PHENOTYPIC SELECTION FOR FUSIFORM RUST RESISTANCE

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Abstract.--Open-pollinated progenies from fusiform-rust-free slash pines selected in a 94-percent infected plantation in Mississippi were all more resistant to artificial inoculation than seedlings from a bulk seed lot. Only one rust-infected parent transmitted any appreciable degree of resistance to its progeny.

Phenotypic selection in heavily infected stands seems an efficient method for finding sources of resistance. Variability among progenies of rust-free parents was sufficient to permit additional gain from culling after progeny testing.

Fusiform rust, caused by Cronartium fusiform Hedgc. and Hunt ex Cumm., remains a serious disease of loblolly (Pinus taeda L.) and slash pines (P. elliottii Engelm.). Most tree-improvement programs in the Southeast attempt to increase resistance to this disease by avoiding the selection of rust-infected trees. The efficiency of this practice depends upon the amount of variation in resistance available to breeders and the degree to which a rust-free phenotype reflects the presence of heritable resistance.

Substantial variation in resistance under field conditions has been observed in loblolly (Barber 1966) and slash pines (Barber 1961). Variation in resistance to infection after artificial inoculation has also been reported for both species (Davis and Goggans 1968; Jewell and Mallett 1967). On the other hand, the selection and breeding of plus trees free of rust has often failed to appreciably increase resistance (North Carolina State University 1970; LaFarge and Kraus 1967; Goddard and Strickland 1970). Apparently, a more intensive method of selection is required.

The probability of finding new sources of resistance might be enhanced by selecting in heavily damaged stands. As such areas usually contain few phenotypes desirable in terms of other traits, the advantages of this approach have not been examined thoroughly. It was attempted with some success in a severely infected stand of slash pine in Mississippi, however (Neelands and Jewell 1961). Open-pollinated progenies from a sample of rust-free selections were consistently less susceptible to artificial inoculation than bulk seedlings. This paper reports the results of more comprehensive tests on similar progenies.

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MATERIALS ANT METHODS

While studying the influence of prescribed burning on rust incidence, Dr. P. V. Siggers established a series of four study plots near Laurel, Mississippi. The old field site had been planted with South Georgia-North Florida slash pines at a 6- by 6-foot spacing in 1941. When established in 1946, each plot contained 110 living trees of which 85.4 percent were galled (table 1). Though the incidence of rust varied somewhat from plot to plot, galled trees were uniformly distributed within plots.

Table 1.--Severity of fusiform rust infection on four slash pine selection plots

Plot	Area	Trees	1946		1954		
			Proportion 2/ per tree	galled	Galls per tree	Proportion 3/ rust-killed	Proportion galled
	Acre	Number	Number	Percent	Number	Percent	Percent
TI-2C	0.158	110	4.4	91.8	7.1	47.3	96.4
TH-3	.153	110	3.6	78.2	7.1	24.3	92.5
TH-4	.167	110	4.6	87.3	4.8	28.4	94.5
TH-3,4C	.175	110	3.9	84.5	5.1	44.0	94.5
Mean	.163		4.1	85.4	6.0	36.1	94.5

Galls per living tree detected by observation from the ground.

2/ Living galled trees and rust-killed trees / original trees less those killed by causes other than rust.

3/ Trees rust-killed original trees less those killed by causes other than rust.

The percentage of trees galled in 1946 probably underestimates the actual incidence of rust. Some galled trees no doubt died and disappeared from the plots and a few may have shed branch galls before the first observation. It seems unlikely, however, that the latter would have remained rust-free. Records taken either annually or biennially from 1946 through 1954 show that both the number of galled trees and the number of galls per tree steadily increased (table 1). Of the trees living in 1954, 91.4 percent were galled. Expressed on a cumulative basis, 94.5 percent of the trees present in 1946 were considered susceptible.

Rust-free phenotypes were selected in 1954. Trees not preserved for study, including several of the least attractive rust-free selections, were removed to provide growing space. The 29 selections currently available include: 16 trees known to have remained rust-free since 1946; 1 rust-free check chosen only on the basis of its appearance in 1954; and 12 rust-infected trees.

