Tolerance of Loblolly Pines to Fusiform Rust

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ABSTRACT. *Loblolly pines (*Pinus taeda *L.) thut were 8 to 17 yr old tolerated one to three fusiform rust* (Cronartium quercuum *[Berk.] Miyabe ex Shirai f. sp.* fusiforme) *galls in theirstems. Families withfourormore galls in their stems lost 2.5%* **or more** *of the trees by age 17. In living trees with less than four stem galls, diameter growth was comparable to that of trees with no galls. Tolerance was indicated by the ability of loblolly pines to maintain the rustfungus in stems that had dbh's similar to asymptomatic trees on the same site. In plantations, the number of galls in the stem was generally one to two per infected tree. This was also true for mature trees (12 to 38 in. dbh) along the Natchez Trace Parkway. These trees have been infected with fusiform rust for nearly 100 yr. On the other hand, the presence of four or more stem galls seems to be a reliable indicator of mortality rather than tolerance. South. J. Applied For. 19 (2): 60–64.*

Over the past 30 years, damage and death in loblolly (*Pinus taeda* L.) and slash (*P. elliottii* Engelm. var. *elliottii)* pines caused by the fusiform rust fungus *(Cronartium quercuum* (Berk.] Miyable ex Shirai f. sp. *fusiforme*) have increased dramatically. In response, foresters first tried to locate geographic sources of pines resistant to the disease (Wakeley and Bercaw 1965). As a result, millions of progeny of moderately resistant loblolly pines from Livingston Parish, Louisiana, were planted over large areas of the South (Wells 1985). Next, pathologists and tree breeders tried to produce strains of loblolly pine that were resistant to the disease as determined by gall formation (Powers and Kraus 1983, Sluder 1989). The USDA Forest Service established the Resistance Screening Center in Asheville, North Carolina, where newly germinated seedlings are exposed to high concentrations of rust spores (Laird and Phelps 1975). Pine families in which a low proportion of exposed seedlings become infected and subsequently develop rust galls are considered for use in rust-resistant seed orchards, where seeds with a high degree of resistance to infection are produced (Powers and Kuhlman 1987).

Overall, this genetic approach has reduced the number of slash and loblolly pines lost to rust in the areas of greatest hazard, but there have been problems associated with the wide genetic variation in the rust fungus (Powers and Matthews 1979). Some slash and loblolly pine families that survive inoculation tests become infected when exposed to different strains of the fungus in the field. Just as there are some geographic areas in which pines appear to be resistant, there are others in which the rust fungus is particularly virulent even among different galls in the same stand (Snow et al. 1975).

As a result, if resistant slash and loblolly pines are planted over a large area (e.g., a county), the fungus strains in that area may eventually overcome the resistance. This problem would most likely develop in subsequent plantings. Part of the problem is that the genetic makeup of the fungus is so variable and adaptable. Furthermore, when pines are selected because they do not become infected, the less virulent fungus strains for which pines are resistant are not reproduced. The result may be some selection pressure for new virulent fungal strains. That it is important to maintain populations of less virulent strains has been demonstrated experimentally (Powers and Matthews 1979).

If the objective of breeding is to prevent gall formation, forest managers must constantly breed new loblolly pines to avoid changes in the rust fungus, which is how crop plant breeders have controlled wheat rust. This may be the only practical approach if a gall on a tree bole usually kills the tree. Loblolly pines, however, often survive for very long periods with one or more galls on the tree bole. Also, infections in branches near the bole are sometimes prevented from entering the boles of loblolly pines. The data presented in this paper suggest a new strategy for managing rust in loblolly pines: instead of breeding pines to resist infection entirely, perhaps we should be breeding trees to minimize rust damage. This tolerance, or ability to maintain the rust fungus and produce good diameter growth, could further reduce damage to stem wood quality if galls remain small.

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To explore the possibility of using gall tolerance in the management of fusiform rust on loblolly pine, some questions need to be addressed: (1) Why do some loblolly pines with several rust galls in their boles live long and productive lives? (2) Do loblolly pine families vary in their tolerance to fusiform rust? (3) What types of rust-tolerance mechanisms exist in loblolly pines? To answer these questions, we collected data from progeny studies, commercial plantations, and natural stands of loblolly pine.

