FUSIFORM RUST EPIDEMICS IN FAMILY MIXTURES OF SUSCEPTIBLE AND RESISTANT SLASH AND LOBLOLLY PINES

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Abstract. Fusiform rust incidence (% trees infected) was measured through age 5 yr for mixtures of susceptible and resistant slash pine *(Pinus elliottii* var. *elliottii)* and loblolly pine *(P. taeda)* planted in seven potentially high-rust-hazard locations in the Coastal Plain of FL, GA and MS. Four mixtures of six open-pollinated pine families were evaluated: rust-susceptible slash (SS), rust-resistant slash (RS), rust-susceptible loblolly (SL), and rust-resistant loblolly (RL). Few trees were infected through age 2 yr; rust increased in years three to five concomitant with an increase in tree height. Average rust incidence at age 5 yr was 46.5, 16.0, 44.2 and 10.4% for SS, RS, SL and RL, respectively. Resistant mixtures had significantly less rust than susceptible mixtures at all locations. Few interactions between rust incidence and age occurred among mixtures within locations. At three locations, slash pine was significantly more infected than loblolly pine; at one location, loblolly pine was significantly more infected than slash pine. Rust incidence on susceptible family mixtures varied among locations reflecting the rust hazard of the site. Rust incidence on RS mixtures varied among locations, increasing significantly with increasing rust hazard, i.e., with increasing rust incidence on SS family mixtures. Rust incidence on RL mixtures increased slightly with increased rust incidence on SL, but differences among locations were not significant. These results suggest that similar mixtures of half-sib rust-resistant slash and loblolly pine families will reduce rust incidence substantially in a variety of locations and rust hazards, but the performance of resistant slash pine family mixtures may be reduced significantly in locations with very high rust incidence.

Keywords: *Cronartium quercuum* f sp. *fusiforme, Pinus elliottii* var. *elliottii, Pinus taeda,* stability of rust resistance.

INTRODUCTION

Fusiform rust of slash pine *(Pinus elliottii* Engeim. var. *elliottii)* and loblolly pine *(P. taeda* L.) caused by the obligate parasite *Cronartium quercuum* (Berk.) Miyabe ex Shirai f sp. *fusiforme*, results in millions of dollars of losses annually in the southeastern USA (Anderson *el al.* 1986, Powers *et al.* 1975). Fusiform rust, of rare occurrence at the beginning of this century Griggs and Schmidt 1977), apparently spread from west to east (Mississippi to Atlantic Coast) Dinus 1974) and increased dramatically as pine management intensified (Schmidt 1978). The fungus exhibits variability in pathogenicity (Kuhlman 1990, Powers 1980) and half-sib (open-pollinated) pine families respond differentially to fungus isolates (Powers 1985). Genetic resistance to the pathogen occurs in slash and loblolly pine (Schmidt and Goddard 1971, Wells and Wakely 1966) and resistant pines are planted to reduce rust impact (Schmidt *et al.* 1985).

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Notwithstanding successes in finding and using fusiform rust resistance, information is needed on the temporal and spatial stability of widely-planted, intensively-managed resistant pine genotypes. The factors affecting stability in the field are especially important now that a major gene for resistance has been identified in the fusiform rust - loblolly pine pathosystem (Wilcox *et al.* 1995), and previously in the white pine blister rust - sugar pine pathosystem (Kinloch and Comstock 1981, Kinloch *et al.* 1970).

Our objective was to assess the disease progress and spatial stability of rust resistant slash and loblolly pine mixtures planted at seven locations in the Southeastern Coastal Plain exhibiting different levels of rust incidence, i.e., rust hazard, and cultural treatments.

METHODS AND MATERIALS

The general methods and materials were reported in previous publications on the influence of oak management on fusiform rust incidence (Schmidt *et al.* 1993) and the stability of resistance in slash and loblolly pine (Hodge *et al.* 1993). Only those methods appropriate to the data on epidemics in resistant and susceptible pine family mixtures are presented here.

