Temporal and Spatial Patterns of Fusiform Rust Epidemics in Young Plantations of Susceptible and Resistant Slash and Loblolly Pines

ROBERT A. SCHMIDT, Professor of Forest Pathology, RENEE C. HOLLEY, Statistician I, MICHAEL C. KLAPPROTH, Graduate Student, Department of Forestry, and THOMAS MILLER, Research Plant Pathologist, USDA Forest Service, Southeastern Forest Experiment Station, School of Forest Resources and Conservation, University of Florida, Gainesville 32611

ABSTRACT

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Fusiform rust incidence data were analyzed from 1,882 predominantly 5-yr-old slash and loblolly pine plantations established on 67,740 ha in eight management areas in Florida and Georgia between 1961 and 1980. In both species, rust incidence increased from east to west within the region. In the northern portion of its range (central Georgia), rust incidence was greater on slash than on loblolly pine, but in the southern portion of its range (northeastern Florida), rust incidence was greater on loblolly than on slash pine. Temporal trends indicate that specific areas are perennially either high or low in rust incidence, although there are periods of increasing and decreasing epidemics. Rust management strategies can be designed for specific areas according to anticipated high or low rust incidence. Rust incidence was significantly lower ($P = 0.01$) among plantations established with seedlings from rust-resistant seed sources than among those established from largely unimproved, susceptible sources.

Additional key words: *Cronartium quercuum* f. sp. *fusiforme*, disease management, disease resistance, epidemiology, *Pinus elliottii* var. *elliottii, P. taeda*

Southern fusiform rust, caused by *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*, is the most destructive disease in the intensively managed southern pine forests (1,4,13). In areas of high rust incidence, the disease is the major obstacle to effective management of slash (*Pinus elliottii* Engelm. var. *elliottii*) and loblolly (*P. taeda* L.) pines. Severely damaged plantations must be destroyed and replanted or grown to rotation age at greatly reduced stocking, yields, and product options. Historical data (3,6,16) suggest that concomitant with intensive forest management, the disease spread from west (Mississippi and Alabama) to east (Florida, Georgia, and South Carolina) and increased dramatically during the last 30 yr. Schmidt (14) suggests that this increase occurred in part because fusiform rust is a "young tree epidemic," and young rapidly growing pine plantations—a success of forest management in the South—provide abundant susceptible tissue and a favorable microclimate for infection and inoculum production.

Survey data (12,16,22) delineate broad geographic areas of rust incidence on a regional basis, but effective rust management requires specific data on rust incidence through time and space in smaller management areas or individual plantations. Unfortunately, limited data exist on which to base rust incidence or hazard predictions, especially for specific sites. Individual components such as soil drainage and fertility (9,20) and abundance of oak (8,23,24), the alternate host, have been investigated, but a comprehensive site-hazard study does not exist.

In 1983, a cooperative project of the Southeastern Forest Experiment Station, Container Corporation of America Inc. (CCA), and the University of Florida was initiated to study fusiform rust site hazard. This paper presents results from an initial phase of this project. The object was to define the temporal and spatial patterns of rust incidence in 5-yr-old plantations. In addition, rust incidence data for plantations of rust-resistant pines planted in areas with high rust incidence are presented. There is abundant evidence from artificial inoculations and progeny tests for rust resistance in loblolly and slash pine seed sources (5,19), but information on their performance in operational plantings is lacking. Preliminary results from a portion of these data were reported (7,17).

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MATERIALS AND METHODS

Data set. These data summarize fusiform rust incidence in 1,882 pine

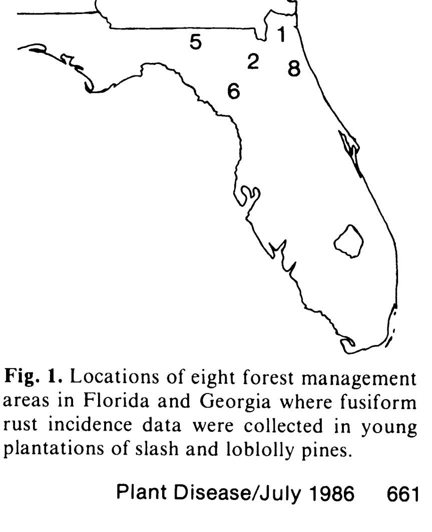

Fig. 1. Locations of eight forest management areas in Florida and Georgia where fusiform rust incidence data were collected in young plantations of slash and loblolly pines.

plantations (1,427 slash and 455 loblolly) encompassing 67,740 ha. The data derive from an ongoing plantation inventory, primarily at age 5 yr, in eight CCA management areas from south central Florida to west central Georgia (Fig. 1). This inventory includes information on species, plantation size, year planted, rust incidence, and seed source. Included are 210 (28 slash and 182 loblolly) plantations ("resistant plantations") established with seedlings from rust-resistant seed sources.