Sufficient open-pollinated seed from 12 rust-free selections, five rust-infected selections, and the rust-free check were available for testing in 1968. Included for comparison were open-pollinated seedlings from a resistant standard, 8-7; a susceptible standard, 18-40; and a bulk lot representative of seedlings currently used for reforestation on Mississippi National Forests. Performance of open-pollinated progenies from the resistant and susceptible standards has been verified in the field and under artificial conditions (Dinus 1969). Thirty-day-old seedlings of uniform size were exposed to the pathogen for 72 hours via the artificial inoculation technique developed by Jewell (1960). Row plots of nine seedlings per family were randomly assigned to nursery flats arranged in a randomized block design. All families were represented in at least three replications, but some in as many as seven. After inoculation, seedlings were transplanted to nursery beds in the same design.

Three hundred days after inoculation, the seedlings were lifted and the number having at least one gall was determined for each family. Mortality averaged only 4.6 percent and was uniformly distributed among blocks and families. Variation among families in terms of the proportion of galled seedlings was evaluated with the Chi Square test for independence in r X 2 tables (Steel and Torrie 1960, pp. 370-371). Variation among the several groups of selections was similarly evaluated. Individual Chi Square tests were used to compare the ratios of galled to rust-free seedlings in specific families to those observed in the standard and bulk lots. Tifferences resulting in Chi Square values larger than that at the 0.05 level of probability were considered significant.

RESULTS

Extensive variation in resistance to fusiform rust was found among families. The incidence of rust averaged 76.6 percent and ranged from a low of 43.5 percent for progeny from a rust-free parent to a high of 91.7 percent for the bulk lot (table 2). Considered as a group, offspring from rust-free parents were less frequently galled than those from rust-infected parents and those from the bulk lot (72.4 versus 86.0 and 91.7 percent, respectively). Progenies from rust-infected parents were also less diseased, on the average, than bulk seedlings. Individual Chi Square tests indicated, however, that the latter difference was largely due to the performance of offspring from one rust-infected selection (J-1-2). The proportion of galled seedlings observed among offspring of this selection was 12.9 percentage points less than the average for its group and approximated that for progenies from rust-free parents. Hence, only one of the five rust-infected selections transmitted any appreciable degree of resistance to its progeny.

Table 2.--Proportions of galled seedlings in open-pollinated slash pine progenies from rust-free selections, rust-infected selections, and four check lots.

Parents: Phenotype and code		Progeny Performance: Alive	Galled	Galled
		Number	Number	Percent
Rust-free:	J-1-3	23	10	43.5
	J-1-4	37	23	62.2
	W-1-20	53	33	62.3
Total, best three rust-free:		113	66	58.4
	W-1-22	60	41	68.3
	W-1-6	60	42	70.0
	W-1-25	63	46	73.0
	W-1-14	71	52	73.2
	W-1-3	44	33	75.0
	W-1-2	52	39	75.0
	W-1-7	45	36	80.0
	W-1-5	65	53	81.5
	W-1-19	62	52	83.9
Total, all rust-free:		635	440	72.4
Rust-infected:	J-1-2	26	19	73.1
	W-1-24	69	59	85.5
	W-1-4	35	30	85.7
	W-1-21	37	33	89.2
	W-1-17	61	55	90.2
Total, rust-infected:		228	196	86.0
Checks:				
Rust-free	W-1-8-1-/	71	62	87.3
Susceptible	18-40	43	36	83.7
Resistant	8-7	70	39	55.7
Bulk		60	55	91.7
Totals		1107	848	76.6

Data for W-1-8 were excluded from gain calculations as it was chosen only on the basis of its appearance in 1954.

Individual Chi Square analyses indicated that fewer seedlings from every family of rust-free parents were galled than from the bulk lot. If the performance of the bulk seedlings estimates the level of resistance in Mississippi slash pines, the degree of improvement resulting from phenotypic selection under the conditions described equals the difference between the mean for offspring from rust-free parents and that for bulk seedlings. In terms of the proportion galled, the reduction amounts to 19.3 percentage points. Stated as a proportion of the bulk mean, the improvement is 21.0 percent.

Had selection been based only on appearance in 1954, two more of the trees tested would have been considered rust-free. The inclusion of these (W-1-8 and W-1-24) as rust-free parents increased the mean proportion of galled seedlings for this group from 72.4 to 75.0 percent. Offspring from these two parents were as frequently galled as those from the susceptible standard and most of the rust-infected parents (table 2). Nevertheless, the absence of early records would not have greatly decreased the effectiveness of phenotypic selections in this 91.4-percent-galled stand.

