THREE INCREMENTS OF GAIN FROM THREE STAGES OF SELECTION IN SLASH AND LONGLEAF PINES AND HERITABILITIES AT AGE 21 YEARS

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Abstract.--Three tandem stages of selection--individual, family, and within-family--performed in slash and longleaf pines produced good increments of gain in most of seven traits in most stages. Gains in d.b.h. and volume per tree were low or negative for the first two increments, but selection within families was very effective in producing gains in these two traits. Selection among families was primarily for rust resistance and produced large gains in that trait. Heritabilities were moderately strong to strong for most traits. Selection among families for a critically important trait needs to be followed by within-family selection to recoup losses and secure desired gains in other traits

Additional keywords: Progeny testing, mass selection, family selection, within-family selection, selection differential, disease resistance, Pinus elliottii var. elliottii, P. palustris, Cronartium quercuum f. sp. fusiforme.

Breeding plans for forest trees can vary from very simple mass selection to very elaborate combinations of selection and progeny testing. Generally, the more elaborate the plan, the greater the genetic gain per generation and the greater the total cost. The choice of plan depends upon the objectives and resources of the particular organization involved.

Breeding plans commonly used for forest trees include one or more of the following three stages: phenotypic selection from a mass population, progeny testing and selection among families, and selection of individuals within selected families. Each stage has its own set of costs and produces its own increment of gain. So there is considerable interest in what happens in each stage and how best to allocate resources among them (Cotterill and James, 1981; Namkoong and others, 1966).

Several progeny test plantations established in central Georgia by the Southeastern Forest Experiment Station are now near pulpwood rotation age and provide an excellent opportunity to evaluate gains from the three stages of selection in slash (Pinus elliottii Engelm. var. elliottii) and longleaf (P. palustris Mill.) pines.

METHODS

Trees used to begin this study were slash pines selected from plantions of unknown provenance in Jones and Dooly counties and longleaf pines selected from natural stands in Bleckley and Dooly counties, Georgia (selection stage one). This first stage of selection was done without a formal selection index. Instead, choices were made by measuring tree size

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and subjectively evaluating several form traits. Almost all the trees selected were free of fusiform rust (Cronartium quercuum (Berk.) Miyabe ex. Shirai f. sp. fusiforme) cankers.

Several progeny tests were established, but for this paper data from only three will be used, two of slash and one of longleaf pine. Each plantation was numbered. Numbers 38 and 50 are slash pine and number 49 is longleaf pine. Plantation 38 contained wind-pollinated progenies from 27 trees and plantation 50 contained wind-pollinated progenies from seven trees plus 11 full-sib progenies from single crosses among 17 trees. Longleaf plantation 49 contained wind-pollinated progenies from seven trees and six full-sib progenies from crosses among eight trees.

Traits evaluated in the progeny tests at age 21 years were survival, height, d.b.h., tree volume, rust-free percentage, stem crook, and volume per hectare. Heritabilities and phenotypic standard deviations on both a family and an individual basis were calculated from the data from wind-pollinated (half-sib) progenies.

Selection among and within families (stages two and three) was performed in the progeny tests. The trait used for selection among families was rust-free percentage. For selection within families, only rust-free trees with good size and form traits were selected. Again, no formal selection index was used. Only one tree per selected family was chosen in plantation 38. In each of the other two plantations the best tree on each plot of each selected family was chosen in all but two plots which had no suitable trees.

For each trait, actual gain produced by each stage of selection was calculated. For stage one, gain was the mean of all the families compared to the check. For stage two, it was the mean of the selected families compared to the mean of all the families and for stage three, it was the mean of the selected trees compared to the mean of the selected families. These gains were calculated for each plantation. Each increment of gain was also expressed as a percentage of its base.

To estimate the gain in performance expected to he inherited by progenies from the second-generation selections, each increment of gain was multiplied by its applicable heritability, the increments summed, and the sums compared to the check mean for each trait.

