GENETIC EVALUATION OF TWO-YEAR HEIGHT OF
SCOTCH PINE SEEDLINGS

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INTRODUCTION

This paper reports the results of genetic analyses of full- and half-sib Scotch pine (Pinus sylvestris L.) seedlings produced from intra- and inter-racial matings. The objectives of the study were to answer the following questions: (1) What is the heritability of 2-year-height growth of progeny grown under nursery conditions; (2) How much within-plot variability is there among the different mating types; (3) Are family variance components high enough to make nursery selection effective?

The plant materials were derived from open-pollinated and artificial matings within and among natural and artificial populations of Scotch pine from Europe. All progenies had one or both parents from the same Spanish population. The matings and seed collections were made between 1962 and 1969. Artificial matings were made using a mini-bag procedure (Gerhold 1968). Seeds were extracted by hand from cones and stored by families in a freezer until planting.

Seeds were sown in wooden flats in a greenhouse early in 1969 and 1970. The seedlings were watered and fertilized periodically. In late May or early June the seedlings were transplanted to the Penn Nursery, Potters Mills, Pennsylvania.[2] The families were assigned to experiments according to parentage (Table 1). The nursery design for each experiment had four randomized complete blocks, two in each of two adjacent nursery beds. In each block a family was represented by ten or fewer seedlings planted five inches apart within and between rows. Adjacent nursery beds were used each year in order to minimize site differences.

Seedling heights were measured to the nearest cm in late fall after the second growing season. The inner 6 seedlings and 8 seedlings per row were measured in 1970 and 1971, respectively. If the required number of seedlings was not available in the middle of a row, then trees at the edge were measured.

The data were analyzed during the method of unweighted means (Searly 1971). The resulting sum of squares, except for within plot error, were multiplied by the harmonic mean of cell frequencies.

Analyses of variance were performed on means of families selected according to parentage, to see if there were any differences between two non-Spanish pollen mixes mated to the same Spanish females, and between Spanish open-pollination and a Spanish pollen mix also mated to the same Spanish females.

The analysis of variance, random model, was used to estimate variance components:

Source	Expected Mean Squares of Individual Tree Analyses
Family	$\sigma^2_W + k\sigma^2_{BF} + kb\sigma^2_F$
Block x Family	$\sigma^2_W + k\sigma^2_{BF}$
Error (within plots)	σ^2_W

k = harmonic mean of number of seedlings/plot.

Heritability was estimated on an individual seedling basis using the following formulas:

$$h^2 \text{ (individual half-sib)} = \frac{4\ \sigma^2_F}{\sigma^2_F + \sigma^2_{BF} + \sigma^2_W}$$

and

$$h^2 \text{ (individual full-sib)} = \frac{2\ \sigma^2_F}{\sigma^2_F + \sigma^2_{BF} + \sigma^2_W}$$

The ratios of family variance (σ^2_F) to phenotypic variance ($\sigma^2_P = \sigma^2_F + \sigma^2_{BF} + \sigma^2_W$) were calculated for comparing all full and half-sib experiments.

Full-sib family means within male parents were regressed on half-sib family means of their respective female parents for families selected according to parentage. This is the method illustrated by Becker (1964), except that we substituted open-pollination half-sib family means of the female parents' progeny rather than using the female parent's records.

Progenies of one Spanish pollen mix and two non-Spanish pollen mixes each were regressed or compared with progenies resulting from wind pollination of common female parents. Regression and correlation coefficients, and paired t-tests using data adjusted to variance equal to one, were calculated.

RESULTS AND DISCUSSION

The analyses of variance revealed that blocks and block x family variance components accounted for a small part of the total variation. This indicated that data from different experiments in the same year could be combined or selected for further analyses with little bias. The estimated variance components are given in Table 2.

The heritability estimate of 0.94 on an individual basis for open-pollinated progeny from one Spanish population is higher than generally reported for pine species of a comparable age (Table 2, 1971-B). Wright (1963) reported family heritabilities of 0.803 and 0.816 for two-year-old seedlings from open-pollinated Scotch pine families from 3 Belgium and 5 East German stands, respectively. Schrum (1969) reported smaller individual heritabilities (approximately 0.75) for 4, 5, and 6 year height of plantation grown Scotch pine.   Kriebel et al. (1972) reported much smaller estimates of heritability (0.16 – 0.59) for 1, 2, and 3 year height in eastern white pine diallel progenies grown in pots and in a nursery. They further reported that reciprocal-maternal effects were generally about the same as general combining ability. Maternal effects probably inflated our heritability estimate. Namkoong (1966) stated that non-additive genetic effects, relatedness of neighboring trees, and failure to recognize inbreeding may lead to over-estimate of true additive genetic variances.

