Survival of Slash Pine Having Fusiform Rust Disease Varies with Year of First Stem Infection and Severity

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ABSTRACT. *Probabilities of death of young slashpine infected byfusiform rustpathogen varied with timing and severity of infection. Trees in nine slashpineplantations varying widely in site quality and initial number oftreesperacre hadsimilarprobabilities ofdeathfrom rust. About 90% oftrees with stem infections in thejirst three growing seasons died by age 15 if the gall spanned more than 50% of the circumference of the stem by age 5. If 50% gall encirclement occurred after age 5, mortality rates dropped to about 30% at age 15. Where first stem infection occurred after the fifth year, probability of death was essentially the same as for rust-free trees. Methods are given for using timing-severity data to estimate future stocking. South. J. Appl. For. 22(2):96–1 00.*

Efficient management of slash pine (*Pinus elliottii* Engelm. var *elliottii)* stands infected by fusiform rust pathogen *(Cronartium quercuum* [Berk.] Miyabe ex Shirai f. sp. *fusiforme)* requires accurate predictions of preharvest rust-associated mortality. Death of trees with early stem infections of fusiform rust is common (Sluder 1977, Wells and Dinus 1978, Nance et al. 1981, Lloyd 1982, Shoulders and Nance 1987). Survival models (Nanceet al. 1983, Devine and Clutter 1985) or mortality simulation models (Geron and Hafley 1988) are available for estimating future stocking of fusiformrust-infected stands. Shoulders et al. (1991), showed however, that trees infected in the third growing season have a lower probability of fusiform rust disease-related mortality than trees infected in the second year. Percent of stem encircled by the gall, an indication of the disease development rate, also affects the survival of pine (Belanger and Zarnoch 1991). Other possible mortality associated factors include site quality, stand density, and host genotype. Applicability of survival prediction models to individual forests depends on the importance of the above factors.

The objectives of this study were: (1) to examine how timing and severity of fusiformrust pathogen infection affect mortality of planted slash pine, (2) to investigate the consistency of rust associated mortality predictions among locations with different stand densities and site qualities, (3) to determine whether probabilities of death vary among seed sources, and (4) to provide guidelines for using timing-severity data to estimate future stocking of slash pine.

Materials and Methods

Probabilities of death of planted slash pines having fusiform rust through age 16 are based on data from a study installed in 1974 at nine locations in coastal counties of Mississippi (Froelich and Snow 1986). Each plantation consisted of 25 rows of trees, with 30 trees per row. Spacing was 6 ft within rows and 10 ft between rows. Trees of one of three seed sources were planted in each row. Two sources originated from different seed production areas. The third source was from open-pollinated seed collected from seed orchard clones whose progeny had shown resistance to fusiform rust in previous tests.

First-year survival of planted seedlings ranged from 236 to 583 trees/ac (33 to 91%, Table 1). Mortality in the first year was due to excessive or inadequate soil moisture after planting. Fusiform rust disease infection, site index, and soil drainage varied substantially among locations (Table 1).

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Table 1. Characteristics of nine plantations of slash pine used to study effects of fusiform rust on tree survival.

	Plantation no.								
Characteristic	1	2	3	4	5	6	7	8	9
No. live trees/ac[1]	421	236	388	320	393	513	583	399	550
Site index[2]	59	67	59	69	67	75	67	67	75
Drainage’	M	W-E	M	M-W	M	M-W	M-W	W	P[4]
Percent rust’	47	71	30	29	31	12	58	68	41

[1] Age 1.
[2] Base age 25 yr.
[3] Drainage: P = poor; M = moderate; W = well; E = excessive.
[4] Drainage and site quality improved by bedding in Plantation 9.
[5] (Cumulative stem infection at age 16)/(number live trees at age 1).

Detailed observations on fusiform rust disease development rate were made each year for 16 yr. Data included: (1) location of each gall (distance above ground and distance to branch galls from the main stem); (2) year (since planted) when each gall developed; (3) year when branch galls spread into main stem; (4) year when more than 50% of the stem was encircled by one or more galls; (5) year of witches’ brooming (multiple stems and no primary stem) due to main stem mortality associated with fusiform rust disease; (6) year of partial crown death at a stem gall; and (7) year of tree death identified as not rust related, broken at rust gall, or dead but standing with a stem gall or canker.

