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Genetic Evaluation of Rapid Height Growth in Pot- and Nursery-Grown Scotch Pine

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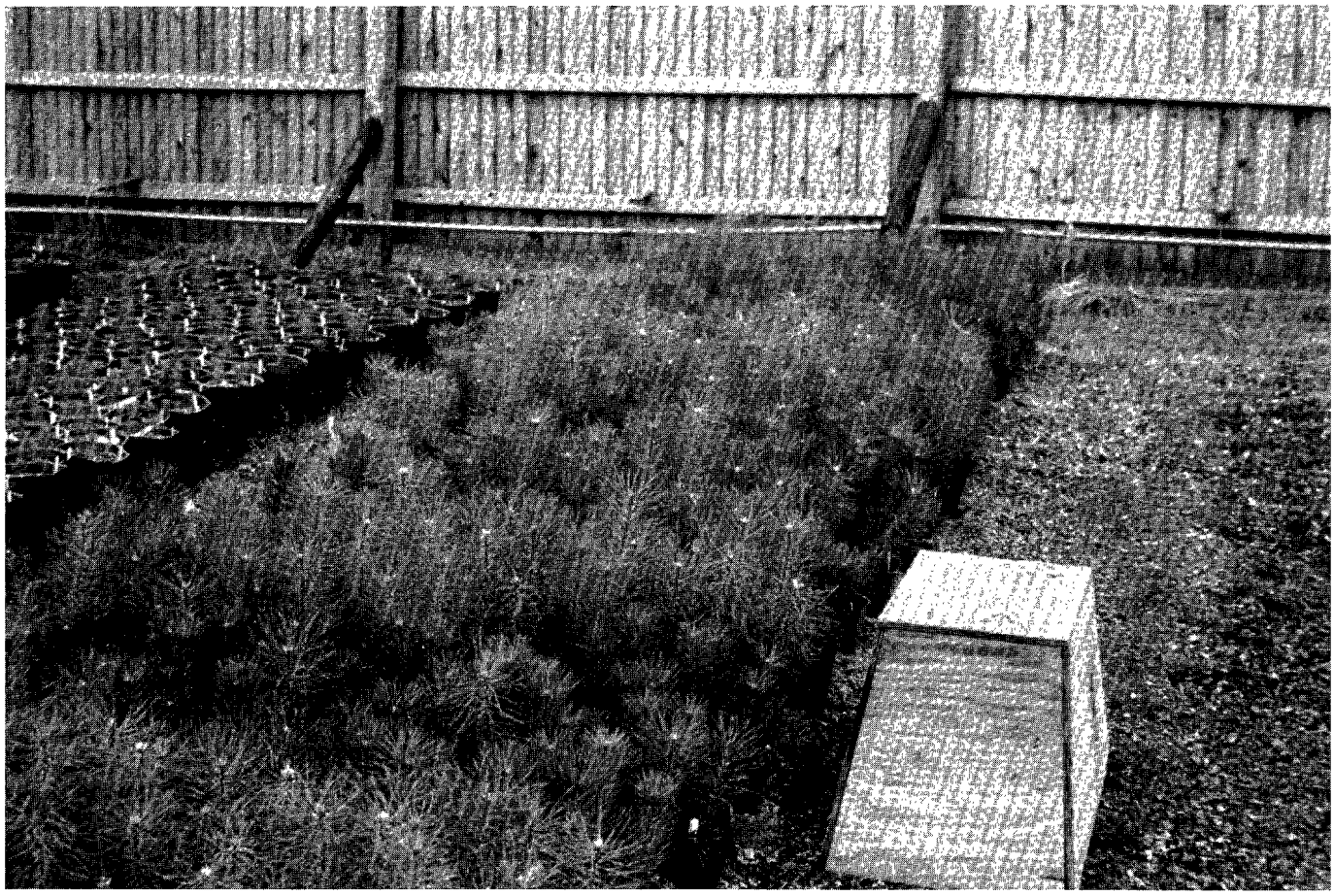

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Abstract

Genetic and environmental components of variance for 2-year heights of offspring from inter- and intra-provenance matings in Scotch pine (*Pinus sylvestris* L.) were studied to determine which provenances and selection methods should be used in a program to improve ornamental and Christmas trees.

The study represents 11 experiments (parental groups), consisting of families from 7 diallel matings minus selfs in 5 different provenances, 3 factorial matings between provenances, and 1 from open pollination. The seedlings for the 11 experiments were grown in pots and in a nursery for 2 years.

Heritability estimates of 2-year height from inter- and intra-provenance matings tended to be larger on a family basis than on an individual basis, with the larger estimates being from nursery evaluations. In general, additive genetic variance was larger than dominance variance, although dominance variance increased in provenance hybrids. Nursery evaluation was preferred to pot evaluation of 2-year height because heritability estimates were larger and error variances were smaller for the experiments evaluated. Individual selection in the nursery within the German provenance seems to be the best method for improvement of 2-year height of the provenances evaluated in this study, although the rate of improvement in the Spanish provenance may be greater. Simple recurrent selection would be a good method for improvement of traits important to the Christmas tree producing industry.