Comparison of family means in full-sib experiments revealed that the performance of trees used as females and males were quite predictable and consistent.   This further indicated that the general combining ability for juvenile height growth may be quite high. Two-year height data from diallel matings in Spanish, French, and German Scotch pine populations have been obtained and will be reported in the near future. These data should furnish additional estimates of genetic population parameters.

Although generally it is not valid to compare variance components among experiments, we feel there is some justification here due to the fact that all the Spanish parents were from the same population. Also, experiments were randomized in the nursery within years, thus giving them comparable environmental conditions. One might expect the ratio of family variance to phenotypic variance to be much larger for full-sib experiments than for half-sib experiments, as it represents twice as much additive variance plus 1/4 of the dominance variance. This was not the case when the 1971-A (full-sib) and 1971-B (open-pollinated half-sib) Spanish population experiments were compared (Table 2). The ratio of family variance to phenotypic variance was almost four times smaller for the full-sib experiment than it was for the half-sib experiment. The lower family variance in the full-sib experiment could be the result of many crosses having common parents.   If the half-sib open-pollination progeny were in reality full-sibs we would expect the ratios of family to phenotypic variance to be rather similar. The ratios of family variance to phenotypic variance from racial crosses were close to what we expected. The ratio of σ^2 / σ^2 for the racial full-sib experiment

(0.35) was less than half, but greater than the ratios from racial half-sib pollen mix experiments (0.27 and 0.25).

Analyses comparing Spanish open-pollination with a Spanish pollen mix, and two non-Spanish pollen mixes, revealed that the pollen sources were not significantly different in either analysis (Table 3).   The lack of differences between pollen sources should be interpreted with caution, since in both analyses males x females were significantly different and there was only one degree of freedom for pollen sources. Seeds from open-pollinations were collected from a plantation less than 10 years of age in which only a few trees were producing large amounts of pollen. The comparison of the six-tree Spanish pollen mix with that of Spanish open-pollination in this young stand indicates that pollen dissemination in this case was adequate for producing progenies whose early growth rates were representative of female parents.

Individual tree heritabilities estimated from these analyses of variance were 0.32 and 1.05 for the intra- and inter-population crosses, respectively (Table 4). Note, however, that each experiment contained only half as many female parents as families. The variation among families therefore is probably reduced, giving lower estimates of heritability.

Means of full-sib families within male parents regressed on half-sib family means of their respective female parents for 1970 (Spanish females and non-Spanish pollen mixes) and for 1971 (Spanish females and Spanish open-pollination and a Spanish pollen mix) gave family heritability estimates of 2.24 and 0.68, respectively.   The high heritability resulting

from half-sib population crosses may be due to dominance bias. The bias would be a function of differences in gene frequencies between the two populations (Stuber 1970).

In correlation coefficients, slopes and intercepts from simple linear regression and paired "t" test for the three pollen mixes compared to Spanish open-pollination are tabulated below.

<div align="center">Experiment</div>

	1	2	3
x values	71 open	71 open	71 open
y values	71 Spanish pollen mix	70 non-Spanish[a] pollen mix (NYE)	70 non-Spanish[b] pollen mix (NE-27)
# values	7	5	6
corr. coef.	0.9935	0.9966	0.9957
slope	0.9867	0.7444	0.7929
intercept	-0.1713	-0.1026	-0.0349
paired "t"	3.415*	3.771*	6.530**

  * Significant at 5 percent.

 ** Significant at 1 percent.

  [a] NYE-Branch is a commercial variety of Scotch pine, its origin probably is central Europe.

  [b] NE-27 pollen is from a regional Scotch pine study; its origin probably is central Europe.

The high correlation coefficient for Experiment One is what is expected if there is little difference between Spanish open-pollination and the Spanish pollen mix on the same females. We also would expect a slope close to one and an intercept near zero if the crosses were similar and the progeny were grown in the same year. The significant difference of the paired "t" test does not support the conclusion that pollens really are no different. The correlation coefficients for Experiments Two and Three were higher than expected; considering the greater possibility of male x female interactions with pollens from different racial backgrounds. The reduction in slopes of Experiments Two and Three compared to One is probably due to environmental effects associated with different years. The seedlings measured in 1970 were considerably smaller than those measured in 1971. Otherwise we would have expected the slope to be greater than one for the two experiments, because pollen mixes were from faster growing populations which could have originated in France or other parts of Europe. The significant paired "t" tests for all the experiments indicates that there were real differences between the Spanish and non-Spanish pollens and Spanish open-pollination and a Spanish pollen mix.