Rust incidence. Rust incidence data were collected from the live trees at five consecutive planting spaces in the row nearest the center of a 78.4-m^2 sample plot. Sample plots were evenly spaced, and their numbers varied with plantation size. For example, averages of 27 (6.75% sample) and 144 (0.50% sample) plots were measured in plantations of 2.43–4.05 and 223–243 ha, respectively. Fusiform rust categories were 1) stem and branch infections or stem only and 2) branch infections only. Combining these categories provided an estimate of cumulative percentage of rust at age 5 yr. Rust incidence (percentage of trees with rust) for each plantation was calculated as a total for all sample plots, i.e., the total number of living trees with rust divided by the total number of living trees. This value underestimates the amount of rust, because trees killed by rust were not included.

To examine temporal and spatial trends, the percentage of rust for each plantation and the mean percentage of rust for all plantations established in a given year (means were weighted by area of plantation) were calculated for each of the eight areas. Appropriate means were compared statistically.

Rust-resistant plantations. CCA planting records indicate that no, some, or all plantations established in an area in a specific year were planted with seedlings from rust-resistant seed sources. Unfortunately, in those years when some but not all plantings were planted with resistant sources, identification of individual resistant or susceptible plantations was not available. In statistical comparisons between resistant and susceptible plantings, mean rust incidence derives only from those years when all plantings were from known sources. Rust-resistant sources of loblolly pine were bulk collections of seed from wind-pollinated provenances from Livingston Parish, LA, and eastern Texas. Resistant sources of slash pine were bulk collections from rust-tested, wind-pollinated seed-orchard clones and a rust-rogued seed production area. Susceptible plantations were derived from unimproved (for rust) and sometimes unidentified sources and included seed-orchard sources.

RESULTS

Characterization of data. Frequency distributions of year planted, plantation size, age at inventory, and rust incidence for all (susceptible and resistant) plantations are shown in Figure 2. Relatively large numbers of slash pine plantations were established from 1961 to 1980; the number of loblolly plantations increased after 1973 (Fig. 2A). Plantation size ranged from 0.4 to 300 ha; 90% were 80 ha or less (Fig. 2B). Plantations were predominantly 5 yr old when inventoried; the range was 4.0–8.5 yr (Fig. 2C). Rust incidence in individual plantations ranged from 0 to 97.8% (Fig. 2D), and the number of plantations of both species decreased with increasing rust incidence.

Spatial patterns. Comparisons among geographic areas and between species are shown in Table 1, which summarizes the mean rust incidence for all susceptible plantations. Rust means ranged from 3.1 to 67.6% in slash pine and from 0 to 49.1% in loblolly pine. Although there were important differences among areas and between species within areas, the overall averages (24.9% for slash and 26.2% for loblolly) were similar. Generally, rust incidence was low in the eastern region on slash pine (areas 1, 2, 4,

