Predictions of Expected Gains in Resistance to Fusiform Rust in Loblolly Pine

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Although properly timed fungicidal sprays are effective in control of fusiform rust in forest nurseries, no economical chemical or silvicultural method of control has been developed to control the disease in plantations. The most promising mode of defense against future losses to this disease is the selection, breeding, and wide-spread distribution of genetically resistant strains of loblolly and slash pines.

Since the causal organism of fusiforme rust (*Cronartium fusiforme* Hedgc. and Hunt ex cumin.) and both loblolly and slash pine (*Pinus taeda* L. and P. *elliottii* Engelm. var. *elliottii*) are indigenous to the same region, it is likely that genetically controlled resistance to rust has evolved in both species of trees. A number of studies have shown that variability in resistance does exist in both loblolly (Kinloch and Stonecypher, 1969; Woessner, 1965; Wells and Wakeley, 1966) and slash pine (Barber, 1964; Goddard and Arnold, 1966; Gansel, et al., 1971). The utilization of this variability depends upon: (i) the degree of additive genetic control of resistance, (ii) the stability of resistance over a range of environments, (iii) the genetic correlations between resistance to rust and other economically important traits, and (iv) the type of breeding program undertaken to provide rust-resistance.

Since genetically controlled resistance to fusiform rust is of major economic value in the Southeast, most tree improvement programs in this region include rust-resistance as an important trait. Accurate estimates of the genetic parameters that describe rust-resistance are required as the basis for the integration of this trait into a breeding program. The present investigation was designed (i) to estimate the degree of genetic control of variability in rust-resistance in a natural stand of loblolly pine and (ii) to predict the gain in resistance that can be expected from the methods of selection commonly used in tree breeding programs.

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MATERIALS AND METHODS

The population of plants used in this investigation is found in the Loblolly Pine Heritability Study carried out cooperatively by International Paper Company and North Carolina State University. The study is located in Decatur County in Southwest Georgia on International Paper Company's Southlands Experiment Forest. Detailed description of the parent trees, mating design, planting design, and outplanting sites was given by Stonecypher (1966). Further description of the study with respect to fusiform rust was provided by Kinloch and Stonecypher (1969); therefore, only the following brief summary will be included in this paper.

Parent Trees

The loblolly pine parent trees were selected at random in a mixed stand of native loblolly with intermixed shortleaf (P. *echinata* Mill.) and a few longleaf pines (P. *palustris* Mill.). Even though located in the Coastal Plain, the trees are growing on a site which has soil and vegetation typical of the southern Piedmont. Much of the area was under cultivation until the 1920's and early 30's. The stand from which the parent trees were chosen originated from seeds from trees surrounding abandoned cultivated fields. The parent trees averaged thirty-five years of age when the study was initiated in 1959. With aid of binoculars, fusiform rust galls were counted on the branches and stem of each tree.

Controlled matings were made among the parent trees according to Comstock and Robinson's (1948, 1952) Design I. Sixty-five male groups were randomly chosen from the parent trees. Each group consisted of a pollen parent (male) that was mated to each of four nearby seed (female) parents. Control-pollinations within male groups were carried out over a three-year period (from 1959 to 1961).

Nursery Treatment and Field Planting Design

Seeds from the controlled matings were collected and planted in nursery beds at Southlands Experiment Forest in 1962-64. Fusiform rust infection was not controlled in the nursery, therefore, some seedlings that were infected while in the nursery were planted in the field. Otherwise, the seedlings were grown using normal nursery procedures.

The seedlings from each control-pollinated family were planted with 12 trees in each of six row-plots. The six plots were distributed in three replications at each of two locations. Field planting was carried out over a three year period beginning in January 1963; each year's planting consisted of a different group of families. The trees were established at an 8' x 8' spacing. Because of the large number of families involved, male groups were confounded in sets to reduce the size of each replication. Since not all matings produced enough viable seeds, two of the three plantings contained unequal numbers of male groups and females per male group.

Planting Sites

Southlands Experiment Forest is divided by the Flint River into two parts which are very different. However, the sites in which the control-pollinated portion of the study were planted differed mainly in previous cultural history. The site east of the river (east planting) supported a sparse stand of loblolly and shortleaf pine which was removed and the site prepared by treatment with a rolling chopper and disk. This site **is less** uniform than the planting site west of the river. During extended periods of wet weather, water stands in the low areas. These areas were avoided during planting so that certain sets were not contiguous within some replications.