Each tree was classified using a numeric/letter code that indicated the timing and severity of the infection, to aid presentation and analysis. The numeric prefix is the age when first stem infection occurred, or when a branch gall spread into the stem. The latter was defined as stem swelling due to assumed presence of the fungus. When stem swelling occurred after a nearby galled branch died, the year of stem infection was considered year of branch death. There were six age classes; 1, 2, 3, 4, 5, and 6+. Trees having stem infections occurring after age 5 were labeled 6+. Annual height measurements were used to reconstruct year of first stem infection when direct stem infection was not detected for one or more years after it occurred. Probabilities of death were computed two ways; By actual year of infection, which includes infections discovered later and assigned to that particular year, and by infection that was actually visible at a given age. The former gives a better perspective of the total effects of rust development on stocking over time, the latter is more useful in using field observations made at a specified early stand age to predict future stocking.

Severity of infection was defined as tree age when at least 50% of the circumference of the main stem of the tree was encircled by a stem gall. “A” is equivalent to 50% encirclement by age 5, “B” is equivalent to 50% encirclement after age 5, “C” is equivalent to not 50% encircled by age 16. Age 5 and 50% are not arbitrary numbers. Experience has shown that 50% encirclement by age 5 results in reduced growth and early tree mortality in plantations (Froelich et al. 1983).

Chi-square tests for independence were used to compare differences in mortality among classes, with the acknowledgment that some differences that are statistically significant are not always important for forest management purposes.

Results and Discussion

After the twelfth growing season, hurricane Elena caused breakage at some galls in all stands, and completely destroyed Plantation 6. Plantation 7 was destroyed by wildfire after season 13 measurements. Moderate to heavy crown scorch from a wildfire probably hastened death of some infected trees in Plantation 1.

Because of the nature of the data, an overall factorial analysis was not feasible. The analysis was broken down into three levels. Mortality in the 18 infection classes (including those free of stem infection-rust-free) was examined for all plantations combined, for plantation differences, and for seed source differences. Class 6+A does not exist, because infection occurred after age 5. Classes 1C, 2C, and 3C (stem infection in growing season 1, 2, or 3 and not 50% stem encircled at age 16) were dropped from the analysis because these classes had too few trees. The early infections nearly always became stem encircling.

Probabilities of Death From Rust-All Plantings Combined

Differences in mortality among infection classes for all plantings combined were large (Figure 1) and statistically significant at age 16 ($P < 0.001$). Mortality in classes 1 A, 2A, and 3A ranged from 90% to 95% at age 16. The differences were not statistically significant ($P > 0.6$). There were important differences, however, in the early time trends of the three. At age 5, 40% of the trees infected the first year (IA) were dead versus 15% for 2A and only 5% for 3A. The differences among these classes at age 5 were significant statistically ($P < 0.001$). These differences show that rust infection has a very serious impact on early stand density when it occurs in the first or second growing season. This early impact has not been considered in growth and yield models that base projections on trees living at ages 3 or 5 or later.

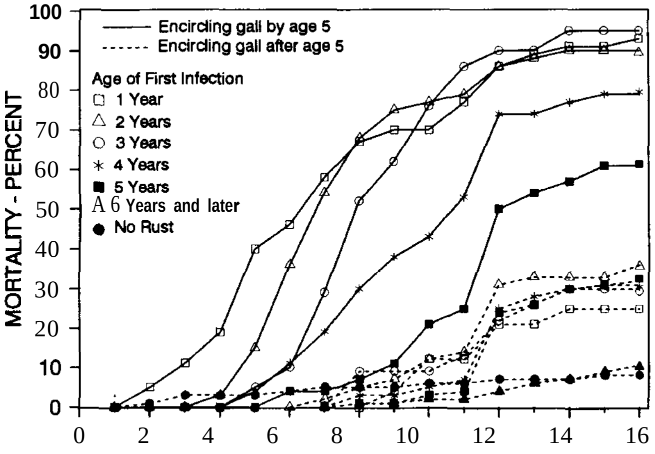

Figure 1. Probabilities of death of fusiform rust pathogen infected slash pine by timing and severity of gall development.