Family mixtures. Pine seedlings of four mixtures - rust-susceptible slash (SS), rust-resistant slash (RS), rust-susceptible loblolly (SL) and rust-resistant loblolly (RL) - were planted in six locations in FL and GA (Figure 1). At the seventh location in MS only loblolly mixtures were planted. Original selections were from the Coastal Plain of NC, SC, FL, GA, AL and MS (see source, Figure 1). Seed were collected from open-pollinated clones established in seed orchards. Seedlings were grown in a nursery in southcentral GA in the spring and planted at the test locations the following winter. One location was planted in 1985, four were planted in 1986 and two were planted in 1987 (Table 2).

Each of the four mixtures consisted of a random mix of equal proportions of seed from six very susceptible or very resistant open-pollinated families, as determined in field progeny trials and/or greenhouse tests. The average rust indices (Hatcher *et al.* 1981) were 92, 28, 77 and 32 for RS, SS, RL and SL family mixtures, respectively (Table 1).

Table 1. Average fusiform rust index for family mixtures of susceptible or resistant slash and loblolly pines planted in seven high-rust-hazard locations in the Coastal Plain of FL, GA and MS.

Family mixture	No. of families in mixture	Rust index' Ave.	Rust index' Range
Resistant slash (RS)	6	92	87-99
Susceptible slash (SS)	6	28	15-39
Resistant loblolly (RL)	6	77	73-86
Susceptible loblolly (SL)	6	32	19-41

'NC State Tree Improvement Cooperative rust index values for loblolly pine (Hatcher *et al.* 1981) and those calculated for slash pine from the University of FL Cooperative Forest Genetics Research Program. An average family (unimproved for rust resistance) would have a value of 50: higher values = greater resistance.

Experimental design and analyses. At each location, two 3.64 ha (9.0 ac) areas, each consisting of thirty-six 0.10 ha (0.25 ac) subplots were installed (Figure 1). One area was treated annually to remove susceptible oaks; in the other area, oaks were allowed to grow. Each area accommodated a 2 (species) x 2 (family mixtures) x 3 (cultural treatments) randomized complete block split-split plot design with three replications. Each area consisted of six main plots arranged in three replications. The main plot was pine species, split into resistant and susceptible pine mixtures. Three cultural treatments were applied at planting to these split plots: control (no treatment); fertilizer + herbicide, and fertilizer + herbicide + Bayleton®. There were 36 subplots on each area or a total of 72 subplots at each location. A preliminary analysis indicated that there were few consistent relations in percentage trees infected or height among the cultural treatments and unless otherwise noted, these treatments were pooled to analyze family mixtures. Thus, there were 72/4 or 18 subplots/family mixture. Data were collected from a 54-tree sample at the center of each subplot of 164 trees. The number of branch and stem galls on each tree was recorded annually at ages 1-5 yr and cumulative rust incidence (% trees infected) was calculated. Tree height was measured at ages 1, 3 and 5 yr.

