

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 ^{f/}
	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 ^{f/}
	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/ Loblolly 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 loblolly 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 loblolly 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 loblolly 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, suspected 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.

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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.

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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

magnitude, while specific combining ability effects were smaller but significant.

Several sizable heterosis values, both positive and negative, were observed among the population hybrids and hybrid families. In general, hybrid superiority was lacking as indicated by many neutral and negative values. Interpopulation hybridization is likely to be important primarily in combining desirable characters and producing genetically diverse populations in future generations.

Key words: Population hybridization, *Pinus sylvestris*, diallel cross, heterosis, variance components, general and specific combining abilities, and polycross.

Zusammenfassung

In drei verschiedenen Baumschulen in Pennsylvania wurde die Höhe und die Nadellänge für Intra- und Interpopulationshybrid-Sämlinge von *Pinus sylvestris* L. ermittelt.

Serienmäßige Populations-Diallel-Analysen wurden benutzt, um die Varianz-Komponenten zwischen Populationen und Individuen zu schätzen, und Informationen von relativer Wichtigkeit für 2 Züchtungseinheiten, d. h. die Populationen und die Individuen innerhalb der Populationen zu erhalten. Die genetische Variabilität bei der Höhe war zwischen Individuen größer als zwischen Populationen. Die allgemeine Kombinationseignung der Individuen war die wichtigste genetische Variationsursache.

Die Variabilitäten bei der Nadellänge von Populationen und Individuen war annähernd gleich. Die allgemeine Kombinationseignung von Populationen und Individuen waren von gleicher Art, während die spezifischen Kombinationseignungseffekte kleiner aber signifikanter waren. Verschiedene beträchtliche Heterosis-Werte, sowohl positiv als auch negativ, wurden zwischen den Populationshybriden und Hybridfamilien beobachtet. Im allgemeinen fehlte eine Überlegenheit der Hybriden, was durch viele neutrale und negative Werte aufgezeigt wurde. Eine Hybridisierung zwischen Populationen ist wahrscheinlich in erster Linie wichtig, um erwünschte Merkmale zu kombinieren und genetisch unterschiedliche Populationen für zukünftige Generationen zu produzieren.

Introduction

Scotch pine (*Pinus sylvestris* L.) is an important ornamental tree in northeastern United States, where it is used primarily for Christmas trees and landscape plantings. Several breeding programs have been initiated to improve commercial and ornamental qualities of the species. Population hybridization may be an important technique in such breeding programs, especially if distinct genetic variation exists among the populations of interest. Genetic variation among populations of the species is well documented (WRIGHT and BALDWIN 1957, GERHOLD 1959, WRIGHT and BULL 1963, KING 1965, STEINER 1974). Studies on crossabilities and precocious flowering patterns among the provenances (GERHOLD 1966, WRIGHT *et al.* 1966, KARRFALT *et al.* 1975) indicate that population hybridization can be a useful breeding method for Scotch pine. Principal benefits of interpopulation hybridization could include heterosis, a combination of desirable characters, and synthetic populations with greater genetic variability for a future breeding program. These possibilities of interpopulation hybridization have received attention (WRIGHT 1964), and early results of such experiments on several species have been reported (NILSSON and ANDERSON 1970, WOESSNER 1975, MORGENSTERN 1975, HOLST and FOWLER 1975).

An effective hybridization program depends on obtaining genetic information for the desired traits from a mating experiment. The diallel cross system is a particularly use-

ful mating design for estimating genetic parameters, although it requires laborious procedures. In the experiment, the diallel cross system was modified to evaluate performances of populations as breeding units, and of individuals within the populations. It was termed a "nested population diallel."

The experiment was designed to provide genetic information about intra- and interpopulation hybrids of Scotch pine. The specific objectives were (1) to estimate genetic and environmental components of variability, (2) to estimate heterosis values for interpopulation hybrids, and (3) to relate the genetic parameters resulting from intra- and interpopulation crosses to selection and breeding methods.

Materials and Methods

Plant materials

Seeds used in this experiment were produced at the Kellogg Forest of Michigan State University where a plantation of 108 Scotch pine provenances had been established in 1961 (WRIGHT and BULL 1963). Geographic flowering patterns and crossability of provenances in the plantation were reported in detail by KARRFALT *et al.* (1975).