Variation in resistance among progenies of rust-free parents was also significant. Since some of this variability is presumably heritable, a further reduction in the average incidence of rust can be expected from selection on the basis of progeny testing. Each of the families from rust-free parents had fewer galled seedlings than the bulk lot. Also, more than half of these families (the best seven) had less rust than offspring of the susceptible standard. Hence, selection on the basis of comparison to the bulk lot or the susceptible standard seemed inefficient. Rather than setting an arbitrary limit in terms of percent galled or, simply, a certain number of parents, the performance of each family was compared to that of the progeny from the resistant standard. Families judged to have an incidence of rust greater than the latter on the basis of individual Chi Square tests were not considered further. Three of the rust-free parents (25 percent) produced progenies which did not differ from the resistant standard. The average proportion of galled seedlings in families from these selections (J-1-3, J-1-4, and W-1-20) was 58.4 percent, 14.0 percentage points less than the mean for all families from rust-free parents (table 2). This reduction is only slightly less than that resulting from phenotypic selection (19.3 percentage points). The total reduction obtained from phenotypic selection combined with elimination on the basis of progeny testing then amounts to 33.3 percentage points. Stated as a percent of the bulk mean, the improvement is 36.3 percent.

TISCUSSION

The open-pollinated progenies of rust-free parents tested in this study were more resistant to artificial inoculation than those from rust-infected parents and, most important, than seedlings representative of the general population. These results agree in general with those from previous studies in which both slash and loblolly pines were tested under artificial (Jewell and Mallett 1967; Kinloch and Kelman 1965) or field conditions (Dinus 1969; Kinloch and Stonecypher 1969). Most previous studies have shown, however,

that progenies from rust-free selections are usually, but not always, more resistant than the other types. Hence, selection of rust-free parents has been said to result in moderate gain, and culling based on subsequent progeny tests is considered essential for maximizing gain (Blair 1970). A similar conclusion can be drawn from the present data. Phenotypic selection resulted in progeny with an average incidence of rust 19.3 percentage points less than that in bulk seedlings. Had three-fourths of the rust-free parents been culled on the basis of progeny testing, the amount of rust in progenies from the remaining parents would have been reduced by an additional 14.0 percentage points.

The improvement resulting from phenotypic selection is especially encouraging in that these were open-pollinated progenies tested under conditions designed to enhance the probability of infection. Most pollen can be assumed to have come from the surrounding, large area of unselected trees. Even so, each family was less susceptible than seedlings typical of those currently used for reforestation in Mississippi. These results suggest that phenotypic selection can be a reliable method for locating new sources of resistance.

For phenotypic selection to be effective, critical attention must be given to stand and individual-tree characteristics. For example, only marginal differences in resistance to artificial inoculation were found among progenies of rust-free and rust-infected loblolly pines (Kinloch and Kelman 1965). The parents were from a 35-year-old stand in which only 62 percent of the trees were galled. In another study, the proportion of galled seedlings in progenies from controlled matings among rust-free parents varied from 9 to 99 percent (Jewell and Mallett 1967). These trees were from a 75-percent-galled stand of slash pine. In neither case were individual tree histories known. Under such circumstances, the phenotype cannot be expected to and did not provide a reliable estimate of the genotype.

Rust incidence averaged 91.4 percent when the present selections were chosen. Individual tree records, available except for the first 5 years, indicated that 94.5 percent of the trees were galled at one time or another. Even under these circumstances, considerable variation was found among progenies. Only 25 percent of the rust-free parents produced offspring as resistant as those from the best standard. Should a similar proportion of the untested selections prove as acceptable, a total of four outstanding selections will have been found. This total represents only 0.9 percent of the trees present in 1946 and approximately 0.5 percent of those originally planted. Of the rust-free parents tested, however, all produced progenies less susceptible than bulk seedlings. All 16 selections available could therefore be useful. Ignoring the several that died before or after selection, these comprise 3.6 percent of the trees present in 1946 or about 2.0 percent of the original stand. Hence, trees that have escaped exposure, that have undetectable galls, or that have shed branch galls via natural pruning will be quite frequent where rust is less severe.

Phenotypic selection then can only be as effective as reported here when rust incidence is as great at the time of selection as in this instance or when records are available on the performance of individual trees during past epidemics. Selection in plantations subjected to more moderate, but uniform exposure over a period of years would probably yield less, but nevertheless substantial, improvement. Existing progeny test plantations in hazardous areas also seem logical places to seek new sources of resistance via phenotypic selection.

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