Reprinted from PHYTOPATHOLOGY, Vol. 59, No. 9, 1246-1255, September 1969
Printed in U. S. A.

# Genetic Variation in Susceptibility to Fusiform Rust in Seedlings from a Wild Population of Loblolly Pine

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Ph.D. thesis by the senior author, North Carolina State University, under the direction of Bruce J. Zobel, Arthur Kelman, and Ellis B. Cowling. Portion of a larger experiment conducted cooperatively by International Paper Company and North Carolina State University. Financial support provided by grants from the Southern Forest Disease and Insect Research Council, the National Science Foundation (grant G-10680), and the National Institute of Health (grant GM-11546).

Cooperation and assistance of Charles Driver and Darwin Fender of the Southlands Experiment Forest of International Paper Company, Bainbridge, Georgia, is gratefully acknowledged.

Journal Series Paper No. 2685 of the North Carolina State University Agricultural Experiment Station, Raleigh.

Accepted for publication 11 March 1969.

ABSTRACT

Striking genetic variation in susceptibility to fusiform rust was observed among 55 controlled-pollinated (CP) and 48 wind-pollinated (WP) families from parent trees of loblolly pine selected at random in a natural forest stand in southwest Georgia. The mating design permitted statistical tests for estimating both additive and total genetic variance. WP families were planted on two different sites, CP families on four sites, including one where a deliberate attempt was made to increase the hazard of fusiform-rust infection. Susceptibility to rust was measured as the percentage of trees infected and the average number of galls per tree.

Variation among both CP and WP families was great on all sites, with family means ranging from 0.5-10.8 galls/tree (17.5-100% of trees infected) on the site with the most severely infected trees. Heritability estimates were high (0.65-0.85) and remarkably uniform on all sites tested. There was a consistent positive relationship between parent and offspring over all sites; on the average, WP progenies from rust-free parents had less rust than those from rust-infected parents, and CP progenies from two rust-free parents had less rust than those with one rust-free parent, which in turn had less than those from two rust-infected parents. Since some notable exceptions to this trend were observed, however, it was concluded that greater gains in resistance to fusiform rust can be obtained by combining phenotypic selection with progeny testing than by the former alone.

Variation in the amount of rust among sites was also great, ranging from a mean of 0.5-3.4 galls/tree (31.6-79.5% of trees infected). The relative rankings of families on the different sites was fairly stable, and the genotype × site interaction was small. Edaphic factors associated with the previous cultural history of the sites apparently influenced the amount of rust that subsequently developed on the trees. Knowledge of this relationship could be used to advantage in progeny testing. Phytopathology 59:1246-1255.

Forest trees offer unique advantages (as well as obvious disadvantages) for the analysis of genetic variation in host-parasite interactions that have evolved naturally in wild plant communities. In contrast to most agricultural crops, which have been domesticated for centuries, the germ plasm and habitats of many existing populations of forest trees remain relatively unaltered by man. It is reasonable, therefore, to assume that the genetic structures of such populations, as well as that of their endemic parasites, have been determined by natural selection alone. The present study was undertaken to analyze the pattern of genetic variation in susceptibility of a wild population of a native tree species, loblolly pine (*Pinus taeda* L.), to fusiform rust —an endemic disease caused by *Cronartium fusiforme* Hedgc. & Hunt ex Cumm.

Fusiform rust is the most important disease of loblolly pine and slash pine (*P. elliottii* Engelm. var. *elliottii*) in the southern USA. It causes direct or indirect losses in excess of $10,000,000 annually (11). In certain areas of South Carolina, Georgia, Alabama, and Mississippi frequent epidemics limit successful economic management of both species. Because silvicultural and chemical means of control are either ineffective or economically unfeasible in forest stands, development of rust-resistant trees appears to be the most promising alternative.

Variation in susceptibility to fusiform rust has been described among wind- and controlled-pollinated families of slash pine, and among hybrid families of slash pine and shortleaf pine (*P. echinata* Mill.) following both natural infection (2, 13, 19) and artificial inoculation (1, 14, 15). Considerable variation in susceptibility has been demonstrated, both among loblolly pine trees from different geographic regions and different stands within regions (7, 18, 27, 28). Results from a few tests (3, 30) have indicated an even greater range of variability among individual trees within stands.

Of primary practical importance to genetic improvement in resistance to rust is the magnitude of the interaction between genotype and environment. Few genetic studies have included the effects of varying environments, although it is known that environmental factors critically affect the intensity of rust infection, and

that the degree of rust hazard varies between regions and different sites within regions.

The specific objectives of this study were to determine (i) the extent of genetic variation in resistance to fusiform rust in sibling offspring of loblolly pine derived from a wild population of randomly selected parent trees, and (ii) the stability of observed resistance over a range of natural environments.

MATERIALS AND METHODS.—Trees used in this study were part of the Loblolly Pine Heritability Study being conducted cooperatively by the International Paper Company and North Carolina State University. This is a large and long-term quantitative genetics study, in which families from controlled-pollinated (CP) and wind-pollinated (WP) matings were established in replicated plantings over several years on two different types of sites in Decatur County, Georgia. The data reported here were taken from a portion of the 1960 and 1963 plantings of the WP and CP families, respectively, involving almost 10,000 individual trees. The scope and design of the entire Heritability Study are described in detail by Stonecypher (26) and Cech et al. (5).