Introduction

Scotch pine (*Pinus sylvestris* L.) is a major timber species in Europe and Asia. It is an important Christmas tree species in the United States and Canada. Large numbers are planted annually along highways and for other landscape and ornamental purposes.

Breeding programs have been undertaken in the United States at the Pennsylvania State University and by the U.S. Forest Service at Lincoln, Nebraska, to improve the ornamental quality of the species. Both programs focus on improving traits important to Christmas tree and amenity uses. Evaluation of the genetic control of growth of different provenances and interprovenance crosses using estimates of components of variance would be very valuable in designing such programs. Evaluation of different provenances allows the breeder to select the most promising ones to work with. Interprovenance hybridization could reveal heterosis, combine desirable traits, and create greater variability for selection purposes. These evaluations and estimates allow the breeder to maximize genetic gain for a given input of resources.

This study was designed to estimate mean heights and genetic and environmental components of variance of 2-year-old seedlings from inter- and intra-provenance matings. The specific objectives were: (1) to estimate additive and dominance genetic components of variance and environmental components of variance from inter- and intra-provenance matings, (2) to estimate heritability on an individual basis and on a family basis, (3) to compare nursery and pot propagation methods to determine the better method for genetic evaluation, and (4) to make recommendations concerning selection and breeding methods.

Materials and Methods

Inter- and intra-provenance crosses made in 1969 and 1970 were grouped by parentage into 11 experiments. The parents were from five introduced provenances of Scotch pine: four provenances growing at the Kellogg Forest of Michigan State University and one provenance growing at the Pennsylvania State University (Table 1). The four provenances at the Kellogg Forest were derived from native European forests and are part of a geographic variation test in Scotch pine (Figure 1) reported by Wright and Bull (1963). The provenance at the Pennsylvania State University is from Sierra de Guadarrama, Valsain Forest, at 1000 meters in central Spain (near 245 of Wright and Bull 1963) and is not part of a formal provenance study. The parents were selected for heavy flowering but not for other growth traits.

Table 1.—Description of plant materials in experiments, showing mating designs and the number of families planted in pots and in the nursery

Experiment No.	Year of mating	Mating design	Provenance	Number of families	
				Pots	Nursery
1	1970	6 × 6 diallel minus selfs	Spanish	30	29
2	1970	6 × 6 diallel minus selfs	Spanish	28	16
3	1970	6 × 6 diallel minus selfs	Spanish	21	12
4	1969	6 × 6 diallel minus selfs	French (212)[a]	18	10
5	1969	5 × 5 diallel minus selfs	French (238)	11	8
6	1969	4 × 4 diallel minus selfs	French (316)	7	6
7	1969	6 × 6 diallel minus selfs	German (250)	24	13
8	1970	5 × 6 factorial	French (212) ♀ × Spanish ♂	13	5
9	1970	3 × 6 factorial	French (212) ♀ × German (250) ♂	18	13
10	1970	6 × 4 factorial	German (250) ♀ × French (212) ♂	22	12
11	1969	open pollination	Spanish	18	17

[a]Numerical identification of provenances as reported by Wright and Bull (1963).