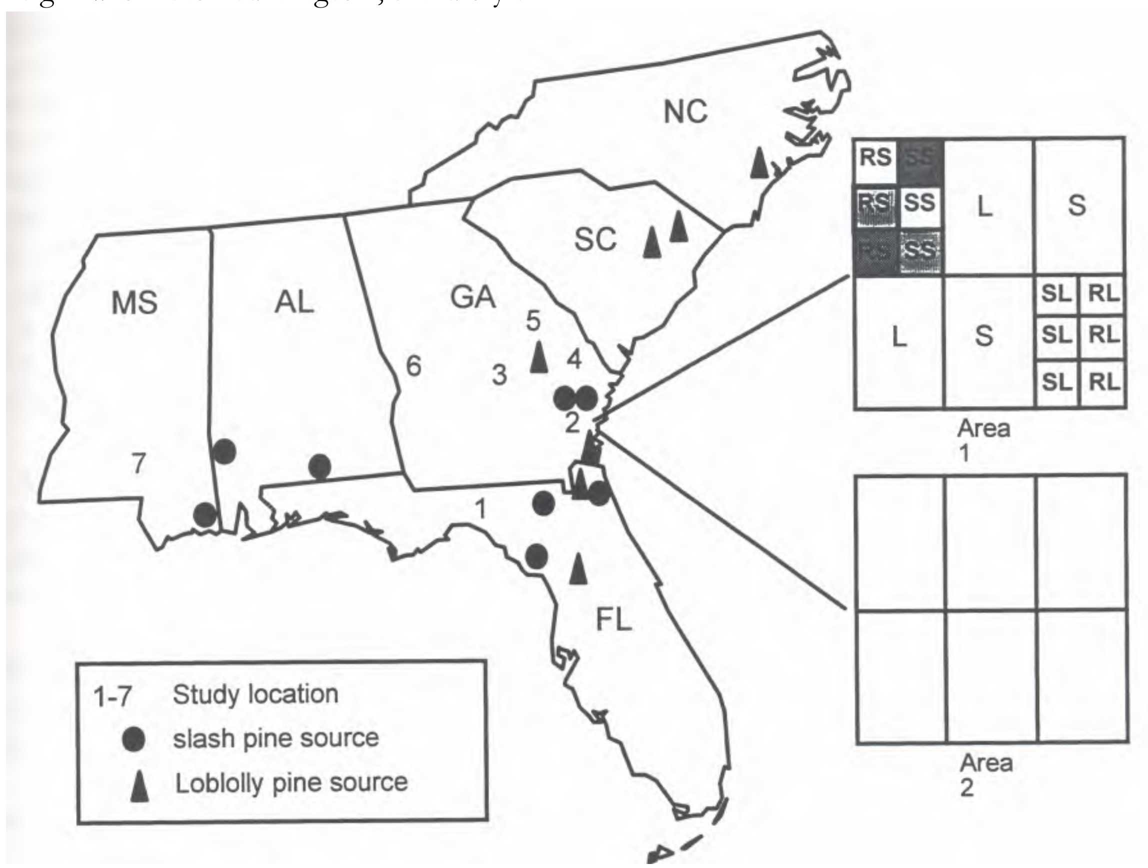

Figure 1. Fusiform rust study locations (1-7) and geographic sources of pine selections in the Southeastern Coastal Plain and experimental design. Increasing intensity of shading represents increasing intensity of cultural treatments (described in text). All replications were similar to the one shown shaded with the exception that Area 1 was treated annually to eliminate oak while Area 2 was not treated for oak control. SS = susceptible slash, RS = resistant slash, SL = susceptible loblolly and RL = resistant loblolly.

Differences in percentage trees infected within and among locations were examined with analysis of variance (Anonymous 1985). Differences in percentage trees infected between species at each location were determined by the F-test using the appropriate mean square error term. Significant differences in percentage trees infected among locations for each family mixture were determined conservatively, using Duncan's Multiple Range test with the location x area interaction mean square as the error term. Because rust incidence on susceptible mixtures (rust hazard) varied among locations, the relative resistance, i.e., percentage of trees infected in resistant mixture/percentage of trees infected in susceptible mixture (R/S ratio) was used in an analysis of variance and regression analyses to evaluate the stability of rust resistance among locations and treatments.

RESULTS

Disease progress age 1-5 Yr . Rust incidence on susceptible mixtures (SS, SL), indicative of rust hazard, remained low through 2 yr at five locations; at Perry and Screven, rust incidence was moderate on these mixtures by age 2 yr (Figure 2). Rust increased substantially on SS and SL mixtures at all locations subsequent to age 3 yr. The pattern of rust increase on these susceptible mixtures after age 2 yr varied among locations; at Perry and Louisville there was little or no increase in rust from yr 3 to 4; at Statesboro, a substantial increase in rust occurred from yr 3 - 5; at McRae, Perkinston and Americus, substantial rust occurred during yr 4 and 5. Rust on SS and SL mixtures increased substantially during yr 4 only at Screven and yr 5 only at Louisville. Overall infection during the first 3 yr resulted in 70 and 43% of the branch galls growing into the stem by age 4 yr at Perry, FL and McRae, GA, respectively, while by age 4 yr only 20% of the branch galls had grown into the stem at Statesboro. Among all locations, the average ranking at age 5 yr, from high to low rust incidence was: SS, SL, RS and RL, although SL SS at two locations (Screven and Louisville). Family mixtures maintained their relative positions of rust incidence throughout age 5 yr with the exception of SL during the fifth year, when at six of seven locations, SL exhibited a differentially high increase in rust incidence.

