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Literature Cited

Brown, A. H. D. and R. W. Allard: Estimation of the mating system in open-pollinated maize populations using isozyme polymorphisms. Genetics **66**: 135—145, (1970). — Brown, A. H. D., A. C. Matheson and K. G. Eldridge: Estimation of the mating system of *Eucalyptus obliqua* L'Herit. by using allozyme polymorphisms. Aust. J. Bot. **23**: 931—949, (1975). — Cheliak, W. M., K. Morgan, C. Strobeck, F. C. Yeh and B. P. Dancik: Estimation of mating system parameters in plant populations using the EM algorithm. Theor. Appl. Genet. **65** 157—161, (1983). — El-Kassaby, Y. A., F. C. Yeh and O. Sziklai: Estimation of the outcrossing rate of Douglas-fir *[Pseudotsuga menziesii* (Mirb.) Franco] using allozyme polymorphisms. Silvae Genet. **30**: 182—184, (1981). — El-Kassaby, Y. A., F. C. Yeh and O. Sziklai: Inheritance of allozyme variants in coastal Douglas-fir *(Pseudotsuga menziesii* var. *menziesii)*. Can. J. Genet. Cytol. **24**: 325—335, (1982a). — El-Kassaby, Y. A., O. Sziklai and F. C. Yeh: Linkage relationships among 19 polymorphic allozyme loci in coastal Douglas-fir *(Pseudotsuga menziesii* var. *menziesii)*. Can. J. Genet. Cytol. **24**: 101—108, (1982b). — El-Kassaby, Y. A., A. M. K. Fashler and O. Sziklai: Reproductive phenology and its impact on genetically improved seed production in a Douglas-fir seed orchard. Silvae Genet. **33**: 120—125, (1984). — El-Kassaby, Y. A. and K. Ritland: Low levels of pollen contamination in a Douglas-fir seed orchard as detected by allozyme markers. Silvae Genet. (in press), (1986). — Ellstrand, N. C., A. M. Torres and D. A. Levin: Density and the rate of apparent outcrossing in *Helianthus annuus (Asteraceae)*. Syst. Bot. **3**: 403—407, (1978). — Ellstrand, N. C. and K. W. Foster: Impact of population structure on the apparent outcrossing rate of grain sorghum *(Sorghum bicolor)*. Theor. Appl. Genet. **66**: 323—327, (1983). — Ennos, R. A. and M. T. Clegg: Effect of population substructuring on estimates of outcrossing rate in plant populations. Heredity **48**: 283—292, (1982). — Epperson, B. K. and R. W. Allard: Allozyme analysis of the mating system in lodgepole pine populations. J. Hered. **75**: 212—214, (1984). — Eriksson, G., A. Jonsson and D. Lindgren: Flowering in a clonal trial of *Picea abies* Karst. Stud. For. Suec. **110**: 5—45, (1973). — Fashler, A. M. K. and W. J. B. Devitt: A practical solution to Douglas-fir seed orchard pollen contamination. For. Chron. **56**: 237—241, (1980). — Fowler, D. P.: Natural self-fertilization in three jack pines and its implications in seed orchard management. For. Sci. **11**: 55—58, (1965a). — Fowler, D. P.: Effects of inbreeding in red pine, *Pinus resinosa* Ait. III Factors affecting natural selfing. Silvae Genet. **14**: 37—46, (1965b). — Franklin, E. C.: Estimates of frequency of natural selfing and inbreeding coefficients in loblolly pine. Silvae Genet. **20**: 194—195, (1971). — Fyfe, J. L. and N. T. J. Bailey: Plant breeding studies in leguminous forage crops. I. Natural crossbreeding in winter beans. J. Agric. Sci. **41**: 371—378, (1951). — Griffith, B. G.: Phenology, growth, and flower and cone production of 154 Douglas-fir trees on the University Research Forest as influenced by climate and fertilizer, 1957—67. Faculty of Forestry, University of British Columbia, B. C., Bull. No. 6, 70 pp., (1968). — Hadders, G.: The situation of pollination in seed orchards of Scotch pine *(Pinus sylvestris* L.). Foren Skogstradsfor Inst Skogsforbat Arsbok 1971: 111 — 139, (1971). — Hamrick, J. L.: Plant population genetics and evolution. Amer. J. Bot. **10**: 1685—1693, (1982). — Jonsson, A., I. Ekberg and G. Eriksson: Flowering in a seed orchard of *Pinus sylvestris* L. Stud. For. Suec. **135**, 38 pp., (1976). — Kendall, M. and S. Stuart: The Advanced Theory of Statistics. Vol. 