Results at Age 15 Years from a Half-Diallel Cross among 10 Loblolly Pines Selected for Resistance to Fusiform Rust (Cronartium quercuum f. sp. fusiforme)

By E. R. SLUDER

Research Plant Geneticist, USDA Forest Service,
Southeastern Forest Experiment Station,
Macon, Georgia 31020, U.S.A.

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Abstract

Ten loblolly pine seed orchard clones selected for their high resistance to the southern fusiform rust fungus were crossed in a half-diallel mating scheme. The 45 crosses were outplanted in a progeny test in 1974 in Houston County, Georgia, an area of very high rust hazard. Fifteenth-year data showed that the 10 clones differed at the 0.01 level in general combining ability for height and for percentage free of fusiform rust infection at 15 or cumulative percentage free to 15. Also, specific combining abilities of the 10 clones varied at the 0.01 level for rust-free percentage cumulative to age 15.

Heritability of percentage rust-free was 0.69 based on 15th-year data and 0.52 based on cumulative records. Heritability of tree height was 0.48 on a family or 0.28 on an individual-tree basis. The 10 clones divided sharply into half with moderate resistance and half with low resistance to rust, even though all had shown high resistance in earlier tests. Mortality percentages of trees with infected stems were not significantly correlated with stem infection percentages, suggesting little or no linkage between susceptibility to stem infection and tolerance of stem cankers. The 3 stages of selection produced a genetic gain of about 32%; that is, 32% more trees were rust-free at age 15.

Key words: *Pinus taeda*, *Cronartium quercuum* f. sp. *fusiforme*, breeding, selection.

Introduction

Intensive management of loblolly (*Pinus taeda* L.) and slash (*P. elliotti* ENGELM. var. *elliottii*) pines in plantations has rapidly increased over the last 40 to 50 years. Coincident with that increase has been an increase in infection by the southern fusiform rust fungus (*Cronartium quercuum* (BERK.) MIYABE ex SHIRAI f. sp. *fusiforme*). Infection is ecpecially high in the Piedmont and Upper Coastal Plain provinces from North Carolina to Mississippi (ANDERSON *et al.*, 1988; DINUS, 1974; PHELPS, 1974; POWERS *et al.*, 1975; SCHMIDT *et al.*, 1974). More recently, incidence has begun to increase in eastern Texas (LENHART *et al.*, 1988). In high-incidence areas, fusiform rust seriously hinders the productive management of loblolly and slash pine plantations (CZABATOR, 1971).

Infections on seedlings in the nursery or during the first 5 years after field planting cause the greatest mortality. Seedlings can be protected from infection in the nursery, and systemic fungicides used in the nursery commonly protect the seedlings for 1 to 2 years after outplanting (KELLY, 1980, 1985; ROWAN, 1982a, 1984; SKOLLER *et al.*, 1983). Established galls, however, do not respond to chemical treatment (ROWAN, 1982b). Even when they are not fatal, early stem infections produce costly losses in fiber production and especially in the supply of wood for solid products (ANDERSON *et al.*, 1986; GERON and HAFLEY, 1988; PHELPS and CHELLMAN, 1975; SLUDER, 1977a).

The most practical way to control losses to the fungus in loblolly plantations is to improve genetic resistance. Loblolly pines vary in resistance to fusiform rust, both geographically and on an individual-tree basis (KINLOCH and STONECYPHER, 1969; POWERS and DUNCAN, 1976; POWERS and KUHLMAN, 1987; SLUDER, 1980, 1987, 1988, 1989; WELLS and WAKELEY, 1966). Selection and breeding for resistance, however, is complicated by variation in the fungus itself. Virulence of the fungus varies geographically (SNOW and KAIS, 1970; POWERS *et al.*, 1977) from one gall to another (KUHLMAN, 1990; POWERS *et al.*, 1977) and even within a gall (POWERS, 1980). It does not appear to vary over time (POWERS and DWINELL, 1978).