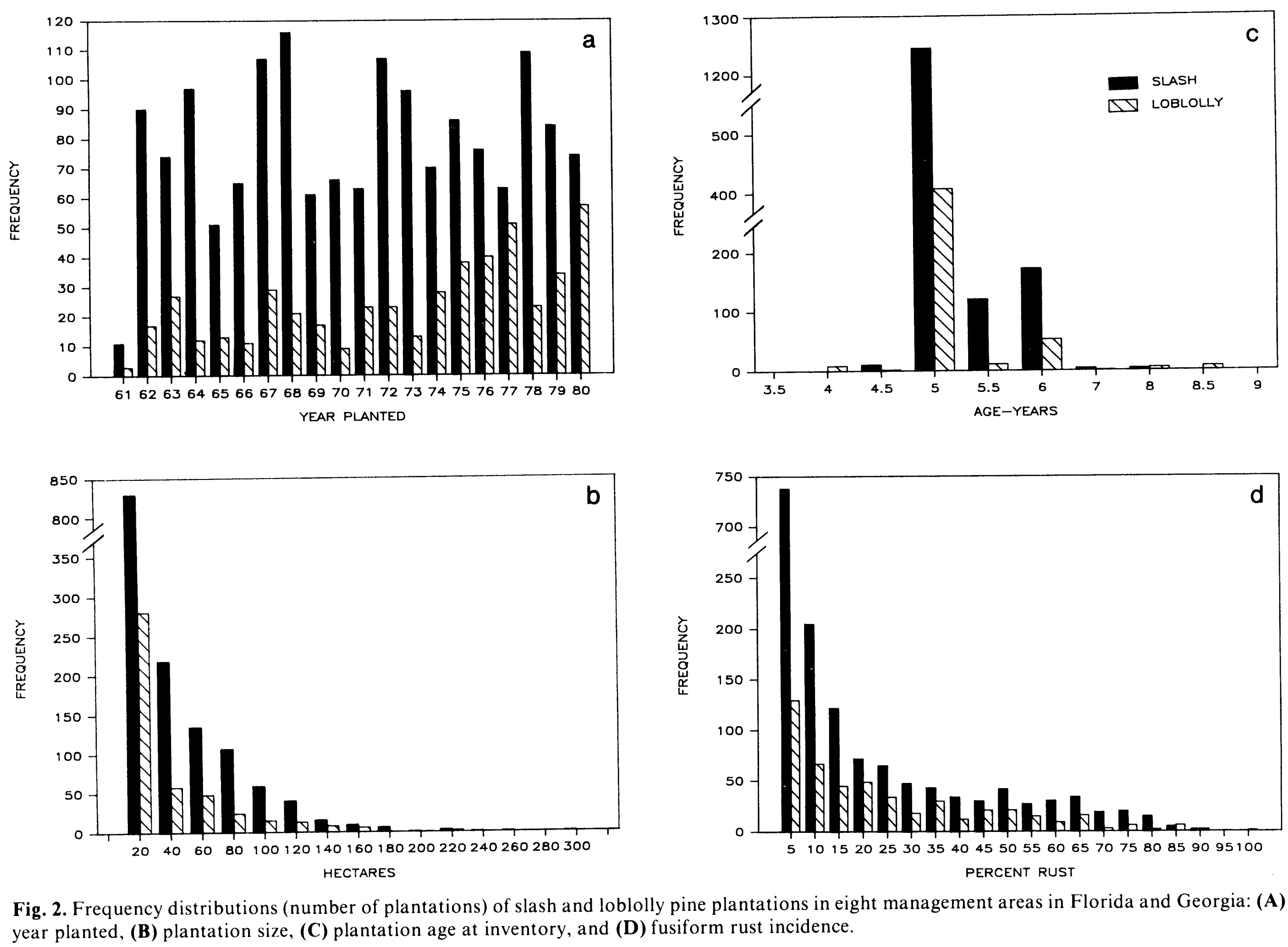

Fig. 2. Frequency distributions (number of plantations) of slash and loblolly pine plantations in eight management areas in Florida and Georgia: **(A)** year planted, **(B)** plantation size, **(C)** plantation age at inventory, and **(D)** fusiform rust incidence.

6, and 8) and on loblolly pine (areas 1, 4, and 8). Rust incidence increased in the western region (areas 3, 5, and 7) on both species. In areas 3, 5, and 7, rust incidence was high on both species but was significantly higher on slash than on loblolly pine. Rust incidence was significantly greater on loblolly than on slash pine in the southern portion of the range in northeastern Florida (areas 2 and 6), whereas rust incidence was greater on slash than on loblolly pine in the northern portion of the range in central Georgia (areas 3 and 7).

Temporal patterns. Figures 3 and 4 summarize the mean, minimum, and maximum percentage of rust as a function of year planted for all plantations (susceptible and resistant) in several exemplary areas.

Figure 3A–D depicts rust incidence in four slash pine areas with perennially low incidence. Mean incidence was 6.2, 7.7, 10.1, and 10.2% for areas 1, 2, 4, and 6, respectively. Within areas, mean rust incidence varied little among years. Only a few plantations showed high incidence. There were periods of increasing and decreasing incidence, but overall, these were not sustained. There were too few data to make similar observations on loblolly pine in areas of low rust incidence.