2 Inference and Relationship. Charles Griffin and Co. Ltd., London, (1979). — Li, C. C.: Population Genetics. University Chicago Press, (1955). — Marx, J. L.: Instability in plants and the ghost of Lamarck. Science **224**: 1415—1416, (1984). — Mitton, J. B., Y. B. Linhart, M. L. Davis and K. B. Sturgeon: Estimation of outcrossing in ponderosa pine, *Pinus ponderosa* Laws from patterns of segregation of protein polymorphisms and from frequencies of albino seedlings. Silvae Genet. **30**: 117—121, (1981). — Moran, G. F., J. C. Bell and A. C. Matheson: The genetic structure and levels of inbreeding in a *Pinus radiata* D. Don seed orchard. Silvae Genet. **29**: 190—193, (1980). — Moran, G. F. and A. H. D. Brown: Temporal heterogeneity of outcrossing rates in Alpine ash *(Eucalyptus delegatensis* R. T. Bak.) Theor. Appl. Genet. **57**: 101—105, (1980). — Müller-Starck, G., M. Ziehe and H. H. Hattemer: Reproductive systems in conifer seed orchards. 2. Reproductive selection monitored at an LAP gene locus in *Pinus sylvestris* L. Theor. Appl. Genet. **65**: 309—316, (1983). — Neale, D. B.: Population genetic structure of the Douglas-fir shelterwood regeneration system in southwest Oregon. Ph. D. thesis, Oregon State University, (1983). — Omi, S. K.: Seed set and the proportion of progeny due to self-fertilization in a Douglas-fir seed orchard. M. Sc. thesis Oregon State University, (1983). — O'Reilly, C., W. H. Parker and J. E. Barker: Effect of pollination period and strobili number on random mating in a clonal seed orchard of *Picea mariana*. Silvae Genet. **31**: 90—94, (1983). — Phillips, M. A. and A. H. D. Brown: Mating system and hybridity in *Eucalyptus pauciflora*. Aust. J. Biol. Sci. **30**: 337—344, (1977). — Ritland, K. and Y. A. El-Kassaby: The nature of inbreeding in a seed orchard of Douglas-fir as shown by an efficient multilocus model. Theor Appl. Genet., **71**: 375—384 (1985). — Roberds, J. H. and M. T. Conkle: Genetic structure in loblolly pine stands: allozyme variation in parents and progeny. For. Sci. **30**: 319—329, (1984). — Shaw, D. V. and R. W. Allard: Estimation of outcrossing rates in Douglas-fir using isozyme markers. Theor. Appl. Genet. **62**: 113—120, (1982a). — Shaw, D. V. and R. W. Allard: Isozyme heterozygosity in adult and open-pollinated embryo samples of Douglas-fir. Silvae Fennica **16**: 115—121, (1982b). — Shaw, D. V., A. L. Kahler and R. W. Allard: A multilocus estimator of mating system parameters in plant populations. Proc. Nat. Acad. Sci. (USA) **78**: 1298—1302, (1981). — Shen, H. H., D. Rudin and D. Lindgren: Study of the pollination pattern in a Scots pine seed orchard by means of isozyme analysis. Silvae Genet. **30**: 7—15, (1981). — Silen, R. R. and G. Keane: Cooling a Douglas-fir seed orchard to avoid pollen contamination. U.S.D.A., For. Serv., Res. Note PNW-101, 10 pp, (1969). — Squillace, A. E. and R. E. Goddard: Selfing in clonal seed orchards of slash pine. For. Sci. **28**: 71—78, (1982). — Steel, R. G. D. and J. H. Torrie: Principles and Procedures of Statistics: A Biometrical Approach. McGraw-Hill Book Company, N. Y., (1980). — Wheeler, N. C.: Variation in seed orchard reproductive bud phenology: limitations to supplemental mass pollination (SMP). Paper presented at the Western Forest Genetics Association, 1984 Annual Meeting, August 7—10, 1984. University of Victoria, Victoria, B. C., (Abstract), (1984). — Witter, M. S. and P. P. Feret: Inheritance of esterase and acid phosphatase isozymes in Virginia pine and the application of the isozyme technique to a seed orchard population. Silvae Genet. **28**: 213—220, (1979). — Wright, S.: Coefficients of inbreeding and relationship. Am. Nat. **56**: 330—338, (1922). — Yeh, F. C., A. Brune, W. M. Cheliak and D. C. Chipman: Mating system of *Eucalyptus citriodora* in a seed-production area. Can. J. For. Res. **13**: 1051—1055, (1983).

