PREDICTED GAINS FOR FUSIFORM RUST RESISTANCE IN SLASH PINE

D. L. Rockwood and R. E. Goddard[1/]

Abstract. --Genotype x environment interactions for fusiform rust resistance were observed, but interactions of progenies were unrelated to mean infection levels. Heritabilities of individuals were very low while heritabilities of progeny means were high. Breeding methods utilizing progeny test evaluations or family selection may increase resistance relative to commercial checks by as much as 50 percent.

Additional keywords: Pinus elliottii Engelm. var. elliottii, forest tree improvement, breeding.

Resistance to fusiform rust, Cronartium fusiforme Hedgc. & Hunt ex Cumm., in slash pine, Pinus elliottii engelm. var. elliottii, is of primary importance to many members of our Program[2/], Particularly relevant at this time are predictions of gain by various breeding methods so that maximum improvement in resistance may be achieved.

MATERIALS AND METHODS

Fusiform rust incidence data were taken from field tests five years after establishment. The tests were planted by members of the Program as part of the progeny testing program of seed orchard clones.

Eight open-pollinated progeny tests of Brunswick Pulp and Paper Company (BPP) were utilized (Table 1). Two tests were established per year over a four year period as randomized complete block designs with five replications and seven-tree row plots. Nineteen progenies were common to tests 6 through 11, and a separate group of 19 progenies were present in tests 8 through 13.

Two full-sib progeny tests of Container Corporation of America (CCA) and one of Continental Can Company (CCC) were also used to estimate genetic variances (Table 2). Each test was a RCB with 10-tree row plots; CCA tests had four replications, the CCC test five. Twenty-two crosses from four males and seven females were common to the CCA tests. Two sets of crosses, one consisting of 12 progenies from three males and five females and another with 12 crosses from four males and four females, were used in the CCC test.

Analyses of variance were applied to each test and combination of tests. Each of the open-pollinated tests had sources of variation and degrees of freedom as shown in Table 3. Combined open-pollinated tests had additional sources

1/Postdoctoral Associate and Associate Professor, respectively, University of Florida.

2/ University of Florida Cooperative Forest Genetics Program.

of variation for years, sites and appropriate interactions (Table 4). The analyses of variance for the control-pollinated tests were as presented in Table 5. Male and Female variance components (σ_M and σ_F) estimated ¼ σ^2, and the male x female variable component σ^2_{MF} was an estimate of 1/4 σ^2_D

Table 1.--BPP open-pollinated progeny tests utilized

Test	Year Established	No. of Families	Ave. Fusiform Rust Incidence	
			Families	Checks
			(% infected)	
1-6	1964	35	34	29
1-7	1964	35	23	14
1-8	1965	56	18	8
1-9	1965	56	16	19
1-10	1966	58	32	22
1-11	1966	57	21	15
1-12	1967	46	59	43
1-13	1967	46	58	46

Table 2.--CCA(3) and CCC(4) full-sib progeny tests utilized

Test	No. Males	No. Females	No. Families	Ave. Fusiform Rust Incidence	
				Families	Checks
				(%infected)	
3-6	4	9	29	16	15
3-7	4	11	38	37	32
4-3	7	11	28	70	55

Data presented here were based on rust observations expressed as percent of trees infected per plot. Within-plot variance for a test was estimated by (mean percent infected) x (100 - mean percent infected). Analyses were also performed as described by Becker and Marsden (1972), namely, adjusting the ratio of the number of trees infected to the number of trees per plot and then transforming the adjusted ratio by arcsin of the square root. Through the use of the constant binomial sampling variance, within-plot variances were estimated. Variance components and heritabilities derived by the two methods were virtually identical.

Heritability estimates and predicted gains for various breeding methods were based on procedures outlined by Shelbourne (1969). Individual contributions to genotype by environment interactions were obtained by a method presented by Shelbourne (1972) for partitioning the interaction sum of squares.

Table 3.--Analyses of variance for open-pollinated tests 6 - 13

Source	d.f.	Mean Squares					
		Test: 6	7	8	9	10	11
Reps	4	1424.6**	740.4*	250.4	1030.9*	977.1	274.4
Progenies	18	1045.4**	594.0**	341.4	421.5	620.4	325.5
Error	72	345.1	231.2	248.7	348.4	482.1	216.4
Total	94						
Ave. Infection		33.1	19.1	16.0	20.9	31.6	16.3
Range of Progeny Means		8.6-66.2	8.4-51.6	0-34.2	0-38.0	5.6-45.4	6.2-92.8
		Test: 8	9	10	11	12	13
Reps	4	262.8	250.7	905.2	523.6*	430.3	496.2
Progenies	18	743.6*	491.6	612.4	800.9**	1252.0**	1138.8**
Error	72	377.1	354.0	403.1	202.3	400.8	435.3
Total	94						
Ave. Infection %		17.8	16.3	32.1	20.9	59.4	58.0
Range of Progeny Means		2.8-48.6	0-35.6	11.4-50.4	0-42.8	25.2-90.4	23.2-83.6

* and ** significant at the 5 and 1% levels, respectively.