*Parent population and mating design.*—The parent population and progeny test sites are located on the Southlands Experiment Forest near Bainbridge, Georgia (Fig. 1).

The stand of parent trees consisted of naturally regenerated, second-growth loblolly pine growing in mixture with shortleaf pine and some putative hybrids between the two species. With one exception, the parent trees were loblolly pine. The exceptional parent was subsequently judged to be a hybrid, based on its flowering phenology and the close resemblance of its WP progeny to shortleaf pine. All parent trees were selected at random within the area shown in Fig. 1.

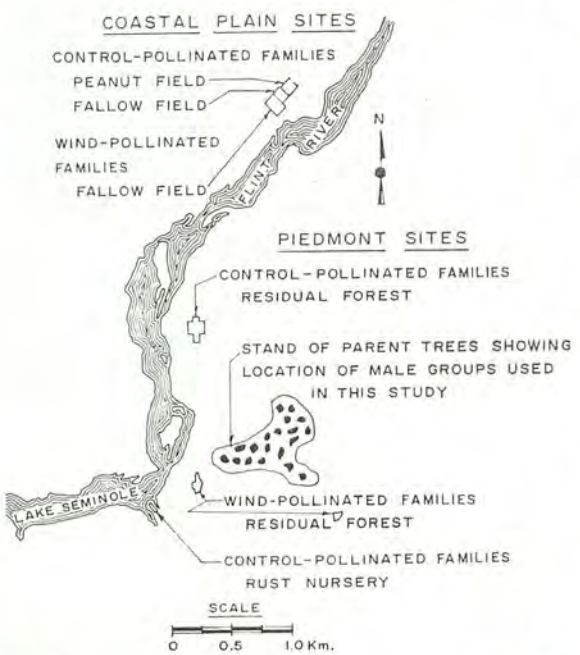


**Fig. 1.** Location of parent trees and planting sites for the controlled- and wind-pollinated families.

Controlled pollinations were made according to mating Design I of Comstock & Robinson (6). Flowers on each of several seed ("female") parent trees were pollinated by a single "male" parent. Both sets of parents constituted a "male group," and produced a family structure of half-sib (male parent in common) and full-sib (both parents in common) progenies. The only departure from random mating was that female parents within the several male groups were spatially related (Fig. 1). Nineteen such male groups were examined, with the number of females per male varying from two to four, providing a total of 55 CP families. After growing one year in a nursery, seedlings were outplanted in three locations with three replications of each family/location. Row plots consisted of 12 trees of each family at two locations, and 10 trees at the other.

Forty-eight WP families (including 32 from the same parents used in the controlled-pollinations) also were studied. Seedlings were outplanted in 1960 in two locations, with two replications of each family/location and 25 trees/square plot.

Spacing between trees in all plantations was $2.5 \times 2.5$ m, except in one plantation of CP families (the rust nursery), where it was $0.4 \times 1.0$ m.

*Planting sites.*—Southlands Experiment Forest is divided by the Flint River into two distinct forest types (Fig. 1). On the west side, the predominant forest vegetation consists of longleaf (*P. palustris* Mill.) and slash pines. The topography is flat, and soils (mainly in the Lakeland, Flint, and Cahaba series) are typical of the lower coastal plain. On the east side, the natural forest cover consists of a mixture of loblolly and shortleaf pines, and soils (mainly Ruston series) are more characteristic of the Piedmont (26).

CP families were established on each side of the river. On the west side, two of the replications were in a field previously planted to peanuts for several years. The third replication was in an adjacent field that had lain fallow for several years prior to planting. Since both the amount of rust and growth of the trees in these two fields were so different when these observations were made, the fallow field was defined as a separate site; data from this replication were handled separately, and excluded from the analysis of variance for this location and all locations taken together. On the east side, three replications were planted on a site which previously supported a stand of scattered loblolly and shortleaf pines.

Three additional replications were planted in a rust nursery, where the amount of inoculum and the environmental conditions conducive to infection were deliberately enhanced (9). The site had been fallow for several years prior to planting.

WP families were replicated twice on each of two sites, the fallow field on the west side of the river and the residual forest on the east.

To study a possible relationship between soil nutrients and the severity of rust infection among sites, soil samples consisting of two 17-cm cores from each

plot in the CP plantings were analyzed for P, K, Ca, Mg, total N, pH, organic matter, and texture.

*Observations and analysis.*—The number of stem and branch galls on all parent trees was recorded first in 1959 (26). Similar data were taken again in 1962 by the first author on 16 of the parent trees whose WP progeny were studied. Finally, 18 parents whose progeny were observed in both CP and WP plantings were re-examined in 1966.

The number of detectable stem and branch galls on each tree of the CP and WP families were recorded throughout 1966. By careful study of a large sample of galls and their location on trees of both CP and WP progenies, it was estimated that over 90% of the observed infection occurred in the 1964 growing season, and most of the remainder in 1965. Total heights of all CP trees, except those in the rust nursery, for which no data were available, were made in the winter of 1964.

The average number of galls/tree, and the percentage of trees with one or more galls, transformed into arc sin $\sqrt{\text{percentage}}$ values, were taken as separate indices of susceptibility.