Comparison of species. Average cumulative rust incidence at age 5 yr on slash pine (SS, RS) was 30.9% and was significantly greater than that (26.4%) on loblolly pine (SL, RL) among all locations, and within locations at Statesboro, McRae and Perry (Table 2). Average cumulative rust incidence on loblolly pine (SL, RL) was significantly greater than that on slash pine at Louisville.

Comparisons of family mixtures. In both species and at all locations, resistant family mixtures had significantly less rust than susceptible family mixtures (Figure 2, Table 2). Among locations, SS ranged from 26.3 - 76.1%, $\bar{x}$ = 46.5%; RS ranged from 5.3 - 34.3% $\bar{x}$ = 16.0%; SL ranged from 22.8 - 62.7%, $\bar{x}$ = 44.2%, and RL ranged from 5.3 - 14.4%, $\bar{x}$ = 10.4% (Table 2). Rust incidence on SS and SL mixtures varied significantly among locations (reflecting rust hazard of the locations). Correlation between SS and SL for rust incidence was 0.86, p = 0.03. Rust incidence on the RS mixture varied significantly among locations and was correlated (r = 0.97, p = 0.001) with rust incidence on the SS mixture. Rust incidence on the RL mixture varied little among locations, but was correlated (r = 0.92, p = 0.003) with rust incidence on the SL mixtures.

Relative resistance of family mixtures (resistance/susceptible ratio). Relative rust resistance (RS/SS ratio of cumulative percentage trees infected at age 5 yr) of slash pine ranged from 0.20 - 0.45 among locations, varied significantly among locations (Table 2) and was correlated (r = 0.80, p - 0.06) with rust incidence on SS. In loblolly pine, the RL/SL ratio ranged from 0.18 - 0.27 among locations, did not vary significantly among locations (Table 2) and was not correlated (r = 0.10, p = 0.83) with rust incidence on SL. The average ratios for slash pine (0.34) and for loblolly pine (0.23) were significantly different (p - 0.05).

Rust incidence in relation to pine growth (height), age and cultural treatments. The positive relation between rust incidence (total number of galls) and height at age 1, 3 and 5 yr at Statesboro, GA for slash pine (Figure 3A) and loblolly pine (Figure 3B) was typical of all locations in that it reflects the increase in rust susceptible tissue with increasing age. The associated number of stem galls at age 5 yr at Statesboro for SS, RS, SL and RL was 253, 126, 152 and 31, respectively. The number of total galls (branch and stem) per infected trees at age 5 yr for SS, RS, SL and RL was 3.6, 2.4, 2.8 and 1.6, respectively. Within species, there was no significant difference between the average heights of susceptible and resistant family mixtures at ages 1, 3 or 5 yr for slash or loblolly pine. Loblolly pine was significantly taller than slash pine at age 5 yr at Statesboro, but this relation between species varied among locations.