The progenies of the 133 clones in the Georgia Forestry Commission's loblolly pine seed orchards were tested for resistance in central Georgia, where the high incidence of fusiform rust in plantations provides a rigorous test (PHELPS, 1974; SOHN and GODDARD, 1979). Fifth-year rust incidence data from these progeny tests were used to select 10 clones whose progenies had above-average resistance to infection at age 5 as well as desirable growth. The 10 clones were crossed in a half-diallel arrangement to study inheritance of rust resistance and other traits in loblolly pine. This report presents the 15-year results of that study. Five- and 10-year results have been previously reported (SLUDER, 1981, 1988).

Materials and Methods

Data from 6 progeny-test plantations were used to select the 10 clones for the study. Five of the plantations contained polycross progenies and one contained single cross progenies. Progenies of the selected clones averaged 4.75 standard deviations above their respective plantation means in percent rust-free or in the number of cankers per tree. Their mean superiority was 64% (*Table 1*), which placed them in the upper 10% in the plantations.

The clones were arranged in the half-diallel cross according to flowering phenology (SLUDER, 1977b). Flowering was earliest for Clone Number 1 and latest for Clone Number 10. Pollen from the earlier flowering clones was used to pollinate the later flowering ones. Thus, all 45 crosses were made in one season (1972), eliminating the need to store pollen.

In 1973 seeds were collected, extracted, and stratified. In February 1974 they were planted in 7.6-cm square peat pots arranged in a greenhouse in a randomized-block

Table 1. — Loblolly pine clones used in the study and the superiorities of their progenies in rust resistance at age 5 over the original progeny-test plantation means[1].

Clone number	GFC[2] serial number	Progeny superiority[3] Percent	SE
1	617	75.8	6.84
2	518	39.2	2.78
3	541	71.9	3.70
4	600	67.2	3.01
5	603	74.1	2.35
6	520	50.2	10.90
7	542	50.9	3.27
8	578	80.5	4.15
9	566	47.9	4.73
10	582	80.9	5.73
Mean		63.9	4.75

[1] The resistance trait was percentage rust-free (four plantations) or galls per tree (2 plantations).
[2] GFC = Georgia Forestry Commission.
[3] Superiority as percentage above and as standard errors (SE) above the plantation mean.

design of 5 replications and 16 seedlings per square plot. In June, 4 of these replications were planted in a disc-harrowed old field in Houston County, Georgia. Spacing in the field was 2.5 m x 2.5 m. Each of the 4 randomized blocks contained the 45 crosses, along with a standard Georgia Crop Improvement Association (GCIA) check lot, and a bulk seed orchard check lot. Both the diallel and the check lot seedlings were started in the greenhouse at the same time. Survival at age 3 years averaged 88.7%.

Traits assessed at age 15 were survival, height, d. b. h., volume per tree, percentage rust-free at 15 (ignoring past records) and cumulative percentage rust-free to 15 (including records of trees killed by rust and trees that had only branch cankers but lost them when the branches dropped off). Percentages were transformed to the arc sines of their square roots for analysis. Plot-mean and individual-tree data were subjected to randomized block and diallel analyses of variance (*Tables 2, 3*). Variance components, heritabilities, combining abilities, breeding values, and the genetic correlation between mean height and rust-free percentage were estimated (Becker, 1984; Griffing, 1956; Schaffer and Usanis, 1969), as were relationships between rust mortality rates and stem infection rates. The genetic assumptions were random effects, no dominance, and no genotype x environment interaction.

Results

Randomized-block analyses of variance of plot means showed significant ($P < 0.01$) differences among the 45 crosses and the 2 check lots in survival, height, and the 2 expressions of fusiform-rust resistance. Differences in d.b.h. and volume per tree were nonsignificant. Ranges for the 47 lots were: survival, 42% to 86%; height, 9.94 m to 13.23 m; d.b.h., 15.3 cm to 19.3 cm; volume per tree, 0.072 m^3 to 0.133 m^3; rust-free at 15, 0% to 54%; and rust-free cumulative to 15, 0% to 40%. The diallel means were higher than the GCIA check means for all traits, especially percentage rust-free, but were higher than the orchard check means only in the survival and rust-free traits *(Table 4)*.