Classes 4A and 5A had 79% and 61% mortality, respectively, by age 16. Hurricane Elena in the twelfth growing season obviously hastened death of trees in these two classes (Figure 1). Classes 1B through 5B also were affected by the hurricane. Eighty percent of the rust-associated mortality during growing season 12 was breakage at rust galls. In nonhurricane years, only 10% of rust-associated mortality was breakage. Classes 6+B and rust-free were not affected by the hurricane. Although losses did occur in the twelfth growing season in classes 1A-3A, the mortality trajectory appeared to be little affected by the hurricane; most of the trees in those classes already were dead. In the classes where encirclement occurred after age 5, mortality was lower than for classes where encirclement occurred earlier. Cumulative mortality at age 16 was 25% to 36% for classes 1B through 5B (Figure 1). The differences among these five classes at age 16 were not significant statistically ($P > 0.93$). Mortality in 6+B was 9% at age 16, almost identical to the 8% mortality in the rust-free class.

In the classes where encirclement did not occur over the life of the study, probabilities of death were 21% and 16% for classes 4C and 5C at age 16, respectively (not shown in Figure 1). Most of the mortality in these classes was hurricane related. Mortality in class 6C+ was only 1%, lower than in rust-free. The lower mortality in class 6C+ than in rust-free is probably due to the fact that the rust-free class contained a greater proportion of small trees than 6C+. Small trees of poor vigor have a lower probability of being infected by the fusiform rust pathogen than larger ones (Nance et al. 1981, Froelich et al. 1983), and a higher probability of death due to competition.

Probabilities of Death From Rust-Differences Among Plantings

Witches'-broom trees and trees having partial crown mortality were deleted for studying probabilities of rust-associated death among locations because of very low probability of survival to age 16 and because proportions varied widely among locations. Following deletions and sorting by location, there were only a few trees in most of the 18 classes, making it necessary to group some of the classes. Classes 1 to 3A, 4 to 5B, and rust-free had a reasonable number of trees for studying variations in probabilities among locations.

Mortality trends for combined classes IA to 3A showed considerable variation in probabilities among the nine locations in the early years, but by age 16 the range was only 84% to 94% for 8 of 9 plantations. In Plantation 1, moderate to heavy crown scorch probably hastened the death of trees in this class (100% mortality by age 16). Variation in probabilities of death of trees among plantations for classes 4B–5B also was narrow among Plantations 2 through 9 at age 16, ranging from 22% to 33%. Probability of death in Plantation 1 was 45%.

Mortality of rust-free averaged 8% (Figure 1) and ranged from 2% to 17% among the nine locations. Three plantations having more than 10% cumulative mortality at age 16 were excessively wet or dry sites. Much of the cumulative mortality in these three plantings occurred early in the study, ranging from 6% to 10% at age 5.

There was no evidence that probabilities of death of either infected or rust-free trees were affected by variations in initial stand density or site index. The plantations with the highest density (6, 7, and 9, with 513 to 583 trees/ac at age I), all on better than average sites, had only 2% to 4% cumulative mortality of rust-free trees at 16 yr. Cumulative mortality for classes 1A to 3A and 4B to 5B for these plantations also was no higher than other locations. The situation may change if these plantings are managed less than optimally and later allowed to become self-thinning.

Probabilities of Death from Rust-Differences Among Seed Sources

Classes 1A to 3A, 4B to 5B, and rust-free were used to evaluate differences in probabilities of death from rust development among the three seed sources. Trees having witches'-brooms and partially dead tops associated with rust development were again omitted.