Analyses of variance were computed for all plot means (except on the single replication of CP families in the fallow field). Since the number of female parents within the 19 male groups varied, male groups with progenies from two, three, and four females/male were each analyzed separately and their sums of squares pooled to give the analysis for all sites taken together. Expected mean squares were derived by pooling expected sums of squares in a corresponding manner. Components of variance were estimated according to conventional assumptions and procedures (6, 26) and the additional assumption that the WP families consisted entirely of half-sibs. Heritability estimates were computed from the ratio of the additive genetic variance to the total phenotypic variance, on the basis of plot means.

RESULTS AND DISCUSSION.—The results of this study justify four major conclusions: (i) Striking variation in susceptibility to fusiform rust that is under strong genetic control exists among individual trees of loblolly pine, so that (ii) substantial improvement in resistance to this disease can be effected by selection of genetically resistant parent trees; (iii) the relative resistance of trees to rust is stable over a range of environments, even though (iv) variation in the edaphic environment can strongly predispose trees to increased susceptibility. Evidence in support of each of these conclusions is summarized in Table 1 and Figs. 2 and 3, and is considered in detail below.

*Variation among families.*—The magnitude of the difference between the most susceptible and least susceptible of either CP or WP families on any given site was at least 6-fold when the amount of rust was measured as the percentage of trees infected, and 13-fold when measured as the average number of galls/tree (Table 1, Figs. 2, 3). Family means ranged from 0.5-10.8 galls/tree (17.5-100% of trees infected) on the plant field and from 0.0-2.2 galls/tree (2.8-75.6% of trees infected) on the residual forest (the sites on which the trees showed the greatest and least amounts of infection, respectively). The family from the parent tree suspected to be a hybrid with shortleaf pine (3C-Figs. 2, 3) was the most resistant on three of the four sites used for the CP families, and on both sites used for the WP families. Differences among means of both CP and WP families were highly significant statistically on all sites tested separately, and also in analyses for all sites taken together (17 for greater detail). The correlation coefficient between the two indices of susceptibility ranged from 0.64 to 0.88, becoming progressively greater at decreasing levels of infection (Table 1).

*Parent-offspring relationship.*—When families were grouped according to the phenotypes of their parents, i.e., whether their parents were (apparently) free of rust or had one or more galls, WP families from parents with no detectable symptoms of rust were more resistant, on the average, than those from rust-infected parents, and CP families from two rust-free parents were more resistant than those with only one rust-free parent; both of the latter groups of progeny were more resistant than those from two infected parents (Table 2). These differences among families grouped accord-

TABLE 1. Variation in the amount of fusiform rust observed in controlled- and wind-pollinated families of loblolly pine on different sites

| Planting site | Replications | % Trees infected | | No. galls/tree | | Correlation between indices of susceptibility | Height of trees[a] |
|---|---|---|---|---|---|---|---|
| | | Average | Range | Average | Range | | |
| | | | | | | | *cm* |
| | | | *Controlled-pollinated families* | | | | |
| Peanut field | 2 | 79.5 | 17.5-100 | 3.4 | 0.5-10.8 | 0.64 | 33.4 |
| Rust nursery | 3 | 61.2 | 14.1-96.7 | 1.6 | 0.2-6.7 | 0.75 | |
| Fallow field | 1 | 48.0 | 0.0-100 | 1.1 | 0.0-3.6 | 0.81 | 27.4 |
| Residual forest | 3 | 31.6 | 2.8-75.6 | 0.5 | 0.0-2.2 | 0.88 | 19.9 |
| | | | *Wind-pollinated families* | | | | |
| Fallow field | 2 | 61.8 | 11.5-88.9 | 1.9 | 0.4-5.2 | 0.81 | |
| Residual forest | 2 | 54.4 | 2.0-95.7 | 1.4 | 0.0-4.5 | 0.88 | |
| | | | *Parent-trees* | | | | |
| | | 60.0 | - | 2.0 | 0-18 | | |

[a] Measurement preceding the growing season of 1964, when most of the observed infection is believed to have occurred.