Gains from First-Cycle Selection in Slash and Longleaf Pines

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Summary

In tree breeding research begun in 1953, three stages of selection--initial, family, and within-family--were performed in slash *(Pinus elliottii* Engelm. var. *elliottii)* and longleaf *(P. palustris* Mill.) pines. Several traits were used in the selection, but no selection index was constructed. Results from three studies, two on slash and one on longleaf pines, were assessed at progeny age 21 or 22 years. Initial selection produced moderate gains in height and resistance to fusiform rust caused by *Cronartium quercuum* f. sp. *fusiforme,* but some losses in diameter. Selection among families, primarily for rust resistance, produced large gains in that trait but low or negative gains in height, diameter, and volume per tree. Selection within selected families produced gains in height and diameter, yielding from 6 to 11 percent gain in volume per tree. Total gains in rust resistance were 144 to 198 percent for slash pine and 65 percent for longleaf pine. For both species, the greatest need revealed in this research was for improved resistance to fusiform rust. Also, selection among families for one critically important trait such as rust resistance needs to be followed by within-family selection for gains in other important traits that were not considered during among-family selection.

Key words: *Pinus elliottii* var. *elliottii, P. palustris, Cronartium quercuum* f. sp. *fusiforme,* heritability, genetic gain, selection differential.

Zusammenfassung

In der Forstpflanzenzüchtung, die 1953 begann, wurden 3 Stadien der Selektion — initiale, Familienselektion und die Selektion innerhalb Familien — bei *Pinus elliottii* Engelm. var. *elliottii* und *Pinus palustris* Mill. durchgeführt. Mehrere Merkmale wurden bei der Selektion verwendet, jedoch wurde kein Selektionsindex konstruiert. Die Ergebnisse von 3 Untersuchungen, 2 von *Pinus elliottii* und eine von *P. palustris,* wurden im Alter von 21 oder 22 Jahren ermittelt. Die initiale Selektion brachte mittleren Gewinn im Höhenwachstum und in der Resistenz gegen den Rostpilz *Cronartium quercuum* f. sp. *fusiforme,* aber einige Einbußen im Durchmesserwachstum. Die Selektion von Familien vornehmlich auf Rostpilzresistenz, brachte großen Gewinn bei dem Merkmal, aber geringen oder negativen Gewinn im Höhen-, Durchmesser- und Volumenzuwachs pro Baum. Die Selektion innerhalb selektierter Familien brachte Gewinne im Höhen- und Durchmesserwachstum, die von 6—11% mehr Volumenzuwachs ergaben. Der Gesamtgewinn betrug für die Rostpilzresistenz 144 bis 198% bei *Pinus elliottii* und 65% bei *P. palustris.* In dieser Untersuchung zeigte sich für beide Baumarten, daß die Notwendigkeit der Verbesserung der Rostpilzresistenz das wichtigste war. Darüber hinaus ist es nötig, daß sich an die Selektion von Familien für ein unbedingt wichtiges Merkmal, wie die Rostpilzresistenz, eine Selektion innerhalb der Familien bei anderen wichtigen Merkmalen anschließen sollte, die nicht während der Selektion von Familien berücksichtigt wurden.

Introduction

Breeding programs for forest trees commonly include first-cycle selection at three stages: among individuals within base populations, among families in progeny test plantations, and among individuals within selected families. There is considerable interest in what happens in each stage and how best to allocate resources among them in practical programs (Cotterill and James 1981; Namkoong *et al.* 1966). Gain expectations for various approaches and stages of selection have been presented by Namkoong *et al.* (1966).