The seven parental populations used in the experiment are identified by Michigan State University designations MSFG numbers: 212 from France, 250 from Germany, 262 from Georgian S.S.R., 269 from England, 316 from France, 318 from Belgium, and 556 from Italy. Controlled pollinations were performed in May 1969, using the "minibag technique" (GERHOLD 1968). The seeds of these matings were harvested in the fall of 1970 and stored in a refrigerator until they were sown.

Mating design

The mating design, the nested population diallel, used to produce these hybrids, was a modification of the diallel cross system. It is similar to the "two-level diallel cross" proposed by HINKELMANN (1974) in that seed parents were nested within the populations; but it differs by using pollen mixtures instead of individual male parents for each population. It may be described as a diallel arrangement of polycrosses with females nested within populations. The pollen mixes enabled estimates of genetic parameters to be based on a larger number of parents than would have been possible with matings among individuals.

The complete matrix of matings can be seen in Table 3. Two trees from each of the seven populations were selected to represent maternal parents of the populations. The criterion in selecting female trees was a sufficient number of flowers to make the required crosses. Each seed parent was crossed with seven pollen mixes. Each mix was composed of equal volumes of pollen from five to nine trees of the same population. A total of 98 families resulted, with progenies in three groups: one set of seven intrapopulation crosses consisting of 14 families, and two sets of 21 population hybrids, which are reciprocal to each other, each set consisting of 42 families.

A "population hybrid", as the term is used here, consists of two "hybrid families" because two seed parents were used for each population. The interpopulation reciprocal hybrids were defined only at the population level, not at the family level, because female parents were nested within the populations but males were the pollen mixes of the populations.

Nurseries and plantings

In March 1974, 12 seeds per plot were sown in 4 randomized blocks in a greenhouse using styrofoam blocks with

40 cc cavities filled with a soil-peat-perlite mixture. The seedlings were later pooled for nursery planting since no apparent block differences were found. Three nurseries were selected in Pennsylvania to expose seedlings to different environments. One was a State-owned nursery, Penn Nursery in Centre County, and two were commercial Christmas tree nurseries, Carino Nurseries in Indiana County, and Strathmeyer Forests in York County.

Transplanting to each nursery was completed in July 1974. Nursery beds, 1.2 m wide, had been prepared using standard practices. A four-tree-plot per family was planted in each of two randomized blocks in each nursery; plot sizes varied according to seedling survival. Spacing between trees and rows was 13 cm.

Seedlings were observed in all nurseries at about 5-week intervals during three growing seasons. Survival and growing conditions were satisfactory except at Strathmeyer Forests where some mortality occurred due to wildlife, and there were persistent weed problems. Hand weeding was done regularly.

In September 1976, individual tree heights and needle lengths were measured in millimeters after growth had ended. Total height was measured from the ground to the terminal bud. Needle lengths were measured on a randomly picked fascicle from the current year's growth.

Statistical models and analyses

To include effects associated with seed parents within the populations, the ordinary diallel model (GRIFFING 1956, COCKERHAM 1963) was modified. The model, "nested population diallel," with experimental design, is

$$Y_{hl(ik)(j-)z} = \mu + N_h + r_{hl} + G_i + G_j + S_{ij} + M_i + M_j + R_{ij} + g_{(ik)} + s_{(ik)(j-)} + e_{hl(ik)(j-)z}$$

where

$Y_{hl(ik)(j-)z}$ = z^{th} observation on the progeny from k^{th} female tree of i^{th} population mated to j^{th} pollen mixture in l^{th} replicate of h^{th} nursery;

μ = experimental mean;

N_h = h^{th} nursery effect, $h = 1, 2, 3$;

r_{hl} = l^{th} replicate effect in h^{th} nursery, $l = 1, 2$;

$G_i(G_j)$ = population general combining ability effect for i^{th} (j^{th}) populations, $i, j = 1, 2, \dots, 7$;

S_{ij} = population specific combining ability effect for cross between i^{th} and j^{th} populations, $s_{ij} = s_{ji}$;

$M_i(M_j)$ = maternal effect for i^{th} population, $M_i^1 = -M_j$;

R_{ij} = population reciprocal effect for reciprocal cross of i^{th} and j^{th} populations, $R_{ij} = -R_{ji}$;

$g_{(ik)}$ = general combining ability effect for k^{th} female within i^{th} population, $k = 1, 2$;

$s_{(ik)(j-)}$ = specific combining ability effect for cross between k^{th} female in i^{th} population and j^{th} pollen mixture; and

$e_{hl(ik)(j-)z}$ = random error component.