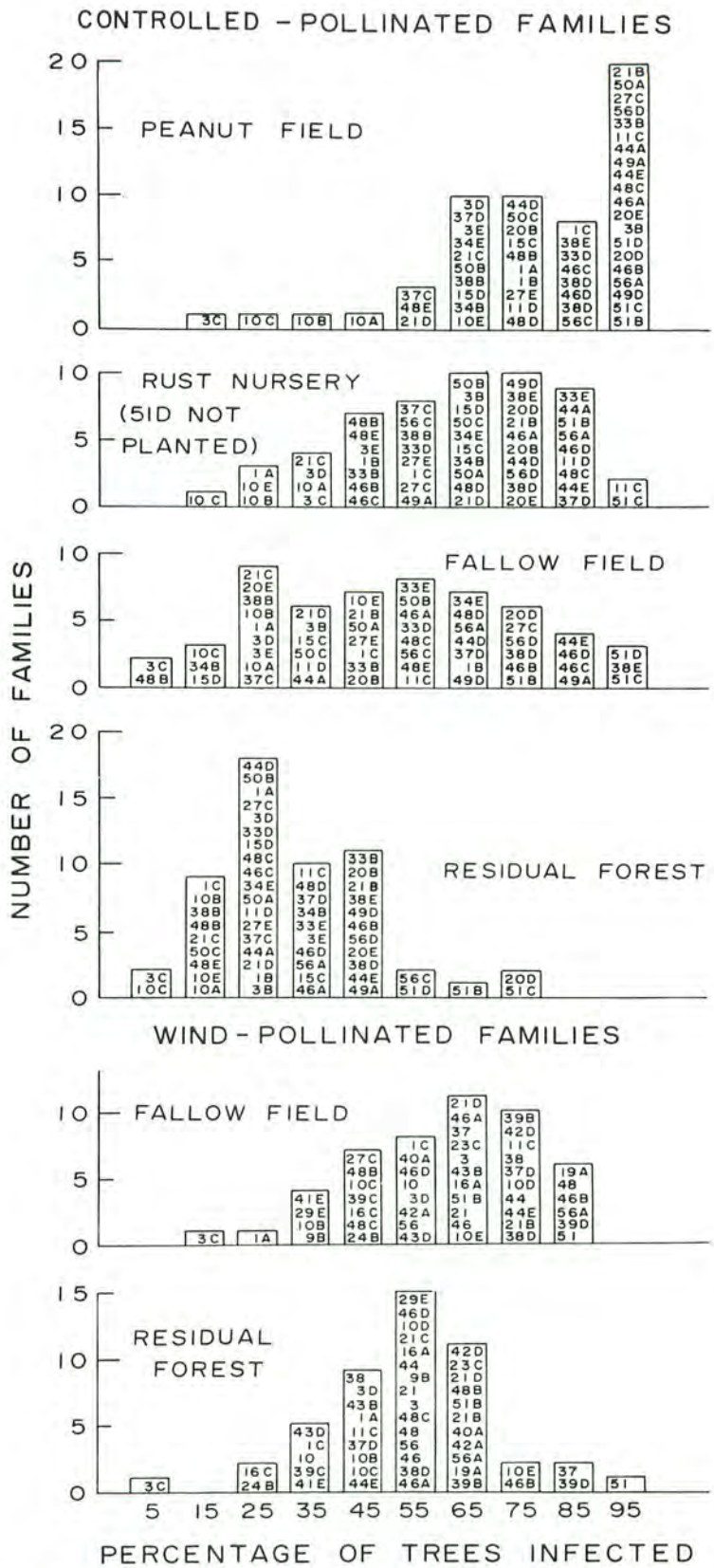


**Fig. 2.** Distribution of individual family means in percentage of trees infected at each site. Families are listed within each bar of the histogram from top to bottom in order of increasing amount of rust observed.