Research on selecting and progeny testing the southern pines in central Georgia was begun by the Southeastern Forest Experiment Station, USDA Forest Service in 1953. Several progeny test plantations established then are now near pulpwood rotation age and provide data for estimating gains from three stages of first-cycle selection in slash pine (*Pinus elliottii* Engelm. var. *elliottii)* and longleaf pine (*P. palustris* Mill.).

Materials and Methods

The original trees for this research were selected in 14- to 18-year-old commercial plantations of slash pine and 25- to 30-year-old natural stands of longleaf pine. The slash pine plantations were of unknown provenance. All the stands were in central Georgia.

Test families from the selected trees included both wind- and control-pollinated progenies. Results reported are from two slash pine tests and one longleaf pine test. One of the slash pine tests (test 38, planted in 1956) contained wind-pollinated progenies from 27 trees. The second slash pine test (test 50, planted in 1959) contained wind-pollinated progenies from 7 trees plus 11 full-sib progenies from single crosses among 17 trees. Progeny test 49, the longleaf pine test which also was planted in 1959, contained wind-pollinated progenies from 7 trees and 6 full-sib progenies from single crosses among 8 trees. Standard check lots from unselected trees were included in each progeny test.

Selection was performed among individuals in the original stands, among families in the progeny tests, and among trees within selected families. The initial selection was on several form and vigor traits. Selection among families was primarily for resistance to southern fusiform rust (*Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme).* Selection among trees within selected families was on size and form traits with the requirement that any tree selected be free of rust infection.

The standard genetic gain formula is $G = i\sigma_p h^2$ where:

G = genetic gain

i = selection intensity

σ_p = phenotypic standard deviation

h^2 = heritability.

Each parameter in the formula is estimated for each stage of selection.

If the proportion of the population selected is known, selection intensity is readily available from tables. An alternative method is to use $i = s \div \sigma_p$, where s equals the selection differential or the selected population mean minus the unselected population mean. Since $s = i\sigma_p$, s can be used directly in the gain formula (Namkoong 1979, p. 79). The formula then becomes $G = sh^2$, which was used in this study because the selection intensity was unknown in some instances.

Gains were estimated for each stage of selection. For gains from initial selection, check means were assumed to reflect the mean performance of the original, unselected populations. The actual gains for that stage were calculated as the mean of all the families in each progeny test minus the check mean for that progeny test. Gains for the other two stages were calculated with selection differentials and heritabilities. For family selection, s equals the mean of selected families minus the mean of all the families. For within-family selection, s equals the mean of the selected trees minus the mean of the selected families. Heritabilities were estimated from analysis of variance data as follows:

Half-sib families

$$h_f^2 = \sigma_f^2 \div (\sigma_f^2/r + \sigma_e^2)$$

$$h_w^2 = 3_f \div (3\sigma_f^2 + \sigma_w^2 + \sigma_e^2)$$

Full-sib families

$$h_f^2 = \sigma_f^2 \div (\sigma_f^2/r + \sigma_e^2)$$

$$h_w^2 = \sigma_f^2 \div (\sigma_f^2 + \sigma_w^2 + \sigma_e^2)$$

where:

h_f^2 = family heritability

h_w^2 = within-family heritability

σ_f^2 = variance among families

σ_w^2 = within-family variance

σ_e^2 = error variance

r = number of replications

In the heritability equations, $\sigma^2_f = 1/4\ \sigma^2_A$ for half-sibs and $1/2\ \sigma^2_A + 1/4\ \sigma^2_D$ for full sibs (σ^2_A = the additive variance and σ^2_D the dominance variance) (NAMKOONG 1979, p. 78). For the two progeny tests with both half-sib and full-sib progenies, heritabilities were estimated for each type of progeny and the weighted mean of the two estimates used as the heritability for the trait. Traits for which gains were estimated were rust-free percentage, height, diameter at breast height (d.b.h.), volume per tree, and volume per hectare. Gains were estimated at age 22 years for progeny test 38 and at age 21 years for progeny tests 49 and 50.