Diallel analyses of plot means from the 45 crosses showed significant ($P < 0.01$) variation in general combining abilities (GCA) of the parents in height and the 2 rust-resistance traits but nonsignificant variation in survival, d.b.h., and volume per tree (*Table 5*). Cumulative rust-free

Table 2. — Ecpectation mean squares (EMS) for the diallel analysis of plot means (n = reciprocal of harmonic mean number plants per cross).

Source	D.f.	EMS
Rep (r)	3	$nV_e + 45V_r$
GCA	9	$nV_e + V_{sca} + 8V_{gca}$
SCA	35	$nV_e + V_{sca}$
Error (e)	132	nV_e

Table 3. — Expectation mean squares (EMS) for the diallel analysis of individual-tree data.

Source	D.f.	EMS
Rep (r)	3	$V_e + 0.61V_{sca} + 1.08V_{gca} + 449.61V_r$
GCA	9	$V_e + 41.63V_{sca} + 319.23V_{gca}$
SCA	35	$V_e + 39.47V_{sca}$
Error (e)	1752	V_e

percentage was the only trait showing any significance in specific combining ability (SCA) variation ($P < 0.05$). With individual-tree data, GCA variation was significant for height ($P < 0.01$) and volume per tree ($P < 0.05$), but nonsignificant for d.b.h.; SCA variation was significant only for height ($P < 0.05$) (*Table 5*).

For the rust-free traits, breeding values of the 10 clones varied from less than 0% to 69% at age 15, and from less than 0% to 44% cumulative to age 15 (*Table 6*). On this test site, the 10 clones divided sharply, half with moderate resistance and half with low resistance. The more resistant clones also averaged better than the less resistant clones in the four other traits (*Table 6*).

The heritability of the rust-free trait was 0.69 if only 15th-year data were considered and 0.52 based on cumulative data. Tree height had a heritability of 0.48 based on family means and 0.28 on an individual-tree basis (*Table 7*). The heritability of rust-free percentage has varied little over time: 0.62 at age 5 (SLUDER, 1981) and 0.69 at age 10 (SLUDER, 1988) and age 15.

The genetic correlation between percentage rust-free and average tree height has varied with time: 0.30 at age 5, 0.57 at age 10, and now 0.39 at age 15 years.

Table 4. — 15-year means for the check lots and the diallel.

Lot	Height	D.b.h.	Vol/tree	Survival	Rust-free At 15	Rust-free Cum. to 15
	m	cm	m^3	Percent	Percent	Percent
Orchard	12.40	17.7	0.129	50.07	4.54	0.00
GCIA	11.25	15.8	.099	69.12	2.27	1.56
Diallel	11.95	16.8	.102	70.87	20.61	10.52

Table 5. — Mean squares and significance tests for diallel analyses of plot mean and individual tree data.

Source	Height	D.b.h.	Vol/tree	Survival	Rust-free At 15	Rust-free Cum. to 15
	m	cm	m^3	Percent	Percent	Percent
Plot mean						
GCA	6.0768**	2.7321Ns	0.000931Ns	194.6778Ns	766.1271**	465.6744**
SCA	0.7118Ns	2.5043Ns	.000474Ns	166.7091Ns	40.5262Ns	48.7910*
Error	0.5109	2.4432	.000444	122.9133	31.3368	22.0872
Individual tree						
GCA	62.3276**	24.8342Ns	0.009427*			
SCA	7.2423*	15.7627Ns	.003394Ns			
Error	2.1345	12.1969	.002079			

Ns = Nonsignificant
*) Significant at the 0.05 level
**) Significant at the 0.01 level

Table 6. — Breeding values of the 10 parent clones, based on 15-year data.