RESULTS

The means for all the families, selected families, trees selected within families, and checks are listed for each plantation in table 1. Gains and other data are shown in tables 2 through 8.

Stage 1, Mass Selection

Gains over checks from mass selection were greatest for survival, percentage rust free, and volume per hectare, three traits which are positively correlated (tables 2 and 3). Moderate gain was made in stem straightness. Gains in height and d.b.h. were low. In fact, there was a loss in mean d.b.h. for the longleaf, associated most likely with the good gain in survival percentage. Survival and d.b.h. were strongly inversely correlated in the longleaf pine.

Table 1.--Data means at age 21 for two slash and one longleaf pine progeny tests

Group	Survival	Height	D.b.h.	Rust free	Stem crook	Volume/ tree	Volume/ ha
	Percent	m	cm	Percent		m3	m3
Slash pine plantation 38							
All families(27) (27)	32.8	18.4	26.7	30.3	3.30	0.372	128.9
Best 7 families	52.8	19.1	25.9	65.9	2.97	.359	200.1
Selected trees. (7)		20.9	31.2		1.29	.606	
Check	25.4	17.6	26.9	20.5	3.49	.362	91.9
Slash pine plantation 50							
All families(18) (18)	48.9	17.8	22.3	21.9	3.15	.247	127.0
Best 4 families	62.7	18.0	21.9	51.5	2.72	.241	158.3
Selected trees (14)		20.0	25.7		1.93	.386	
Check	39.1	17.4	21.6	12.6	3.69	.231	93.2
Longleaf pine plantation 49							
All families(13) (13)	46.9	17.7	23.3	25.9	2.90	.270	129.1
Best 4 families	45.7	18.0	23.7	42.5	2.84	.287	131.7
Selected trees (14)		19.4	26.2		2.14	.384	
Check	32.7	17.3	24.6	22.6	3.33	.295	98.5

a/ Best in rust resistance.

Selection differentials were less than one standard deviation for all traits except height in plantation 38; stem crook and volume per hectare in plantation 50; and survival, stem crook, and volume per hectare in plantation 49 (table 4). Family heritabilities were moderate to high for most traits, but height in plantation 50 and stem crook and volume per hectare in plantation 49 had zero heritabilities (table 6).

Stage 2, Selection Among Families

Since selection among families was based primarily on rust resistance, by far the greatest percentage gain from this stage *was* in the rust free percentage (table 3). Good gains also were realized in survival and volume per hectare for slash pine plantations 38 and 50, but not for longleaf pine plantation 49. In all three plantations, this stage of selection yielded little or no gain in height and d.b.h. Again, selection differentials were low except for the rust-free and associated traits (table 4). However, a high selection differential for rust-free percentage was not accompanied by high selection differentials for survival and volume per hectare in longleaf pine. Heritabilities and phenotypic standard deviations were the same for this stage as for stage one (tables 5 and 6).

Table 2--Actual gains at age 21 from three stages of selection

Selection Stage	Trait						
	Survival	Height	D.b.h.	Rust free	Stem crook	Volume/ tree	Volume/ ha
	Percent	m	cm	Percent		m^3	m^3
			Plantation 38				
Mass[a/]	7.4	0.8	-0.2	9.8	0.19	0.010	37.0
Family[b/]	20.0	.6	- .8	35.6	.13	- .013	73.2
Within family[c/]		1.8	5.3		1.88	.247	137.7[d/]
			Plantation 50				
Mass	9.8	.4	.7	9.3	.54	.016	33.8
Family	13.8	.2	- .4	29.6	.43	-.006	31.3
Within family		2.0	3.8		.79	.145	95.2[d/]
			Plantation 49				
Mass	14.2	.4	-1.3	3.3	.43	-.025	30.6
Family	-1.2	.3	.4	16.6	.06	.017	2.6
Within family		1.4	2.5		.70	.097	44.5[d/]

a/ Means of all the families compared to the means of the check.
b/ Means of selected families compared to the means of all the families
c/ Means of selected trees compared to the means of selected families.
d/ Gains if all trees in selected families were as large as selected trees.

