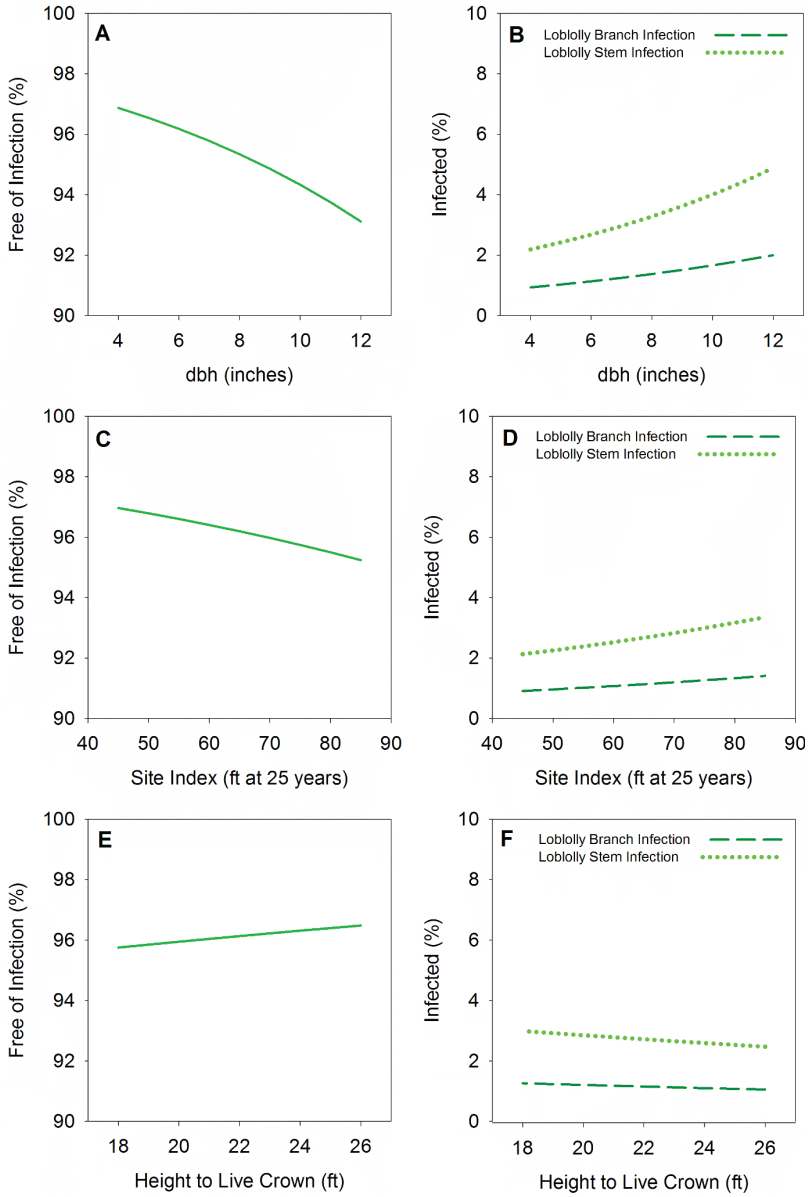


**Figure 2. Changes in rust infection probabilities for loblolly pine trees following the changes in (a, b) tree DBH, (c, d) site index, and (e, f) tree height to living crown.**

1970). With the extensive planting of susceptible pine and an aggressive site preparation that increased the oak abundance, the disease became widespread, resulting in a quick increase during 1970s and 1980s (Figure 1; Hunt and Lenhart 1986, Coble and Lee 2002) and a maximum prevalence around 1987 (Figure 1; Lenhart et al. 1994, Coble and Lee 2002). In the 1990s, the proportions decreased, starting at a slow rate and then at a greater rate (Figure 1; Coble and Lee 2002). Starting in 2002, the overall infection rate remained 3–4 percent for loblolly pine and further declined to about 14 percent for slash pine (Figure 1). Overall, we came to three conclusions: (1) Even though rust incidence varies among years depending in part on favorable or unfavorable weather at critical periods in the rust life cycle (Figure 1; Dinus and Schmidt 1977), overall rust infection rates for both pines decreased with increasing stand age (Figure 1). (2) Substantially more rust infections occurred on slash pine than on loblolly pine (Figure 1; Hunt and Lenhart 1986, Coble and Lee 2002, Bridgewater and Smith 2002). And (3), more stem-infection than branch-infection occurred (Figure 1). Higher fusiform rust infection for slash pine compared with loblolly pine was also reported elsewhere in the US South (Starkey et al. 1997, Randolph et al. 2015). It is important to note that the temporal trend results from a combination of effects including environment (such as year-to-year variation in weather), tree age, growth, and their interactions. Also, similar to previous studies (Schmidt et al. 1986, Coble and Lee 2002), dead trees were removed and not included in proportion calculations, possibly resulting in underestimating infection ratios. Infection ratios would be underestimated if effected trees died but overestimated if uninfected trees died.