Table 4.--Analyses of variance for combined open-pollinated tests

Source	d.f.	Tests 6-11		Tests 8-13	
		MS	2	MS	
Years	2	2978.8	-22.3	90560.9**	465.8
Sites/Years	3	7220.4**	67.8	2063.4*	16.7
Reps/Sites/Years	24	873.0**	24.8	478.1	6.1
Progenies	18	1214.1**	24.7	2247.1**	48.3
Years x Progenies	36	474.6	5.3	799.5**	26.8
S/Y x Progenies	54	395.0	16.6	397.8	7.1
R/S/Y x Progenies	432	312.0	312.0	363.1	362.1
Total	569				
Ave. Infection		22.8		34.1	
Range of Progeny Means		14.0-31.5		13.4-51.5	

* and ** significant at the 5 and 17 levels, respectively.

RESULTS AND DISCUSSION

Environments strongly influenced observed rust levels in the combined tests. For BPP tests 6-11, infection levels between sites within years were different (Table 4). In BPP tests 8-13, sites within years were also important, but variation among years was greater. Here, the year to year differences were attributable to tests 12 and 13, which had much higher rust than tests 8-11. However, since the sites were not common across years, the higher rust in tests 12 and 13 cannot be attributed necessarily to yearly variation in rust. The effect may also be due to differing sites. The sites in the two county region of southeastern Georgia where the BPP tests are located do differ (Goddard and Vande Linde, 1967).

Differences among progenies were observed in both combined tests and most individual tests. Segregation of progenies into resistant and susceptible categories was easier in tests with higher rust levels due to greater ranges among progeny means.

Genotype x environment interaction variance components were large relative to the progeny variance component for both combined analyses (Table 4). The Sites/Years x Progenies variance component was considerable for tests 6 to 11, in which variation due to Sites/Years was great. In tests 8 to 13, where variation among years was large, the Years x Progenies interaction was the major interaction component. Apparently, whichever environmental factor is most influential will be the source of most interaction with progenies. The overall magnitude of interaction components indicates that selection of resistant progenies may depend on particular environmental conditions.

The above interactions of the open-pollinated progenies were unrelated to their mean infection levels. Correlations between infection percentages and Years x Progenies and Sites/Years x Progenies interactions were .04 and .26 for Tests 6-11 and -.19 and .38 for Tests 8-13. Variation of resistant progenies from test to test seems comparable to that of susceptible progenies.

Furthermore, the correlations between Years x Progenies and Sites/Years x Progenies interactions were .13 and .03, respectively, for the two combined tests. No apparent advantage would result from testing progenies over several sites per year as compared to testing on fewer sites per year over several years.

Specific crosses among genetic lines may offer no more resistance to disease at high levels of infection than general crosses. Table 5 shows that the magnitude of the Male x Female variance component decreased as infection rates increased. Further indication of the relative lack of dominance genetic variance at high levels of infection is the nonsignificance of Testers x Clones interaction in progeny tests with 90+ percent rust (Weir and Zobel, 1972).

Narrow-sense heritabilities tended to increase with rising infection rates (Table 6). Correlations among heritabilities of individuals and infection rates exceeded .4, while for heritabilities of progeny means, the correlations were about .35. The positive trend was evident up to the maximum infection rate in the present study, 70 percent.

Individual tree selection will not be a productive method of increasing resistance, based on the low heritabilities for individuals noted here, usually

Table 5.--Analyses of variance for full-sib progeny tests

Source	d.f.	3-6 MS	3-6 h^2	3-7 MS	3-7 h^2
Reps	3	327.95		252.04	
Males	3	965.95*	33.20	1678.21*	78.21
Females	6	358.90	9.04	2050.30*	164.88
Males x Females	12	245.48	17.75	-19.00	-93.82
Error	63	174.18	174.18	450.08	450.08
Total	87				
Ave. Infection %		16.1		35.2	

Source	d.f.	4-3 MS	4-3 h^2
Reps	4	422.60	
Progenies	23		
Sets	1	10,603.20*	
Males/Sets	5	4,928.45**	306.96
Females/Sets	7	906.05**	79.61
Males x Females/Sets	10	-136.44	-82.58
Error	92	193.86	193.86
Total	119		
Ave. Infection %		69.5	

and ** significant at the 5 and 17$_0$ levels, respectively.