Table 3--Actual gains at age 21 from three stages of selection, expressed as percentage of the base

Selection Stage	Trait						
	Survival	Height	D.b.h.	Rust free	Stem crook	Volume/ tree	Volume/ ha
	Percent						
Plantation 38							
Mass[a/]	29.1	4.6	-0.01	47.8	5.4	2.8	40.3
Family[a/]	61.0	3.5	-0.03	117.4	4.0	- .03	56.8
Within family[a/]		9.6	20.3		59.3	68.8	68.8[a/]
Plantation 50							
Mass	25.1	2.3	3.2	73.8	14.6	6.9	36.3
Family	28.2	1.1	-1.8	135.1	13.6	-2.4	24.6
Within family		11.1	17.3		29.0	60.2	60.2[a/]
Plantation 49							
Mass	43.4	2.3	-5.3	14.6	12.9	-8.5	31.1
Family	-2.6	1.2	1.7	64.1	2.1	6.3	2.0
Within family		7.8	10.5		24.6	33.8	33.8[a/]

a/ See footnotes to table 2.

Table 4--Selection differentials used at three stages of selection

Selection Stage	Trait						
	Survival	Height	D.b.h.	Rust free	Stem crook	Volume/ tree	Volume ha/
			Plantation 38				
Mass[a/]	.47	1.08	-0.12	0.40	0.49	0.19	0.62
Family[a/]	1.27	.87	- .46	1.45	.33	- .24	1.24
Within family[a/]		.88	1.00		1.55	1.24	2.33[a/]
			Plantation 50				
Mass	.71	.53	.49	.70	1.93	.43	1.08
Family	1.01	.27	- .28	2.22	.22	- .16	1.00
Within family		1.23	.94		.81	1.20	3.04[a/]
			Plantation 49				
Mass	1.09	.78	- .98	.26	1.54	.64	1.61
Family	- .09	.59	.30	1.29	.21	.44	.14
Within family		.96	.66		.83	1.07	2.34[a/]

a/ See footnotes to table 2.

Table 5--Phenotypic standard deviations among and within families for the traits at age 21 years

Basis	Trait						
	Survival	Height	D.b.h.	Rust free	Stem crook	Volume/ tree	Volume/ ha
	Percent	m	cm	Percent		m^3	m^3
			Plantation 38				
Family	15.7	0.75	1.73	24.5	0.39	0.053	59.2
Within family		2.08	5.28		1.21	.199	
			Plantation 50				
Family	13.7	.75	1.42	13.3	.28	.037	31.3
Within family		1.62	4.04		.97	.121	
			Plantation 49				
Family	13.0	.51	1.33	12.9	.28	.039	19.0
Within family		1.46	3.80		.84	.091	

Table 6--Heritabilities at age 21 years, on a family mean and an individual tree basis

Basis	Trait						
	Survival	Height	D.b.h.	Rust free	Stem crook	Volume/ tree	Volume/ ha
	Percent	m	cm	Percent		m^3	m^3
			Plantation 38				
Family	0.86	0.19	0.55	0.82	0.34	0.45	0.89
Within family		.25	.24		.13	.20	
			Plantation 50				
Family	.84	0	.61	.88	.77	.43	.78
Within family		0	.20		.28	.19	
			Plantation 49				
Family	.70	.43	.83	.80	0	.91	0
Within family		.36	.33		0	.57	

Stage 3, Selection Within Families

Selection within families produced good gains in the four individual-tree traits--height, d.b.h., stem crook, and volume per tree. Selection differentials generally were higher and heritabilities lower than for the same traits in stages one and two.