Estimates of within plot variation (σ^2_w) were quite different depending on the parentage of plant material. Within plot variation for racial and population full‾sibs was smaller than within plot variation for comparable racial and population half-sib progeny within years (Table 2). This is what is expected since the genetic variance not in the family components falls into error.   It is also expected that with greater diversity in germ plasm there will be larger variation in within plot variances.

CONCLUSIONS

Heritability estimates of two-year nursery height ranged from 0.32 to 0.94 for a Spanish population depending on the method of estimation. The more realistic estimate is probably 0.68 obtained when means of full-sib families within male parents were regressed on half-sib family means of their respective female parents.   Inter-population heritability estimates of two-year nursery height were higher than intra-population estimates.   Intra-population heritability estimates were all greater than one except for the 1970-B full-sib experiment. The difference between the intra‾population and inter-population heritability estimates is probably due to differences in gene frequencies between the two populations used to obtain the inter-population progeny.

Estimates of within-plot variation were quite different depending on the parentage of the plant material. In general, with greater diversity in germ plasm there was larger variation within plots.

Estimates of heritability indicated that mass selection for early height growth would be effective under the conditions of this experiment.

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Table 1.--Mating types in experiments.

Expt.	No. Families	Sib Type	Female Parents	Male Parents
1970 A	34	half	16 Spanish trees	3 non-Spanish pollen mixes (26 families) and Spanish open-pollinations (8 families)
1970 B	39	full	17 Spanish trees	7 selected non-Spanish trees
1970 C	40	half	16 Spanish trees 12 non-Spanish trees	3 non-Spanish pollen mixes (20 families) 1 Spanish pollen mix (20 families)
1971 A	31	full	9 Spanish trees	12 Spanish trees (6 same as females)
1971 B	31	half	30 Spanish trees	open-pollination, overwhelmingly Spanish

Table 2.--Estimated variance components of two-year seedling height by year and experiment.

Experiment	Sib Type	Experiment mean in cm	Harmonic mean of # seedlings/plot	σ^2_F	σ^2_{BF}	σ^2_W	σ^2_F/σ^2_P	h^2
1970 A	half	19.7	5.97	8.87	1.84	21.86	0.27	1.09
1970 B	full	18.8	5.93	9.34	0.97	16.61	0.35	0.69
1970 C	half	18.6	5.98	8.41	1.79	23.09	0.25	1.01
1971 A	full	22.5	6.91	1.78	2.34	26.48	0.06	0.12
1971 B	half	25.2	7.47	10.78	1.66	33.62	0.23	0.94

Table 3.--Analyses of variance of two-year seedling height for comparing pollen types.

	1970 Non-Spanish Pollen Mixes				1970 Spanish Open-Pollination vs Spanish Pollen Mix		
Source	d.f.	MS	F	Source	d.f.	MS	F
Blocks	3	21.118	4.092*	Blocks	3	2.961	$0.646^{n.s.}$
Females	12	66.058	12.800*	Females	6	22.960	5.010*
Males	1	18.613	$3.607^{n.s.}$	Males	1	12.355	$2.696^{n.s.}$
M x F	12	9.773	1.894*	M x F	6	12.380	2.701*
Error	75	5.161		Error	39	4.583	

* significant at 5 percent.

n.s. nonsignificant

Table 4.--Estimated variance components of two-year seedling height for selected families.

Year	Experiment	# families	Harmonic mean of # seedlings/plot	σ^2_F	σ^2_{BF}	σ^2_W	$4\sigma^2_F/\sigma^2_P$
1970	Non-Spanish pollen mixes	26	5.99	8.00	1.68	20.86	1.05
1971	Spanish pollen mix + Spanish open-pollination	14	7.02	3.06	0	35.24	0.32

RECENT GENETICS APPOINTMENTS IN THE NORTHEAST

Dr. Kim Steiner, Penn State Univ., Forest Resources Laboratory, University Park, Pennsylvania 16802.

Dr. David Karnosky, The Cary Arboretum, N. Y. Botanical Garden, Box 609, Millbrook, New York 12545.

Dr. Thomas Adams, Univ. New Hampshire, School of Natural and Environmental Resources, Dept. of Forestry, Durham, New Hampshire 03024.

Dr. David Canavera, Univ. Maine, School of Forestry, Orono, Maine 04473.

Mr. William Sayward, St. Regis Paper Co., Woodland, Maine 04694.

Dr. William Lowe, formerly with Univ. New Hampshire, has been appointed Hardwood Geneticist with the Texas Forest Service, College Station, Texas, to replace Dr. Ron Woessner who is now with the Jari Project in Brazil.