Results

In *Table 1* the means for all the families, selected families, trees selected within families, and checks are listed by trait. These means were used to calculate the selection differentials listed in *Table 2*. Analysis of variance data yieded the heritability estimates in *Table 3*. Except that gains from initial selection are the same as the selection differentials, gains shown in *Table 4* are the products of the appropriate selection differentials and heritabilities.

Although worthwhile gains in rust-free percentage were produced by initial selection, selection among families produced three to four times as much gain in the trait as did initial selection *(Table 4)*. Conversely, initial selection produced considerably greater gains in height than did family selection because height was emphasized in initial selection but was almost ignored in family selection when rust resistance was the trait emphasized. Height was again emphasized in selection within families and in all instances greater genetic gains in height were realized than in family selection. Similar results are seen in d.b.h. and volume per tree, although some losses occurred in these two traits for the first two stages. Gains in volume per hectare were fairly evenly distributed among the three selection stages for slash pine but occurred mostly in the initial stage for longleaf pine.

Genetic gain comparisons among traits can be made in *Table 5*, where gains are shown as percentage of the base. Total relative gains were rather moderate for tree-size traits. Total gain in rust resistance was 65 percent of the

Table 1. — Data means for three progeny tests.

Progeny test number	Data base group[a/]	Trait				
		Rust-free	Height	D.b.h.	Vol./tree	Vol./ha
		Percent	m	cm	m^3	m^3
38[b/]	All families (27)	30.3	18.4	26.7	0.375	124.1
	Selected families (7)	65.9	19.1	25.9	.359	202.1
	Selected trees (7)	100.0	20.9	31.2	.606	---
	Check	20.5	17.6	26.9	.362	91.9
50[c/]	All families (18)	21.9	17.8	22.3	.247	126.1
	Selected families (4)	51.5	18.0	21.9	.241	154.0
	Selected trees (14)	100.0	20.0	25.7	.386	---
	Check	12.6	17.4	21.6	.231	93.2
49[d/]	All families (13)	25.9	17.7	23.3	.281	134.4
	Selected families (4)	42.5	18.0	23.7	.298	137.0
	Selected trees (14)	100.0	19.4	26.2	.384	---
	Check	22.6	17.3	24.6	.298	100.7

a/ Numbers of families or trees.
b/ Slash pine, age 22 years.
c/ Slash pine, age 21 years.
d/ Longleaf pine, age 21 years.

Table 2. — Selection differentials at three stages of selection in three progeny tests.

Progeny test number	Selection stage	Trait				
		Rust-free	Height	D.b.h.	Vol./tree	Vol./ha
		Percent	m	cm	m^3	m^3
38[a/]	Initial[c/]	9.8	0.8	-0.2	0.013	32.2
	Family[d/]	35.6	0.7	-0.8	- .016	78.0
	Within-family[e/]	34.1	1.8	5.3	.247	--
50[a/]	Initial[c/]	9.3	0.4	0.7	.016	32.9
	Family[d/]	29.6	0.2	-0.4	- .006	27.9
	Within-family[e/]	48.5	2.0	3.8	.145	--
49[b/]	Initial[c/]	3.3	0.4	-1.3	- .017	33.7
	Family[d/]	16.6	0.3	0.4	.017	2.6
	Within-family[e/]	57.5	1.4	2.5	.086	--

a/ Slash pine.
b/ Longleaf pine.
c/ All families compared with checks.
d/ Selected families compared with all families.
e/ Selected trees compared with selected families.

Table 3. — Family and individual tree heritabilities in three progeny tests.

Progeny test number	Basis	Type of progeny	Trait				
			Rust-free	Height	D.b.h.	Vol/tree	Vol/ha
38[a]	Family	Half-sibs	0.82[d]	0.91	0.55	0.45	0.89
	Individual	Half-sibs	--	.20	.19	.16	--
50[a]	Family	Half-sibs	.88	0	.61	.43	.78
		Full sibs	.94	.86	.66	.79	.82
		Mean[c]	.92	.52	.64	.65	.81
	Individual	Half-sibs	---	0	.16	.15	---
		Full sibs	---	.33	.07	.14	---
		Mean[c]	---	.20	.10	.14	---
49[b]	Family	Half-sibs	.80	.44	.83	.90	.09
		Full sibs	.76	.76	.59	.72	.83
		Mean[c]	.78	.58	.72	.82	.43
	Individual	Half-sibs	---	.30	.27	.33	---
		Full sibs	---	.22	.02	.08	---
		Mean[c]	---	.26	.15	.21	---

[a] Slash pine.
[b] Longleaf pine.
[c] Weighted mean of half-sib and full-sib progenies.
[d] Not individual-tree traits.