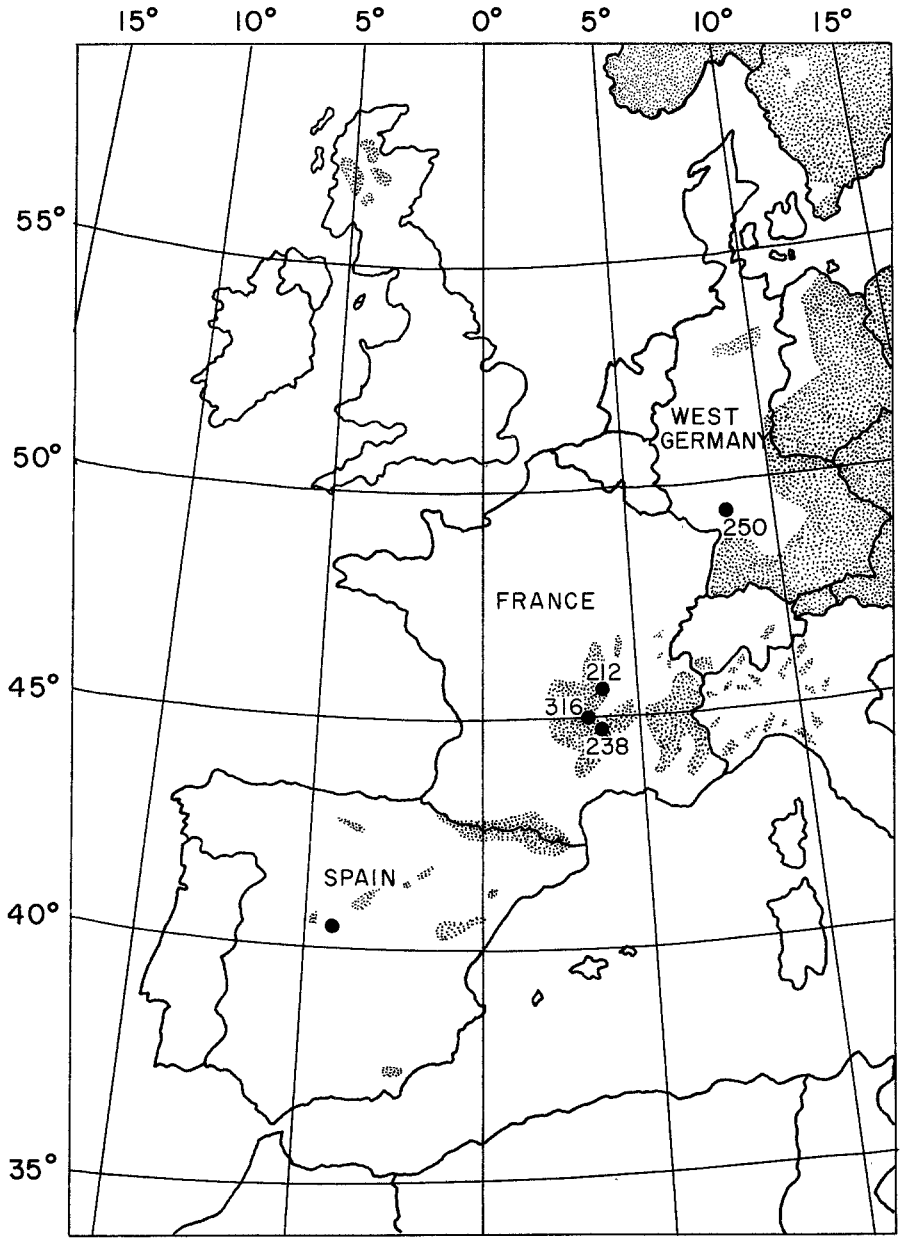

Figure 1.—Natural distribution of Scotch pine in eastern Europe (shaded) (Critchfield and Little, 1966) and provenances included in this study (large dots).

In mid-May 1969 and 1970, female strobili were isolated on the trees, pollen was collected and extracted, and pollinations were made. The pollination procedure was identical to that reported by Gerhold (1968). Pollinated strobili were marked with colored plastic rings.

Cones were protected from squirrels by window screening and were collected in September 1970 and 1971 from matings made in the previous years. Cones that did not open readily were dissected, and all full seeds were extracted.

In March 1972, seeds were sown in a greenhouse in Styroblock "2" containers filled with a 2:1 peat-perlite mix and covered with 1/8 inch of sand. In early June 1972, seedlings were transplanted to 6-inch pots filled with 1:1:2 mix of peat, perlite, and loam soil. Each family was represented by four seedlings in a pot in each of six blocks. The seedlings were watered and fertilized when necessary.

About 2 weeks later, additional seedlings were transplanted to standard nursery beds at the Penn Nursery, Potters Mills, Pennsylvania. Each experiment consisted of families randomized within six replications in 10-tree row plots. The seedlings received standard nursery care.

In October 1973, 2-year heights were measured and recorded to the nearest centimeter for seedlings in pots and in the nursery.

Analyses of variance of 2-year height data were performed for each experiment using plot means for trees in pots and those in the nursery. Analyses of variance were also performed by combining the three 6 × 6 Spanish diallel experiments into an 18-parent disconnected diallel using plot means for pots and for the nursery. Also, analyses of variance were performed on the combined pot and nursery data, treating the two different environments as location effects. A general least-squares program for diallel data was used to analyze the seven diallel experiments (Schaffer and Usanis 1969). A least-squares program using unequal subclass numbers was used to analyze the other four experiments. The program follows the outline of the methods published by W. R. Harvey (1960).

Heritability estimates using only intrapopulation methods were calculated for each experiment at each location (pots and nursery) on an individual basis and on a family basis, using standard formulas (Table 2). Heritability estimates on an individual basis are commonly used for estimating the ratio of additive genetic to total variance and are appropriate for estimating gain from mass selection among randomly placed seedlings in either environment (pots or nursery). Heritability estimates on a family basis are appropriate for estimating gain from selection among half-sib families. For this study, 4 seedlings per plot in pots with replication or 8 of the 10 seedlings per nursery row with replication were assumed for estimates of heritability on a family basis. If all seedlings in nursery rows were present, the border or outside trees were not measured.

Table 2.—Formulas for estimating heritability on an individual basis and a family basis.

Mating design	Heritability	
	Individual basis	Family basis
diallel	$\frac{4\,\sigma^2_{gca}}{2\sigma^2_{gca}+\sigma^2_{sca}+\sigma^2_{mat}+\sigma^2_{rec}+\sigma^2_{p}+\sigma^2_{w}}$	$\frac{\sigma^2_{gca}}{\frac{rn+1}{rn}\sigma^2_{gca}+\frac{1}{rn}\sigma^2_{sca}+\frac{rn+1}{rn}\sigma^2_{mat}+\frac{1}{rn}\sigma^2_{rec}+\frac{1}{r}\sigma^2_{p}+\frac{1}{rn}\sigma^2_{w}}$
factorial	$\frac{4\,\sigma^2\text{ (male or female)}}{\sigma^2_{male}+\sigma^2_{female}+\sigma^2_{mf}+\sigma^2_{p}+\sigma^2_{w}}$	$\frac{\sigma^2\text{ (male or female)}}{\frac{rn+1}{rn}\sigma^2_{male}+\frac{rn+1}{rn}\sigma^2_{female}+\frac{1}{rn}\sigma^2_{mf}+\frac{1}{r}\sigma^2_{p}+\frac{1}{rn}\sigma^2_{w}}$
O.P.	$\frac{4\,\sigma^2_{fam}}{\sigma^2_{fam}+\sigma^2_{p}+\sigma^2_{w}}$	$\frac{\sigma^2_{fam}}{\sigma^2_{fam}+\frac{1}{r}\sigma^2_{p}+\frac{1}{rn}\sigma^2_{w}}$

