Gains in Volume Growth and Rust Resistance to Age 10 in Progeny Tests of Selected Slash Pines

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In the applied tree breeding program at Macon, Georgia, the objectives of the early work were to make phenotypic selections for a catalog of breeding material and to progeny test the selections, both to determine their breeding values and to demonstrate the inheritance of characteristics. The 10-year results of slash pine progeny tests reported here show that traits are inherited and that considerable gains in rust resistance and wood production can be realized through selection.

Materials and Methods

Materials for this study were 21 phenotypic selections of slash pine (Pinus elliottii ENGELM.) made in plantations in Jones (J) and Dooly (D) Counties, Georgia. Selections in Jones County were from one 18-year-old plantation. The Dooly County selections were from several plantations ranging from 14 to 18 years in age. All were of unknown provenance.

The Jones County plantation occupied several hectares. A total of 25 trees were selected in this plantation, 12 of which were used in this study. Along with each selected tree, 10 check trees were measured. Including 250 randomly selected check trees, a total of 275 trees well distributed over the plantation were measured. Population parameters were estimated from the 275-tree sample and selection intensities for three traits were calculated (Tab. 1). Based on height and diameter, the 12 Jones County trees used in this study represent approximately the upper 50 percent of the population.

Table 1. — Estimates of population parameters, selected mean, and standardized selection intensities for the Jones County trees.

	Total height	D.b.h.	Volume per tree
	Meters	Centimeters	Cubic meters
Population mean	15.24	29.84	0.57
Population standard dev.	2.49	6.12	0.27
Selected mean	17.04	34.54	0.81
		Standard deviations	
Selection intensity	0.72	0.77	0.89

The Dooly County trees were selected from several plantations with unknown population structures, but the bases for selection, and therefore selection intensity, were at least as high as those in the Jones County selections.

Thirty progenies were derived from the 21 selected trees. Seventeen were single-cross and 13 were open-pollinated progenies. These along with three control stocks, which were representative of seed being sown commercially at the time, were divided into two groups and outplanted in 1959 in Bleckley County, Georgia. Eight progenies and two controls were common to both plantations. The field designs were randomized blocks with four replications of 25-tree square plots in one plantation and five replications of 5-tree row plots in the other. Spacing was 10 by 10 feet.

At 5 and 10 years of age, height, presence or absence of rust on stems andlor branches, and survival were measured. Fifth-year results appear in a report by WEBB and BARBER (1965). D.b.h. was measured at 10 years. The volume of each tree at age 10 was calculated with the formula constructed by SCHMITT and BOWER (1970) for young slash pine grown in plantations (standard error of estimates of tree volume = 0.106 cubic foot or 3 cubic decirneters). Percentages were transformed to arcsin of their square roots for analysis. Data from the two plantations were combined for analysis according to the method of GOMEZ (1970). Data from the progenies and controls common to both plantations were used to adjust data from the other progenies for a combined multiple comparison test (DUNCAN, 1955). Progenies significantly better than controls were identified by DUNNETT's (1955) test. Family averages for the progenies were analyzed as an incomplete diallel to estimate breeding values (GILBERT, 1967)[1]). In the diallel analysis, wind was treated as one parent. Gains were estimated for three hypothetical intensities of individual tree selection and for each of the three stages of selection actually performed on this material.

Results

Family Means

Mean survival at 10 years was 92 percent. There were no significant differences in survival among families or between families and check lots.

Family means did differ significantly in volume per unit area, volume per tree, height, d.b.h., and percent rust-free (Tab. 2). Volume per hectare varied from 40 to 83 cubic meters (577 to 1192 cubic feet per acre). Twelve progenies were better than the average of controls in volume per unit area. Average volume per tree ranged from 42 to 92 cubic decimeters (1.47 to 3.27 cubic feet) and 12 of the progenies were better than controls. Average heights varied from 7.1 to 10.4 meters (23 to 34 feet) and 13 of the progenies were significantly taller than controls. The range in average d.b.h. was 12 to 17 centimeters (4.9 to 6.8 inches), with seven

[1]) Dr. E. B. SNYDER, Institute of Forest Genetics, Gulfport, Mississippi, did the diallel analysis.

progenies testing better than controls. Rust incidence varied from all trees infected in the two most susceptible families to 57 percent of the trees free of rust in the most resistant family. Only three families were significantly more resistant to rust than were the controls.

resistance are J2, J18, J20 and D28. These five trees also have good to acceptable breeding values for the other four traits listed in *Tab. 2*. J22 has the highest breeding values for volume growth, height, and d.b.h. but has a low breeding value for rust resistance.