Probabilities of death from rust development for classes 1A to 3A were almost identical among the three seed sources (88% to 92% at age 16). For trees in classes 4B to 5B, mortality at age 16 ranged from 30% to 33% among seed sources. Mortality of rust-free trees was identical among sources, 8%. Seed source 2 was collected from trees whose progeny had shown low infection to fusiform rust. In the current study, this source did not achieve expectations; it did not differ in infection rate from the other two sources (Froelich and Snow 1986). It is possible that more rust-resistant families of slash pine have lower rust associated mortalities once infected, but given the lack of difference of infection rates among the seed sources in this study, more definitive timing-severity data would be needed to test this hypothesis.

Comparisons with Other Studies

It is important to compare probabilities of death of infected and noninfected trees from the present study with values in Nance et al. (1981) that had been developed from the large data sets described by Shoulders (1976). Establishment densities at age 3 or 5 usually exceeded 800 trees/ac (out of 1210 planted trees/ac), which is considerably higher than the present study (Table 1). Comparisons between studies therefore provide some evidence regarding the possible effects of stand density on probabilities of death from rust development.

To compare studies, probabilities were computed according to the criteria in Nance et al. (1981). Probabilities in their Tables 3 and 4 had been based on all stem infections visible on trees living at age 3 (100 experimental plots of slash pine in Mississippi), or at age 5 (87 slash pine plots in Louisiana).

Probabilities of death in the current study, when based on the infections that were detectable at ages 3 or 5, are lower, but generally within 10% of the values in Nance et al. (1981). These minor, but consistent, differences may be due to failure to detect smaller, less aggressive infections in the 1981 study. Rust associated mortality would be higher for the larger, more highly developed infections, biasing their mortality rates upward.

There are other factors that could have resulted in higher probabilities of death in the Nance et al. (1981) study. Greater average density of their plots might have increased tree-to-tree competition, resulting in the higher rates of death. There also may have been more early mortality in the plots than in those in the study reported here. The differences in mortality rates between studies from all possible causes are small, however, implying that probabilities of death up to age 15 should not be influenced greatly by the differences in establishment densities commonly found in planted slash pine. This assumption is supported by the survival model that Nance et al. (1983) developed from their data. That survival model indicates that variations in age 3 or age 5 densities from 400 to 1200 trees/ac do not affect probabilities of death of either infected or noninfected trees up to age 20. Effects of site index on mortality also are not apparent in their model.

Predicting Future Stocking

Because probabilities of death of infected and rust-free trees to at least age 15 do not seem to be affected by variations in site quality or by variation in stand density, a complex model is not necessary for estimating future stocking. A simple table can be used to estimate probabilities of death for the important classes of infection. The values in Table 2 should provide reasonable estimates of future stocking for most stands of slash pine. These probabilities are based on the percent infection that was visible on living trees at age 5. Timing-severity classes exclude witches'-broomed trees (usually developed in growing season two or three) because such trees had only a 2% chance of survival to age 16. Trees whose crown had partially died when the main stem broke or died at a rust gall were also excluded. Most of these trees also died by age 16.

Although annual tree heights are very helpful for correctly assigning year of first stem infection (1 to 3, or 4 to 5, Table 2), it should be possible to estimate with reasonable accuracy the year infected by considering heights above ground, distances of branch galls to the stem, and by annual growth of stems and branches. Southern pines do not produce definitive whorls, but one may still distinguish annual growth increments because branches of the first flush are usually larger than branches of subsequent flushes in a year. Only 2% of all year 1 to 3 stem galls were more than 4 ft above ground; therefore galls above 4 ft can be assigned to year classes 4 to 5 with reasonable accuracy. Branch-into-stem infections in years 4 to 5 also may occur below 5 ft, however, making it necessary to consider height above ground, distance to the stem, and branch and gall vigor.

Assigning trees to severity class B is uncertain because these are the trees expected to become encircled by subsequent development after age 5. Class B in Table 2 includes trees that became 50% encircled between ages 5 and 10. Unless a stem gall is close to 50% encircling at age 5, or obviously growing rapidly in circumference, the tree should be classed as rust-free rather than 1B to 5B.