The experimental mean, nurseries, and replicates within the nurseries were considered as fixed effects, and all the remaining terms were assumed to be random effects. The intrapopulation progenies were excluded from this analysis.

Because the data were unbalanced with a few missing cells, they were subjected to a generalized least squares analysis to obtain solutions including expected mean squares. The size of the variance-covariance matrix ($X'X$ matrix) was the limiting factor for using a full rank model.

Therefore, the sum of squares for error in this model contains within plot error and remainders due to all possible interactions.

For computing sum of squares and expected mean square coefficients, a computer program was written to compute design and variance-covariance matrices, then the forward solutions were obtained by applying an algorithm from DIALL (SCHAFER and USANIS 1969). Significance tests were performed approximately by using the conventional F-test although the data were unbalanced (TIETJEN 1974).

Heterosis at both population and individual family levels was examined using data from two nurseries, excluding Strathmeyer nursery where most missing data occurred. Separate analyses of variance were performed to examine differences among families prior to estimation of heterosis. The heterosis value for population was defined as the average difference of a population hybrid and its midparent value, allowing negative heterosis and considering reciprocal population hybrids separately. The midparent values were calculated as the average of intrapopulation progenies of the parental combination in consideration. For example, the heterosis

value of i^{th} and j^{th} population hybrid (H_{ij}) is defined as:

$$H_{ij} = \bar{Y}_{ij} - \frac{1}{2}(\bar{Y}_{ii} + \bar{Y}_{jj}),$$

where

\bar{Y}_{ij} = progeny mean of i^{th} and j^{th} cross

$\bar{Y}_{ii}(\bar{Y}_{jj})$ = progeny mean of i^{th} (j^{th}) intrapopulation cross.

The standard error of the estimates is calculated as:

$$S.E.(H_{ij}) = \sqrt{\sigma_e^2 \left(\frac{1}{N_{ij}} + \frac{1}{4N_{ii}} + \frac{1}{4N_{jj}} \right)},$$

where

$S.E.(H_{ij})$ is standard error of H_{ij} ,

σ_e^2 is error variance from analysis of variance,

N_{ij} , N_{ii} , and N_{jj} are number of observations for progeny mean of i^{th} and j^{th} cross, i^{th} and j^{th} intrapopulation crosses, respectively.

The estimated heterosis value was declared significant if its absolute value exceeded twice the standard error, as 95% of the t -distribution fell within approximately two standard deviations. Similarly, heterosis values for individual hybrid families were computed as the average difference of hybrid families between the average of intrapopulation family and intrapopulation cross progenies, for females and males, respectively.

Results

Components of variance

Nurseries, population general combining abilities (GCA), and individual general combining abilities (gca) were the significant sources of variation in height (Table 1). The mean square for the remainder, which includes all the interactions, was also significant when compared with that for within plot error. Large differences among the nursery environments were indicated, with no differences between the replicates within nurseries. Average seedling height at Carino was 337 mm, at Strathmeyer 293 mm, and at Penn 211 mm.

The largest genetic source of variation in height was the general combining ability of individual seed parents, which amounted to 10% of the total phenotypic variance, followed by the general combining ability associated with parental populations (3.2%). Population reciprocal effects (RECP) and specific combining abilities involving seed

parents and pollen mixes (sca) were the same magnitude, amounting to 1.2% of the total phenotypic variance. The estimates of population specific combining abilities (SCA) and population maternal effects (MAT) were negative. Most of the total variation was due to genetic/environmental error (84.4%).

Significant sources of variation in needle length were nurseries, GCA, SCA, gca, sca, and remainder due to interactions. The nursery means ranged from 47 mm at Strathmeyer to 54 mm at Penn. Population general combining ability was the largest genetic source of variance and amounted to 12.1% of the total phenotypic variance, followed by individual general combining ability (9.2%). The variances for SCA, MAT, and sca were 2.4, 0.1, and 3.8%, respectively. Genetic/environmental error amounted to 72.4%, and was the largest contribution to total phenotypic variance.