σ^2_{gca} = general combining ability
σ^2_{sca} = specific combining ability
σ^2_{mat} = maternal effects
σ^2_{rec} = reciprocal effects
σ^2_{p} = among-plot variance
σ^2_{w} = within-plot variance
σ^2_{male} = male variance
σ^2_{female} = female variance
σ^2_{mf} = male × female variance
σ^2_{fam} = family variance
r = number of replications
n = numbers of trees/plot

Results

A. **Mean Height.** Large differences in 2-year mean height were found among the Scotch pine seedlings of the five original provenances and also between those provenances grown in pots and in the nursery (Table 3). Seedlings from every experiment were shorter in the nursery than those grown in pots. There were no significant changes in ranking of provenances between the two environments. Spanish seedlings were the shortest and German seedlings were the tallest. The three French provenances were intermediate in height between the Spanish and German provenances with French (212) seedlings being the tallest, next French (316) seedlings, and finally French (238) seedlings, the shortest of the French provenances.

Table 3.—Two-year heights and error variances for Scotch pine seedlings grown in pots and in the nursery

Experiment	Pots		Nursery	
	Mean (cm)	σ_e^2	Mean (cm)	σ_e^2
Spanish diallel #1	19.05	6.89	15.88	2.65
Spanish diallel #2	19.74	7.32	15.72	1.81
Spanish diallel #3	19.93	8.93	16.78	2.62
Spanish open pollination	19.69	7.05	17.12	3.35
French (212)♀ × Spanish ♂	24.48	8.15	20.64	—[a]
French (212) diallel	25.78	20.47	21.29	3.85
French (212)♀ × German (250)♂	28.28	14.69	22.86	3.48
German (250)♀ × French (212)♂	30.13	16.29	23.58	5.12
German (250) diallel	31.21	19.69	26.86	11.97
French (316) diallel	21.42	8.82	19.44	—[a]
French (238) diallel	20.34	10.38	17.15	3.47

[a]No analysis of variance was conducted on these data because of the large number of missing cells.

Mean 2-year heights of interprovenance seedlings were intermediate between those of their two parental provenances (Table 3). There was a slight tendency for the hybrid seedlings to be closer to the height of the female parent's provenance.

There was a slight heterotic response for 2-year height for the French × Spanish seedlings grown in pots. French × Spanish hybrid families averaged 107 percent of the average provenance mid-parent value. Individual hybrid families grown in pots ranged from 83 to 136 percent of their respective mid-parent values. There seems to be no clear heterotic response in the German × French hybrid seedlings grown in pots and in the nursery. The German female × French male hybrid families averaged 106 and 98 percent of their average provenance mid-parent values in pots and in the nursery, respectively. Individual German female × French male families ranged from 87 to 114 percent and 81 to 103 percent of their respective mid-parent values in pots and in the nursery, respectively. The French female × German male hybrid families averaged 99 and 95 percent of their average provenance mid-parent values in pots and in the nursery, respectively. Individual French female × German male families ranged from 83 to 109 percent and 78 to 102 percent of their respective mid-parent values in pots and in the nursery, respectively.

B. **Estimates of Components of Variance.** Within experiments and locations, within-plot variances (σ_w^2) generally were less than among-plot variances (σ_p^2), although in most instances these variances were quite similar in magnitude (Table 4). In only one instance, the German (250) nursery diallel, was among-plot variance more than twice the within-plot variance. Across all experiments, the among-plot variances were from 8 to 58 percent of their respective total variances. Also, within-plot variances ranged from 9 to 42 percent of their respective total variances. There was quite a range in magnitude of components of variance between locations and among experiments. This is a reflection of differences in the error terms of each experiment. The ratios of among-plot and within-plot components of variance to their respective error components of variance were quite consistent.

Table 4.—Within-plot and among-plot components of variance for experiments as a percentage of total variance.

Experiment	Pots		Nursery	
	σ_w^2	σ_p^2	σ_w^2	σ_p^2
Spanish diallel #1	35	37	23	34
Spanish diallel #2	40	45	22	21
Spanish diallel #3	41	45	30	36
Spanish diallels Combined	39	43	24	39
Spanish open pollination	42	37	26	44
French (212)♀ × Spanish ♂	34	22	—[a]	—[a]
French (212) diallel	32	48	26	35
French (212)♀ × German (250)♂	30	27	9	8
German (250)♀ × French (212)♂	35	35	18	18
German (250) diallel	33	52	24	57
French (316) diallel	37	58	—[a]	—[a]
French (238) diallel	30	34	41	48

[a]No components of variance were estimated because no analyses of variance were conducted on these data.