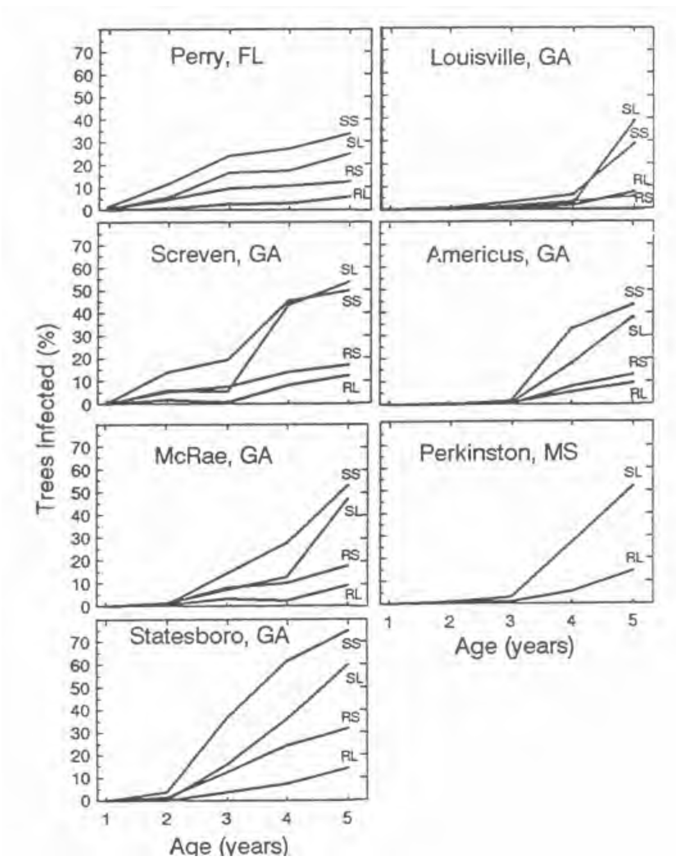

Figure 2. Disease progress (cumulative percentage trees infected) from ages 1-5 yr in family mixtures of rust-resistant or susceptible slash and loblolly pines planted (1985-87) at seven locations in the Coastal Plain of FL, GA and MS. SS = susceptible slash, RS = resistant slash, SL = susceptible loblolly, and RL = resistant loblolly.

Table 2. Fusiform rust incidence (cumulative percentage trees infected) and relative performance (resistant/susceptible ratio) at age five years in mixtures of open-pollinated progenies of resistant and susceptible slash and loblolly pines planted at seven locations in the Coastal Plain of FL, GA and MS'.

	Year	Average		Slash		Loblolly		Resist/Susc ratio	
Locations'	planted	Slash	Loblolly	Susc.	Resist.	Susc.	Resist.	Slash	Loblolly
Statesboro, GA Bulloch Co. (4)	86	59.5A[3]	38.4B	76.1a[4]	34.3a	62.7a	14.1a	0.45a	0.22a
McRae, GA Wheeler Co. (3)	86	35.8A	26.4B	53.6b	18.0b	44.7bc	8.6a	0.34ab	0.19a
Screven, GA Wayne Co. (2)	86	32.1A	32.4A	49.1b	15.1bc	52.0abc	12.8a	0.3 lab	0.25a
Perkinston, MS Stone Co. (7)	87					54.5ab	14.4a		0.26a
Americus, GA Sumter Co. (6)	87	26.6A	24.6A	42.4bc	11.6bc	36.0cd	9.7a	0.27ab	0.27a
Perry, FL Taylor Co. (1)	85	21.6A	14.0B	31.7cd	11.4bc	22.8d	5.3a	0.36ab	0.23a
Louisville, GA Jefferson Co. (5)	86	16.2B	24.0A	26.3d	5.3c	37.2cd	7.0a	0.20b	0.18a
Average		30.9A	26.4B	46.5A	16.0B	44.2A	10.4B	0.34A	0.23B

'Average of 18 plots (excluding missing plots) per family mixture: 54 measurement trees per plot (excluding rust-unrelated mortality).

[2](#) refers to study location in Figure 1.

[3]Means within each location (within each row) followed by different capital letters are si gnificantly differen (p = 0.05) according to F-test.

'Means among locations (within a column) followed by different lower-case letters are si gnificantly differen (p = 0.05) according to Duncan's Multiple Range test.