Clone	Trait				Rust-free	
	Height	D.b.h.	Vol/tree	Survival	At 15	Cum. to 15
	m	cm	m^3	Percent		
1	12.94	16.81	0.1090	73.26	2.56	-2.25
2	11.97	16.28	.0960	63.21	12.49	5.86
3[1]	12.21	16.68	.1032	81.87	37.42	18.34
4[1]	13.09	17.24	.1150	77.96	33.22	16.96
5	12.32	17.19	.1090	58.65	-0.61	-0.39
6[1]	12.00	18.09	.1150	75.30	30.93	17.55
7	10.21	16.53	.0842	59.57	-1.94	-5.43
8[1]	11.07	16.27	.0906	73.96	23.84	16.42
9	11.35	16.21	.0922	65.45	-0.39	-5.48
10[1]	12.36	17.10	.1076	76.61	68.57	43.63
Mean	11.95	16.84	.1022	70.58	20.61	10.52
5 Best[1]	12.15	17.08	.1063	77.14	38.80	22.58
5 Worst[2]	11.76	16.60	.0981	64.03	2.42	-1.54

[1]/ Most resistant clones.
[2]/ Least resistant clones.

The crosses among the 5 clones with the highest rust resistance averaged 25.9% rust-free cumulative to age 15, ranging from 15.0% to 39.7% (*Table 8*). Their resistance compares very favorably with the cumulative percentage rust-free for both check lots (0.0% for the orchard and 1.6% for the GCIA) (*Table 4*).

The data in *tables 8* and *9* are the result of selection at three stages: the original selection to establish the seed orchard, selection of the 10 clones in the half-diallel (*Table 1*), and selection of the 5 most rust-resistant clones of the 10. Genetic gains from each of these selection stages can be estimated from the data. For the first 2 stages, the selection differentials (orchard check mean — GCIA check mean; and diallel mean — orchard check mean) directly estimate the genetic gains, since reproduction of the selected phenotypes actually took place. The third-stage selection differentials (5-clone mean — diallel mean) must be multiplied by the appropriate heritabilities (*Table 7*) to estimate genetic gains.

Genetic gain in fusiform rust resistance was substantial in Stages 2 and 3 (*Table 9*). Stage 1 produced a small gain if only 15th-year data were considered but a small loss based on cumulative results. Stage 1 produced a noticeable gain in tree size, which was the major trait for that selection. Some loss in tree size occurred in Stage 2, but no further change in the trait occurred in Stage 3. Selection of the largest rust-free phenotype from each family shown in *table 8* should produce more gain in rust resistance as well as some gain in tree size.

Analyses of rust mortality percentages yielded some *interesting* results. There were significant differences ($P < 0.01$) in mortality among the 45 crosses, wich was consistent with its negative correlation to percentage rust-free ($r = —0.49$). Also, GCA variation in rust mortality among the 10 parents was significant ($P < 0.01$). However,

Table 7. — Family and individual-tree heritabilities estimated from 15-year data.

Basis of heritability	Height	D.b.h.	Vol/tree	Survival	Rust-free At 15	Rust-free Cum. to 15
	m	cm	m^3	Percent	Percent	Percent
Family	0.48	0.01	0.11	0.02	0.69	0.52
Individual	0.28	0.01	0.03	--	--	--

Table 8. — Rust-free percentages cumulative to age 15 of the 10 crosses among the 5 most rust-resistant clones.

Male Clone	Female clone 4	Female clone 6	Female clone 8	Female clone 10
	Percent	Percent	Percent	Percent
3	18.79	14.96	20.76	39.58
4		23.75	15.20	36.14
6			16.46	33.33
8				39.69
	Mean = 25.87			

variation among the 45 crosses in percent mortality of trees *with infected stems* was significant only at the 0.05 level, and the 10 clones did not vary significantly in GCA for the trait. Furthermore, percentage mortality of infected stems was not significantly correlated with percentage of stems infected ($r = 0.22$). Apparently, genes that control susceptibility to stem infections do not directly control the development of established stem cankers or the sensitivity of the stem to them.

Discussion

The site of this study is an area of extremely high fusiform rust hazard, providing a rigorous test for rust resistance. For half of the clones, these site conditions may have overcome the resistance seen in earlier tests (Sohn *et al.*, 1975). The remaining clones, those that tested well in this study, should have stable resistance in central Georgia.