Heterosis

The analyses of variance for both height and needle length revealed significant differences among the 98 families. Mean height of the families ranged from 194 mm (262 GEO 2 × 556 ITA, abbreviations explained in tables) to 421 mm (269 ENG 1 × 318 BEL) with a grand mean of 288 mm. Needle length ranged from 33 mm (556 ITA 2 ×

316 FRA) to 79 mm (250 GER 2 × 250 GER) with a grand mean of 52 mm.

As mentioned earlier, heterosis values were calculated using family means at two nurseries. The magnitude of heterosis values in the population hybrids varied from -86 to 79 mm for height and from -7.8 to 7.5 mm for needle length (Table 2). Most were not significant.

The largest positive heterosis value for height was obtained by crossing 316 FRA × 212 FRA, and amounted to 30% of the mid-parent value. In 34 of 42 crosses the estimates were negative. The largest negative heterosis value (250 GER × 318 BEL) was -26% of its mid-parent value. Fourteen of the 42 estimates were relatively large in magnitude, exceeding twice their respective standard errors. Such large heterosis values among the population crosses occurred more or less at random, and generally were unrelated to their geographic distribution. However, all heterosis values for the hybrid populations that had 262 GEO as the common male and 250 GER or 262 GEO as the common female were negative and frequently large.

The frequency of the negative and positive heterosis values for needle length was equal among population hybrids. Eight of the 42 estimates were relatively large in magnitude and exceeded twice their respective standard errors. There was only one large positive heterosis value (250 GER × 212 FRA), amounting to 13% of its mid-parent

Table 1. — Analyses of variance of height and needle length for nested population diallel experiment.

Sources of variation	Degrees of freedom	Height			Needle length		
		Mean squares	Variance components	VC% ^a	Mean squares	Variance components	VC% ^a
Nurseries	2	2 507 472 *			5 011 *		
Replications	3	15 094 ns			137 ns		
Populations	41						
GCA	6	82 463 *	255.6	3.2	5 514 *	21.0	12.1
SCA	14	4 297 ns	<0.0	0.0	406 *	4.2	2.4
MAT	6	24 500 ns	<0.0	0.0	818 ns	0.2	0.1
RECP	15	12 246 ns	91.6	1.2	185 ns	<0.0	0.0
Individuals	42						
gca	7	50 422 *	785.0	10.0	1 063 *	15.9	9.2
sca	35	7 578 ns	93.9	1.2	192 *	6.6	3.8
Pooled error	849	6 622	6,622.0	84.4	126	125.5	72.4
Remainder	320	9 905 *			180 *		
Within plot error	529	4 636			93		

^aVC % = $(\sigma_i^2/\sigma_p^2) \times 100$, where σ_i^2 is the i^{th} variance component; σ_p^2 is the total phenotypic variance,

$$\text{i.e., } \sigma_G^2 + \sigma_S^2 + \sigma_M^2 + \sigma_R^2 + \sigma_G^2 + \sigma_S^2 + \sigma_e^2.$$

*Significant at 0.05.

^{ns}Not significant at 0.05.

Table 2. — Heterosis values of height and needle length and their standard errors (in parentheses) for population hybrids, and means of intrapopulation crosses in the main diagonal.