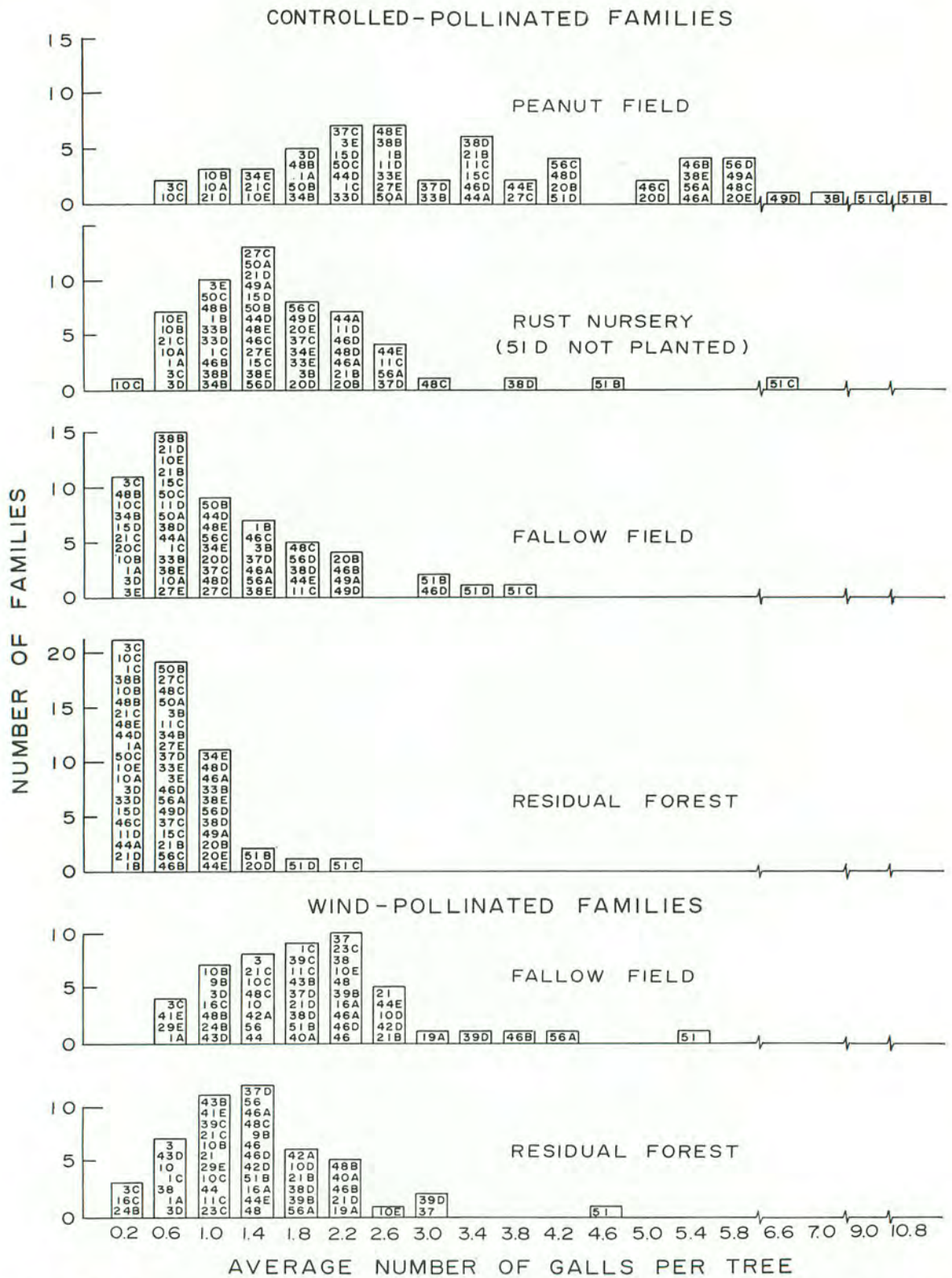


**Fig. 3.** Distribution of individual family means in average number of galls per tree at each site. Families are listed within each bar of the histogram from top to bottom in order of increasing amount of rust observed.

TABLE 2. Relationship of the phenotype of parent loblolly pine trees (rust-free or rust-infected) to the amount of fusiform rust observed on their offspring

| Site | Controlled-pollinated families[a] | | | Wind-pollinated families[a] | |
|---|---|---|---|---|---|
| | Free × free (6) | Free × infected (25) | Infected × infected (23) | Free (19) | Infected (29) |
| | | | *% Trees infected* | | |
| Peanut field | 54.3 | 74.4 | 86.5 | | |
| Rust nursery | 44.6 | 61.4 | 65.2 | | |
| Fallow field | 23.8 | 47.0 | 55.9 | 55.4 | 66.0 |
| Residual forest | 21.3 | 28.9 | 36.0 | 48.0 | 58.9 |
| | | | *Avg. No. galls/tree* | | |
| Peanut field | 2.7 | 3.0 | 4.0 | | |
| Rust nursery | 1.2 | 1.5 | 1.9 | | |
| Fallow field | 0.8 | 0.8 | 1.3 | 1.5 | 2.0 |
| Residual forest | 0.4 | 0.5 | 0.6 | 1.2 | 1.5 |

[a] Numbers in parentheses indicate families in each group.

ing to their parental phenotypes were highly significant on all sites tested. Furthermore, as the amount of rust on the different sites increased, so did the magnitude of the difference among the families that were grouped according to their parental phenotypes. Although these trends held consistently over all sites tested by both indices of susceptibility, notable exceptions occurred among individual families. For example, highly resistant progeny were derived from parent 10B in both controlled and wind pollinations; but this parent had four times the number of galls as the average for all parent trees (Table 1), and more galls than parent 51—the parent of the most susceptible families in both CP and WP crosses (Fig. 2, 3). Therefore, although phenotypic selection of rust-free parent trees would usually result in moderate gains in resistance in their progeny, maximum gains would be obtained by progeny testing. This conclusion is consistent with earlier observations that progeny from rust-free parents were generally, although not always, more resistant than those from rust-infected parents following artificial inoculation (15, 16).

It is not surprising that the phenotype of the parent was not a consistently good estimator of its genotype. Most fusiform rust galls occur on branches, so that detection of galls in the crowns of mature trees is difficult. Furthermore, the number of branch galls observed at any given time may be only a fraction of the total that have developed; some usually are lost by natural pruning. Also, the susceptibility of individual trees may vary greatly according to their age when infected. Since the frequency and severity of rust epidemics fluctuate widely in different years and regions, different stands may be subjected to varying degrees of selection pressure from the pathogen. It is unlikely that a stand subjected to a severe epidemic while young would have the same genetic structure with respect to resistance as one which escaped until relatively mature. Thus, estimates of the genetic value of individual trees from different stands that are based on their phenotypes may not be comparable or will be imprecise at best.

*Estimates of heritability.*—Differences among male groups were highly significant by both indices of susceptibility on all sites tested separately and by the percentage-of-trees-infected index in the analysis for all sites taken together. Differences among females within the male groups were highly significant by both indices of susceptibility on the peanut field and by the percentage-of-trees-infected index in the analysis for all sites taken together; they were of marginal significance on the residual forest site by the percentage-of-trees-infected index, and nonsignificant in the remainder of the analyses. Further details of the statistical analyses are available in the dissertation from which this paper is derived (17).

Although genetic differences among families are indicated clearly, evaluation of the estimates of the components of variance (Table 3) and heritability (Table 4) should be made with caution. The degrees of freedom for reliably estimating the genetic components of variance were fewer, and the standard errors of the estimates larger, than desirable; the error variances were also large, and, by the average number-of-galls/tree index, so heterogeneous as to preclude an analysis of the data for all sites taken together; finally, in the controlled pollinations, estimates of the genetic variance based on half-sib progenies (male groups) and full-sib progenies (females with male groups) were grossly discrepant, possibly resulting from biases in the mating of parents.