The clones used in this study were selected for resistance to fusiform rust, introducing the possibility of bias in estimated heritabilities. However, these heritabilities (0.69 at age 15 and 0.52 cumulative to age 15) are only slightly lower than the 0.65 to 0.85 range that Kinloch and Stone-

Table 9. — Genetic gains from the 3 stages of selection in this study.

Selection stage	Height	D.b.h.	Vol/tree	Survival	Rust-free At 15	Rust-free Cum. to 15
	m	cm	m^3	Percent	Percent	Percent
1. Orchard	1.15	1.9	0.030	-19.05	2.27	-1.56
2. 10 Clones	-0.45	-0.9	-0.027	20.80	16.07	10.52
3. 5 Clones	0	0	0	0.08	13.50	7.98
Total	0.70	1.0	0.003	1.83	31.84	16.94

Table 10. — Rust-free data cumulative to age 15 years, cross means.

Male clone	Female clone 2	3	4	5	6	7	8	9	10
	Percent								
1	0	1.67	0	1.67	3.12	0	5.01	3.45	28.70
2		19.36	2.50	6.97	11.69	3.59	2.50	0	29.46
3			18.79	6.47	14.96	0	20.76	4.35	39.58
4				11.61	23.75	3.12	15.20	9.37	36.14
5					7.05	1.78	3.59	0	11.92
6						10.79	16.46	1.67	33.33
7							7.46	0	4.17
8								7.71	39.69
9									4.17

Mean = 10.52

Table 11. — Specific combining abilities for rust-free cumulative to age 15 years.

Male clone	Female clone 2	3	4	5	6	7	8	9	10
	Percent								
1	-1.81	-6.37	-7.36	2.99	-4.53	3.84	-2.08	7.31	8.01*
2		7.26	-8.91*	4.23	-0.02	3.37	-8.65*	-0.19	4.71
3			1.14	-2.50	-2.98	-6.45	3.37	-2.08	8.68*
4				3.32	6.49	-2.65	-1.50	3.62	5.84
5					-1.53	4.69	-4.43	2.93	-9.70*
6						4.73	-0.53	-4.37	2.74
7							1.95	5.45	-14.93*
8								2.23	9.65*
9									-14.93*

*) Values ± 1.96 standard error or greater.

CYPHER (1969) reported after randomly sampling a natural population of loblolly pine in southwest Georgia. Apparently, selection has caused little decrease in variation in rust resistance among these clones compared with an unselected population.

One probable explanation of the positive correlation between mean height and rust-free percentage in this study is the negative effect that stem cankers have on height growth (SLUDER, 1977a). The correlation indicates that the 2 traits likely can be improved simultaneously.

Apparently, high susceptibility to stem infection does not predispose loblolly families or individuals to die after cankers form, since percentage mortality of infected stems was not significantly correlated with percentage of stems infected. Neither is low susceptibility to stem infections strongly linked to high tolerance of them, at least in these 10 genotypes. The results of this and other similar studies point to a lack of knowledge about resistance mechanisms-how genes prevent infection by the fungus and how growth of cankers is controlled once infection has occurred.

However, SCA values may give some hints about gene action. Of the 45 crosses among the 10 clones in the half-diallel, 8 had high SCAs for percentage rust-free, cumulative to age 15 (*Tables 10, 11).* Of these 8 crosses, all involved at least one clone with a high GCA for rust resistance. Two of the 8 crosses involved high GCAs for both clones and had high, positive SCAs. Of the remaining 6 crosses — each involving a high and a low GCA for rust resistance — 5 had rust-free percentages that were lower than expected, based on the mean GCA of their parents. In low x high crosses, apparently, susceptibility tends to be dominant over resistance.

Intensive selection and breeding programs have produced significant gains in resistance to fusiform rust. What is lacking now is an understanding of the genes involved and the resistance mechanisms that they control. Some of the clones used in this study produced crosses with large negative SCA values. These could prove useful as genotypes for studying resistance mechanisms, either by exposure to fungal strains of differing virulence or by analyzing DNAs or isozymes to find chemical markers associated with genes that control reaction to infection.

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