Methods

In order to determine tolerance, loblolly pines were observed in control-pollinated progeny tests near Greenwood, Florida, and in the DeSoto, Bienville, and Homochitto National Forests of Mississippi. Additional loblolly pines from progeny tests of open-pollinated seedlots were measured at Madison, Florida, and Savannah, Georgia, as an adjunct to forest industry tests. Loblolly pine stands were also observed in Argyle, Florida; Bainbridge, Georgia; and Lumberton, McComb, and McHenry, Mississippi. Mature loblolly pines (approximately 100 yr old) were examined on the Natchez Trace Parkway in Mississippi. This variety of readings was made to obtain differences in percentages of infected trees and different age classes.

Evaluation of tolerance to fusiform rust in loblolly pines required a survey of tree and gall traits. The observable variables were total number of trees; trees with fusiform rust galls in the stem; branch galls within 12 in. of the stem; girdling of the stem expressed as a percentage of the stem circumference covered with gall tissue; diameter at breast height (dbh); and dead trees due to rust-associated mortality (RAM).

Analyses of variance (fixed effects model) and regression analyses were used to estimate family effects and to test possible relationships among observable variables.

Control-Pollinated Progeny Tests

Florida Test.-The design at the Greenwood, FL, progeny test consisted of 49 full-sib crosses in IO-tree row plots, spaced at 6 x 10 ft with 4 replications. Trees were evaluated at ages 4, 12, 15, and 17 yr.

Mississippi Test.-In the progeny tests in the national forests of Mississippi, 8 full-sib crosses in 1 O-tree row plots with 3 replications were observed at 8, 9, and 10 yr. Spacing was 8 x 8 ft.

Open-Pollinated Progeny Tests

Madison, FL Test.-Livingston Parish, LA, and Marion County, FL, loblolly pines were observed at a planting at Madison, FL. Livingston Parish seed sources are grown in large numbers, possess good growth, and have above-average fusiform rust resistance (Wells 1983). The test design was 4 blocks of 49 trees in 7-tree rows. Spacing was 6 x 10 ft. Trees were evaluated in their 17th growing season. Five-year infection of these trees was reported in a previous paper (Pait and Draper 1983).

Savannah, GA Test.-Livingston Parish source and loblolly pine family 7-56 (Zobel et al. 197 1) were compared in IO-ac paired plots with a 6 x 10 ft spacing in Savannah, GA Three random rows of 100 trees in a straight line were measured at the end of the 10th growing season. In addition to these 2 seed sources, 20 open-pollinated pine families were observed. These were second-generation loblolly selections. The design of the test was 2 blocks, 6 replications, and 6-tree row plots. Spacing was 6 x 10 feet.

Forest Industry Stands

Commercial stands of loblolly pines in Florida, Georgia, and Mississippi had spacings of 6 x 8 ft or 6 x 10 ft. Tree dbh ranged from 5 to 10 in. and ages ranged from 8 to 12 yr. Twelve random rows of 25 trees per row were observed. Also, at Lumberton, MS, 200 loblolly pine saplings between 2 and 4 yr old were observed at an early age.

Naturally Regenerated Stands

Twenty-five loblolly pines on the Natchez Trace Parkway were measured at each of 12 stops that extended for 110 mi north from Natchez. Only trees that were greater than 12 in. dbh were measured.

Results

Tolerance and Tree Growth

Highly infected loblolly pines had no significant differences in their dbh values during the 17th growing season in Florida (Table 1). The means fordbh values indicated similar rates of growth of all crosses regardless of their percent of infection. Susceptible check trees that survived RAM at 17 yr were the largest in the test. The susceptible check at Mississippi also was the largest in diameter at 7.2 in. compared to 4.8 in. for selected family 209, a resistant family. The trees largest in diameter among the resistant families were from parent 236 (Table 3).

When 144 Livingston Parish, LA, and 148 Marion County, FL, trees were measured, the average dbh of the trees with galls was the same as that for asymptomatic trees of both seed sources. The mean dbh values at 17 yr were 7.9 and 7.5 for the two seedlots.

Measurements of rust-infected loblolly pines along the Natchez Trace Parkway that were 100 yr old averaged 21 in. (12 to 38 in.). Asymptomatic trees ranged from 14 to 28 in. and also averaged 21 in. in dbh.

