A HALF-DIALLEL CROSS AMONG LOBLOLLY PINES SELECTED FOR RESISTANCE TO FUSIFORM RUST

Earl R. Sluder[1]

Abstract.--Fifth-year infection data from progeny tests of seed orchard clones of loblolly pine were used to select 10 clones for further breeding for rust resistance. At age 5, the 45 progenies from a half-diallel cross showed no significant differences in survival but differed significantly in height and highly significantly in percentage of rust-free trees and number of cankers per tree. General combining abilities of the clones were nonsignificant for survival, significant for height, and highly significant for rust traits. Specific combining abilities were nonsignificant for all traits. Heritability was low for survival, moderate for height, and high for rust-resistance traits.

Additional keywords: Pinus taeda, Cronartium quercuum fusiforme, heritability, progeny testing, variation.

Southern fusiform rust *(Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme)* has become a major problem in plantations of loblolly pine *(Pinus taeda* L.) in the Southeastern United States (Czabator 1971; Powers and others 1975). No effective cultural practices to control infection and damage by the fungus have been found. The use of planting stock that is genetically resistant to fusiform rust appears to be the only way to handle the problem.

Practical breeding programs were begun a number of years ago concurrently with research on variation in and inheritance of resistance to fusiform rust in loblolly pine. Stonecypher (1966) described a large study conducted in Georgia. Results from that study showed that loblolly pine varies in resistance to fusiform rust (Kinloch and Stonecypher 1969), heritability of resistance is under moderately strong additive control (Blair 1970), and family plus within-family selection should result in considerable improvement in resistance (Blair and Zobel 1971). Progenies from three single crosses among five loblolly pines of known resistance to fusiform rust had greater resistance to infection than did wind-pollinated progenies from the same five trees (Powers and Duncan 1976). Furthermore, there was high correlation between single cross progeny and mid-parent in degree of resistance (r = 0.98).

---

[1] Plant Geneticist, Southeastern Forest Experiment Station, USDA Forest Service, Macon, Georgia.

The clones in the Georgia Forestry Commission's loblolly pine seed orchard were progeny tested for rust resistance and other traits. The clones with above-average rust resistance were determined from the test data and 10 of them were crossed in a half-diallel (no reciprocals or selfs), producing 45 progenies. Based on the amount of information per experimental unit, the partial diallel is the best of four commonly used experimental designs for estimating heritability (Pederson 1972). This is a report of the 5th-year results from the outplanting of that diallel cross.

MATERIALS AND METHODS

The 10 clones used in the study were evaluated on the basis of 5th-year rust data from their progenies in several progeny test plantations located in Bleckley and Houston Counties, Georgia. Progenies of the clones ranged from 39 to 81 percent above their respective plantation means in rust resistance traits (table 1).

The clones were arranged in the half-diallel cross according to flowering phenology (Sluder 1977). Pollinations were made in 1972. Seedlings for the study were grown in peat pots in the greenhouse and field planted in Houston County, Georgia, in June 1974. The field design was randomized blocks, four replications, and 16-tree square plots with a tree spacing of 2.5 by 2.5 meters (8.2 by 8.2 feet). The study included the 45 crosses and three checklots. The checklots were two standard lots and a bulk seed orchard lot.

Progenies were assessed at age 5 for survival, height, number of rust cankers per tree, and the percentage of rust-free trees. Standard randomized block analysis of variance was made for all traits. In addition, diallel analysis was made for all traits according to methods of Griffing (1956) and Becker (1975), with clonal effects assumed to be random (table 2). Heritabilities (h^2) were estimated on family means for survival and percentage of rust-free trees. For height and numbers of rust cankers per tree, heritabilities were estimated on a family mean and on an individual tree basis.1/

1/ $h^2_{fam.} = \sigma^2_{GCA} \div (\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{e})$

$h^2_{ind.} = 4\sigma^2_{GCA} \div (\sigma^2_{GCA} + \sigma^2_{w} + \sigma^2_{p})$

σ^2_{GCA} = general combining ability variance

σ^2_{SCA} = specific combining ability variance

σ^2_{e} = error variance

σ^2_{w} = within-plot variance

σ^2_{p} = variance among plots

Table 1.--*Loblolly pine clones used in the study and the superiority of their progenies in rust resistance at age 5 in the original progeny test plantations*[a]

Clone		Superiority of progeny over plantation mean	
G.F.C. serial number	Tree identification	Percent	SD
518	Coweta 1	39.2	1.13
520	Coweta 3	50.2	3.45
541	Greene 5	71.9	1.51
542	Greene 6	50.9	1.46
566	Heard 15	47.9	1.93
578	Morgan 3	80.5	1.69
582	Morgan 7	80.9	2.34
600	Morgan 57	67.2	1.22
603	Putnam 4	74.1	0.96
617	Sumter 1	75.8	2.79
Mean		63.9	1.85

[a]/ Resistance was based on percentage of rust-free trees or on the number of cankers per tree.

