FUSIFORM RUST IN HALF-DIALLEL CROSS PROGENIES OF RESISTANT OR SUSCEPTIBLE LOBLOLLY AND SLASH PINES[1/]

E. R. Sluder

ABSTRACT. Progenies from a half-diallel cross among six loblolly pines and another among six slash pines were field-tested in central Georgia for fusiform-rust resistance. Three of each set of six parents had been typed as resistant (R) and three as susceptible (S) to the fungus in previous progeny tests that included check lots. At age 5 years, the 15 progenies of each species varied significantly in percentage infection and number of galls per tree. The RXR slash crosses produced highly resistant offspring but the RXR loblolly crosses produced progenies that were 79 percent infected. All SXS crosses of both species produced very susceptible progenies and RXS progenies were intermediate in susceptibility. Each set of parents varied significantly in general and specific combining abilities. The mean breeding values for the R slash parents were 25.5 for percent infection and 0.57 for galls per tree. For loblolly R parents, the corresponding values were 79.4 and 3.05. For the S parents, the respective breeding values were 94.1 and 3.26 for slash and 96.1 and 6.43 for loblolly.

Keywords: *Pinus taeda*, *Pinus elliottii*, *Cronartium quercuum* f. sp. *fusiforme*.

The fusiform-rust fungus (*Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*) seriously decreases wood production in plantations of loblolly (*Pinus taeda* L.) and slash (*P. elliottii* Engelm. var. *elliottii*) pines in much of the Southeastern U. S. (Anderson and others 1986). Losses occur as mortality, decreased growth of infected stems, and altered wood properties and decay in cankered tissue (Sluder 1977a). Breeding for genetic resistance to the fungus is considered the most practical way to reduce losses in commercial plantations of these two pine species. Both research on and applied breeding programs for rust resistance in slash and loblolly pines are being conducted. This paper reports the rust resistance in a half-diallel cross among six loblolly pine clones and another among six slash pine clones. In each species, half of the clones were typed as resistant and half were typed as susceptible to rust.

[1/] In cooperation with the Georgia Forestry Commission and the Georgia Pacific Company.

[2/] Principal Plant Geneticist, Macon, GA.

MATERIAL AND METHODS

The parents in this study were seed orchard clones that had been progeny tested for resistance to fusiform rust. Six loblolly and six slash pine clones were selected for study. In field tests of each set of six clones, progenies of three had proven more resistant and three less resistant than the check lot to fusiform rust (Table 1).

The **six** clones of each species were crossed in a modified half-diallel (no selfs) arranged according to flowering phenology (Sluder 1977b). Seedlings from the crosses were field-planted in 1978 in Houston County, Georgia, in an area of known high incidence of fusiform rust. Plantings included four replications in randomized complete blocks. Each replicate had a 16-tree plot of each progeny. Each plot had two rows of 8 trees spaced 2.5 m between and 1.25 m within rows. Study sites for the two species were adjacent.

At age 5 years the number of galls on each tree was recorded and the percentage of the trees infected in each plot was calculated. Analyses of variance and diallel analyses (Model I) were performed on the data for each half-diallel. From the diallel analyses, variance components were calculated and used to estimate heritabilities of percentage infection and galls per tree at age 5 years (Becker 1984). Breeding values of each clone were calculated for these two traits.

RESULTS

For each species, the progenies varied significantly both in percentage infection and galls per tree (Table 2). The resistant x resistant (RXR) and the resistant x susceptible (RXS) crosses of slash pine had less rust than did the same types of crosses of loblolly pine. The SXS crosses were very susceptible in both species. Relative susceptibility of the three types of crosses was RXR<RXS<SXS for each species (table 2).

Table 1.--Rust infection and galls per tree on progenies of loblolly and slash pine parents in previous progeny tests (percent differences from check lots).

Parent	Rust rating[1/]	Rust trait			
		% infected		Galls/tree	
		(%)[2/]			
		loblolly	slash	loblolly	slash
1	R	-2	-44	-24	-28
2	S	1	31	59	96
3	R	-10	-58	-50	-21
4	R	-39	-35	-44	-6
5	S	3	26	81	74
6	S	21	134	35	49
MEAN	R	-17	-46	-39	-18
	S	8	64	58	73

[1/] R = resistant, S = susceptible to fusiform rust.

[2/] Percent = [(progeny mean - check mean)/check mean]x100. Negative values are desirable, positive values are undesirable.

Table 2.--Mean fifth-year fusiform-rust data from half-diallel crosses among six loblolly and six slash pines.