Since the component of variance for male groups ($\sigma^2$m, Table 3) estimates a quarter of the additive genetic variance, while the component of variance for females within male groups ($\sigma^2$f) estimates a quarter of the additive plus a quarter of the dominance genetic variance (6, 26), the component for females within male groups should be at least as large as the component for males even if there is no dominance variance. The fact that it was much smaller in all of the analyses (Table 3) is perplexing. Stonecypher (26) reported a similar result for the traits of survival and height growth after 1 year in the field in this same population of trees. He also discussed the possibility that the relative proximity to each other of the parent trees within male groups might have resulted in matings between relatives, i.e., trees with some degree of common ancestry.

TABLE 3. Components of variance for amount of fusiform rust observed in the controlled- and wind-pollinated families of loblolly pine

| Component of variance ($\sigma^2$)[b] and its standard error ($S\sigma^2$) | % Trees infected[a] | | | | Avg. No. galls/tree | | |
|---|---|---|---|---|---|---|---|
| | All sites taken together | Peanut field | Rust nursery | Residual forest | Peanut field | Rust nursery | Residual forest |
| | | | | *Controlled-pollinated families* | | | |
| $\sigma^2m$ | 68.85 | 93.26 | 93.39 | 58.20 | 2.11 | 0.86 | 0.12 |
| $S\sigma^2m$ | 31.38 | 44.66 | 41.27 | 28.42 | 0.96 | 0.30 | 0.04 |
| $\sigma^2f$ | 39.87 | 79.44 | 36.20 | 24.13 | 1.12 | 0.07 | 0.02 |
| $S\sigma^2f$ | 14.32 | 36.68 | 25.90 | 16.30 | 0.55 | 0.12 | 0.02 |
| $\sigma^2e$ | 154.38 | 132.23 | 194.96 | 122.05 | 1.99 | 1.08 | 0.13 |
| $\sigma^2ms$ | 7.44 | | | | | | |
| $\sigma^2fs$ | 2.45 | | | | | | |
| $\sigma^2s$ | 282.97 | | | | | | |

| Component of variance ($\sigma^2$)[b] and its standard error ($S^2$) | % Trees infected[a] | | | Avg. No. galls/tree | |
|---|---|---|---|---|---|
| | All sites taken together | Fallow field | Residual forest | Fallow field | Residual forest |
| | | | *Wind-pollinated families* | | |
| $\sigma^2p$ | 74.90 | 72.43 | 103.73 | 0.70 | 0.51 |
| $S\sigma^2p$ | 19.43 | 20.82 | 26.43 | 0.20 | 0.13 |
| $\sigma^2e$ | 40.27 | 53.77 | 49.50 | 0.54 | 0.26 |
| $\sigma^2ps$ | 18.49 | | | | |
| $\sigma^2s$ | 0.80 | | | | |

[a] Transformed into arc sin $\sqrt{\text{percentage}}$ values.
[b] m = Male groups; f = females within male groups; e = error; ms = male groups × sites interaction; fs = females within male groups × sites interaction; s = sites; p = families (wind-pollinated); ps = families × sites interaction.

An assumption basic to the design and analysis of this experiment was that the matings were random. If trees within male groups were in fact genetically similar, the component of variance for females within male groups would be reduced in proportion to the degree of similarity. Since pine forests in much of the South commonly are regenerated by relatively few seed trees following abandonment of agricultural fields or logging operations, it is likely that the resulting genetic structure of such stands consists of clusters of relatives derived from one or few proximal seed trees. Since parent trees within each male group in this study were not widely separated (the minimum distance between them was only about 16 m), common ancestry among parents within a male group is not only possible, but is suggested by the consistency of the data (Table 3). The distance between male groups (Fig. 1), on the other hand, was probably sufficient to preclude any substantial degree of co-ancestry among them. If this hypothesis be correct, the increased covariance of females within male groups would seriously underestimate dominance variance, if it exists, and in any case overestimate both the additive variance and heritability.

The error variances were large in most analyses, but were generally considerably lower in the analyses of the WP than in the CP families (Table 3). Although this may be attributable simply to the larger size of the plots in the WP plantings (25 trees) than in the CP plantings (12 trees), it also may indicate that the error variance decreases with increasing age of the host. The WP families had been in the field 3 years longer than the CP families at the time most of the observed infection occurred.

In spite of the above disparities, the relatively large standard errors of the components of variance, and the possibility of biased estimates of additive genetic variance, the 12 estimates of heritability were high and remarkably uniform over all sites by both indices of susceptibility (Table 4). It is reasonable to expect that biases due to common ancestry of parents would be less in the WP families than in the CP families, since the former presumably result from a wider range of parents. Therefore, the close agreement of the estimates of heritability for the CP and WP families is considered particularly significant, and indicates that substantial improvement in resistance to fusiform rust in loblolly pine is possible through selection of genetically resistant trees.