Females	Males (pollen mixtures)						
	212 FRA ^a	250 GER	262 GEO	269 ENG	316 FRA	318 BEL	556 ITA
Height (mm)							
212 FRA	<u>263</u>	-2 (24)	-35 (21)	2 (19)	-32 (17)	-28 (21)	2 (19)
250 GER	-14 (19)	<u>375</u>	-44* (19)	-36 (19)	-47* (18)	-82* (21)	-26 (18)
262 GEO	-22 (21)	-86* (22)	<u>287</u>	-25 (20)	-18 (18)	-41 (23)	-57* (21)
269 ENG	-2 (16)	-15 (18)	-73* (23)	<u>321</u>	-20 (15)	36* (18)	-5 (18)
316 FRA	79* (17)	18 (19)	-48* (19)	-22 (16)	<u>264</u>	7 (16)	-29 (18)
318 BEL	26 (17)	-80* (22)	-38 (23)	-55* (22)	-29 (22)	<u>363</u>	-27 (23)
556 ITA	43* (17)	-53* (19)	-60* (22)	-8 (18)	21 (18)	-5 (19)	<u>268</u>
Needle Length (mm)							
212 FRA	<u>48</u>	1.2 (3.5)	-3.5 (3.0)	2.7 (2.7)	-2.9 (2.5)	-1.4 (3.0)	-2.4 (2.8)
250 GER	-7.5* (2.8)	<u>69</u>	1.8 (2.7)	5.9 (2.8)	0.4 (2.6)	-7.8* (3.0)	-0.6 (2.7)
262 GEO	-7.5* (3.0)	0.0 (3.2)	<u>48</u>	5.0 (3.0)	0.8 (2.6)	0.3 (3.3)	3.5 (3.0)
269 ENG	-2.1 (2.4)	-5.0 (2.7)	-5.9 (3.3)	<u>56</u>	-4.7* (2.2)	-5.6* (2.6)	-2.2 (2.6)
316 FRA	3.1 (2.4)	-4.0 (2.7)	4.5 (2.8)	1.1 (2.4)	<u>38</u>	1.8 (2.4)	4.1 (2.7)
318 BEL	-5.1 (2.5)	3.4 (3.2)	-3.7 (3.3)	5.8 (3.2)	0.1 (3.3)	<u>66</u>	1.8 (3.3)
556 ITA	-2.6 (2.5)	-7.7* (2.8)	1.0 (3.3)	-6.4* (2.6)	-5.7* (2.7)	-3.5 (2.8)	<u>50</u>

* Absolute value of heterosis exceeding twice its standard error.

^a Populations are identified by MSFG accession number, e.g., MSFG 212, and abbreviations of place of origin, e.g., France, Germany, Georgian U.S.S.R., England, Belgium, Italy.

Table 3. — Heterosis values of height and standard errors (in parentheses) for hybrid families and means of intrapopulation families in the main diagonal.

Females	Males (pollen mixtures)						
	212 FRA	250 GER	262 GEO	269 ENG	316 FRA	318 BEL	556 ITA
	(mm)						
212 FRA 1 ^a	212	70* (29)	-31 (34)	58 (29)	-18 (24)	7 (33)	50 (31)
212 FRA 2	<u>288</u>	-69* (30)	-38 (24)	-30 (23)	-33 (22)	-45 (24)	-22 (22)
250 GER 1	-16 (25)	<u>338</u>	-34 (26)	50 (30)	-35 (25)	-72* (30)	21 (24)
250 GER 2	-4 (27)	<u>405</u>	-51* (24)	-88* (23)	-56* (23)	-91* (25)	-71* (24)
262 GEO 1	-5 (33)	-96* (30)	<u>293</u>	4 (27)	-4 (25)	28 (36)	-23 (29)
262 GEO 2	-27 (25)	-75* (31)	<u>280</u>	-53 (28)	-25 (24)	-73* (29)	-80* (27)
269 ENG 1	7 (22)	-20 (21)	-126* (30)	<u>389</u>	-19 (21)	45* (22)	-79* (27)
269 ENG 2	-3 (22)	-34 (27)	-20 (30)	<u>253</u>	-18 (20)	14 (25)	52* (22)
316 FRA 1	53* (21)	31 (31)	-61* (25)	-57* (22)	242	-58* (21)	-29 (23)
316 FRA 2	113* (23)	6 (21)	-34 (27)	16 (23)	<u>289</u>	79* (22)	-27 (28)
318 BEL 1	61* (23)	-46 (32)	-1 (36)	-107* (36)	-31 (30)	<u>334</u>	41 (36)
318 BEL 2	-9 (24)	-104* (28)	-59* (26)	-33 (26)	-23 (30)	<u>383</u>	-60* (26)
556 ITA 1	74* (22)	-75* (26)	-39 (32)	10 (25)	11 (22)	31 (24)	<u>253</u>
556 ITA 2	-6 (27)	-42 (24)	-79* (28)	-26 (24)	-74* (28)	-47 (26)	<u>288</u>

* Absolute value of heterosis exceeding twice its standard error.

^a Populations are identified by MSFG accession number, e.g., MSFG 212, and abbreviations of place of origin, e.g., France, Germany, Georgian U.S.S.R., England, Belgium, Italy. Female parents designated 1 or 2.

Table 4. — Heterosis values of needle lengths and standard errors (in parentheses) for hybrid families and means of intrapopulation families in the main diagonal.