Parent			Trait	
Female	Male		Percent Infected	Galls/Tree
			Loblolly	
4 (R)[1/]	3 (R)[1/]		62.0 a[2/]	1.67 a[2/]
5 (S)	4 (R)		76.5 b	2.56 ab
6 (S)	4 (R)		82.8 bc	3.50 a-c
3 (R)	1 (R)		84.0 b-d	3.59 a-c
5 (S)	1 (R)		87.5 b-e	6.11 c-e
2 (S)	1 (R)		88.2 b-e	4.69 b-d
6 (S)	1 (R)		89.4 c-e	5.06 b-d
4 (R)	1 (R)		90.6 c-e	4.09 a-d
6 (S)	3 (R)		91.4 c-e	4.38 b-d
6 (S)	2 (S)		92.0 c-e	5.86 cd
5 (S)	3 (R)		92.1 c-e	4.30 b-d
4 (R)	2 (S)		92.2 c-e	5.11 b-d
3 (R)	2 (S)		93.4 c-e	6.52 de
6 (S)	5 (S)		96.9 de	5.18 b-d
5 (S)	2 (S)		98.4 e	8.46 e
		Mean: RXR	78.9 a[3/]	3.12 a[3/]
		RXS	88.2 b	4.69 b
		SXS	94.0 c	5.91 c
			Slash	
4 (R)	3 (R)		18.1 a	0.49 a
3 (R)	1 (R)		28.6 ab	0.78 ab
4 (R)	1 (R)		39.2 bc	1.02 ab
6 (S)	3 (R)		42.5 bc	0.89 ab
4 (R)	2 (S)		46.5 bc	1.16 a-c
3 (R)	2 (S)		47.8 bc	1.33 a-c
5 (S)	3 (R)		52.9 cd	1.05 ab
2 (S)	1 (R)		55.6 cd	1.00 ab
6 (S)	1 (R)		58.6 cd	2.02 cd
5 (S)	4 (R)		59.2 cd	2.04 cd
5 (S)	1 (R)		70.5 d	1.70 b-d
6 (S)	4 (R)		94.1 e	3.18 ef
6 (S)	2 (S)		98.3 e	2.54 de
5 (S)	2 (S)		99.2 e	3.61 f
6 (S)	5 (S)		100.0 e	4.68 g
		Mean: RXR	28.6 a	0.76 a
		RXS	58.6 b	1.60 b
		SXS	99.2 c	3.61 c

[1/] R = rated resistant, S = rated susceptible to fusiform rust.
[2/] Within a column, means followed by a common letter do not differ at the 0.05 level, Duncan's Multiple Range Test.
[3/] Within column, cross type means not followed by a common letter differ at the 0.05 level.

The diallel analyses of plot means revealed highly significant differences among the **six** parents in general combining abilities (GCA) for both traits in both species (table 3). The only instance of nonsignificant variation in specific combining ability (SCA) of the parents was for galls per tree in loblolly pine. With individual-tree data, the loblolly as well as the slash pine parents showed highly significant GCA and SCA variation in number of galls per tree (Table 3). GCA and SCA estimates based on plot means are shown for the two traits in Tables 4 (loblolly) and 5 (slash).

Table 3.--Diallel analyses of variance of fusiform-rust data from half-diallel crosses among **six** loblolly and among six slash pines, age 5 years.

Source of variation	Trait			
	% Infected		Galls/tree	
	Mean square			
	Plot Means[1/]			
	loblolly	slash	loblolly	slash
GCA[2/]	122.43**	1691.30**	5.65**	3.14**
SCA[3/]	58.47**	144.21*	1.12	0.50**
Error (BXC)[4/]	17.99	38.57	0.66	0.09
	Individual tree[5/]			
GCA	--	--	293.66**	88.85**
SCA	--	--	115.16**	25.04**
Error (BXC)	--	--	32.80**	5.03*
Within plot			17.46	3.52

[1/] The Model I (fixed effects) analysis was used: both the GCA and SCA mean squares were tested against the BXC error mean square.

[2/] General combining ability.

[3/] Specific combining ability.

Blocks x crosses interaction.

[5/] The GCA, SCA, and BXC mean squares were tested against the within-plot mean square (Model I).

**Significant at the 0.01 level.

*Significant at the 0.05 level.

Table 4.--General (GCA) and specific (SCA) combining abilities based on plot means at age 5 years for a half-diallel cross among six loblolly pines.

Male parents	Female parents (S) 2	(R) 3	(R) 4	(S) 5	(S) 6	GCA
			SCA - - - - - -			
			Percent infected			
1 (R) [1/]	-6.03		11.39	-3.53	-1.91	0.14
2 (S)		3.36	6.86	1.24	-5.43	6.27
3 (R)			-13.01	5.26	4.29	-4.06
4 (R)				-5.63	0.39	-8.76
5 (S)					2.66	3.07
6 (S)						3.34
			Galls/tree			
1 (R)	-1.75	-0.30	1.08	0.68	0.29	-0.04
2 (S)		0.85	0.32	1.25	-0.69	1.74
3 (R)			-0.57	-0.36	0.38	-0.81
4 (R)				-1.22	0.38	-1.69
5 (S)					-0.36	0.73
6 (S)						0.07

1/ B= rated resistant, S = rated susceptible to fusiform rust.

Table 5.--General (GCA) and specific (SCA) combining abilities based on plot means at age 5 years for a half-diallel cross among six slash pines.