Table 4. — Estimated genetic gains from three stages of selection in three progeny tests.

Progeny test number	Selection stage	Trait				
		Rust-free	Height	D.b.h.	Vol./tree	Vol./ha
		Percent	m	cm	m^3	m^3
38[a]	Initial	9.80	0.80	-0.20	0.0130	32.20
	Family	29.19	.13	- .44	- .0072	69.42
	Within family	---	.36	1.01	.0395	22.23[c]
	Total	38.99	1.29	.37	.0453	123.85
50[a]	Initial	9.30	.40	.70	.0160	32.90
	Family	27.23	.10	- .26	-.0039	22.60
	Within family	---	.40	.38	.0203	12.97[c]
	Total	36.53	.90	.82	.0324	68.47
49[b]	Initial	3.30	.40	-1.30	- .0170	33.70
	Family	12.95	.17	.29	.0139	1.12
	Within family	---	.36	.37	.0181	8.32[c]
	Total	16.25	.93	- .64	.0150	43.14

[a] Slash pine.
[b] Longleaf pine.
[c] Assuming the same relative response in volume/ha as in volume/tree.

base for longleaf pine and 144 to 198 percent of the base for slash pine. Volume per hectare was another trait with high relative gains.

Discussion

There were some differences between heritability estimates from half-sib and full-sib progenies but the differences were not consistent. There are 16 pairs of heritabilities in *Table 3* for comparison. Heritabilities are about the same in five pairs, those from full sibs are the greatest in five pairs, and those from half-sibs are the greatest in six pairs. Apparently, sampling variation is a greater source of difference between the two kinds of heritability estimates than is dominance variance.

In the initial stage of selection, strong selection pressure was not applied on any single trait. Generally, choices were based on a combination of size and form traits, although no selection index was constructed. Consequently, gains in height and d.b.h. in the initial selection probably were not as great as they could have been had these two traits been the only ones involved.

The total gains in rust-free percentage do not include an increment from within-family selection *(Table 4)*. Since only rust-free trees were selected at this stage, selection differentials were high *(Table 2)*. Since there is no way to estimate heritability of rust-free percentage on an individual basis, no gains for that trait at that stage are shown. There should have been some gains, though, probably at least as great as gains from initial selection.

Similarly, direct estimates of gains in volume per hectare from within-family selection were not possible, but it seems reasonable to assume that volume per hectare would have about the same relative response to within-family selection as did volume per tree *(Table 5)*. Under that assumption, the third stage of selection produced genetic gains of 8 to 22 m³ per hectare *(Table 4)*.

Percentages of infection by fusiform rust were about the same in longleaf pine as in slash pine *(Table 1)*. Total gain in rust-free percentage for longleaf, however, was less than half the gain for slash pine *(Table 4)*. That is because the the selection differentials for the first two stages were considerably lower for longleaf than for slash pine *(Table 2)*, which probably means less variation in the trait in longleaf pine.

The level of fusiform rust infection on longleaf pine may be surprizing, since the disease generally is not a serious problem on the species if rust inoculum levels increase over study site, however, and should longleaf pine be planted extensively, fusiform rust could become a more general problem on the species. It was a serious problem on this time as it has in slash pine plantations.

Selection among families on the rust-resistance trait produced substantial gains in volume per hectare for slash pine despite losses in d.b.h. and volume per tree for that

Table 5. — Estimated genetic gains from three stages of selection in three progeny tests, expressed as percentage of the base.