Females	Males (pollen mixtures)						
	212 FRA	250 GER	262 GEO	269 ENG	316 FRA	318 BEL	556 ITA
	(mm)						
212 FRA 1 ^a	54	4.7 (4.3)	-2.9 (4.9)	8.8*(3.5)	4.2 (3.5)	4.1 (4.9)	-4.8 (4.5)
212 FRA 2	<u>45</u>	-5.1 (4.3)	-3.6 (3.5)	-1.5 (3.3)	-3.3 (3.3)	-4.3 (3.5)	-1.7 (3.3)
250 GER 1	9.9*(3.7)	58	0.6 (3.7)	15.9*(4.4)	8.0*(3.6)	-2.4 (4.4)	4.1 (3.5)
250 GER 2	7.2 (3.9)	<u>79</u>	3.1 (3.4)	-0.9 (3.4)	-5.7 (3.3)	-12.1*(3.7)	-4.1 (3.6)
262 GEO 1	-8.3 (4.8)	2.9 (4.5)	<u>48</u>	-1.7 (4.0)	-1.9 (3.7)	-3.0 (5.3)	2.8 (4.2)
262 GEO 2	-6.9 (3.7)	-2.6 (4.6)	<u>47</u>	11.9*(4.1)	2.9 (3.5)	2.2 (4.2)	4.1 (4.0)
269 ENG 1	-6.3 (3.2)	-8.2*(3.2)	-16.0 (4.4)	62	7.7*(3.1)	-11.9*(3.3)	-5.4 (4.0)
269 ENG 2	-0.9 (3.2)	-1.5 (4.0)	1.1 (4.4)	<u>51</u>	-4.5 (3.0)	-2.0 (3.6)	-0.9 (3.2)
316 FRA 1	1.7 (3.1)	0.6 (4.7)	0.1 (3.6)	2.1 (3.2)	<u>39</u>	1.7 (3.1)	1.7 (3.3)
316 FRA 2	4.8 (3.4)	-5.1 (3.1)	9.0*(4.0)	-0.1 (3.4)	<u>37</u>	2.0 (3.3)	7.9 (4.1)
318 BEL 1	-11.1*(3.4)	-2.9 (4.8)	-16.3*(5.3)	-6.2 (5.2)	-2.3 (4.4)	<u>63</u>	-18.9*(5.9)
318 BEL 2	0.8 (3.5)	8.0 (4.1)	0.8 (3.8)	10.8*(3.8)	1.5 (4.3)	<u>67</u>	10.0*(3.7)
556 ITA 1	-4.4 (3.2)	-1.1 (3.9)	1.0 (4.7)	-3.7 (3.6)	-3.8 (3.3)	-1.4 (3.5)	<u>53</u>
556 ITA 2	0.0 (4.0)	-11.7 (3.5)	2.1 (4.0)	-7.9*(3.5)	-9.3*(4.1)	-5.4 (3.8)	<u>46</u>

* Absolute value of heterosis exceeding twice its standard error.

^a Populations are identified by MSFG accession number, e.g., MSFG 212, and abbreviations of place of origin, e.g., France, Germany, Georgian U.S.S.R., England, Belgium, Italy. Female parents designated 1 or 2.

value. All of the population hybrids that had 269 ENG as the common female parent consistently produced negative estimates.

The range of estimated heterosis values for the hybrid families was greater than for the population hybrids in both height and needle length, and included large differences between pairs of female parents (Table 3). The largest positive heterosis value (114 mm) for height was obtained by crossing 316 FRA 2 × 212 FRA, which was 41% larger than its mid-parent value; and the largest negative heterosis estimate was -126 mm (269 ENG 1 × 262 GEO), which was 32% smaller than its mid-parent value. Twenty-eight of 84 hybrid families had relatively large heterosis values, exceeding twice their respective standard errors, and 8 of those were positive.

Heterosis values for needle length of hybrid families (Table 4), ranged from -18.9 (318 BEL 1 × 556 ITA) to 15.9 mm (250 GER 1 × 269 ENG), and these were 29% less than and 26% more than their mid-parent values, respectively. Seventeen of these estimates were larger than twice their respective standard errors, and 8 of these were positive.