*Genotype × environment interaction.*—The magnitude of the genotype × environment interaction is important, since it measures the degree of genetic control of variation in susceptibility exerted in diverse environ-

TABLE 4. Estimates of heritability of resistance to fusiform rust in loblolly pine

| Planting site | % Trees infected | Avg. No. galls/tree |
|---|---|---|
| | *Controlled-pollinated families* | |
| Peanut field | 0.65 | 0.74 |
| Rust nursery | 0.72 | 0.85 |
| Residual forest | 0.72 | 0.84 |
| All sites taken together | 0.75 | |
| | *Wind-pollinated families* | |
| Fallow field | 0.73 | 0.72 |
| Residual forest | 0.81 | 0.80 |
| All sites taken together | 0.80 | |

ments with respect to disease hazard. In the CP families, in which the amount of rust was most variable among sites, the family × site interaction was not significant (17). Although the family × site interaction was highly significant in the WP families, its component of variance was only a quarter of the genetic component (Table 3). These results are consistent with those of several previous studies. Kraus (18) found no significant interaction between 18 seed sources and 10 planting locations in Georgia, though the variability in amount of rust observed both among seed sources and planting locations by themselves was highly significant. Similarly, there was no significant interaction among nine widely separated seed sources and planting locations in one of the two series of the Southwide Seed Source Study (28). In the other series, the interaction of seed source × planting location was highly significant, but again the component of variance for the interaction was smaller than the component of variance for seed sources. The significant interaction was apparently due to scale effects in the amount of rust between locations rather than to changes in the relative susceptibility of the various seed sources.

In this study, the stability of genetic control of resistance to fusiform rust was most conspicuous in some of the families that were consistently at the extreme tails of the distribution of relative susceptibility (e.g., 3C, 10B, 10C, 51B, and 51C, Fig. 2, 3). Even though the amount of rust observed on some families varied as much as 8-fold among different sites, the relative order of susceptibility of most families did not change appreciably. In applied breeding programs, selections will undoubtedly be made among the most highly resistant families or individuals. These data indicate that this resistance will be quite stable.

*Influence of site factors on susceptibility to rust.*— A major objective of the Heritability Study was to test for genotype × environment interactions of any trait, including susceptibility to fusiform rust. Accordingly, the planting sites used were selected for diversity, and more particularly to be representative of those commonly found in the Coastal Plain and Piedmont physiographic regions (Fig. 1). The rust nursery was designed specifically to provide a rapid and efficient method for screening for genetic differences among families in resistance to fusiform rust alone, by attempting to raise the hazard of rust artificially (9).

The results differ from those expected in that trees in the peanut field had much more rust (3.4 galls/tree) than those in the rust nursery (1.6 galls/tree) and seven times the amount in the residual forest site (0.5 galls/tree, Table 1). This unexpectedly large variation within a small geographic area could have resulted from any one or a combination of differences among sites in (i) amount of inoculum, (ii) amount of host tissue exposed, (iii) meteorological conditions affecting the dissemination and germination of rust spores, and (iv) edaphic factors that predispose trees to increased susceptibility. The following circumstantial evidence is most consistent with the last hypothesis.

The decreasing amount of rust observed in the peanut field, rust nursery, and fallow field, respectively, indicates that differences in either the amount of inoculum or meteorological conditions among sites were not primarily responsible for the observed differences in the amount of rust. Although both the amount of inoculum and meteorological conditions were presumably most favorable for infection in the rust nursery, the average number of galls/tree was only slightly greater on this site (1.6) than on the fallow field (1.1), but was less than half of that observed on the peanut field (3.4). Since the fallow field was adjacent to the peanut field and had similarly flat topography and proximity to sources of inoculum, the more than 3-fold difference in the amount of rust between these two sites cannot reasonably be attributed to comparable differences in either the amount of inoculum or meteorological conditions. Therefore, any possible influence of these factors on the amount of disease observed apparently was less limiting than other factors on these two sites.

Since there were considerable differences among sites in the average height growth of trees planted at the same time (CP families, Table 1), and between WP families (planted 3 years earlier) and CP families, differences in the amount of rust observed among sites could be related to the amount of susceptible tissue exposed to rust spores (assuming this to be a function of rate of growth). The average number of galls/tree on the CP families planted on the peanut field, fallow field, and residual forest sites (Table 1) are correlated, and WP families on the residual forest site had more galls/tree (1.4) than genetically related CP families on the comparable residual forest site (0.5). But the coefficient of determination between the average height and number of galls/tree for CP families within any site ranged only from 0.04-0.23, and CP families on the peanut field had much more rust than those on either of the sites used for the WP families, even though the latter were considerably taller. Thus, both growth in height and the number of galls/tree were correlated with differences among sites, but not with each other directly. From this it can be inferred that although the amount of host tissue exposed to inoculum may have been a significant factor in determining the amount of rust observed, it was not the most important.

Direct evidence of variation in the edaphic environment of the various sites used in the CP plantings is indicated by the large differences among sites in the average height of the trees (Table 1). These differences were associated with differences in the amount of rust infection and also in the amount of calcium, magnesium, and phosphorus (but not nitrogen) in the soil of the peanut field, fallow field, and residual forest sites (Table 5). The severity of rust infection observed on all sites was also associated strongly with their previous cultural history, particularly with the length of time since cultivation before planting the trees. Thus, in the CP plantings the peanut field was highest, the fields that had lain fallow for several years (including the rust nursery) intermediate, and the relatively undisturbed residual forest site lowest in amount of rust observed. The same trend was evident in the WP plant-

TABLE 5. Nutrients in the soil of sites used for the controlled-pollinated families[a]

| Site | Ca | Mg | P | K | N |
|---|---|---|---|---|---|
| | *me/100 g* | *me/100 g* | *ppm* | *me/100 g* | *%* |
| Peanut field | 1.89 | 0.47 | 4.0 | 0.04 | 0.073 |
| Fallow field | 1.72 | 0.47 | 2.5 | 0.05 | 0.093 |
| Residual forest | 1.13 | 0.35 | 1.7 | 0.06 | 0.067 |
| Rust nursery | 0.64 | 0.17 | 8.0 | 0.04 | 0.048 |

[a] Analyses for total N were made by the Department of Soil Sciences, North Carolina State University, Raleigh; all other analyses were made by the Soil Testing Laboratory, North Carolina Department of Agriculture, Raleigh.

ings; although the difference among the two sites was relatively small and not significant statistically, trees in the fallow field had more rust than those in the residual forest site.