Tolerance and Number of Galls in the Stem

Mean values for galls in the stem differed among loblolly pine crosses in Florida (Table 1). These values were related to RAM in the Argyle and Lumberton plantings, R^2=0.85 and 0.87. These high numbers of galls in the stem were found only in these three plantings. Examples of incidence of stem galls at other locations are shown in Table 2.

Variations in tolerance were indicated by the differences between families in percentages of galls that grew into the stem. These differences were significant (P = O.OOl), and the number of these galls was positively related to the percent infection (r^2=0.70). The fourreplications had 3,650 galls that grew to the main stem but died without causing significant swelling of the stem. These galls are shown in Figure 1 A- 1 C. When RAM trees were found intact at these locations, their stems had four or more galls.

Table 1. Comparison of fusiform rust, stem diameters, rust-associated mortality (RAM), and number of stem galls in control-pollinated loblolly pines during the seventeenth growing season in Florida.[1]

Pine cross[2]	Trees with galls (%)	dbh (in.)	RAM (%)	Mean no. of stem galls
3-36x1-11	90	6.8	12	2.6
3-36 x 1 l-20	78	7.8	10	3.1
3-36 x 1-14	a7	71	18	3.0
3-36 x 12-l 2	78	7.8	8	2.5
3-36 x 12-13	92	7 5	25	2.8
3-36 x 1-64	77	6.8	20	2.4
3-36 x 5-33	77	7.5	8	2.1
3-36 x 5-5	92	6.7	15	3.4
3-36 x 7-2	81	7.7	10	2.3
3-36 x 7-34	83	6.8	18	3.2
3-36 x 7-56	86	8 2	2	2.8
Mean	84	7.3	13.3	2.7
3-2 x l-l 1	95	6.8	22	3.8
3-2 x 1 l-20	92	6.5	30	4.2
3-2 x l-14	88	6.8	22	4.4
3-2 x 12-12	100	8.0	22	3.8
3-2 x 12-13	94	7.0	25	2.6
3-2 x 1-64	90	8.0	22	3.6
3-2 x 5-33	98	7.2	38	3.2
3-2 x 5-5	91	7.6	28	3.4
3-2 x 7-2	97	7.2	25	3.8
3-2 x 7-34	97	6.4	28	4.0
3-2 x 7-56	95	6.8	20	4.8
Mean	94	71	25.6	3 8
10-8 x W	100	a.4	25	3.8

1 Means of 4 replications of 10-tree row plots

2 Pine females 3-36 and 3-2 have been assigned average rust performance values in other tests (Zobel et al. 1971) Pine IO-8 is the susceptible check Differences among crosses for trees with galls and dbh were not significant at the 5% level. Differences for RAM and stem galls were significant ($P = 0.009$ and $P = 0.027$, respectively)

Tolerance and Tree Mortality

Rust-associated mortality (RAM) occurred when high percentages of trees became galled (Tables 1 and 4). RAM was absent at 60% infection in commercial stands (Table 4). Low RAM values (3%) were found in Mississippi national forests where infection was less than 50% (Table 3). Family differences for RAM values in Table 1 were significant (P = 0.009). Cross 3-36 x 7-56 with 2% RAM and cross 3-36 x 12-13 with 25% RAM clearly illustrate this difference (Table 1). Progeny of parent 3-36 had a much lower RAM than those of parent 3-2 (Table 1).

Tolerance and Stem Girdling

Growth of gall tissue to encompass the main stem was generally incomplete. Even when infection was high, the percentage of stems girdled by galls was significantly different among crosses (*P* = 0.005). For example, branch galls that grew into the stems of cross 3-36 x 7-56 girdled 47% of the tree circumference, whereas those in stems of 3-2 x 7-56 girdled 74% of the circumference. The comparable value for the susceptible check, family 10-8, was 60% girdled. One of these trees with four stem galls is shown in Figure 1D.

When less than 50% of the trees in a plantation were infected, galls encompassed 40 to 55% of the stem after 10 growing seasons. This growth of gall tissue was highly variable in older trees. Of galls in the stems of 95-yr-old infections, 48 were small, encompassing only 13% of the circumference; 163 galls encompassed 40% of the stem.

Table 2.