Table 2. — Average 10-year data from two plantations, data adjusted for joint analysis[1]).

Progeny[2])	Volume per hectare	Volume per tree	Height	D.b.h.	Rust-free
	m^3	dm^3	m	cm	pct
J20 × W	83.42a *	82a—d*	9.88a—b*	16.18a—d	39.0a—b
D7 × D27	83.07a *	87a—b*	10.41a *	16.56a—b*	11.6b—f
J5 × W	80.80a—b*	78a—e*	9.63b—d*	16.18a—d	19.3a—e
J2 × W	80.03a—b*	82a—c*	9.65b—d*	16.53a—c*	12.6b—f
J11 × J2	79.43a—b*	81a—d*	9.63b—d*	16.46a—c*	38.4a—b
J14 × W	79.20a—b*	80a—d*	9.49b—d*	16.18a—d	57.1a *
J 18 × D104	78.33a—c*	83a—c*	9.59b—d*	16.38a—c*	14.8b—e
J22 × J12	76.76a—c*	77b—e*	9.74a—c*	15.75b—e	0.4e—f
J6 × W	74.75a—c*	72b—f	9.26b—d	15.65b—e	2.6d—f
J14 × J11	73.69a—c*	79a—d*	9.58b—d*	16.20a—d*	50.6a *
J18 × W	73.18a—d*	92a *	9.72a—c*	17.27a *	31.6a—c
J5 × D38	73.18a—d	74b—f	8.93d—g	16.00a—e	32.2a—c
J12 × J22	72.22a—d*	77b—e*	9.62b—d*	16.03a—d*	20.1a—d
D28 × W	72.03a—d	74b—f	9.25b—e	16.23a—d	26.8a—d
D7 × W	69.87a—d	77b—e*	9.20b—e	16.13a—d	11.1b—f
J20 × J6	69.68a—d	69c—g	9.52b—d*	15.26b—f	17.2b—e
D28 × D36	68.83a—d	71c—f	9.11c—e	15.59b—e	37.8a—b
J11 × W	65.84a—e	70c—f	8.96d—f	15.67b—e	6.3c—f
J18 × D27	62.09b—f	69c—g	9.36b—d	15.21b—f	21.3a—d
J18 × J6	60.11c—f	64e—g	9.01d—f	14.81d—g	49.9a *
Commercial	58.59c—g	65d—g	9.02c—f	14.99b—g	22.2a—d
Cont. D. 5	56.68d—g	61f—g	8.56e—g	14.81d—g	14.0b—e
J12 × W	55.66d—h	63e—g	8.89d—g	14.35f—g	11.3b—f
D12 × W	54.13d—h	58f—i	8.38f—h	14.27e—g	0.0f
J5 × J9	54.10d—h	57f—j	8.84d—g	13.89f—h	3.9c—f
Cont. D. 2	51.90e—h	57f—i	8.46f—g	14.43e—g	8.0c—f
D104 × D27	50.82e—h	54g—k	9.42b—d*	13.45g—h	1.3d—f
J26 × W	50.61e—h	55g—j	7.83h—i	14.83c—g	1.0e—f
D104 × W	49.23f—h	58f—i	9.32b—d	14.43e—g	3.4c—f
J5 × D111	44.94f—h	49h—k	8.44f—h	13.41g—h	1.2d—f
J26 × J25	44.20g—h	46i—k	7.49i—j	13.89g—h	23.9a—d
D104 × D9	43.38g—h	42j—k	8.17g—h	12.45h	0.0f
J25 × J26	40.41h	42k	7.08j	13.49g—h	18.2b—e
Average	64.54	68	9.07	15.24	18.4
Select average	65.46	69	9.11	15.29	18.8
Control average	55.72	61	8.68	14.73	14.7

[1]) Within each column, means not sharing a common letter differ significantly at the 5-percent level according to Duncan's new multiple range test. An asterisk(*) indicates family means that are better than the average of controls according to Dunnett's test at the 5-percent level.
[2]) J = Jones County, D = Dooly County, and W = wind pollinated.

The eight progenies and two control lots common to both plantations showed no progeny-by-plantation interactions in any of the traits except d.b.h.. The interaction in d.b.h. was caused by only two of the progenies.

The correlations between 5- and 10-year data were statistically significant for both height and rust. The coefficient for height was 0.90. For rust r was 0.62, with a considerable increase in rust incidence between ages 5 and 10. For example, in the larger plantation the rust-free percentages ranged from 60 to 98 at 5 years but at 10 years varied from less than 1 to 72.