Most of the area west of the river (west planting) had been cultivated to peanuts immediately prior to planting, but one replication of the 1963 planting had lain fallow several years prior to 1963. The difference in amount of rust in these replications is discussed in detail by Kinloch and Stonecypher (1969).

Measurement of Rust Susceptibility

In 1967 and again in 1968 each tree in the 1963 and 1964 plantings was examined for fusiform rust galls. The amount of rust was measured by three indices of susceptibility: (i) the number of rust galls per tree, (ii) "c-score," and (iii) the percentage of trees infected. Part of the 1968 measurement was made during the early spring when the rust galls were sporulating and thus easily visible. This measurement was thus more reliable and was used in the following analyses.

Separate records were made of the number of stem galls, branch galls considered likely to grow into the stem, and branch galls considered unlikely to grow into the stem before the branch died. Only the total number of galls per tree was used for the following analyses.

"C-score" is an index devised by personnel at Southlands to reflect the economic and biological impact as well as the incidence of disease. Numerical values were assigned as follows:

1 no galls

2 = branch galls

3 severe branch galls

4 - one stem gall

5 - two or more stem galls

6 - one stem gall and branch galls (4 and 2)

7 = one stem gall and severe branch galls (4 and 3)

8 - two or more stem galls and branch galls (5 and 2)

9 - two or more stem galls and severe branch galls (5 and 3)

10 = dead because of rust infection or with multiple stems as a result of severe rust infection

The last score (No. 10) also includes all trees which had rust at an earlier date but were missing at the time of the 1968 measurement. The scorer was required to decide subjectively whether or not branch galls were severe (scores 2 or 3 and 8 or 9) and whether the tree had multiple stems because of rust infection.

The percentage of infected trees per plot was calculated based on the c-score dates i.e. all trees with a score greater than one were considered infected. It also includes all trees having been recorded as diseased in earlier measurements even though the tree may have been missing or evidence of rust infection may no longer have been present at the 1968 measurement. The raw percent data were transformed to arcsins of the square root of the percentage of infected trees. The transformed data were used for all analyses except gain computations.

Analysis

The form of analysis of variance, tests of significance and estimates of components of variance and their standard errors, are described in detail elsewhere (Blair, 1970). Estimates of heritability (on an individual tree basis) were computed for the c-score and number of galls per tree indices utilizing components of variance as estimates of the genetic parameters. For the percent infected index, Robertson and Lerner's (1949) method for all-or-none traits was employed.

Predicted gains were computed from the estimated genetic parameters using three systems of selection. The first was based on the mass selection of rust-free trees. Resistance to rust as measured by the percentage of trees infected is considered a threshold trait in the method presented by Dempster and Lerner (1950) and progress in achieving resistance is obtained by selecting all or a random sample of rust-free parent trees and using them to produce the next generation.

Gains in resistance to rust from mass selection as measured by the number of galls per tree and c-score indices were computed by conventional gain prediction formulae (see Namkoong et al., 1966). Again, only rust-free parent trees are selected and used to produce the next generation.

The second system of selection involved mass selection combined with progeny testing. Mass selection is carried out as above i.e., rust-free male parent trees are selected. The half-sib progeny from each of the selected trees is then used as **a** basis for further selection. Approximately half of the parent trees were culled on this basis.

If mass selection and mass selection combined with progeny testing produce gains in resistance in the first generation of progeny from selected trees, continued selection among first generation progeny -- both among and within families -- should produce increased resistance in the second generation (Stonecypher, 1969). In this study each male parent was mated to a series of female parents producing full-sib families. Consequently, gain predictions were based on selection among and within full-sib families. Since recombination has occurred in production of the first generation progeny, the genetic variation was assumed to be reconstituted. The parameters estimated for the first generation were then used in the prediction formula (modified from Namkoong et al., op. cit.) to estimate the **gains in** resistance that might be expected when using progeny tests as a source of second generation selections.

RESULTS AND DISCUSSION

The results of this study support the following conclusions:

1. Substantial variation in resistance to fusiform rust in loblolly pine as reported in earlier studies are confirmed. In the population used in this investigation, resistance to fusiform rust in loblolly pine is under moderate to weak genetic control.