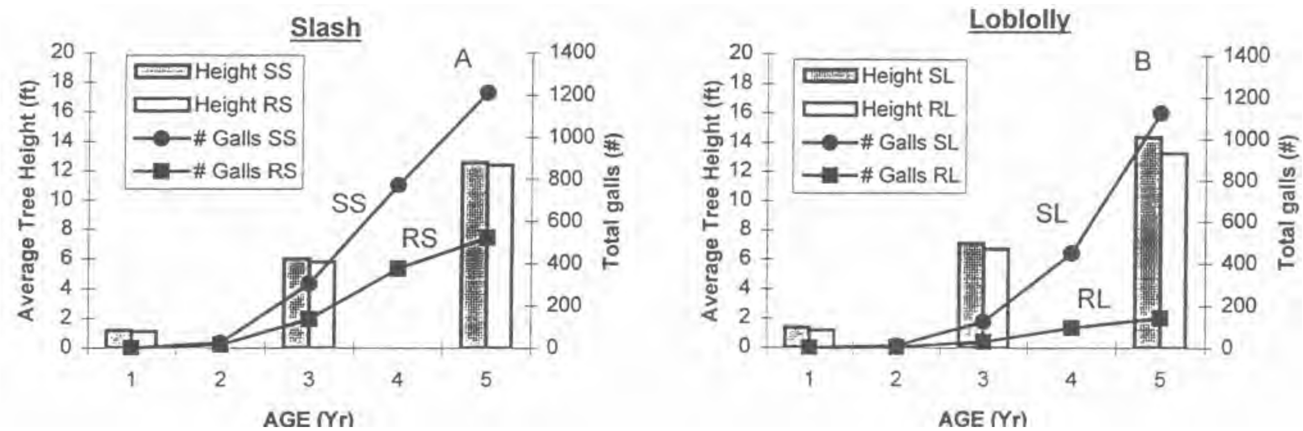

Figure 3. Cumulative fusiform rust incidence (total number of galls {branch and stem}) at ages 1-5 yr and height at ages 1, 3 and 5 yr of rust-susceptible and rust-resistant slash pine (A) and loblolly pine (B) family mixtures at Statesboro, GA.