Table 2.--*Expected mean squares for the diallel analysis of variance*

Source	df	Expected mean squares[a]
GCA	9	$0.0211\sigma^2_w + \sigma^2_{sca} + 8\sigma^2_{gca}$
SCA	35	$0.0211\sigma^2_w + \sigma^2_{sca}$
Error	33	$0.0211\sigma^2_w$

[a]/ σ^2_w = variance among full sibs within plots; σ^2_{gca} = general combining ability variance; σ^2_{sca} = specific combining ability variance. The coefficient 0.0211 is the reciprocal of the harmonic mean number of full-sibs per cross, 47.45.

Variance components, general and specific combining abilities, and breeding values also were estimated. Confidence limits for combining abilities were calculated by multiplying their standard deviations which were calculated according to Griffing (1956) by the appropriate value from a standard t-distribution table. Genetic correlations between percentage of rust-free trees and number of cankers per tree and between percentage rust-free and height were calculated. Genetic gains in rust resistance with different intensities of selection were estimated.

RESULTS

Randomized Block Analysis

Differences among the 45 diallel progenies were nonsignificant for survival, significant for height, and highly significant for percentage rust-free and number of cankers per tree (table 3).

Table 3.--*Mean squares of randomized block analysis of variance and of diallel analysis of 5th-year data*

Source	df	Survival	Height	Rust-free	Cankers/tree
			ANALYSIS OF VARIANCE		
Block	3	996.44**	3.47**	653.00**	72.86**
Progeny	44	253.31	0.20*	659.00**	19.14**
Error	132	220.92	0.12	152.18	3.83
			DIALLEL ANALYSIS		
GCA	9	72.95	0.098*	628.59**	17.35**
SCA	35	60.86	0037	45.46	1.55
Error	33	55.23	0.031	38.04	0.96

GCA = general combining ability; SCA = specific combining ability.
* Significant at the 0.05 level.
** Significant at the 0.01 level.

Diallel Analysis

Neither general nor specific combining ability variation was significant for survival (table 3). For height, general combining ability (GCA) was significant but specific combining ability (SCA) was nonsignificant. GCA was highly significant both for percentage rust-free and number of cankers per tree, but neither trait exhibited significant variation in SCA,

Estimates of variance components for GCA and SCA and their standard deviations are shown in table 4. For SCA, the standard deviation is greater than the variance component for all traits except number of cankers per tree. For GCA, the standard deviation is greater than the variance component for survival only. Variance components expressed as percentage of total including error indicate that relative GCA variance is low for survival, moderate for height, and high for rust resistance (table 5). Relative SCA variance is low for all traits.

Table 4.--*Variance components for GCA and SCA and their standard deviations*

Variance source	Component	Standard deviation
	SURVIVAL	
GCA	1.5111	4.2714
SCA	5.6259	19.3522
	HEIGHT	
GCA	0.0077	0.0054
SCA	0.0063	0.0113
	PERCENTAGE RUST-FREE	
GCA	72.8911	33.5298
SCA	7.4133	13.9431
	CANKERS PER TREE	
GCA	1.9753	0.9261
SCA	0.5955	0.4271

GCA = general combining ability; SCA = specific combining ability.

Table 5.--*variance components by trait expressed as percentage of total*

Variance source	Variance component			
	Survival	Height	Rust-free	Cankers/tree
		Percent		
GCA	2.4	17.3	61.6	56.0
SCA	9.0	14.1	6.3	16.9
Error	88.6	68.6	32.1	27.1

GCA = general combining ability; SCA = specific combining ability.

Mean data for the 10 clones are shown in table 6 and their general combining abilities in table 7. Two clones had general combining abilities for survival which exceeded the 0.05 confidence limits even though analysis of variance indicated no significant variation in GCA for that trait. Two or more combining abilities exceeded confidence limits in all instances where analysis of variance indicated significance.

Table 6.--*Fifth-year data means by clone and trait*

Clone	Trait			
	Survival	Height	Rust-free	Cankers/tree
	Percent	*m*	*Percent*	*No.*
617	90.9	3.39	10.9	7.75
518	85.1	3.21	12.6	5.34
541	85.1	3.31	25.4	4.22
600	86.3	3.47	19.3	5.15
603	86.8	3.25	14.2	5.96
520	83.9	3.26	22.8	5.30
542	85.6	3.21	10.1	7.21
578	84.7	3.15	24.2	3.88
566	80.4	3.19	16.1	4.73
582	83.4	3.36	34.8	3.94
Mean	85.2	3.28	19.0	5.35

[a/] Means for the nine crosses involving the clone.