Discussion

The nested population diallel analysis provided important information on the population components of variance relative to the individual components of variance. The genetic variance percentage for populations may be defined as the percentage of total population variance components to total phenotypic variance [i.e., $(\sigma^2_G + \sigma^2_S + \sigma^2_M + \sigma^2_R) \times 100/\sigma^2_P$] and similarly the genetic variance percentage for individual variability was defined as $(\sigma^2_g + \sigma^2_s) \times 100/\sigma^2_p$. For height, the genetic component for individuals (11.2%) was more than twice that for populations (4.4%). These ratios for needle lengths were about equal, i.e., 14.6% for populations and 13.0% individuals.

It should be noted that interpretation of the population components of variance is different from that of the ordinary intrapopulation diallel crosses, because genetic interpretation in an ordinary mating experiment is based on covariance of relatives in panmixia. However, the covariance structure among the offsprings in this experiment is different since the males are represented by different populations. HINKELMANN (1974) suggested a "coefficient of as-

sociation" in interpreting population components of variance, which is based on some degree of similarity of gene pools in different populations. STUBER and COCKERHAM (1966) compared gene action and variances in a hybrid population under two definitional systems. In one system, gene effects were defined according to origin (reference population), and in the other system gene effects were defined uniquely in the hybrid population. They showed different partition of genetic variances between the two systems, although the total genetic variance was the same, and suggested a different selection system. In addition, the variances could not be directly related among generations because they are gene-frequency and gene-distribution dependent.

Although a simple way to describe genetic structure of the population is not yet available, the population GCA variance (σ^2_G) seems to be associated with additive effects of the populations. Such an extension of general combining ability variance to the population level seems to be useful in a breeding program based on populations, and may provide the average breeding value of the populations. The significance of population general combining ability for both height and needle length indicated that additive effects associated with populations are real, and that selection for population general combining ability may be effective. Similarly, gca variance of individuals (σ^2_g) is interpreted as the average effects of individual trees in a series of crosses. The significant σ^2_g indicates the large differences among seed parents in the average contribution to their offspring. Thus, a breeder can utilize both population and individual general combining ability estimates in screening the populations and individuals, respectively, whose average contribution to their offspring is large in a hybrid breeding program.

Population maternal effects (σ^2_M) and population reciprocal effects (σ^2_R) are associated with an additional influence of population females on the progenies, and on the differences in specific combining abilities of reciprocal population crosses. These variances are often considered as environmental sources of variation (FALCONER 1960) and have little use in plant breeding. In this experiment, these variances were negligible in both characters, and thus offer support for simplifying mating designs by excluding them from the model. Use of half-diallel or factorial mating designs, in practice, may save time and cost, and yet provide the necessary information.

Interaction variance of the populations may be an important component in needle length as suggested by a significant population specific combining ability (σ^2_S). This component represents an interaction effect between the populations of different genetic structure, and a portion of it may indicate average dominance relationships among the populations. The specific combining ability variance of individuals (σ^2_s) results from interaction between the seed parents and pollen mixture of the populations. This interaction variance was large in needle length. These interaction variances may relate to heterotic effects limited to specific crosses of populations or individuals.

There were several large heterosis values among the population hybrids and hybrid families; however, heterosis in most cases was negative for height, indicating a general lack of hybrid superiority. NILSSON (1975), ZEASER (1976), and DEMERITT and GERHOLD (1985) reported that the mean heights of hybrid populations in Scotch pine were generally intermediate between the mean heights of the parental popu-

lations. Negative heterosis in interprovenance hybridization in loblolly pine was reported by WOESSNER (1975). CRESS (1966) indicated that a negative contribution to heterosis can be expected at certain loci with more than two alleles at a locus even when alleles in pairs have partially dominant, completely dominant, or overdominant effects.

Such lack of hybrid superiority might also be explained by gene actions within the populations. The intrapopulation progenies used to calculate mid-parent values seem to be highly heterozygous with some degree of nonadditive gene action, and probability are less inbred than if they had been produced in natural populations. That is because the outbreeding tendency of the species was exaggerated by using pollen mixtures consisting of several individuals of the same population, excluding those used as females, probably a less closely related group of parents than would normally occur in nature. Individual populations may have high frequencies of favorable linkage maintained through the evolutionary process. Therefore, mid-parent values based on intra-population progenies may be inflated relative to interpopulation progenies.