Location	Stem galls	Seedlot
Madison, FL	1.4	Livingston Parish
	1.3	Marion County
Savannah, GA	1.5	Livingston Pansh
	14	7-56
Bainbridge, GA	1.6	7-56
McComb, MS	2.1	Bulk seedlot
McHenry, MS	1.6	Bulk seedlot
Lumberton, MS	1.3-1.9	Bulk seedlot (seedlings)
Natchez Trace Parkway	1.2	Natural (95+ years old)

Discussion

Results from this study answer some of the questions that were raised in the beginning of this paper. Tolerance varies with pine family and number of galls in the stem. First, infected loblolly pines on most of the sites had ony one or two galls per stem. These galls did not completely girdle the trees, even those that were infected for approximately 95 years. These pines did not die. Four or more galls seemed to cause RAM in trees, but this severe level of infection was unusual in most of the observed sites. Thus, RAM was low in most of the loblolly plantations we observed.

Secondly; loblolly pine families differed significantly in their ability to live with fusiform rust as indicated by the data on RAM and on galls in the stem (summarized in Table 1). Lack **of** tolerance in infectedloblolly pines was characterized

Figure 1. Reaction of loblolly pines to fusiform rust: (A) Failure of a gall on a large branch to cause swelling in the stem; (B) Three dead galls at the stem of a 15-yr-old loblolly pine; (C) Large number of galls dying at the stem in a 25-ft-tall loblolly pine, (D) Row plot of loblolly pine 10-8 in the 17th growing season. These trees had an average of 3.8 galls in their stems after 12 yr.

Table 3. Occurrence of fusiform rust galls in control-pollinated progeny tests for 9-yr-old loblolly pines in Mississippi National Forests.'

Region 8 pine crosses	Total trees (no.)	Galled trees (%)	Galls in the stem	Growth rank by diameter
209 x 203	74	2	0	7
209 x 239	116	5	40	8
250 x 245	60	12	25	4
216x245	58	12	77	6
236 x 228	81	29	55	2
236x231	65	22	40	1
203 x 223	125	54	22	3
3-3-2 (ck)	154	52	36	5

[1] Crosses are sorted from least galled to most galled Pooled infection ranged from 4 to 43% for these crosses at DeSoto, Bienville, and Homochitto National Forests RAM averaged 3%

by RAM values of 20% or more. Death of large numbers of galls attached to the stem was also a sign of intolerance because the fungus did not survive.

Thirdly, some evidence was obtained on the types of rust-tolerance mechanisms in loblolly pines. Tolerance has not developed in seedlings that formed stem galls from infection of the terminal shoot. These galls completely girdled seedlings, as noted in other studies (Geron and Hafley 1988, Kuhlman 1988). Tolerance in loblolly pine appears to be the ability of the infected trees to support growth of the fungus within the cambium while allowing diameter growth of the tree to proceed normally.

One of the most interesting results was the occurrence of small galls on the old loblolly pines. Findings of Snow et al. (1990) suggest that one type of resistance in loblolly pine seedlings is the restriction of gall tissue to a small volume of the stem. If this restriction is under genetic control, as suggested by their greenhouse data, then it should be expressed in plantation trees. Many of the galls we found indicate this restriction trend. The observations of Snow et al. (1990) were made on fast growing seedlings in the greenhouse and nursery. Extrapolation from these juvenile trees to adult field trees may not be valid (Loo et al. 1984). However, we routinely observed restriction of gall growth in field trees among juvenile and adult individuals.

Even when galls remain small, they may impact yield for lumber products. Trees with 1 to 3 galls in their stem had diameters that were similar to asymptomatic ones. Such infected trees should compete equally within stand dynamics with those uninfected, but if stocking is adequate, they should be removed in thinnings due to potential product degrade.

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Table 4. Number of stem galls in commercial stands of loblolly pines.'

Location	Trees with galls[2]	No of galls in stem: 1	2	3	4+	Asymptomatic trees
		No. of trees				
Argyle, FL	247	71	50	39	61	53
Lumberton, MS	260	74	4:	31	79	40
McComb, MS	200	74	46	22	26	100
McHenry, MS	181	75	35	14	4	119

[1] A total of 300 trees in rows of 25 each were observed at each site Spacing was 6 × 8 or 6 × 10 feet Trees with branch galls only are Included in trees with galls
[2] The RAM was 12, 20, 6 and 0%. respectively These trees are Included in the 4+ column of stem galls