The use of an ordinal, multinomial logit model using GLMMs was found to be a sound methodology to predict the probabilities of rust infections. Generalized linear mixed models are an extension of the linear mixed models to situations with a distribution other than normal by combining the properties of linear mixed model (which incorporates random effects) and generalized linear model (which handles non-normal data by using linking functions and exponential family). Therefore, GLMMs can account for hierarchical structure of data and allow for nested and crossed random-effect terms (Zuur et al. 2009, Vonesh 2012) and non-normal data. In previous studies, logistic regressions (Borders and Berry 1986, Arabatzis et al. 1991) have often been used, in which each observation is assumed to be independent, which is not always completely true in longitudinal data collected from permanent plots. The variances among plots and trees within plots in this study were significant, suggesting the importance of incorporating these sources of variation into modeling. While the ordinal, multinomial logit model using GLMMs is appropriate for construction of models, it does not provide residuals for evaluating the precision of predictions. Further work should, therefore, include evaluation of the predictions at a tree or stand level.

As expected, our results showed that fusiform rust infections for both pines were affected significantly by tree and stand variables. Two variables, SI and HLC, correlated significantly with rust infections for both pines (Table 2). The rust infected probabilities increased with increasing SI for both pines (Figures 2 and 3). The majority of previous studies found SI to be positively correlated with rust infection (Nance et al. 1981, Borders and Baily 1985, 1986, Arabatzis et al. 1991), whereas others found a negative correlation (Schmidt et al. 1988) or no relationship at all (Miller 1972, Froelich and Schmidtling 1998). Our

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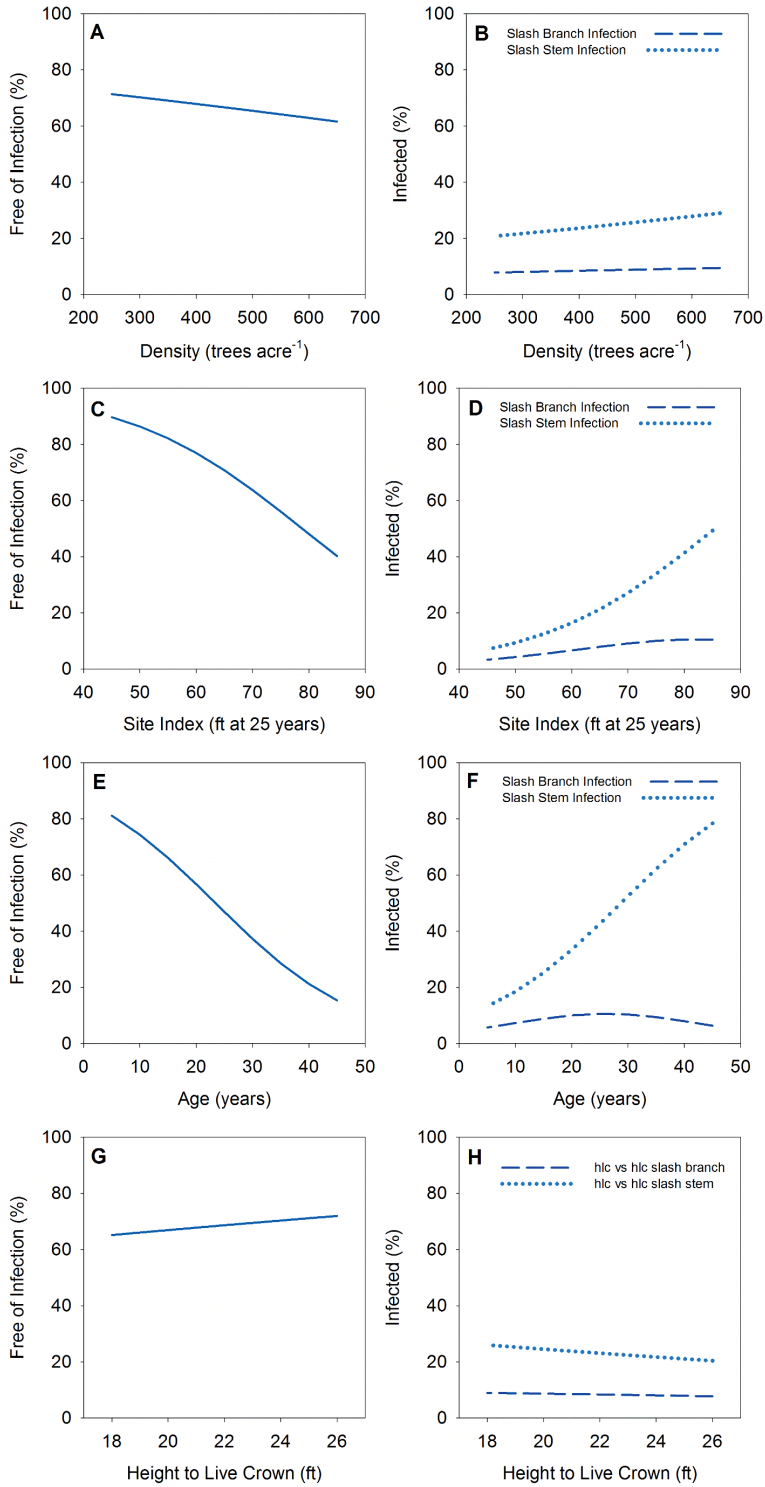