Table 7.--*General combining abilities by trait for the 10 clones*

Clone	Trait			
	Survival	Height	Rust-free	Cankers/tree
	Percent	m	*Percent*	*No.*
617	6.4*	0.12*	-9.6**	2.70**
518	-0.2	-0.07	-7.2**	-0.01
541	-0.1	0.03	7.2**	-1.27**
600	1.2	0.21**	0.3	-0.22
603	1.7	-0.04	-5.3*	0.68*
520	-1.5	-0.02	4.3*	-0.05
542	0.5	-0.08	-10.0**	2.09**
578	-0.6	-0.14*	5.9**	-1.65**
566	-5.4*	-0.10	-3.4	-0.69*
582	-2.1	0.08	17.8**	-1.58**

* Exceeds the 0.05 confidence limits.
** Exceeds the 0.01 confidence limits.

Combining abilities are expressed as values above or below the diallel mean. Breeding values of the clones, however, are absolute values and can be compared with check means as well as among themselves (table 8). None of the clones showed a serious deficit in survival ability and height growth, in comparison with checks, but clones 518, 542, 603, and 617 proved low in rust resistance at this planting site. Clones 520, 541, 578, 582, and 600 showed good to high rust resistance.

Table *8.--Breeding values of the 10 clones by trait*

Clone	Trait			
	Survival	Height	Rust-free	Cankers/tree
	Percent	*m*	*Percent*	*No.*
617	98.0	3.52	-0.3	10.7
518	84.9	3.14	4.6	5.3
541	84.9	3.34	33.4	2.8
600	87.6	3.70	19.7	4.9
603	88.7	3.20	8.3	6.7
520	82.3	3.24	27.6	5.2
542	86.2	3.12	-1.1	9.5
578	84.1	3.00	30.7	2.0
566	74.3	3.08	12.4	4.0
582	81.1	3.44	54.6	2.2
Diallel mean	85.2	3.28	19.0	5.3
Check mean	87.5	3.09	6.3	8.7
Percentage gain over check	-3	6	202	64

The correlation between the percentage of superiority of the clone progenies over their respective plantation means (table 1) and the breeding values calculated with the data from this diallel (table 8) was 0.48, non-significant, for the rust-free trait. This is a rather weak agreement between results from the original progeny tests and this diallel cross. The mean breeding value for the 10 clones, however, was 202 percent above the check mean for percentage rust-free, a good indication that some gain in rust resistance has been made.

Heritability was very low for survival in this study, moderate for height, and strong for rust-resistance traits (table 9). For height and cankers per tree, heritability was lower on an individual tree basis than on a family basis.

Phenotypic standard deviation of the traits are also shown in table 9. These values were used to estimate expected genetic gain in rust resistance for various intensities of selection which might be done on these families and individuals (table 10).

The genetic correlation between percentage rust-free and average number of cankers per tree was 0.87. It was 0.30 between percentage rust-free and average height.

Table *9.--Heritability and phenotypic standard deviation of the traits at age 5 based on family means and individual trees*

Trait	Heritability		Phenotypic SD	
	Family	Individual	Family	Individual
Survival (%)	0.02		7.90	
Height (m)	0.17	0.09	0.21	0.58
Rust-free (%)	0.62		10.89	
Cankers/tree (No.)	0.56	0.26	1.88	5.53

Table *10.--Expected genetic gain in rust resistance for six intensities of selection*

Selection intensity	Upper percentage	Trait gain		Percent of mean	
		Family	Individual	Family	Individual
		PERCENTAGE RUST-FREE			
1.16	30	7.83		41.2	
1.40	20	9.45	--	49.7	
1.76	10	11.88	--	62.5	
2.06	5	13.91	-	73.2	
2.42	2	16.33		85.9	
2.64	1	17.82		93.8	
		CANKERS PER TREE			
1.16	30	-1.22	-1.67	-22.8	-31.2
1.40	20	-1.47	-2.01	-27.5	-37.6
1.76	10	-1.85	-2.53	-34.6	-47.3
2.06	5	-2.17	-2.96	-40.6	-55.3
2.42	2	-2.55	-3.48	-47.8	-65.0
2.64	1	-2.78	-3.80	-52.0	-71.1

DISCUSSION

Statistical significance in GCA and nonsignificance in SCA in this study indicate that variation in rust resistance among these clones is largely additive and standard selection procedures should be effective in producing gains in rust resistance. The high genetic correlation between percentage rust-free and number of cankers per tree indicates that either measure of rust resistance can be successfully used for selection purposes. The low genetic correlation between percentage rust-free and height indicates that both traits can be improved with little if any correlated response of one to the other.