The 3,222 trees in Table 2 classified as rust-free included 12% that developed a stem gall after tree age 5, 2% that developed stem galls in years 1 to 5 and continued encirclement after age 10, and 15% with stem galls that were not visible at age 5. Inclusion of these infected trees in the rust-free class had very little effect on the probabilities of death of the rust-free class.

To estimate future stocking of a young rust-infected plantation of slash pine it is necessary to survey for number of trees/ac by rust pathogen infection class. The survey should be conducted at the end of the fifth or sixth growing season. Season six allows additional time for stem infections to become visible. Trees with witches'-broom and broken tops need not be tallied since these trees have a nearly 100% probability of dying by age 16.

Since fusiform rust is randomly distributed in most plantations of pine, Yandle and Roth (1971) found that a sample of three 100-tree rows was sufficient for defining incidence of rust. Rectangular or fixed radius plots, however, would be more desirable for computing the number of trees/ac because of the more accurate measurements of area that they provide. Having tallied the number of trees of each class per acre, the final step is to compute expected mortality over a desired time frame. Multiplying the number of trees in each class by the appropriate probabilities (Table 2) gives the expected mortality. Subtraction of each class from trees living at age 5 or 6 gives the expected future stocking.

When the object of management is to grow sawtimber, predicting future numbers of living trees having rust also is important. Under intensive forest management, sawtimber yield depends on an adequate number of rust-free trees after sanitation-salvage thinning removes defective trees, including those having stem cankers (Froelich 1987). Probabilities in Table 2 for 1A to 3A, 4A to 5A, and 1B to 5B can be used to estimate future living infected trees for those classes. Of the trees in the rust-free class in Table 2, 30%, however, had visible or latent stem infection at age 5, or developed a stem gall after age 5. The rust-free component could be tallied separately to account for these trees. Mortality can be assumed to be the same as "rust-free" in Table 2.

There was a 15% latent infection on trees otherwise scored as rust-free in our data, but this can be expected to vary from

Table 2. Probabilities of death of slash pine from fusiform rust disease development by timing and severity of infection (projections based on trees living at age 5).

	Year											
Class[1]	N	6	7	8	9	10	11	12	13	14	15	16
IA-3A	313	0.22	0.41	0.56	0.65	0.68	0.12	0.75	0.76	0.78	0.79	0.80
4A–5A	52	0.06	0.15	0.26	0.34	0.43	0.53	0.60	0.62	0.66	0.68	0.68
1B–5B	240	0.00	0.01	0.06	0.09	0.13	0.14	0.16	0.20	0.22	0.23	0.24
Rust-free	3,222	0.00	0.02	0.02	0.02	0.03	0.03	0.05	0.05	0.06	0.07	0.07

[1] The numbers 1-3 or 4-5 indicate that first stem infection occurred in growing seasons 1 to 3 or 4 to 5. The letters indicate severity of infection: A = 50% stem encirclement by the gall by age 5, B = 50% stem encirclement between years 6 and 10. Rust-free includes trees having no stem galls visible as well as trees having stem infections discovered after age 5 and infected trees not 50% encircled by a stem gall at age 10. Trees having witches'-brooms and partial crown mortality were excluded from the data.

stand to stand according to the timing of the last severe rust infection year. Followup inspections would be desirable for determining this component. Most of the first-time stem infection that was recorded in our plots after age 5 was attributed to branch galls present at age 5 that grew into the stem. Proximity of galls to the stem (usually less than 12 inches), vigor of the galls and the branches on which they occur are therefore important considerations in estimating future branch-into-stem infections, and gall development.

Conclusions

The long-term, detailed nature of the data in this study gives an excellent picture over time of fusiform rust disease associated mortality on planted slash pine. The importance of early stem infection on mortality is certainly verified. The data provide useful estimates of mortality for management decisions up to age 16 and have impact implications beyond age 16. For example, the leveling off of the mortality trajectories in Figure 1 suggests that most of the mortality due to fusiform rust can be expected to occur by age 1.5, at least until self-thinning becomes important, and thus managers may want to thin their plantings accordingly if producing sawtimber is the goal.

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