Figure 4A–D depicts high rust incidence in four areas; three contain a substantial number of plantations established with seedlings from rust-resistant sources after 1974–1975 (Table 2). Mean rust incidence was relatively high and varied greatly among years throughout the sample period in area 3 (slash pine) and prior to the establishment of resistant materials in area 5 (slash pine) and areas 3 and 7 (loblolly pine). Also, prior to the establishment of resistant plantations, variability of rust incidence among plantations was high, with very high or very low rust incidence in the same areas and in the same year.

Data from susceptible slash pine in high-rust-incidence areas 3 and 5

Table 1. Number of plantations, total area, and fusiform rust incidence for 5-yr-old susceptible slash (S) and loblolly (L) pine plantations planted between 1961 and 1980 in eight management areas in northern Florida and southern Georgia[w]

	Plantations					Fusiform rust incidence[x]		
	Number		Total area (ha)			Mean[y]		
Area	S	L	S	L		S	L	t^z
1	279	30	11,740	640		10.1 c	12.7 bc	1.2 ns
2	271	23	9,563	494		7.7 cd	28.1 ab	4.3 **
3	240	92	6,097	1,743		44.7 b	33.0 ab	4.9 *
4	286	7	11,769	212		10.2 c	16.7 bc	6.1 ns
5	88	14	2.458	310		49.1 b	35.6 ab	2.3 *
6	152	23	7,126	1,375		6.4 cd	34.2 ab	6.4 **
7	14	80	241	1,845		67.6 a	49.1 a	2.8 **
8	69	4	2,075	25		3.1 d	0 c	5.6 **
Total	1,399	273	51,069	6,644	Average	24.9	26.2	

[w] Planted by Container Corporation of America, Fernandina Beach, FL.
[x] Percentage of live trees with one or more branch and/or stem galls.
[y] Means within species among areas were compared with Tukey's studentized range test. Means with dissimilar letters are significantly different at $P = 0.05$.
[z] Means between species within areas were compared with the t statistic as appropriate for equal or unequal variances as determined by the F statistic; * = significant at $P = 0.05$ and ** = significant at $P = 0.01$; ns = not significant.