The influence of different edaphic environments on the amount of fusiform rust observed in this study is consistent with results of earlier reports. Siggers & Lindgren (25) found that slash pine on abandoned agricultural fields had twice the number of galls/tree as trees in nearby plots with no previous history of cultivation. Trees in fertilized and cultivated plots had a significantly greater percentage of trees infected than those in untreated plots (65 vs. 42%); also, there was no relation between height and amount of rust observed among trees within the treated and untreated plots (12). Miller (20) showed that the relative intensity with which sites were prepared for planting was directly correlated with subsequent rust infection of the trees; trees on plots receiving the most intensive preparation had almost twice the number of galls as trees on untreated plots in areas of moderate rust hazard. Siggers (24) suggested that the primary effect of disturbed edaphic conditions on trees was phenological; i.e., trees on sites that had been disturbed by cultivation, fertilization, and fire broke dormancy earlier, thus exposing more succulent, susceptible tissue to inoculum for a longer period of time. No critical evaluation of this hypothesis has been made, however.

Although the underlying causal mechanisms remain obscure, the evidence from this and previous studies points to the conclusion that pines susceptible to fusiform rust are extremely sensitive to predisposing factors in the edaphic environment, especially when the natural environment has been disturbed by intensive cultivation. In the CP plantings of this study, the largest component of variance was the site component (Table 3). In the relatively less disturbed sites of the WP plantings, on the other hand, differences between sites were small and not significant, and the component of variance for sites was negligible. Undoubtedly, the component of variance for sites in the CP plantings was highly inflated by the atypical and artificial environments of the peanut field and rust nursery.

*Implications.*—The results of this study illustrate the range of heritable variation in resistance that may be typical of wild host populations to endemic diseases. Similar patterns of variation have been found in wild populations of oats (*Avena sterilis* L.) to *Puccinia coronata* Cda. var. *avenae* Fraser & Led. (32), and cottonwood (*Populus deltoides* Bartr.) to *Melampsora medusae* Thum. (29). These examples are consistent with theoretical expectations. Person (23) argued that the complimentary gene-for-gene relationship for resistance in the host and virulence in the pathogen demonstrated by Flor (10) for flax (*Linum usitatissimum* L.) and its rust (*Melampsora lini* Desm.) should be expected in any host-parasite combination that has evolved under the mutually antagonistic selection pressures imposed on each other. Gene-for-gene systems have subsequently been demonstrated or strongly implicated in 11 other host-parasite combinations, most of which involve obligate or highly specialized parasites of cultivated species (23). Mode (21) showed by a mathematical model that complimentary genes in a wild, heterozygous, and randomly mating host-parasite population would eventually reach a stable equilibrium at intermediate frequencies as a necessary condition for their co-evolution, since fixation of one complement of genes in one symbiont would lead to its own or the other's extinction. Although no direct evidence of the mode of inheritance of resistance to fusiform rust is available from these data, the range and distribution of families on the scale of susceptibility (Fig. 2, 3), and the high heritability values obtained are consistent with a population segregating at several major polymorphic loci conditioning resistance and susceptibility, as proposed by Mode and Person.

This is in sharp contrast to the patterns of variation in susceptibility to white pine blister rust, a closely related but nonendemic disease in North America caused by *Cronartium ribicola* Fisch. Although resistance has been found in both eastern (*Pinus strobus* L.) (22) and western (*P. monticola* Dougl.) white pines, the high heritability values reported (4) were derived from a parent population that was highly selected for resistance. The relative infrequency of parent trees in these species that transmit a high degree of resistance to their progeny indicates that progress from selection may be much less efficient, and the mode of inheritance of resistance fundamentally different than with fusiform rust of southern pines.

The results of this study also illustrate how artificial disturbance of the natural environment of a wild host species can cause an endemic disease to become epidemic, presumably through predisposing the host to increased susceptibility. The 7-fold difference in the amount of rust that was observed in this study and associated with edaphic differences among sites is similar to the dramatic increase in the incidence of powdery mildew and stem rust that Yarwood (31) found in another wild species, *Baccharis pilularis* DC., resulting from tillage. Donaubauer (8) found that ni-

trogen fertilization markedly increased the amount of rust caused by *Melampsora allii populina* Kleb. on both resistant and susceptible clones of poplars, but that the sensitivity of the relatively susceptible clone was proportionately much greater than the resistant clone; this is similar to the responses of families 51C and 10C on the peanut field and residual forest sites, respectively, in the present study (Fig. 3). These results have important implications for the future silvicultural management of second growth stands and plantations of forest trees, particularly as they relate to decisions concerning the merits of fertilization and cultivation for increased yields, and place increased emphasis on the need for stable genetic resistance to important diseases.

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