There was no significant correlation between family height and rust infection rate at age 10.

Breeding Values; Parent-Progeny Relations

The breeding value — two times the general combining ability plus the general mean — of each of the 21 parent trees is shown in *Tab. 3*. Chck- lot averages are listed for comparison. J14 has the highest breeding value for rust resistance. Other trees with good breeding values for rust

The correlation between breeding values and superiority percentages of selected trees over their surrounding checks was calculated for height and d.b.h.. The correlation coefficients were 0.47 (significant) for height and 0.35 (nonsignificant) for d.b.h..

Gains

Under the assumption that these 21 trees represent the best 50 percent of the populations from which they were selected *(Tab. 1)*, percentages of gain from selection intensities in the original population were estimated by comparing average breeding values of the corresponding proportions of the 21 selected trees with the check-lot averages. Estimated gains from selecting the upper 50 percent of individuals were unimpressive, but were quite substantial when selected percentages were the upper 25 or 10 *(Tab. 4)*.

Gains listed in *table 4* were estimated independently for each trait. The bases for selection were the breeding value of the individual trees or genotypes selected from a base population. Second-generation selection, however, is

Table 3.—Breeding values of the selected trees, based on 10-year measurements of their progenies, for the traits evaluated

Selection	Volume per hectare	Volume per tree	Height	D.b.h.	Trees rust-free
	m^3	dm^3	m	cm	pct
J2	94.03	92	10.17	17.21	39.43
J5	91.19	81	9.96	16.33	29.45
J6	57.49	51	8.81	13.81	9.26
J9	17.00	32	7.72	11.45	-21.59
J11	62.83	68	9.00	15.65	16.02
J12	43.16	51	8.53	12.79	15.18
J14	87.46	88	9.96	16.60	96.14
J18	78.36	95	9.54	17.52	56.69
J20	90.34	88	10.38	16.58	48.02
J22	105.82	103	10.80	18.99	5.22
J25	51.71	53	8.12	13.64	47.70
J26	33.04	34	6.44	13.74	-5.40
D7	90.12	98	10.10	17.85	18.85
D9	35.90	29	6.97	11.13	8.77
D12	40.23	42	7.54	12.63	-6.91
D27	57.54	58	9.79	13.77	0.46
D28	75.86	73	9.28	16.54	46.17
D36	61.80	59	8.94	14.64	29.43
D38	55.16	67	7.90	15.67	35.00
D104	50.92	54	9.37	13.77	-8.42
D111	-13.15	17	6.92	10.49	-27.00
General mean	61.21	64	8.89	14.85	19.88
Check mean	55.72	61	8.68	14.73	14.70

Table 4.—Percentages of gain over checks for individual traits estimated for various proportions of the population selected on the basis of breeding values.

Trait	Proportion selected 1/		
	0.50	0.25	0.10
	Percent		
Volume per unit area	10	46	71
Volume per tree	5	36	59
Height	2	13	19
D.b.h.	1	13	21
Decrease in rust	6	32	56

1/ Proportions of the original population. The proportions 0.50, 0.25, and 0.10 represent, respectively, all 21 of the selected trees, the best 11, and the best 4. To calculate percentages of gain, breeding values of the 21, 11, and 4 trees were averaged and compared with the check-lot average.

based on family means, and the different traits can not be treated independently. Families must either be selected for one primary trait or for some combination of traits. In this study, families were selected for rust resistance, then culled to five on the basis of volume production. The results are shown in *Tab. 5*. These families were the best 16.7 percent for rust resistance, but for average volume per tree they were only the best 27 percent. Selection intensities for the other traits also were lower than for rust resistance.

The best rust-free tree in each family listed in *Tab. 5* was selected on the basis of tree size with some consideration given to form. The five selected trees averaged 103

Table 5.—Percentages of gain from family selection in slash pine 1/

Family	Volume per unit area	Tree volume	Height	D.b.h.	Rust 2/
	pct				
J14 x wind	42	31	9	10	50
J14 x J11	32	29	10	10	42
J18 x J6	8	5	4	1	41
D28 x D36	23	16	5	6	27
J18 x wind	31	51	12	17	20
Average	27.2	26.4	8.0	8.8	36

1/ Family averages compared with checklot average.

2/ Rust gains expressed as percentages of decrease in infection rates.

percent greater in volume per tree than the check-lot average. The genetic gain, however, would be less than 103 percent, depending upon heritability of volume per tree. A selection response equation (Falconer, 1960, p. 193) and data from *tables 1, 4,* and *5* were used to calculate two heritability estimates for volume per tree.