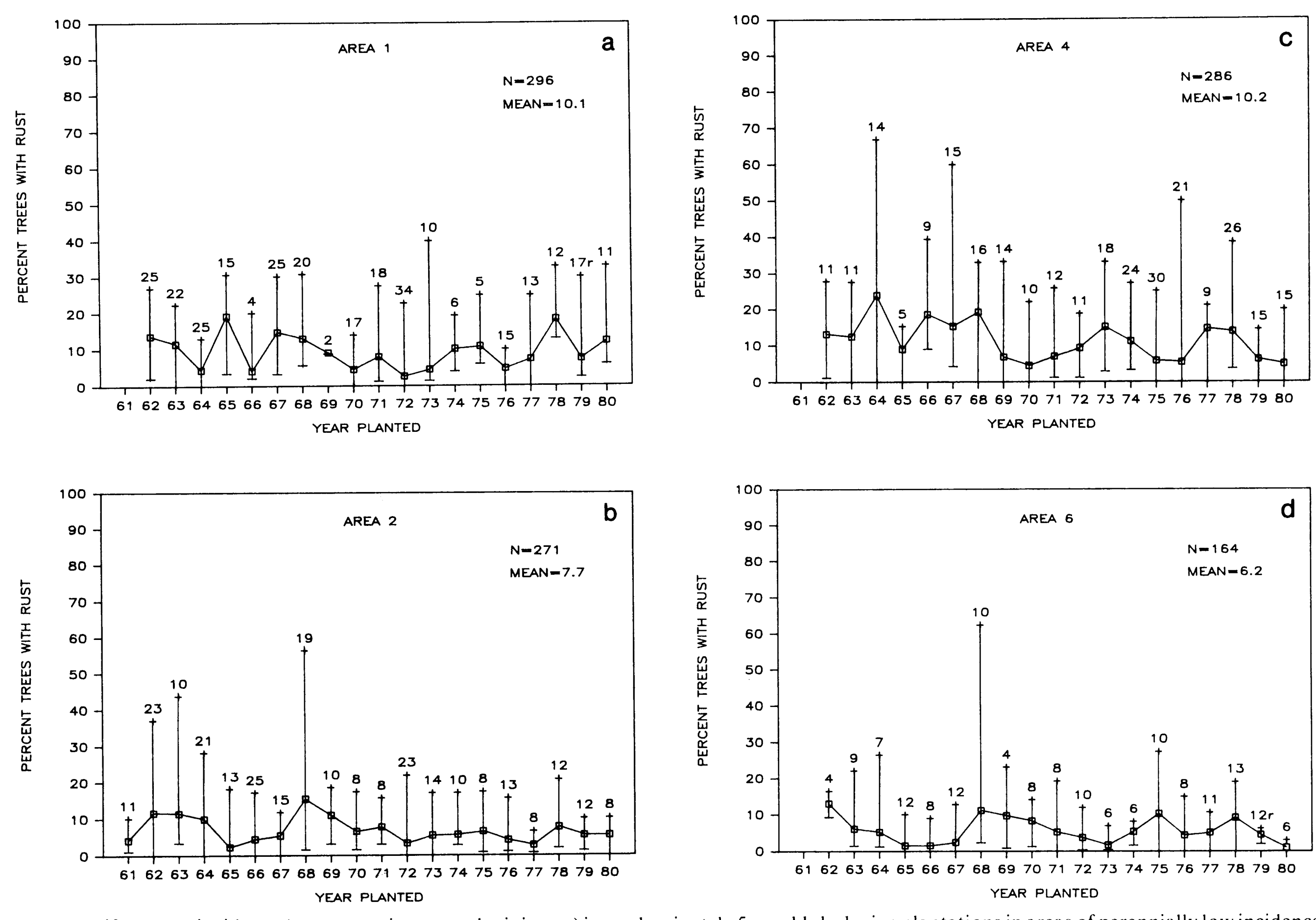

Fig. 3. Fusiform rust incidence (mean, maximum, and minimum) in predominately 5-yr-old slash pine plantations in areas of perennially low incidence in **(A, B, and D)** Florida and **(C)** Georgia. Above the range bars are the numbers of plantations; r = some plantations established with seedlings from rust-resistant seed sources.

Table 2. Comparison of fusiform rust incidence after 5 years in plantations[a] of susceptible and resistant slash and loblolly pines in Florida and Georgia

	Plantations					Fusiform rust incidence[b]		
Area	Species	Susceptibility[c]	Years planted	Number	Total area/(ha)	Mean	$S\bar{x}$[d]	t[e]
1	Loblolly	S	1962–1964, 1967, 1969, 1970, 1974, 1976, 1977, 1979	30	640	12.7	11.2	
		R	1980	4	231	3.0	0.0	4.78**
3	Loblolly	S	1962–1971, 1976	92	1,743	33.0	17.6	
		R	1974, 1975, 1977–1980	59	2,826	13.5	9.9	8.68**
5	Slash	S	1963–1974	88	2,458	49.1	21.1	
		R	1976, 1977, 1979, 1980	28	902	26.5[f]	15.8	5.20**
	Loblolly	S	1963, 1972–1974	14	310	35.6	18.4	
		R	1975–1977, 1979, 1980	30	689	10.2[f]	6.4	5.04**
6	Loblolly	S	1963–1968, 1970, 1973, 1974, 1976	23	1,375	34.2	20.7	
		R	1977, 1978	8	291	8.4	7.2	5.14**
7	Loblolly	S	1967–1973	80	1,845	49.1	23.1	
		R	1974–1977 1979, 1980	81	5,083	11.7	8.4	13.60**
Total susceptible				327	8,370			
Total resistant				210	10,018			

[a] Container Corporation of America, Fernandina Beach, FL.
[b] Percentage of live trees with one or more branch and/or stem galls.
[c] S = rust-susceptible; R = rust-resistant; resistant slash pine seed origins were wind-pollinated seed orchard and seed production areas; resistant loblolly pine seed origins were provenances from eastern Texas and Livingston Parish, LA.
[d] $S\bar{x}$ = standard deviation of the mean.
[e] Susceptible and resistant means within areas were compared with the t statistic as appropriate for equal or unequal variance as determined by an F statistic; ** = significant at $P = 0.01$.
[f] Resistant slash and loblolly means for area 5 were compared with the t statistic ($t = 5.10$**).