**Figure 3. Changes in rust infection probabilities for slash pine trees following the changes in (a, b) stand density, (c, d) site index, (e, f) age, and (g, h) tree height to living crown.**

results, while in parallel to the majority of studies overall, further confirmed that the SI's impacts on rust infection probability were weaker on branch-infection than on stem-infection and were weaker on loblolly pine than on slash pine. Differently, HLC strongly and negatively related to rust infection for both pines (Table 2; Figure 2). This specific relationship has not been previously reported. One possible, although speculative, explanation is that lower branches containing galls died and self-pruned before they could infect the main stem, which occurs more in trees with a larger HLC. The fact that it is more difficult to observe symptoms on branches at greater heights may also contribute to this. For both species, effects of HLC on branch-infection were small but could be serious on subsequent stem infection.

Our results also show that some variables were significant for one pine species but not the other. Unlike the temporal trend (Figure 1), holding constant with other stand variables, fusiform rust incidence increased with stand age for slash pine (Figure 3). A similar relationship, although statistically weakly significant ($P$ = 0.058), was also found for loblolly pine (data not shown). In the literature, the relationship between rust infection and age was found to be positive for both species (Dinus and Schmidt 1977, Borders and Baily 1985, Lenhart et al. 1994, Adams et al. 1996). It is generally reported that rust incidence is unrelated to stand density (Wakeley 1969, Miller 1972, Border and Baily 1986, Froelich and Schmidtling 1998). Our results confirmed this for loblolly pine but contradicted these studies for slash pine, for which rust incidence was positively correlated to stand density. One possible explanation, although speculative, is that slash pine does not self-prune infected branches as strongly as loblolly pine. It is also possible that higher stand densities facilitate the spread of rust, even though diseased trees are not a direct risk to the surrounding healthy ones since spores that infect pines come only from oak leaves. Plantation density for slash pine varies substantially in east Texas, but it mostly ranges between 350 and 650 trees per acre; within these densities, changes 2 percent or lower in branch-infection—but greater than 6 percent in stem-infection—were observed. Overall it is unknown why slash pine rust infection did not respond as expected to stand density or why it varied from loblolly pine.

Individual tree DBH showed positive relationships with rust infection levels for loblolly pine. At a given stand density and site quality, more rapid growth is reflected by larger DBH in a monoculture. Fusiform infection is greater in rapidly growing trees than in those with slower growth (Schmidt 1998, Adams et al. 2010). There was a significant correlation between rust incidence and diameter, which is logical considering the positive relationship between fast growth of young trees and rust infection.