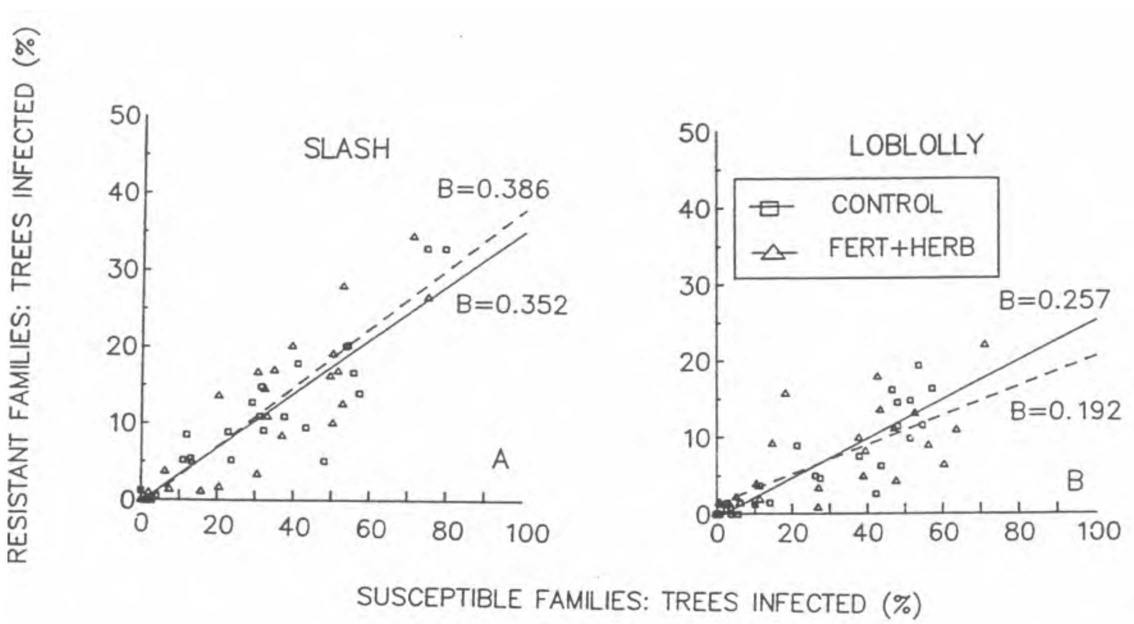

Figure 4. Relationship between cumulative percentage trees infected at age 3 and 5 yr on fusiform rust susceptible and resistant slash pine family mixtures (A) and susceptible and resistant loblolly pine family mixtures (B) receiving cultural treatments to promote growth at high-rust-hazard locations in the Coastal Plain of FL, GA and MS. Control = no treatment; Fert + Herb = fertilizer and herbicides applied at planting.

The relation among cultural treatments (fertilizer and herbicides vs control) at planting, pine height and rust incidence varied among locations. At some locations, fertilizer and herbicide increased pine heights significantly over that of the control with or without a significant increase in rust incidence. At other locations, fertilizer and herbicide did not increase pine height significantly with or without significant increases in rust incidence. Overall, this variation resulted in a linear R/S ratio with increased rust incidence, and did not result in significant differences in regression coeficients for slash pine (Figure 4A) or lobloly pine (Figure 4B).

DISCUSSION

Rust incidence was low at all locations through age 2 yr and increased substantially during ages 3-5 yr at most locations. Others (Griggs *et al.* 1978, Schmidt *et al* 1979) reported similar patterns of disease progress for fusiform rust. Our pine height data suggest that this pattern of rust increase is a function of the availability of susceptible tissue, given the presence of inoculum. Within this typical pattern of rust increase, variation among years occurs (Schmidt and Allen 1991) and is assumed to be related primarily to availability of inoculum as conditioned by weather (Davis and Snow 1968, Froelich and Snow 1986). Percentage trees infected at age 5 yr on susceptible family mixtures ranged from 22.8 to 76.1 among locations and averaged 46.5 and 44.2 on susceptible slash and loblolly pine, respectively. This amount of rust incidence was sufficient to compare resistance among family mixtures and locations (Schmidt and Goddard 1976, Sohn *et al.* 1990).

The greater height of loblolly pine compared to slash pine at Statesboro may explain the greater increase in rust incidence on loblolly pine during the 5th yr compared to slash pine at this location and perhaps other locations. For example, Colbert *et al* (1990) found that dry matter partitioning to the crown (foliage and branches) was greater in 4-yr-old loblolly pine when compared to slash pine which partitioned more dry matter into the stem. Dalla-Tea and Jokela (1991) found that loblolly pines (at 6 yr) produced more branches compared to slash pines. The greater number of succulent terminals associated with these branches could provide a greater number and area of potential infection sites on loblolly pine compared to slash pine. Evaluation prior to age 5 yr would have underestimated rust incidence on susceptible loblolly in several locations and changed the rankings of family mixtures at Louisville and Screven. It is not appropriate to define species comparisons from our data which are derived from a small number of select families. Nevertheless our data with similar genetic material at all locations show that rust incidence on slash pine was significantly greater than that on loblolly pine at the most southern location (Perry, FL) and at two locations (Statesboro and McRae) in central GA. Loblolly pine exhibited significantly greater rust incidence than slash pine at the most northern location (Louisville, GA). Overall, rust incidence on slash pine (30.9%) was significantly greater than that (26.4%) on loblolly pine. This difference resulted from significantly less rust incidence on resistant loblolly pine (10.4%) compared with that (16.0%) on resistant slash pine.

Rust incidence on resistant slash pine family mixtures differed significantly among locations. Similar interactions in slash pine were reported by Sohn and Goddard (1979). Our data indicate that resistance in slash pine is closely related to disease hazard, i.e., the resistance/susceptible ratio increased as rust incidence on susceptible material increased. This decrease in relative resistance could result from quantitative or qualitative changes in inoculum potential among locations. Others have reported the "erosion" of fusiform rust resistance with increased amounts of inoculum in naturally inoculated field progeny tests of slash pine (Sohn and Goddard 1979) and

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