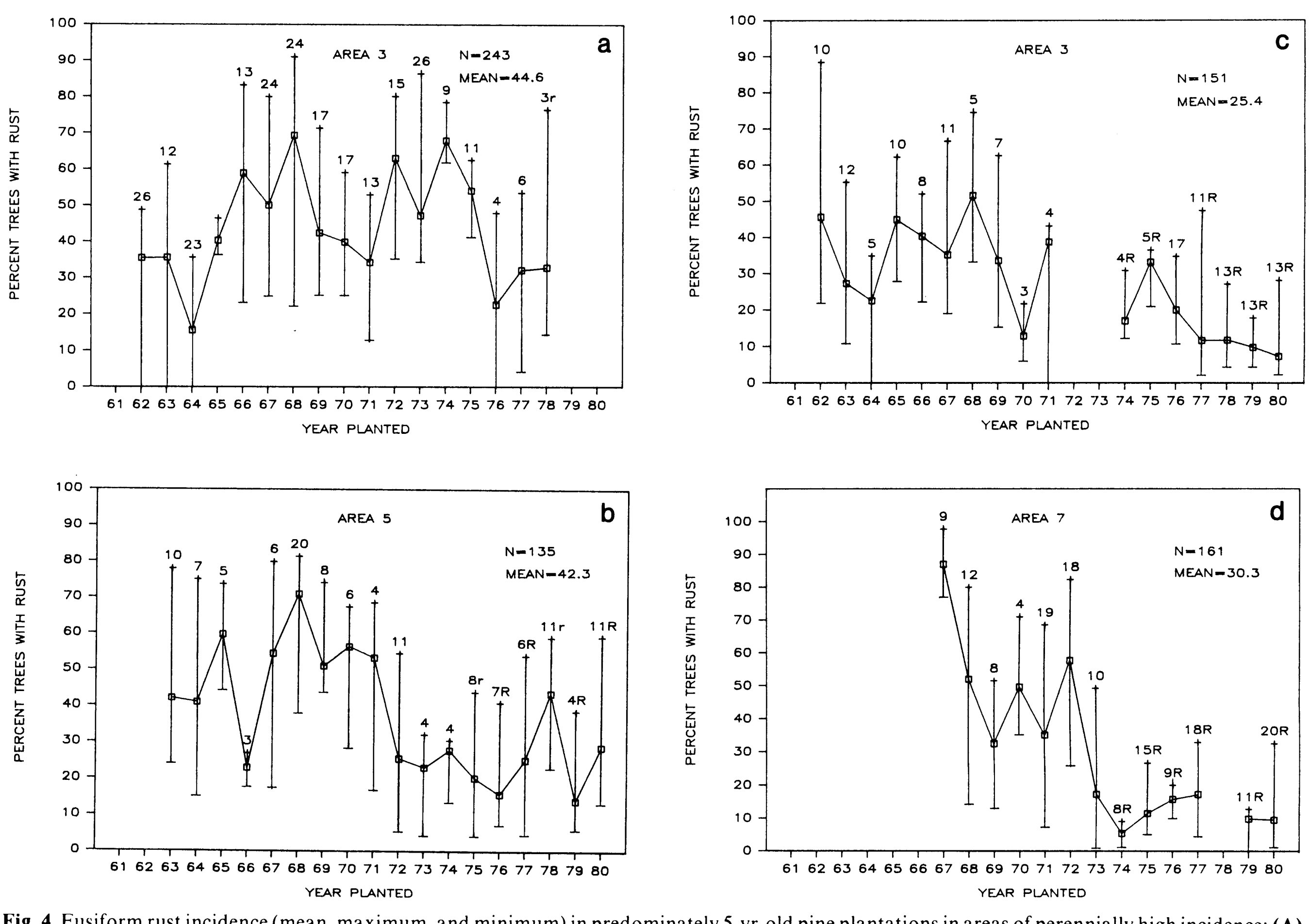

Fig. 4. Fusiform rust incidence (mean, maximum, and minimum) in predominately 5-yr-old pine plantations in areas of perennially high incidence: **(A)** slash pine in Georgia, **(B)** slash pine in Florida, and **(C and D)** loblolly pine in Georgia. Above the range bars are the numbers of plantations; R = all plantations, r = some plantations established with seedlings from rust-resistant sources.

(1963–1974), prior to the establishment of resistance, indicate periods of increasing and decreasing epidemics. Overall, these data from areas with high rust incidence do not provide conclusive evidence for a sustained increasing or decreasing epidemic. Although these trends appear similar for susceptible loblolly pine plantations, there are fewer data on which to judge.