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Therefore, DBH was a common explanatory variable in both the present model and a previous model for occurrence of pine fusiform rust in plantations in Southeastern US (Choi et al. 2008). However, for slash pine, such a relationship was not statistically significant.

Obviously, many factors may contribute to the rust incidence, which makes it difficult to model. Our models explained only a small proportion of variation (around 20 percent). Most of the plantations for the plots were established between 1970 and 1985. During that period, the likely seed lots planted in east Texas were elite provenances or the 1st generation seed orchard seed lots (Fox et al. 2007). Resistance to fusiform rust of these plantations might be improved by genetic selection, resulting in a lower rust incidence compared with natural stands, but that was not the primary focus of tree improvement programs at the time (Fox et al. 2007). Possibly, other variables such as associated oak (Hollis and Schmidt 1977, Froelich and Snow 1986), soil drainage (Schmidt et al. 1988), geographic variables (Borders and Bailey 1986), and climate variables like temperature and moisture (Schmidt 2003) would explain additional variation. However, some of these variables are not included in most forest inventories because they require additional effort and expense. For practical purposes, predicting the infection probability from variables that are collected in most standard forest inventories will be most relevant. Only common variables observed on the tree and stand levels were used in this study, rather than those that are more difficult to derive at the stand level. Also, the observed relationship between these predictors and the multilevel rust infections may not necessarily be causal. A mechanistic interpretation of each significant variable in the model cannot be easily made because the independent variables (i.e., DBH, SI, and TPA) may express multicollinearity, which may mask the effects of some predictors by the others. Unfortunately, using the GLMM procedure, we cannot assess multicollinearity using the variance impact factor value. The problem of covariation is connected to, yet not unique to, this study. However, most of the relationships found in this analysis have simple and logical biological explanations, correspond well with other investigations (Border and Baily 1986, Arabatzis et al. 1991), and aid our understanding of rust prevalence and management. Results of this study can provide information to assist forest managers in planning and implementing silvicultural practices to slow the increase of rust or even convert the plantations to another more rust-resistant species (Dinus and Schmidt 1977).

According to anticipated high or low rust incidence, results can be used to develop rust management strategies for specific conditions. Our results show, for loblolly pine, even though rust infections varied significantly with some tree or stand variables, their actual impacts were small (Figure 2), suggesting that rust infections for this species in east Texas may not be a serious problem. For slash pine, however, rust infection probabilities varied substantially with some tree or stand variables (Figure 3). Furthermore, once a slash pine stem has a gall, there is a higher probability of mortality than is true for a stem-infected loblolly pine (Lenhart et al. 1988). Therefore, the practical meaning in incorporating the findings into managing east Texas slash pine plantations could be substantial. Given the fact that rust incidence is higher for slash than loblolly pine, particularly on better sites, favoring loblolly pine or other rust resistant species (i.e., longleaf pine [*Pinus palustris L.*]) over slash pine is a possible management recommendation, particularly on highly productive sites. Silvicultural activities such as selecting suitable thinning schedules and thinning intensity or delaying fertilization in very young plantations can also be helpful in reducing rust infection loss for slash pine plantations.

Even though our study focused on identifying tree and stand variables that correlated to rust infections in pine plantations for the purposes of forest management planning, our models can also be used as an interim tool for rust infection prediction. Lee and Coble (2002a, b) developed stand level survival models for loblolly and slash pine plantations in east Texas that require the number of uninfected and infected trees at the beginning of a designated projection period. Our rust prediction models can be used to predict the initial estimate of the proportion or number of rust-infected trees per acre, which can then be inserted into Lee and Coble's survival models for predicting growth and yield.

Since the late 1940s, pine silviculture has been changing substantially (Fox et al. 2007). Starting in the 1990s, intensive silvicultural practices such as planting improved rust-resistance seedlots, applying fertilization and weed control, intermediate thinning and other practices have routinely been applied to pine plantations. Note that data reported here represent extensively (nonintensively) managed pine plantations in east Texas and do not represent intensively managed pine plantations. To fill the knowledge gap, the ETPPRP recently initiated its Phase II plots in intensively managed pine plantations across the Western Gulf region. Fusiform rust infections in the Phase II plots will continually be recorded every three years, and the resulting data will provide more precise temporal trends for intensively managed pine plantations.