When plot and nursery data were combined, general combining ability (GCA) was the largest component of variance in the Spanish diallels and in the German (250) diallel experiments (Table 5). Specific combining ability (SCA) was the largest component of variance in the French (212) diallel experiment. Reciprocal effects were the largest component of variance in the French (238) diallel experiment. Components of variance were quite consistent among the three Spanish diallel experiments, with few exceptions. GCA by location components of variance were small for all provenances.

In pot analyses, GCA was the largest component of variance in the Spanish #2, #3, and combined Spanish diallel experiments and in the French (316) experiment (Table 5). SCA was the largest component of variance in the Spanish #1 diallel and the French (212) diallel experiments. Reciprocal effects were the largest component of variance in the French (238) diallel experiment.

In nursery analyses, GCA was the largest component of variance in the Spanish #1, #2, and combined Spanish diallel, the French (212) diallel, and the German (250) diallel experiments (Table 5). SCA was the largest component of variance in the Spanish #3 diallel experiment. Maternal effects were the largest component of variance in the French (238) diallel experiment.

Table 5.—General and specific combining ability, maternal, reciprocal, and general combining ability by location components of variance for 2-year height in diallel experiments as a percentage of total variance.

Location	Component of Variance	Spanish				French			German
		#1	#2	#3	Combined	212	238	316	250
Pots	σ^2_{gca}	7	12	12	8	−1	7	5	7
	σ^2_{sca}	11	1	0	4	13	−12	−5	7
	σ^2_{mat}	4	2	−1	2	6	−10	0	1
	σ^2_{rec}	6	−2	1	4	−14	29	—[a]	−4
Nursery	σ^2_{gca}	32	45	−5	26	38	−2	—	15
	σ^2_{sca}	7	12	18	7	−2	−17	—	5
	σ^2_{mat}	0	−1	16	−2	−2	10	—	−1
	σ^2_{rec}	4	—[a]	—[a]	4	—[a]	—[a]	—	—[a]
Pots and nursery	σ^2_{gca}	18	23	17	15	5	−1	—	14
	σ^2_{sca}	11	6	2	7	19	−3	—	10
	σ^2_{mat}	4	1	−5	3	8	−5	—	0
	σ^2_{rec}	3	2	10	4	−16	15	—	−1
	$\sigma^2_{gca\ by\ Loc.}$	1	1	−2	1	−4	3	—	−4

[a]Variance components due to reciprocal effects were not estimated because the matrices of coefficients of the expected mean squares were singular and could not be inverted.

Family components of variance for the Spanish open pollination experiments from pots, nursery, and combined analyses were 21, 28, and 25 percent of their total variances, respectively (Table 6). The family component of variance from the nursery analysis accounted for a larger percentage of the total variance than did the same component in the pots or combined analyses.

Female components of variance were larger than either male or male × female components of variance in all French (212) female × German (250) male hybrid analyses and the German (250) female × French (212) male hybrids in pots and combined analyses (Table 6). In the two other analyses, the male × female components of variance were small.

C. **Estimates of Heritability.** In the diallel experiments, most estimates of heritability of 2-year height in pots were smaller than heritability estimates of height in the nursery (Table 7). Heritability estimates on an individual basis ranged from 0 to 0.45 in pots and from 0 to 1.25 in the nursery. Heritability estimates on a family basis ranged from 0 to 0.55 in pots

Table 6.—Male, female, and male × female components of variance for 2-year height in provenance hybrids and open pollination experiments as a percentage of total variance.

Location	Component of variance	Spanish open pollination	French (212) ♀ × Spanish ♂	French (212) ♀ × German (250) ♂	German (250) ♀ × French (212) ♂
Pots	σ^2_{males}	—	−16	6	9
	$\sigma^2_{females}$	21[a]	17	26	13
	$\sigma^2_{m \times f}$	—	27	12	8
Nursery	σ^2_{males}	—	—	23	4
	$\sigma^2_{females}$	28[a]	—	50	7
	$\sigma^2_{m \times f}$	—	—	10	52
Pots and nursery	σ^2_{males}	—	—	18	8
	$\sigma^2_{females}$	25[a]	—	35	19
	$\sigma^2_{m \times f}$	—	—	12	15

[a]Component of variance due to open pollination families.

Table 7.—Estimates of heritability of 2-year height on an individual and family basis in diallel experiments

Location		Spanish Diallels				French Diallels			German Diallel
		#1	#2	#3	Combined	212	238	316	250
Pots	Individual	0.27	0.45	0.43	0.29	0	0.26	0.19	0.25
	Family	0.32	0.52	0.55	0.40	0	0.46	0.31	0.37
Nursery	Individual	0.97	1.25	0	0.82	1.11	0	—	0.51
	Family	0.81	0.90	0	0.77	0.84	0	—	0.58

and from 0 to 0.90 in the nursery. Estimates of heritability were different among the provenances studied. The six heritability estimates of zero seem inconsistent with observed patterns, especially those for the nursery, but may be due in part to small sample sizes.

Heritability estimates from the Spanish open pollination experiment were slightly larger when estimated in the nursery compared to pot estimates (Table 8). Heritability estimates on an individual basis were 0.84 and 1.19 from pot and nursery evaluations, respectively. Heritability estimates on a family basis were 0.70 and 0.79 for pot and nursery evaluations, respectively.