One estimate was from individual tree selection data (selection intensity = 0.89, gain = 3 cubic decimeters or 5 percent), and one from family selection data (S.I. = 1.17, gain = 13 cubic decimeters or 26 percent). The two estimates of heritability were 0.12 and 0.41, respectively, and averaged 0.26. With the value 0.26 for heritability and the within-family selection intensity used (1.90, or best one in 22)[2]), the estimated additional genetic gain in volume per tree from within-family selection was 23 percent. The total estimated gain in volume per tree in response to three stages of selection (initial phenotypic + family + within-family) performed on the material in this study was 54 percent *(Tab. 6)*.

Table 6. — Gains in volume per tree from three stages of selection in slash pine.

Stage of selection	Proportion selected	Selection intensity	Gain
			pct
Initial phenotypic	0.50	0.89	5
Family	0.27	1.17	26
Within-family	0.05	1.90	23
		Total	54

Discussion

The differences in breeding values *(Tab. 3)* of the 21 trees used in this study amply demonstrate the inheritance of fusiform rust, volume per tree, and volume per unit area. These and other published results leave no room for doubt that tree breeding could result in substantial gains in a number of traits. The relevant questions: "How much gain and will it pay?"

Namkoong (1970) questions whether progeny testing can be justified on the basis of gain per unit cost. The gain from family selection shown in *Tab. 6* could justify considerable progeny testing expense, particularly for a seed orchard that would be used to reproduce large areas. Had not

[2]) With 25-tree plots, selected trees were compared only with the others on the plot. With 5-tree plots, selected trees were compared with all the trees in the family on five plots. On the average, about 22 trees were surviving in each case.

these selections been progeny tested, gain in volume per tree would have amounted to only 5 percent. Granted, initial individual tree selection intensities normally are much higher than that used here and gains in volume per tree would be expected to be more than 5 percent; but based on this study, progeny testing can be expected to yield as much gain as individual tree selection.

To compare initial phenotypic selection and progeny testing, I selected the best 25 percent of these trees on the basis of their phenotypic superiorities in tree height and d.b.h. to their neighboring check trees. Their breeding values (*Tab. 3*) showed only about half as much gain in volume per tree (19 percent) as did the best 25 percent of the trees selected on the basis of breeding values (36 percent gain, *Tab. 4*). Selection within families would add still more gain to be utilized in a second-generation seed orchard. Thus, individual tree selection followed by family and within-family selection should yield at least double the gain in volume per tree that would result from individual tree selection alone. With progeny testing, one generation of approximately 39 years would accomplish that which would require at least two generations of individual tree selection spanning at least 50 years (NAMKOONG *et al.*, 1966). The cost per unit gain no doubt would be less with the latter approach (Namkoong, 1970), but the greater gain with progeny testing should yield a good return on the greater investment required to do it.

Rust resistance shows about the same response to selection as does volume per tree (*Tab. 4*). Large gains in rust resistance are urgently needed for seedlings to be planted in many areas. The gains can be obtained quickly only by progeny testing, as indicated by this study and by data reported by BLAIR and ZOBEL (1971) for loblolly pine and by ROCKWOOD and GODDARD (1973) for slash pine. The cost with combined selection for rust resistance and volume per tree will be high, but so will be the return in greater volume production per unit area.

Six of the 21 original selections in this study should be used for further breeding work. Five of them — J2, J14, J18, J20, and D28 — have good breeding values for rust resistance and the other, J22, has a very high breeding value for volume production. No crosses among these six trees have been made. They should be crossed in a half-diallel to generate a population for further selection for rust resistance and other traits.

Abstract

At 10 years of age, 30 wind- and cross-pollinated families from 21 selected slash pine (*Pinus elliottii* ENGELM.) trees differed significantly in volume per hectare, volume per tree, height, d.b.h., and percent rust-free. Breeding values of the trees varied greatly for the five traits. Estimated gains in the individual traits, based on breeding values, were one to 10 percent if the upper 50 percent of the original population were selected but were 19 to 71 percent if the upper 10 percent were selected. After an initial selection intensity of 0.89, selection among families (S.I. = 1.17) and within families (S.I. = 1.90) gave an added gain of 49 percent in volume per tree compared with the commercial check lots. The gain in rust resistance was 36 percent when the best 16.7 percent of the families were selected.

Key words:Pinus elliottii ENGELM., Cross-pollinated Families, Breeding value, Rust resistance.

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