2. Selection of uninfected parent trees from natural stands will yield an important initial gain (approximately fifteen percent of the mean) in resistance to fusiform rust. Selection based on subsequent progeny testing will yield an additional gain of similar magnitude (between fifteen and twenty percent of the mean). It is essential to combine mass selection and progeny testing if maximum progress is to be obtained in the first generation of selection.

3. Family plus within-family selection will result in substantial improvement in rust-resistance and is recommended for second generation selection.

Variation in Resistance to Rust

Great variation in resistance to fusiform rust was observed by all indices of susceptibility on both planting sites and in both years of planting (Table 1). Differences between the most resistant and most susceptible families (8 percent infected vs. 91 percent infected) were greater than differences among provenances in any of the planting locations of the Southwide Pine Seed Source Study (Wells and Wakeley, 1966). This comparison emphasizes the importance of within-stand variation in the search for rust-resistance.

Table 1. Variation in amount of fusiform rust measured by the three indices of susceptibility. The data given are means and ranges for the families included in each year of planting

Year of Planting	West Location Mean	West Location Range	East Location Mean	East Location Range	Locations Combined Mean	Locations Combined Range
		Number of Galls Per Tree				
1963	2.7	0.3-9.0	0.8	0.0-3.4	1.7	0.2-6.2
1964	1.6	0.3-3.3	0.5	0.0-1.4	1.0	0.3-2.3
	2.1		0.6		1.4	
		C -Score				
1963	4.0	1.2-7.4	2.0	1.1-4.7	3.0	1.2-6.0
1964	2.8	1.4-5.3	1.6	1.0-2.9	2.2	1.3-4.0
	3.4		1.8		2.6	
		Percent of Trees Infected				
1963	66	8-100	34	5-58	50	8-91
1964	57	13-90	25	0-68		13-79
	62		30		46	

The degree of additive genetic control in rust-resistance ranged from moderate to weak, depending on the index and year of planting being considered (Table 2). Heritabilities on an individual tree basis were computed for the number of galls per tree and c-score using components of variance and for the percentage of trees infected using Robertson and Lerner's (1949) approach.

The heritability estimates for the combined locations for the number of galls per tree, c-score, and percentage of trees infected were 0.29, 0.22, and 0.20 respectively for the 1963 planting and 0.09, 0.04, and 0.12 for the 1964 planting. These estimates are remarkably consistent among indices, particularly considering the different methods of computation. The heritability estimates for the percentage of trees infected also agree very well with the 0.199 estimate reported by Goddard and Arnold (1966) for slash pine.

Table 2. Estimates of heritability (individual tree basis) and standard errors for resistance to fusiform rust. Shown for two planting years and three indices of susceptibility

	INDEX		
Year of Plantin	No. Galls	C-Score	
1963	.29 ± .13	.22 + .09	.20 + .05
1964	.09 + .06	.04 + .03	.12 + .03

It is important to note that estimates obtained for the percent infected index include a certain portion of non-additive variance (Dempster and Lerner, 1950) so is not strictly comparable to the gall count and c-score. The comparison of these estimates in the 1963 planting suggests that genetic control is strictly additive while the 1964 planting would appear to have some non-additive genetic variance. The comparisons of heritabilities in this manner are somewhat tenuous, however, in view of the large standard errors of estimates of the components of variance used in their estimation.

The heritability estimates based on an individual tree are not unexpectedly low and are encouraging in the framework of existing selection programs.

Predictions of Gain

Gain from the Selection and Mating of Rust-Free Individuals

In the absence of better information, the logical procedure for breeding for rust-resistance is the selection and mating of rust-free trees. In the study reported here, a grouping of progenies by the mating type of their parents (Table 3) shows that mating rust-free with rust-free individuals varies from no increase in resistance to thirty-eight percent of the mean depending upon the index of susceptibility and year of planting.

An examination of the results of mass selection and progeny testing can be carried out with the combined plant material of the 1963 and 196)4 plantings. The following assumptions must first be made:

1. The 37 male parents of the trees in the two years' plantings constitute a population from which selection for rust-resistance is proposed.

2. The combined control pollinated progenies of each male group approximate a wind-pollinated progeny test.

3. The progeny from the 1964 planting can be made comparable to the progeny of the 1963 planting by a simple addition of the difference between the means of the two years' plantings to the 1964 progeny means.