Table 6.--Relationship of heritability to infection level in open-pollinated tests

Test	h^2 Individual	h^2 Progeny Mean	Ave. Infection %
Tests 6-11:			
6	.238	.670	33.1
7	.181	.611	19.1
8	.052	.271	16.0
9	.035	.174	20.9
10	.048	.223	31.6
11	.052	.335	16.3
Combined	.054	.623	22.8
Tests 8-13:			
8	.173	.493	17.8
9	.074	.280	16.3
10	.073	.342	32.1
11	.277	.747	20.9
12	.262	.680	59.4
13	.213	.618	58.0
Combined	.083	.685	34.1

less than .1. At high infection rates with concommitant higher heritabilities and more reliable identification of resistant trees, gains by individual selection would be greater but still not appreciable.

The original field selections made for BPP provide an example for the response resulting from phenotypic selection. Most of the trees were taken from stands with less than 30% rust infection, and, consequently, selection intensity was low. With heritability also low, the theoretical gain in resistance is minimal, about 9.47 relative to commercial checks. Realized response from BPP's clonal orchard has been a -28.2%; realized gains have not matched the expected. Similar responses from original selections have been observed for other companies.

While heritabilities for individuals were low, heritabilities of progeny means were high, often exceeding .6 (Table 6). Thus, progeny testing identifies genetic variation existing for rust resistance, and breeding methods relying on select tree evaluation via progeny testing should result in appreciable gains in resistance.

Roguing established clonal orchards, or establishing reconstituted orchards, is an expedient method of increasing rust resistance. In the case of BPP, and most cooperators in the Program, roguing of existing orchards allows recouping of the resistance lost in the first generation selections, and more. Specifically, BPP is establishing a new orchard including their top 31% resistant clones (25 of 81), and an improvement of as much as 28% over commercial checks could result.

While long-term efforts to capture specific combining ability for resistance appear unnecessary, short-term utilization of certain specific crosses showing exceptional resistance has potential. In fact, a number of biclonal orchards, with resulting seed being bulked, is a fast method of increasing resistance. Assuming no dominance genetic variance and an infection rate of 35%, production of specific progenies could result in an infection level of 14%, or a 45% improvement relative to the checks.

A seedling seed orchard composed of bulked open-pollinated progenies has been established by Buckeye Cellulose Corporation (BCC). Seed was collected from 50 clones in each of two orchards - BCC and University of Florida (UF), bulked by orchard, and planted in alternate rows. Subsequent thinning will retain one tree in an interval of 10. Separate rust evaluations indicate that the BCC clones contributed were more resistant than the UF clones. Observations in the orchard show 35.2% infection for the BCC progenies and 54.2% for the UF lines. Estimated gains from thinning are 2.4% for BCC and 8.2% for UF, or, assuming that the orchard production will be the average of the two, the total gain may reach 3.5%, an 8.2% gain relative to checks lots. This relatively low improvement is due to the inability to identify individual clone contributions (a consequence of the bulking of seed) and the high susceptibility of UF clones.

A full-sib seedling seed orchard is under development by BCC, and substantial improvement in rust resistance is expected. Twelve tested highly-resistant males in the Program are being crossed with eight known resistant females from the BCC orchard according to a factorial mating system to produce

96 full-sib families. Rust infection at the orchard site is expected to be about 50%. At that assumed infection level, our data suggest minimal dominance genetic variance will exist. Families will be rogued to approximately the best one in 10, and one tree in a row-plot of 10 in the selected families will be retained. Most of the gain to be realized from this orchard will result from the selection of families with a small increment coming from within-family selection. Total gain may reach 55% relative to commercial checks.

A seedling seed orchard consisting of open-pollinated progenies of 50 of the more resistant clones in the Program is being established by St. Joe Paper Company. The orchard will be thinned to the best 20 progenies and the best tree in a 10-tree row plot. Seventy percent infection at the site is expected. Total gain of 30% relative to commercial checks is anticipated.

The responses predicted here suggest that fusiform rust impact on slash pine management can be appreciably reduced if appropriate breeding programs are followed. Adequate progeny testing is essential in order to identify good general combiners. Employment of these good general combiners in subsequent breeding may lower infection levels by as much as 50%.

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