Effect of resistance on rust epidemic. The impact of rust-resistant plantations established after 1974–1975 is summarized in Table 2 and Figures 4 and 5. Although the effect of resistance is confounded with year planted, as seen in Figure 4, comparisons between resistant and susceptible plantations are possible because in certain years and certain areas, only resistant or only susceptible plantations were established. Because a specific source of resistance was not identified, comparisons among resistant sources are not possible.

Table 2 compares rust incidence in 210 plantations established with seedlings from rust-resistant seed sources and in 327 plantations established with seedlings from susceptible seed sources. In loblolly pine in areas with high rust incidence, rust decreased from 33.0 to 13.5% (area 3), from 35.6 to 10.2% (area 5), from 34.2 to 8.4% (area 6), and from 49.1 to 11.7% (area 7). Similarly, in slash pine (area 5), mean rust incidence was reduced from 49.1 to 26.5%. Even in a location with low rust incidence (area 1), where a few plantations of loblolly pine were established with resistant sources, rust incidence was reduced from 12.7 to 3.0%. Frequency distributions of percentage of rust in susceptible and resistant populations (Fig. 5A–D) show that both the mean and range of rust incidence were greatly reduced in plantations established with seedlings from resistant sources.

DISCUSSION

Although confounded with management practices in some cases, these data from 1,882 pine plantations provide a representative and credible basis on which to delineate temporal and spatial trends in rust incidence for a 20-yr period within populations of plantations in a portion of the southeastern United States. Rust incidence data are the percentage of trees with galls after exposure to rust for five growing seasons. Therefore, the relations between annually occurring independent variables and rust incidence cannot be examined. For example, the effect of weather in one year is not discernible because rust incidence was related to the cumulative influence of weather during five seasons. Also, the role of nursery infection (outplanting infected trees) cannot be assessed.

Data from plantations established with seedlings from rust-susceptible sources showed that areas with low and high rust incidence exist. This conclusion is better supported for slash pine since data are abundant. In areas with low rust incidence, occasional plantations show relatively high incidence, but incidence generally remains low with little variations among and within years. Apparently, these are areas with perennial low incidence, and forest management practices have not changed the incidence of rust in these areas during the period represented by these data. Precautions should be taken to maintain low rust incidence in such areas, e.g., by avoiding the planting of rust-infected seedlings and silvicultural practices that favor the increase of susceptible oak or inoculum.

In areas with high rust incidence, large variation in mean incidence existed among and within years. Periods of increasing incidence, as reported by Schmidt et al (16) and Griggs and Schmidt (6), occurred as did periods of decreasing rust incidence. In these areas, rust incidence generally remained high, although both years and individual plantations with relatively low rust incidence occurred. Apparently, these areas have perennially high rust incidence and should be managed accordingly