Male parents	Female parents (S) 2	(R) 3	(R) 4	(S) 5	(S) 6	GCA
			SCA - - - - - -			
			Percent infected			
1 (R) [1/]	-3.21	9.08	2.89	3.05	-11.79	-12.78
2 (S)		4.58	-13.53	7.99	4.19	10.92
3 (R)			-2.52	1.09	-12.24	-28.47
4 (R)				-9.42	22.57	-11.63
5 (S)					-2.72	19.50
6 (S)						22.47
1 (R)	-0.29	0.76	0.17	-0.45	-0.19	-0.66
2 (S)		0.53	-0.47	0.68	-0.45	0.12
3 (R)			0.13	-0.57	-0.82	-1.16
4 (R)				-0.45	0.63	-0.32
5 (S)					0.83	0.98
6 (S)						1.04

1/ R = rated resistant, S = rated susceptible to fusiform rust.

The family heritability for percentage of progeny infected was considerably higher for slash than for loblolly pine. Heritability of number of galls per tree was nearly the same for the two species on a family basis, but was twice as high for slash as for loblolly pine on an individual-tree basis (Table 6).

In slash pines, the R and S parents differed greatly in breeding values. The R parents, when crossed with each other or trees of equal genetic value, are expected to produce offspring which would average only about 25 percent infection when planted on high-hazard sites (Table 7). Offspring from the S slash parents would average about 94 percent infection under similar conditions. Breeding values for galls per tree showed a similar contrast between R and S slash pine parents.

Table 6.--Heritabilities of rust traits at age 5 years for slash and loblolly pines.

Basis	Trait	
	Percent infected	Galls/tree
	Loblolly pine	
Family	0.25	0.56
Individual tree		0.17
	Slash pine	
Family	0.68	0.50
Individual tree		0.36

Table 7.--Breeding values for fusiform-rust traits of six loblolly and six slash pines as calculated from fifth-year data from half-diallel crosses.

Parent number		Trait			
		Percent infected		Galls/tree	
		Loblolly	Slash	Loblolly	Slash
1	(R)[1/]	88.1	35.2	4.66	0.51
2	(S)	100.0	82.6	8.21	2.07
3	(R)	79.7	3.8	3.12	0.00
4	(R)	70.3	37.5	1.36	1.19
5	(S)	93.9	99.8	6.20	3.79
6	(S)	94.5	100.0	4.88	3.91
Mean:	R	79.4	25.5	3.05	0.57
	S	96.1	94.1	6.43	3.26

[1/] R = rated resistant and S = rated susceptible to fusiform rust.

The contrast between mean breeding values of the R and S parents was not nearly as great with loblolly pine as with slash pine for percentage infection. The loblolly pine R clones averaged 79 percent infection and the S clones 96 percent (Table 7). The contrast between R and S parents for number of galls per tree was similar for the two species, but progenies from the loblolly parents are expected to average about twice *as many* galls per tree as progenies from the slash pine parents.

DISCUSSION

The breeding values in Table 7 indicate that progenies from the R loblolly parents would be much more likely to get at least one fusiform rust infection per tree than would be progenies from the R slash parents. The number of parents screened in selection was not large in either case, so these results do not necessarily indicate that it is easier to find highly resistant slash pines than it is to find highly resistant loblolly pines. The heritability estimates (Table 6) are quite high for slash pine, promising large gains per generation from selecting and breeding for resistance to fusiform rust in these families. One might argue that these parents had an unusually wide spread in resistance, resulting in inflated heritability estimates. But when resistant slash pines were crossed with other resistant ones, they produced resistant offspring. These heritabilities, of course, apply only to this study.

Selection for rust-free individuals is expected to produce lower gains per generation in the loblolly than in the slash pine families. A family heritability of 0.56 for galls per tree, however, indicates that selection to reduce the number of galls per tree would produce large gains in loblolly pine. In another loblolly study involving a half-diallel cross among 10 parents, with the progenies planted in the same area as this study, the heritability of the family mean galls-per-tree trait was 0.56. Heritability of the rust-free percentage trait, however, was 0.62 in that study, much higher than the 0.25 in the present study (Sluder 1981).

The significant variation in specific combining abilities indicates that some nonadditive variation in rust resistance is present in both species. It may be that only a few loci control resistance to fusiform rust. Nonadditive variation is difficult to use in applied breeding programs. Perhaps the SCA variation would be useful in studies of such subjects as dominance, mechanisms of resistance, or number and location of resistance genes.

LITERATURE CITED

Anderson, Robert L.; McClure, Joe P.; Cost, Noel; Uhler, Robert J. Estimating fusiform rust losses in five Southeast states. Southern Journal of Applied Forestry. 10:237-240; 1986.

Becker, Walter A. Manual of quantitative genetics. Fourth Edition. Academic Enterprises, Pullman, Washington. 1984. 186 p.

Sluder, Earl R. Fusiform rust in loblolly and slash pine plantations on high-hazard sites in Georgia. Res. Pap. SE-160. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station; 1977a. 10 p.

Sluder, Earl R. Easier pollination of half-diallel crosses by ranking flower phenology. Southern Journal of Applied Forestry. 1(4):16; 1977b.

Sluder, Earl R. A half-diallel cross among loblolly pines selected for resistance to fusiform rust. In: Proceedings of the Sixteenth Southern Forest Tree Improvement Conference; 1981 May 27-28; Blacksburg, VA; 1981:97-106.