Most heritability estimates for the interprovenance experiments were moderately high for 2-year height, regardless of whether they were calculated on an individual or family basis or from pot or nursery data. Heritability estimates were higher when female components of variance were used to estimate additive variance than when male components were used. Heritability estimates for provenance hybrids were quite variable, but similar to estimates from the diallel analyses for pots and generally less than estimates for the nursery.

Heritability estimates on an individual basis for provenance hybrids based on males ranged from 0 to 0.35 and from 0.17 to 0.93 for pots and nursery data, respectively (Table 8). Family heritability estimates of males derived from pots and the nursery ranged from 0 to 0.29 and from 0.26 to 0.30, respectively. Heritability estimates on an individual basis based on females ranged from 0.52 to 1.06 and from 0.28 to 1.99 for pots and nursery data, respectively. Family heritability estimates based on females ranged from 0.43 to 0.71 and from 0.44 to 0.65 for pots and nursery data, respectively.

Discussion

Statistical developments and analyses in this study included populations generated by crossing presumed random individuals within provenances and by crossing presumed random individuals from two-parent provenances. Intraprovenance estimates of genetic parameters can be related to the provenances from which the parents are a random sample. For interprovenance estimates of genetic parameters, the reference provenance is a theoretical population formed from the union of all possible gametes from one population with those of a second population. Intrapopulation theory is quite satisfactory for interpopulation studies if the same alleles are present in the two-parent populations and if the gene frequencies do not differ greatly. If the gene frequencies in the two-parent populations are different, frequencies at linked loci in the interpopulation will not reach Hardy-Weinberg equilibrium in one generation. The genetic interpretation of the covariances

Table 8.—Estimates of heritability of 2-year height on an individual and family basis in open pollination and provenance hybrid experiments.

Location		Spanish open pollination	French (212) ♀ × Spanish ♂		French (212) ♀ × German (250) ♂	German (250) ♀ × French (212) ♂
Pots	Individual	0.83	males[a]	0.00	0.22	0.35
			females[b]	0.68	1.06	0.52
			combined[c]	0.34	0.64	0.44
	Family	0.70	males	0.00	0.14	0.29
			females	0.71	0.67	0.43
			combined	0.36	0.41	0.36
Nursery	Individual	1.19	males	—	0.93	0.17
			females	—	1.99	0.28
			combined	—	1.46	0.23
	Family	0.79	males	—	0.30	0.76
			females	—	0.65	0.44
			combined	—	0.47	0.35

[a] $\sigma^2_{males} = 1/4\ \sigma^2_A$ [b] $\sigma^2_{females} = 1/4\ \sigma^2_A$ [c] $\sigma^2_{males} + \sigma^2_{females} = 1/2\ \sigma^2_A$

among relatives for the interpopulation will differ from the intrapopulation interpretations (Stuber and Cockerham 1966). We used intrapopulation theory to study interpopulation crosses because we had no objective evidence that our interprovenance crosses violated intrapopulation genetic theory.

Estimates of interprovenance parameters can be very useful. Reciprocal recurrent selection (RRS) used performance of test cross progeny as a basis for selection and has been successful in maize breeding programs (Stuber 1970).

Shelbourne (1969) reviewed tree breeding strategies including RRS with quantitative genetic expectations of gain. He predicted gain in *Pinus radiata* for stem straightness and diameter using various strategies. The greatest gains for both traits were predicted for a second stage clonal orchard; slightly smaller gains were predicted for clonal propagation and testing.

There seemed to be little heterotic response for 2-year height in the interprovenance crosses of Scotch pine when all families are considered. Heterosis was measured as the difference between the provenance hybrid family and the average of the two parents (mid-parent) calculated from intraprovenance full-sib families in diallels. All interprovenance mean heights were intermediate between the mean heights of the parent provenances (Table 3). There were a few differences between the average height of seedlings of hybrid families and the calculated mid-parent values for those families, but the number of families was not greater than one might expect purely by chance. Zeaser (1976) found no real differences between the average of 13 *haguenensis* × *iberica* hybrid families and calculated mid-parent values for 8-year height. This is further evidence that there is little chance of finding heterotic responses in early height growth among the interprovenance crosses of Scotch pine from this area of its natural range.

In the Spanish open pollination experiment, the contribution of male parents by wind pollination may not have been a random process. A considerable proportion of the progeny within families may, in fact, be full-sibs. As the proportion of full-sibs increased, the component of variance due to families would approach half the additive variance plus one-quarter the dominance variance rather than one-quarter the additive variance. This would result in overestimation of true additive variance and of heritability. Heritability estimates from open pollination progeny in pots were considerably larger than estimates from controlled matings in pots. Heritability estimates from open pollination and controlled matings were similar in the nursery. Comparison of genetic parameters generated from the 18 parent Spanish disconnected diallel analyses and the same 18 parents in the Spanish open pollination analyses provided similar heritability estimates for 2-year height only in the nursery evaluation. These limited evaluations seem to indicate that genetic estimates from open pollination experiments probably do not greatly overestimate true genetic parameters when evaluations are made in the nursery.