4. Saving 50 percent of the selected parents constitutes a reasonable milling level based on progeny test information.

Of the 37 male trees, 11 are rust-free and thus qualify for mass selection. These selected male groups have means of 149, 2.73, and 45 percent for number of galls per tree, c-score, and percentage of trees infected, respectively (Table 4, Part A)€ The means of all families in the 1963 planting were 1.73, 2.95, and 49 percent, respectively (see Tables 1 and 4); thus, a small gain for each index (0.24, 0.22, and 4 percent) was realized through selection of uninfected parent trees. Selection of the five "best" males of this group based on the means of their progeny, however, showed a larger increment of gain (Table 4, Part A). The additional gain due to progeny testing in units of the three indices of susceptibility was 0.49 for number of galls per tree, 0.50 for c-score, and 9.4 for the percentage of trees infected. The importance of progeny testing is reflected in an examination of the trees rejected because of poor progeny performance. Trees 20 and 39 would be chosen as rust-free phenotypes (Table 4, Part A). Their progeny, however, were greatly inferior by all three indices of susceptibility and the rejection of these two trees is essential if substantial gain in rust-resistance is to be made in the first generation of selection.

Table 3. Means[a] and differences from grand means[b] of families recorded by the phenotype of their parents (type of mating) and summarized by year of planting and index of susceptibility

Type of Mating	1963 Planting: No. Of Families	1963 Planting: Mean	1963 Planting: Difference from Grand Mean	1963 Planting: % Change in Mean	1964 Planting: No. Of Families	1964 Planting: Mean	1964 Planting: Difference from Grand Mean	1964 Planting: % Change in Mean
Number of Galls Per Tree								
	Grand Mean = 1.73				Grand Mean = 1.01			
Rust-free x rust-free	6	1.08	-o.65c	-38%	13	0.88	-0.13	-13%
Rust-free x infected	3)4	1.46	-0.27	-16%	30	0.93	-0.08	- 8%
Infected x infected	34	2.12	+0.39	+23%	17	1.22	+0.21	+21%
C-Score								
	Grand Mean = 2.95				Grand Mean = 2.24			
Rust-free x rust-free	6	2.17	-0.78	-26%	13	2.04	-0.20	- 9%
Rust-free x infected	34	2.78	-0.17	- 6%	30	2.07	-0.17	- 8%
Infected x infected	34	3.26	+0.31	+11%	16	2.57	+0.33	+45%
Percentage of Trees Infected								
	Grand Mean = 49%				Grand Mean = 41%			
Rust-free x rust-free	6	32%	-17%	-35%	13	41%	0%	o%
Rust-free x infected	3)4	45%	- 4%	- 8%	30	38% .	-2%	- 5%
Infected x infected	34	56%	+ 7%	+14%	16	46%	+5%	+12%

[a] Mean susceptibility for a given mating type

[b] Mean for all families taken together for a given year of planting

Minus indicates increase in resistance compared to the mean

Table 4. Means[a] of the half-sib progeny of trees selected as "best" on the basis the trees' phenotype and its half-sib progeny performance

Male Tree	Half-Sib Progeny Mean No. Gans	C-Score	% Infected
Part A -- Trees selected because they were rust-free. Best five chosen on the basis of progeny performance			
10	0.61*b	1.67*	28*
3	1.03*	2.06*	34*
19	1.34*	2.42*	40*
22	1.31*	2.50*	38*
50	0.73*	2.52*	38*
1)4	1.49	2.65	)i)i
12	1.63	2.77	42
30	1.71	2.99	50
42	1.90	3.21	56
39	2.25	3.54	66
20	2.47	3.67	63
Overall Mean	1.49	2.73	45
Mean of Best Five	1.00	2.23	35.6
Part B -- Trees selected on the basis of progeny performance only			
10	0.61**	1.673i*	2841-*
3	1.03N*	2.06**	31 *
1	1.11.$1*	2.30**	43
21	0.96**	2.3634*	44
19	1.34	2.42-x*	40**
22	1.31	2.50	38**
50	0.73**	2.52	38**
Mean of Best Five Male Trees	0.89	2.16	35.6