## Literature Cited


Adams, J.P., S.B. Land Jr., and H.W. Duzan Jr. 2010. Spacing and family affect fusiform rust incidence in loblolly pine at age 17. P. 297–300, in *Proc. of the 14th biennial southern silvicultural research conf.* Stanturf, J.A. (ed.). USDA Forest Service Gen. Tech. Rep. SRS-121, Southern Research Station, Asheville, NC, 614 p.

Adams, D.E. 1989. *A whole stand survival model from a system of differential equations for pine plantations infested with fusiform rust*. MS thesis. University of Georgia, Athens, GA. 64 p.

Adams, D.E., J.D. Lenhart, A.B. Vaughn, and J. Lapongan. 1996. Predicting survival of east texas loblolly and slash pine plantations infected with fusiform rust. *South. J. Appl. For.* 20:30–35.

Agresti, A. 2013. *Categorical data analysis*. John Wiley & Sons, Inc., Hoboken, NJ. 714 p.

Arabatzis, A.A., T.G. Gregoire, and J.D. Lenhart. 1991. Fusiform rust incidence in loblolly and slash pine plantations in east Texas. *South. J. Appl. For.* 15:79–84.

Borders, B.E., and R.L. Bailey. 1985. *Stand density effects in slash and loblolly pine plantations*. University of Georgia, School of Forest Resources, Athens, GA. PMRC Res. Pap. 1985–1.

Borders, B.E., and R.L. Bailey. 1986. Fusiform rust prediction models for site-prepared slash and loblolly pine plantations in the Southeast. *South. J. Appl. For.* 10:145–151.

Bridgwater, F.E., and W.D. Smith. 2002. Decline in values of slash pine stands infected with fusiform rust. *South. J. Appl. For.* 26(3):134–139.

Choi, J.K., H.E. Burkhart, and R.L. Amateis. 2008. Modeling trends in stem quality characteristics of loblolly pine trees in unthinned plantations. *Can. J. For. Res.* 38: 1446–1457.

Clutter, J.L., J.C. Fortson, and L.C. Shackelford. 1984. *Survival predictions for fusiform infected loblolly pine plantations on prepared sites in the coastal plain of South Carolina, Georgia, and Northern Florida*. University of


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Georgia, School of Forest Resources, Athens, GA. PMRC. Res. Pap, 1984–4. 23 p.

Coble, D.W. and Y.J. Lee. 2004. *Fusiform rust trends in east Texas: 1969 to 2002*. USDA Forest Service Gen. Tech. Rep. SRS-71, Southern Research Station, Asheville, NC. 5 p.

Devine, O.J., and J.L. Clutter. 1985. Prediction of survival in Slash pine plantation infected with fusiform rust. *For. Sci.* 31(1):88–94.

Dinus, R.J., and R.A. Schmidt. 1977. *Management of fusiform rust in southern pines*. Pines: Symp. Proc., University of Florida, Gainesville.

Edgar, C.B., R. Parajuli, R. Zehnder, A.B. Carraway, and E. Taylor. 2017. *Texas harvest trends 2015*. Texas A&M Forest Service, Texas A&M University System, College Station, TX.

Fox, T.R., E.J. Jokela, and H.L. Allen. 2007. The development of pine plantation silviculture in the southern United States. *J. For.* 105(7):337–347.

Froelich, R.C., V.L. Nance, and G.A. Snow. 1983. Size and growth of planted slash pines infected with fusiform rust. *For. Sci.* 29:527–534.

Froelich, R.C., and R.C. Schmidtling. 1998. Survival of slash pine having fusiform rust disease varies with year of first stem infection and severity. *South. J. Appl. For.* 22:96–100.

Froelich, R.C., and G.A. Snow. 1986. Predicting site hazard to fusiform rust. *For. Sci.* 32:21–35.

Hollis, C.A., and R.A. Schmidt. 1977. Site factors related to fusiform rust incidence in north Florida slash pine plantations. *For. Sci.* 23:69–77.

Hollis, C.A., W.H. Smith, and R.A. Schmidt. 1975. Soil and tissue nutrients, soil drainage, fertilization and tree growth as related to fusiform rust incidence in slash pine. *For. Sci.* 21:141–148.

Hunt, E.V. Jr. and J.D. Lenhart. 1986. Fusiform rust trends in East Texas. *South. J. Appl. For.* 10:215–216.