Intrapopulation genetic theory may not be satisfactory for estimation of genetic and environmental components of variance for interpopulation studies. Genes and gene frequencies which determine height appear to be different among the provenances because of the differences in mean heights among provenances. Heritability estimates for 2-year height from interprovenance studies using intrapopulation genetic theory were more variable than estimates from intraprovenance studies. Heritability estimates from nursery data tended to be less variable for provenance diallel experiments than for interprovenance experiments. Dominance variance may increase in importance compared to additive genetic variance in interprovenance crosses if the populations are different in genetic structure. Interprovenance crosses may not be in Hardy-Weinberg equilibrium and therefore no predictions for F_2 performance can be made.

Estimates of the relative magnitude of genetic components of variance in seedling height of Scotch pine can probably be obtained by evaluating at least 30 families at two locations. However, reliable estimates of genetic components of variance can probably be obtained by evaluating 90 families at two locations. Estimates of components of variance were quite consistent for combined analyses for the three Spanish population 6 × 6 diallel experiments (Table 5). Pederson (1971) stated that an 8- to 10-parent diallel mating design is probably the minimum size to obtain good estimates of genetic components of variance. Work at North Carolina State University with yield of corn suggests that at least 256 full-sib families are necessary to obtain reliable estimates of additive and dominance variance and that these families need to be tested in at least 2 years and two locations (Dudley and Moll 1969). Inconsistencies in estimates of components of variance among Spanish diallel experiments within locations may be the result of using too few parents to produce too few families. Namkoong (1979) states that "the geneticist may want to estimate means and several components for several traits from a reasonable population sample. Thus, given the capability for estimating variances and means, but with multiple demands for estimates, either some compromises on efficiency or several different experiments will have to be run".

Differences in the relative importance of the genetic components of variance for combined analyses among populations suggest that the provenances evaluated in this study differed in genetic makeup.

The similarity of genetic components of variance among the three Spanish diallel experiments and the combined Spanish diallel experiment combined over locations strengthened the evidence that the five provenances were different.

There is little reason to doubt the validity of the assumptions that are required for the estimates of additive genetic variance in the diallel mating designs used in this study. However, additive genetic variance estimated from open pollinated families probably is inflated somewhat by full-sibs and maternal effects. Also, estimates of additive genetic variance using the female component of variance from factorial mating designs may be inflated by maternal effects. The parent trees are most likely random members of some non-inbred population, although the parents were not chosen randomly. Parents were selected only for adequate flowering to make the necessary pollinations for the particular mating design being used. However, some might argue that selecting trees with adequate flowering increases the chances that their parents are related. It is assumed for this study that there was no correlation between the flower production of the parents and 2-year height of the resulting progeny. In many applications, it is difficult to conceptualize a population from which a given set of parents could be chosen at random (Baker 1978). Any inbreeding that occurred would not be abnormal, moreover. Each provenance or stand collection consisted originally of seed from 10 or more average trees from an area of several acres (Wright and Bull 1963). It is difficult to estimate just what the relatedness of the parent trees might be and what effect it had, if any, on provenance variances estimated from their progeny.

Maternal effects probably inflated the estimates of additive genetic variance of 2-year height in the open pollination experiment and also in interprovenance experiments where the female component of variance was used to estimate additive genetic variances. Maternal effects were positive in many of the diallel analyses. It is not known to what extent maternal effects may inflate estimates of additive genetic variance. Estimates of maternal effects from diallel analyses indicated that they could greatly influence estimates of additive genetic variance.

GCA was larger than SCA in some diallel experiments. This same relationship was found for 2-year height in eastern white pine (Kriebel et al. 1972) and black spruce (Morgenstern 1974).

Nilsson (1970) found for 2-year height of Scotch pine that additive effects were significantly greater than specific combining effects mainly within provenances, and the same trend held to a lesser extent within a geographical range of 2½ ° latitude and 400 meters in altitude. He also found no case where female effects were greater than male effects, which indicated that maternal effects for his study were fairly small. This study, however, showed that female effects were greater than male effects, which indicated that maternal effects were important.

Dominance variance was much larger in interprovenance matings than in intraprovenance matings of Scotch pine. In a western white pine experiment where the pollen parents were from a stand 65 miles from the female parents, estimates of dominance variance from the interaction of males × females for 1-year height was larger than either the male or female components of variance (Hanover and Barnes 1963).

Narrow-sense heritability estimates for 2-year heights were variable among the five provenances used in this study. There is, however, enough consistency in the estimates when comparisons are made within locations and method of estimation to make reasonable estimates of the range of genetic control of 2-year height. Two-year height is under strong genetic control in some Scotch pine provenances, especially when the seedlings are grown in the nursery. Heritability estimates on an individual basis for pot and nursery evaluations of Spanish open pollination progeny are similar to the estimate of 0.94 previously reported for a similar experiment in the same provenance (Demeritt et al. 1975). Heritability estimates of 2-year height from pot evaluation of diallel matings are similar to estimates on an individual basis of 0.24 and 0.30 reported for 2-year height from diallel matings in eastern white pine (Kriebel et al. 1972). Also, family heritability estimates from nursery evaluations are slightly larger than the heritability estimate of 0.59 reported for black spruce from 7 × 7 nursery diallel experiment (Morgenstern 1974).