Total Gains Over Checks

Among the seven traits, total gain percentages over checks were the greatest for the rust free trait (tables 7 and 8). Good total gains were made in all other traits as well, particularly in survival and volume per hectare. Gains were higher in slash than in longleaf pine. After gains were weighted with heritabilities, the data showed that plantations from seed produced by the trees selected from these families are expected to be about 50 percent rust free for slash pine and about 40 percent rust free for longleaf pine. These two figures compare with 20 percent or less rust free for the checks (table 1), which are assumed to be representative of the general population. The only traits not expected to show some gain were height for progenies of trees selected in plantation 50 and stem crook for progenies of trees selected in plantation 49--heritabilities in these instances were zero.

Table 7--Gains x heritabilities at age 21 years for three stages of selection[a]

Selection Stage	Trait						
	Survival	Height	D.b.h.	Rust free	Stem crook	Volume/ tree	Volume/ ha
	Percent	m	cm	Percent		m^3	m^3
			Plantation 38				
Mass[b]	6.4	0.15	-0.11	8.0	0.06	.004	32.9
Family[b]	17.2	.12	- .44	29.2	.04	- .006	65.1
Within family[b]		.46	1.26		.24	.049	27.5[b]
			Plantation 50				
Mass	8.2	0	0.43	8.2	.42	.007	26.4
Family	11.6	0	- .24	26.0	.33	-.003	24.4
Within family		0	.76		.22	.027	18.1[b]
			Plantation 49				
Mass	9.9	.17	-1.08	2.6	0	-.023	0
Family	- .8	.09	.33	13.3	0	.015	0
Within family		.50	.82		0	.055	25.4[b]

a/ These are increments of gain expected to be expressed in plantations established from bulk seedlings from the second-generation selections
b/ See footnotes to table 2.

DISCUSSION

Cost per unit gain is lowest in stage one (Namkoong, 1970), but tree breeders may not want to choose among the three stages of selection done here. Rather they may want to know whether the gains from each stage would pay the costs involved and still be profitable in a forestry operation. The gains reported here were substantial in all stages for slash pine when viewed as the end product, volume per unit area. Even the third stage should increase volume per unit area. The expected gain is: gain in volume per tree x its heritability x the number of trees per unit area. That *was* the only source of expected gain in volume per hectare in the longleaf pine (table 7).

Gain in some traits may require more than the simplest stage of selection. Until better technology is developed, proper evaluation of selections for rust resistance requires at least some form of progeny testing. By far the greatest gains in that trait were made in selection among families in these plantations (table 7).

Table 8.--Total heritable gains over checks at age 21 years, amounts and percentages

	Trait						
	Survival	Height	D.b.h.	Rust free	Stem crook	Volume/ tree	Volume/ ha
	Percent	m	cm	Percent		m^3	m^3
Plantation 38							
Amount	23.6	0.7	0.7	37.2	.35	.048	125.6
Percent	92.8	4.2	2.6	181.6	10.0	13.3	136.7
Plantation 50							
Amount	19.8	0	.9	34.2	.97	.035	68.9
Percent	50.6	0	4.4	271.7	26.2	15.1	73.9
Plantation 49							
Amount	9.1	.8	.5	15.9	0	.048	25.4
Family	27.8	4.6	2.0	70.4	0	16.3	25.8

If only simple mass selection were done, good gains in a combination of traits in one generation would require use of an elaborate and accurate selection index. Such an index may not be effective for some critical traits such as rust resistance. With the use of two or more stages there is flexibility in concentrating on different traits in the most effective stages. One very beneficial effect of using the third stage in this study was the recovery of some losses in height and d.b.h. which occurred when families were selected primarily on the rust resistance trait.

Gains from the first two stages of selection would be realized in a rogued first-generation clonal seed orchard. Gains from all three stages would be realized in a seedling seed orchard, a good reason to include seedling seed orchards as part of a tree improvement program.

Literature Cited

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