The average breeding value of 19 percent rust-free for the 10 parents in this diallel does not reflect a level of rust resistance high enough to meet the needs for central Georgia. One generation of selection was not enough, but these study results show that further gains in rust resistance can be made in subsequent generations of selection and progeny testing.

For example, selecting the best 30 percent of these families will result in a gain in percentage rust-free of 41 percent of the mean (Table 10). In terms of cankers per tree, the same selection intensity for families will produce a 23 percent gain, with another 65 percent gain possible by selecting the best 2 percent of individuals within the selected families. These gains are similar to predicted gains reported by Blair and Zobel (1971).

There are two possible sources of inaccuracy in predicting gains with data from this study. One is that the clones do not represent a completely random population. They are a sample of clones which on the average have a degree of rust resistance somewhat above the general population mean. I have assumed, however, that variances have not been significantly altered by the degree of selection already effected. Another possible source of inaccuracy is that only one test site was used. This can lead to a genotype x environment interaction component in the numerator of the heritability equation (Namkoong and others 1966). however, the block x family interaction was not significant on this site for number of cankers per tree even though there were highly significant differences among the block means for the trait. Infection levels differed among the blocks, indicating differences in inoculum level. Therefore, differences in inoculum level among test sites probably would cause little if any nonadditive genetic variance in the heritability numerator but differences among locations in genotype of the fungus might (Snow and Kais 1970; Powers and others 1977).

CONCLUSIONS

Ten loblolly pine clones with above-average resistance to fusiform rust were crossed in a half diallel. At age 5, the 45 progenies from the half-diallel cross showed no significant differences in survival but differed significantly in height and highly significantly in percentage of rust-free trees and number of cankers per tree. General combining abilities and heritability of the 10 clones were high or highly significant for rust-resistance traits. Selection among and within these or similar progenies coupled with further breeding should produce large gains in resistance to southern fusiform rust.

LITERATURE CITED

Becker, W. A. 1975, Manual of quantitative genetics. 3rd ed. 170 p. Wash, State Univ. Press, Pullman.

Blair, R. L. 1970, Quantitative inheritance of resistance to fusiform rust in loblolly pine. Diss. Abstr, 31:5737-B,

Blair, R. L., and Zobel, B. J. 1971. Predictions of expected gains in resistance to fusiform rust in loblolly pine. p. 52-67, Proc. Eleventh Conf. South. For. Tree Improv., Atlanta, Ga.

Czabator, F. J. 1971, Fusiform rust of southern pines: a critical review, USDA For. Serv, Res. Pap. SO-65, 39 p.

Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Aust. J. Biol. Sci, 9:463-493.

Kinloch, B. B., and Stonecypher, R. W. 1969. Genetic variation in susceptibility to fusiform rust in seedlings from a wild population of loblolly pine. Phytopathology 59(9):1246-1255,

Namkoong, G., Snyder, E. B., and Stonecypher, R. W. 1966. Heritability and gain concepts for evaluating breeding systems such as seedling orchards, Silvae Genet, 15:76-84,

Pederson, D. G. 1972, A comparison of four experimental designs for the estimation of heritability. Theor. Appl. Genet. 42:371-377.

Powers, H. R,, Jr., and Duncan, H. J. 1976. Increasing fusiform rust resistance by intraspecific hybridization, For. Sci, 22:267-268.

Powers, H. R., Jr., Matthews, F. R,, and Dwinell, L. D. 1977, Evaluation of pathogenic variability of *Cronartium fusiforme* on loblolly pine in the southern USA. Phytopathology 67:1403-1407.

Powers, H. R,, Jr,, McClure, J. P„Knight, H. A,, and Dutrow, G. F. 1975. Fusiform rust: forest survey incidence data and financial impact in the south. USDA For, Serv. Res. Pap. SE-127, 16 p.

Sluder, E. R. 1977, Easier pollination of half-diallel crosses by ranking flower phenology. South. J. Appl. For. 1(4):16.

Snow, G. A., and Kais, A. G. 1970. Pathogenic variability in isolates of *Cronartium fusiforme* from five southern states. Phytopathology 60:1730-1731.

Stonecypher, R. W. 1966. The loblolly pine heritability study. Southlands Exp. For. Tech. Bull. 5, 128 p. Int. Pap. Co., Bainbridge, Ga.