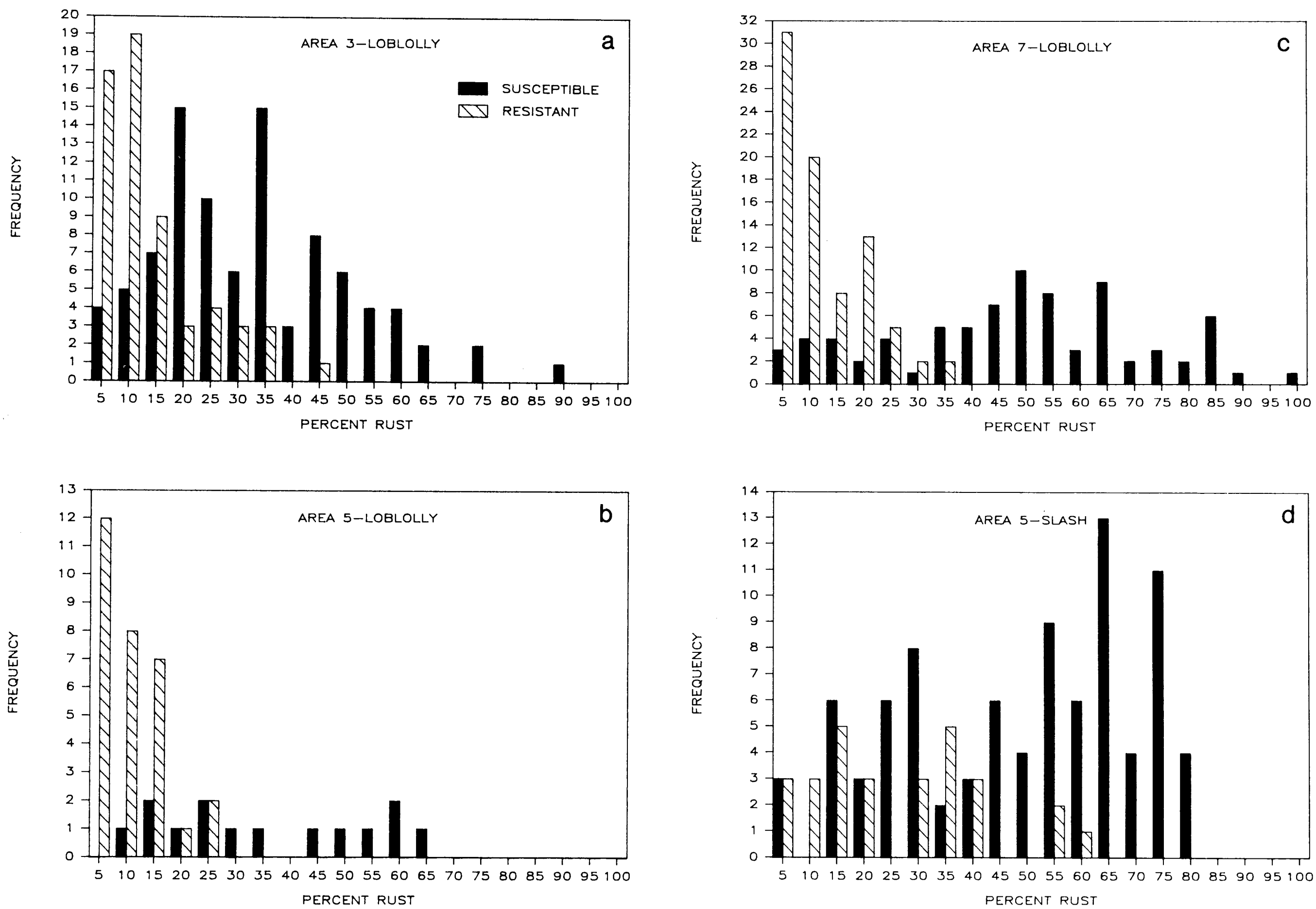

Fig. 5. Frequency distribution (number of plantations) of rust incidence for populations of loblolly or slash pine established in **(A and C)** Georgia and **(B and D)** Florida with seedlings from rust-resistant and susceptible seed sources.

(2,18).

With respect to geographic patterns, our data compare favorably with previous data (12,22). In general, rust incidence increased to the west and north within the region. Comparing species, loblolly pine was more frequently diseased in the southern portion of the range and slash pine was more frequently diseased in the northern portion. The reason for this differential performance is unknown but could be related to pathogenic variability of the rust fungus, pine phenology, or other factors. Rust incidence was greater on slash than on loblolly pine in areas of high rust incidence for both species, regardless of geographic location.

As suggested in a preliminary report (17), these data provide substantial evidence that operational plantings of resistant slash and loblolly pines can significantly suppress the rust epidemic in areas of high rust incidence. The evidence is consistent with many reports from artificial inoculations and field progeny tests (5,19), but until now, comprehensive operational data were unavailable. Unfortunately, rust incidence in resistant plantations and year of planting are confounded. Thus it is possible that long-term trends for decreased rust incidence of unknown cause, e.g., improved rust control in nurseries, coincided with years when rust resistant seedlings were planted. In fact, in some areas, the temporal trends suggest that average rust incidence decreased prior to the planting of resistant pines. This reduction may have occurred if resistant plantations were established, but not identified, or if the 5-yr means for susceptible plantations reflected the effect of inoculum reduction in adjacent resistant plantations. Neither hypothesis could be verified.

Recent progeny test data (11) indicate that plantations representing the Livingston Parish resistant seed source were severely diseased in the area with high rust incidence in Madison County, Florida (area 5). Neither the cause nor the long-term consequences of this increased incidence are known. Nonetheless, consideration should be given to management practices that enhance inoculum reduction in concert with the use of resistant seed sources in areas with high rust incidence (15), especially because results from artificial inoculations (10,21) indicate that the percentage of seedlings with rust, including those from resistant seed sources, increases with increased amounts of inoculum.

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