[a] The male group means from the 1964 planting have been adjusted so as to be comparable to the 1963 planting means. This has been accomplished by adding the difference between the two years of planting (9 percent for the percent infected index) to the 1964 male group means.

b Best five (based on progeny performance); (*)

Male trees selected as best for each index; (**)

The suggestion has often been made that in selecting only rust-free phenotypes for use in a tree improvement program, the tree breeder may be rejecting many otherwise excellent phenotypes because they have only minor rust infection. The belief has been expressed that many of these rejected trees are likely to produce progeny that would be as resistant as the progeny of rust-free trees. To test this hypothesis, five male trees with the least severely infected progeny were chosen regardless of the phenotype of the male parent itself (Table 4, Part B). For the percentage of trees infected, the same five male trees (Nos. 10, 3, 19, 22, and 50) were chosen on the basis of progeny performance as were chosen when the 11 rust-free male trees were selected and only these rust-free trees progeny tested. For c-score and number of galls per tree, male trees 1 and 21 were included among the five best (their progeny were among the least infected), although both had minor rust infection. It is important to note that their inclusion resulted in a reduction of rust severity over the five rust-free selections of only 0.11 galls per tree and 0.07 c-score units. Thus, for all three indices the initial selection of rust-free trees greatly reduced the number of trees to be progeny tested without seriously affecting the ultimate gain in resistance (see Table 11). No exceptionally good genotypes were rejected by mass selection as was the case in height growth for longleaf pine (Snyder, 1969).

It is apparent, however, that some infected x infected matings and many more rust-free x infected matings were less severely infected than the mean (Table 3). Evidence has been reported that suggests that techniques of artificial inoculation (Dinus, 1969) may soon allow the rapid identification of rust-resistant genotypes without long term field testing. This would allow selection for rust-resistance to proceed regardless of the phenotype of the candidate tree and at a more rapid rate than is possible in field testing. However, until the methods of artificial inoculation have become more adequately tested and until their relationship to field infection has become confirmed, including infected trees in a selection program should be avoided.

Predicted Gains

One of the objectives of this study was to predict the gain to be expected from different selection procedures. Because of the large differences in estimates of components of variance between the years of planting, the parent trees from each year were regarded as separate populations in these gain estimations; predicted gains were computed accordingly. A procedure similar to that followed in the construction of Table 4 was used; the 22 male trees of the 1963 planting and the 15 males of the 1964 planting comprised the populations in which selection took place. The families that resulted from the mating of the selected (rust-free) males with the rust-free females in their respective male groups were used as the **basis** for progeny testing the original selections. Since only rust-free x rust-free matings were included in the progeny testing, the progeny approximate those resulting from wind-pollination in a seed orchard consisting of rust-free selections.

The computation of predicted gain was carried out using the selection intensities dictated by the procedure described above. The 1963 planting consisted of 22 male parents, only four of which were rust-free, while the 1964 planting had 15 male parents, seven of which were rust-free. Approximately 50 percent of the selected parent trees were then culled on the basis of the performance of their progeny. Of the four selections in the 1963 planting, two were culled, while three of the seven selections in the 1964 planting were culled.

The predicted gains following these criteria (using the selection intensities shown above and the estimated components of variance for each year) are summarized for all three indices of susceptibility in Table 5, Parts 1 and 2. Gains are presented in units of the index of susceptibility and as a percent of the mean (the average of all families taken together for each year of planting).

The value of progeny testing is demonstrated by these gain predictions. Since the objective of progeny testing is to remove a relatively few poor performers, the selection intensities used in gain computations were low. In spite of this, the realized gain expressed as a percent of the mean is at least doubled in nearly every case by the addition of progeny testing to mass selection; therefore, the additional effort required to progeny test appears to be well worthwhile.

Predicted gains are much lower for the 1964 planting than the 1963 planting (Table 5) reflecting the difference in inheritance patterns. Additive genetic variation, hence general combining ability, was utilized in the selection procedures presented above. The parents of the 1963 planting contained males with good general combining ability, thus selection would be relatively successful in this population. The parent trees of the 1964 planting, on the other hand, showed a great deal more specific combining ability. The progeny reacted unexpectedly to exposure to rust. Rust-free male trees in certain specific crosses with the rust-free females occasionally produced progenies which were severely infected.