Combining desirable traits for a specific breeding objective is an important aspect of hybridization. ZEASER (1976) reported that *haguenensis* × *iberica* Scotch pine hybrids were better suited for Christmas tree or ornamental uses because of a combination of desired characters, including growth rate, foliage color, and trunk form. In our experiment, height and needle length were correlated characters ($r = 0.94$). However, population hybridization is likely to be more important in combining desirable characters for two or more traits with little correlation between them or some qualitative trait such as disease resistance, especially when desired traits are absent from otherwise promising populations. WOESSNER (1975), working with interprovenances hybrids in loblolly pine, found some evidence that desirable parental characteristics had been combined in the hybrids when grown in different edaphic conditions. Such possibilities of extended adaptabilities in Scotch pine interpopulation hybrids will be examined in a subsequent paper.

Genetic diversity among the parental populations is necessary to obtain heterosis; but a lack of heterotic response does not infer an absence of genetic divergence between populations (STUBER 1970). Such genetic diversity among these populations was supported by large differences among intrapopulation crosses. The performances of hybrid populations thus can be accounted for mainly by additive effects, with the exception of a few nonadditive effects which were large in certain cases.

The hybrid populations provide genetically variable materials for an advanced generation breeding program in addition to the possibilities for immediate utilization of the F_1 progenies. This was indicated by large differences between the population hybrids and hybrid families, and some useful heterosis. However, quantitative genetic theory has limitations in formulating genetic effects characterizing the populations and their hybrids (STUBER 1970, STUBER and COCKERHAM 1966). Also, no pattern that would aid in predicting the occurrence of heterosis was discovered. Although the frequency and magnitude of heterosis were large enough to warrant further interest in developing ways to exploit it, population hybridization in Scotch pine is likely to be important primarily in combining desirable characters and producing genetically diverse breeding populations.

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Geographic Variation in Green Ash in the Southern Coastal Plain of the United States

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Abstract

A progeny-provenance test of green ash near Stoneville, Mississippi, is described. Nine seed sources (provenances) from the southern coastal plain were selected. Both latitude- and nonlatitude-related differences in 10 year height was demonstrated. Trees from a southern Mississippi seed source were about 3 feet taller than those from comparable latitude in Louisiana.

There was also evidence of considerable within-seed source variation in height. Statistically significant differences in height were noted among half-sib families from over one-half of the seed sources.

At 5 years, progeny of a putative pumpkin ash had markedly straighter stems than any of the other progenies in the test but at 10 years stems of all progenies had straightened to the point where differences were no longer discernible.

Key words: Progeny test, hardwoods, *Fraxinus profunda*, *Fraxinus pennsylvanica*.

Zusammenfassung

Es wird über die Ergebnisse aus einem Provenienzversuch mit 9 Herkünften von *Fraxinus pennsylvanica* MARSH., in der Nähe von Stoneville, Mississippi, berichtet, wobei

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das Saatgut von jeweils 10 Einzelbäumen geerntet worden war. 3 Herkünfte stammen aus der Küstenebene von North und South Carolina und 6 Herkünfte aus dem Mississippi-Tal vom südlichen Illinois bis zum südlichen Louisiana. Im Alter zehn war die Nachkommenschaft von einer Herkunft vom südlichen Mississippi 3 Fuß höher als Herkünfte aus vergleichbarer geographischer Breite in Louisiana. Offenbar gab es eine beträchtliche Variation in der Baumhöhe innerhalb der Herkünfte. Statistisch signifikante Unterschiede in der Baumhöhe wurden bei Halbgeschwisterfamilien von über der Hälfte der Herkünfte festgestellt.

5 Jahre alte Bäume einer Nachkommenschaft von einer mutmaßlichen *Fraxinus profunda* hatten deutlich geradere Stämme als einige andere Nachkommenschaften des Versuchs, aber bei den 10 Jahre alten Stämmen aller Nachkommenschaften, die sich bis zu diesem Alter gestreckt hatten, waren solche Unterschiede nicht mehr sichtbar.

Introduction

Green ash (*Fraxinus pennsylvanica* MARSH.) is a wide ranging species distributed from the Atlantic coast to the plains states and from Canada to the Gulf of Mexico. It is one of a small group of bottomland hardwood species that has been selected for culture in intensively managed plantations in the southeastern United States (MALAC and HEEREN 1979). Such use makes it a candidate for genetic