Progeny test number	Selection stage	Trait				
		Rust-free	Height	D.b.h.	Vol./tree	Vol./ha
				Percent		
38[a]	Initial[c]	47.80	4.54	-0.74	3.59	35.04
	Family[d]	96.34	.71	-1.65	- 1.92	55.94
	Within family[e]	---	1.88	3.90	11.00	11.00[f]
	Total	144.14	7.13	1.51	12.67	101.98
50[a]	Initial[c]	73.81	2.30	3.24	6.93	35.30
	Family[d]	124.34	.56	-1.16	-1.58	17.92
	Within family[e]	----	2.22	1.73	8.42	8.42[f]
	Total	198.15	5.08	3.81	13.77	61.64
49[b]	Initial[c]	14.60	2.31	-5.28	-5.70	33.47
	Family[d]	50.00	.96	1.24	4.95	0.83
	Within family[e]	---	2.00	1.56	6.07	6.07[f]
	Total	64.60	5.27	-2.48	5.32	40.37

a/ Slash pine.
b/ Longleaf pine.
c/ All families compared with checks.
d/ Selected families compared with all families.
e/ Selected trees compared with selected families.
f/ Assuming the same relative response in volume/ha as in volume/tree.

stage (*Table 4*). The more rust-resistant, selected families had better survival than the nonselected families. Family selection in longleaf pine, however, produced little gain in volume per hectare although it did produce some gain in d.b.h. and volume per tree. Apparently survival was not affected as much by rust infection in longleaf pine as in slash pine.

Theoretically, a selection index combining traits and selection stages, all with proper economic weights, should produce more gain in total value than selecting on different traits at different stages. In such an index, for application in high-rust-hazard areas such as central Georgia, resistance to fusiform rust would likely have a very high economic weight relative to other traits. If so, the gain produced by the index probably would not be much greater than that of the method used here. Selection applied to these materials produced total gains in volume per hectare of 40 to 120 percent, which is quite acceptable.

The greatest need revealed by this study is for genetic improvement in resistance to fusiform rust in slash and longleaf pines. It is futile to improve growth and form traits only to have the trees die from fungal stem infections. The severity of the problem became evident after this study was begun (Czabator 1971; Powers *et al.* 1975; Schmidt *et al.* 1974).

Those who established this study, however, suscepted that fusiform rust was an important factor and so selected mostly rust-free trees. Three slash pine trees infected at time of selection produced highly susceptible progenies, as did many of the rust-free initial selections of both species. Some form of progeny testing of all selections for rust resistance is needed for these two species if their progenies are to be planted in high-hazard fusiform rust areas.

Literature Cited

Cotterill, P. P. and J. W. James: Optimizing two-stage independent culling selection in tree and animal breeding. Theor. Appl. Genet. 59: 67—72 (1981). — Czabator, F. J.: Fusiform rust of southern pines-a critical review. USDA For. Serv. Res. Pap. SO-65, 39 pp. (1971). — Namkoong, G.: Introduction to quantitative genetics in forestry. USDA For. Serv. Bull. 1588, 342 pp. (1979). — Namkoong, G., E. B. Snyder and R. W. Stonecypher: Heritability and gain concepts for evaluating breeding systems such as seedling orchards. Silvae Genet. 15: 76—84 (1966). — Powers, H. R., Jr., J. P. McClure, H. A. Knight and G. F. Dutrow: Fusiform rust: forest survey incidence data and financial impact in the south. USDA For. Serv. Res. Pap. SE-127, 16 pp. (1975). — Schmidt, R. A., R. E. Goddard and C. A. Hollis: Incidence and distribution of fusiform rust in slash pine plantations in Florida and Georgia. Univ. Fla. Agric. Exp. Stn. Bull. 763 (tech), 21 pp. (1974).

Population Hybridization in Scotch pine (Pinus sylvestris L.)[1]): I. Genetic Variance Components and Heterosis

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Summary

Height and needle length of intra- and interpopulation hybrid Scotch pine (*Pinus sylvestris* L). seedlings were evaluated in three different nurseries in Pennsylvania.

Nested population diallel analyses were used to estimate components of variance among populations and individuals, and provide information on the relative importance of the two breeding units, the populations and individuals within populations.

Genetic variability in height among individuals was larger than that among populations. General combining ability of individuals was the most important source of genetic variance.

The variabilities in needle length of populations and individuals were approximately equal. The general combining abilities of populations and individuals were of similar

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