Family Plus Within-Family Selection

The methodology and effectiveness of the first generation of a tree breeding program influences subsequent progress; therefore, consideration must be given in the first generation to the procedures planned for later generations. In an examination of recurrent selection as applied to forest trees, Stonecypher (1969) presented analyses based on third-year height growth which showed that a combination of family plus within-family selection produced good results. This selection procedure was applied to the data from this study to give an indication of the progress that might be expected from second generation selection for resistance to fusiform rust (Table 4, Part 3). The selection intensity for the family selection stage was equal to selecting 11 of the 131 full-sib families

Table 5. Predictions of gain using three methods of selection and three indices of susceptibility

	Predicted Gain			
	In Index Units		In % Of Mean	
	1963	1964	1963	1964
1. Mass Selection				
Gall Counts	0.97	0.09	56%	9%
C-Score	0.71	0.07	24%	3%
Percent Infected (as threshold trait)	8%	4%	16%	9%
2. Mass Selection + Progeny Testing				
Gall Counts	1.67	0.25	91%	25%
C-Score	1.40	0.26	47%	12%
Percent Infected	18%	8%	36%	18%
3. Family + **Within-Family**				
Gall Counts	1.69	0.46	98%	46%
C-Score	0.88	0.37	30%	17%

in both planting years. The intensity used for within-family selection was based on the assumption that the best individual in each family (judged on the basis of its performance corrected for replication effect) would be chosen for use in a second generation seed orchard. Therefore, based an the conservative estimate that each family was represented by a total of 48 individuals over the six replications in the study, a selection intensity of 1 in 48 would result. Even the most severely infected of the best 11 families would probably not have more than 20 percent of its members infected with rust. Therefore, of the 48 individuals in each family, 38 would be rust-free so that within-family selection would result in the random choice (if resistance to rust is the only trait under selection) of one of the 38 rust-free individuals. The effective selection intensity was 38 out of 48 even though only one individual would actually be selected.

The following factors must be considered when interpreting the results of the family plus within-family selection procedure. First, the selection scheme utilized variance components estimated from a highly variable, unselected population. Since a second generation scheme as considered here would be applied to a selected and progeny tested population, the components of variation may be over-estimated when used for predictive purposes. The importance of these over-estimations would depend upon the intensity of the selection that took place in the first generation, but probably would not be serious in that the first generation selection intensities were relatively low. Secondly, the distributions of the number of galls per tree and c-score are skewed to the right and have lower limits of one and zero, respectively. The non-normality of these distributions probably would cause an over-estimation of the gain to be expected from selection designed to increase resistance; i.e., move the mean toward one or zero. Such an over-estimation would make complete resistance appear more easily attainable than it probably is (note the gain of 98 percent of the mean predicted for the gall count index, Table 4, Part 3).

Consideration of these factors is important in the appraisal of the predictions of gain for family plus within-family selection. Gains in c-score were 30 and 17 percent of the mean for the 1963 and 1964 planting, respectively, while the number of galls per tree showed gains of 98 and 45 percent. Such gains can be interpreted as an indication that this method of selection will result in continued progress in attaining rust-resistance but should not be considered as exact predictions of expected progress.

Implications for an Applied Breeding Program

A number of reports have shown that the variability in resistance to rust is wide-spread. These reports have ranged from the intensive sampling of a single stand in this study to the region-wide sampling of the Southwide Pine Seed Source Study. The conclusion (Barber, 1966) that inherent variation in resistance is probably widely distributed throughout the Southeast has been substantiated by this and other reports 1/. In addition to the obvious importance of the existence of sufficient variation to allow selection to be successful, the existence of local variability indicates that the tree breeder can select for resistance within a seed source adapted to grow best under local conditions.

The additive genetic control of resistance estimated on an individual tree basis was lower than desirable for rapid advances from mass selection alone. The estimated gains when combining mass selection and progeny testing, however, are encouraging.

The indication of probable continued improvement through family plus within-family selection in the second generation suggests that two generations of selection may well decrease fusiform rust to an amount that can be tolerated on all but sites with the most severe rust hazard. This projection, of course, excludes the possibility of any unforeseen change in the host-parasite relationship.

1/ Several examples based on extensive progeny tests are given in the Thirteenth Annual Report, N. C. State University-Industry Cooperative Tree Improvement Program. May 1969, pages 9-13.

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