Randolph, K.C., E.B. Cowling, and D.A. Starkey. 2015. Long-term changes in fusiform rust incidence in the Southeastern United States. *J. For.* 113(4):381–392.

Lee, Y.J., and D.W. Coble. 2002a. A survival model for unthinned loblolly pine plantations that incorporates non-planted tree competition, site quality, and incidence of fusiform rust. *Bioresour. Technol.* 85(3):301–308.

Lee, Y.J., and D.W. Coble. 2002b. Modeling survival for unthinned slash pine plantations in east Texas under the influence of non-planted tree basal area and incidence of fusiform rust. *Texas J. Sci.* 54:325–338.

Lenhart, J.D., T.G. Gregoire, G.D. Kronrad, and A.G. Holley. 1994. Characterizing fusiform rust incidence and distribution in East Texas. *South. J. Appl. For.* 18:29–34.

Lenhart, J.D., W.T. McGrath, and T.L. Hackett. 1988. Fusiform rust trends in East Texas: 1969–87. *South. J. Appl. For.* 12:259–261.

Lenhart, J.D., E.V. Hunt Jr., and J.A. Blackard. 1985. *Establishment of permanent growth and yield plots in loblolly and slash pine plantations in East Texas*. USDA Forest Service Gen. Tech. Rep SO-54, Southern Res. Station, New Orleans, LA. 2 p.

Mason, G.N., and J.K. Griffin. 1970. Evaluating the severity of fusiform rust in East Texas pine plantations. *Forest Farmer.* 29:8–9.

Miller, T. 1972. Fusiform rust in planted slash pines: influence of site preparation and spacing. *For. Sci.* 18:70–75.

Nance, W.L., R.C. Froelich, and E. Shoulders. 1981. *Effects of fusiform rust on survival and structure of Mississippi and Louisiana slash pine plantations*. USDA Forest Service Res. Pap. SO-172. 11 p.

Pye, J.M., J.E. Wagner, T.P. Holmes, and F.W. Cubbage. 1995. *What's rust hazard prediction worth? A bioeconomic simulation of resistant seedling allocation across the south*. USDA Forest Service Gen. Tech. Rep. SRS-1, Southern Research Station, Asheville, NC. 6 p.

Schmidt, R.A. 1998. *Fusiform rust disease of southern pines: Biology, ecology and management*. Univ. Fla. Agric. Exp. Stn. Rep. 903. IFAS, University of Florida, Gainesville, FL.

Schmidt, R.A. 2003. Fusiform rust of southern pines: A major success for forest disease management. *Phytopathology.* 93:1048–1051.

Schmidt, R.A., R.C. Holley, M.C. Klapproth, and T. Miller. 1986. Temporal and spatial patterns of fusiform rust epidemics in young plantations of susceptible and resistant slash and loblolly pines. *Plant Dis.* 70:661–666.

Schmidt, R.A., T. Miller, R.C. Holley, R.P. Belanger, and J.E. Allen. 1988. Relation of site factors to fusiform rust incidence in young slash and loblolly pine plantations in the coastal plain of Florida and Georgia. *Plant Dis.* 72:710–714.

Siggers, P.V. 1949. Weather and outbreaks of the fusiform rust of southern pines. *J. For.* 47:802–806.

Starkey, D.A., R.L. Anderson, C.H. Young, et al. 1997. *Monitoring incidence of fusiform rust in the south and change over time*. USDA Forest Service Protection Rep. R8-PR 30.

Stroup, W.W. 2012. *Generalized linear mixed models: Modern concepts, methods and applications*. CRC Press, New York, USA. 550 p.

Vonesh, E.F. 2012. *Generalized linear and nonlinear models for correlated data: Theory and applications using SAS*. SAS Institute Inc, Cary, NC.

Wakeley, P.C. 1969. Results of southern pine planting experiments established in the middle twenties. *J. For.* 67:237–241.

Walterscheidt, J.J. and E.P. van Arsdale. 1976. Distribution of fusiform rust on slash and loblolly pines in Texas. *Plant Dis. Rep.* 60:718–720.

Zhao, D.H., B. Borders, and M.L. Wang. 2006. Survival model for fusiform rust infected loblolly pine plantations with and without mid-rotation understorey vegetation control. *For. Ecol. Manage.* 235:232–239.

Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev, and G.M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York. 574 p.

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