For evaluating progeny, the nursery is preferred to pots because error variances were smaller and heritability estimates for 2-year height were larger. Genotype by environment interaction was of relatively minor importance because GCA by location components of variance were small. Larger nursery than pot heritability estimates mean that a seedling's phenotypic value is probably a more reliable indication of its breeding value if it is grown in the nursery than if it is grown in a pot. There is no conclusive evidence that this is the situation. It may be that we are evaluating a different sort of genotype and environment interaction and nursery is just another environment; i.e., no better or no worse than pots.

The best selection method for improving 2-year height among the provenances evaluated in this study is by individual selection of superior phenotypes from nursery evaluation of German (250) provenance seedlings. The German provenance (250) height in the nursery was 114 percent of the next tallest provenance, the hybrid provenance German (250) female and French (212) male. Narrow-sense heritability of 0.51 for the German (250) nursery diallel experiment means that a seedling's phenotypic value will be a reliable indication of its breeding value for that age. High heritability estimates in the Spanish provenance indicate promising possibilities for improving height in that provenance, even faster than in the German (250) provenance.

No appreciable parent-progeny correlations were found in studies of 2- to 8-year Scotch pine progeny heights in the Netherlands (Squillace et al. 1975). However, the parents

were growing some distance from the progeny and probably in different environments. They indicated that progeny testing of many selections would be required to make any appreciable genetic gain. Progeny testing of selections may be necessary in this program if parent-progeny correlations of heights at different locations are low. Juvenile-mature correlations would be an important consideration if selection on the basis of 2-year data were used for predicting performance later in life.

Squillace and Gansel (1974) reported 3- versus 25-year correlations computed between families, within families, and for all trees regardless of families for wind-pollinated and control-pollinated progeny slash pine. Between-family, within-family, and all-tree correlations for wind-pollinated progeny were 0.00, 0.14, and 0.10, respectively. Between-family, within-family, and all-tree correlations for control-pollinated progeny were 0.53, 0.14, and 0.10, respectively. Between-family correlations indicate the reliability of early selection of families; within-family correlations relate to early selection of individuals within families; and all-tree correlations indicate the reliability of early mass selection.

Wright and Baldwin (1957) reported a correlation of 0.861 for 4- versus 17-year height of 50 Scotch pine provenances computed from plot averages. They concluded that 17-year heights could be forecast with accuracy from nursery measurements. Reliable between-family, within-family, and all-tree correlations are needed for 2- versus 8- to 12-year heights in Scotch pine to judge the reliability of early nursery selection for Christmas tree and ornamental uses.

For Christmas tree or ornamental use, provenance hybridization may be a useful method for combining desirable traits from different provenances. Zeaser (1976) found that *haguenensis* × *iberica* Scotch pine varietal hybrids were better suited for Christmas or ornamental use than either parental variety because of their combination of desired height, foliage color, and trunk form. Provenance hybridization would be especially useful in programs where certain desired traits were absent from promising provenances, such as resistance to a disease.

Once superior-provenance hybrid families or trees are selected, they could be mated to produce F_2 progeny for further evaluation. Also, selected F_1 hybrids with desired traits could be backcrossed with selected trees in one of the parental varieties. Higher order filial generations could be produced and then a recurrent selection program could be conducted in the composite population which might be a useful alternative for combining useful traits in different populations.

The best possibility for improvement of early height growth for Christmas tree or ornamental uses would be in the Spanish provenance. This study indicated that 2-year height growth was under strong genetic control, especially in the nursery evaluation. Spanish Scotch pine already has desirable needle color for ornamental purposes. Large numbers are planted each year to be harvested in 8 to 12 years for Christmas trees.

Simple recurrent selection with or without progeny testing would be a good method of improving height growth, needle color and density, and trunk form for Christmas tree or ornamental uses. Superior quality Christmas trees could be identified in plantations and saved for seed production after the remainder of the trees have been removed. Plantation-grown Scotch pines flower and produce seed at approximately the same age as they are harvested for Christmas trees. Seedlings produced from this improved seed would serve as planting stock for the next Christmas tree plantation.

Conclusions

From the analysis of 2-year height of Scotch pine provenances and provenance hybrids studied in pots and in the nursery, the following conclusions can be supported:

1. Heritability estimates from inter- and intraprovenance matings tend to be larger on a family basis than on an individual basis, the higher estimates being from the nursery evaluation.

2. In general, additive genetic variance was larger than dominance variance, although dominance variance increased in interprovenance crosses.

3. Individual nursery selection within the German (250) provenance seems to be the best method of improving 2-year height because it was the tallest and most variable of the provenances evaluated in this study. The rate of improvement in the Spanish provenance could be greater, however, because heritability estimates were generally higher.

4. Provenance hybridization may be especially useful in programs where desired traits are absent from promising provenances.

5. Simple recurrent selection with or without progeny testing within the Spanish provenance seems to be the best method for improving provenances used for Christmas tree or ornamental purposes.

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Genetic and environmental components of variance for 2-year pot and nursery heights of offspring from inter- and intra-provenance matings in Scotch pine were studied to determine which provenances and selection methods should be used in an ornamental and Christmas tree improvement program. Nursery evaluation was preferred to pot evaluation because heritability estimates were larger and error variances were smaller for the experiments evaluated. Simple recurrent selection would be a good method for improving traits important to the Christmas tree industry.

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