Genetic Variation Among 140 Half-Sib Scotch Pine Families Derived from 9 Stands')

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In the past decade there has been a great amount of interest in the development of seed orchards and in the improvement of trees by selective breeding. There have been several good experiments showing the presence of sufficient genetic variation among individual trees to make selective breeding worthwhile. However, the subject is still in its infancy and there are relatively few experimental data bearing on the question of how best to approach such an improvement project. The present study was undertaken to obtain some of this needed information.

This report covers the nursery performance of 140 half-sib Scotch pine (Pinus *sylvestris* L.) progenies grown seed collected in 9 European stands. The report stresses variation patterns which can be deduced wiht a fair degree of certainty from nursery data. Information on mature performance will have to wait until later.

Materials and Methods

Seed collection. — In the summer of 1958 the forestry department of Michigan State University organized a range-wide geographic origin study of Scotch pine. Researchers in various parts of Europe were asked to furnish seed from stands (preferably native) in their vicinities. Four of those contacted kept the seed separate by individual tree and by stand. The 140 open-pollinated seedlots from 9 stands furnished the material for the present experiment.

The parents were randomly chosen from an 8- to 10-acre area within each stand. The degree of genetic relationship among parents within a stand is unknown but probably not as close as a first-cousin relationship.

Abbreviated descriptions of the parental stands follow. More information is available upon request.

MSFG 275 to 284. Eksismoeii, Eidsverket, N. Høland, Norway. 50^0 50' N. latitude, 11^0 34' E. longitude. 220 meters elevation. Ten parent trees. Stand native. Seed sent by Tollef Ruden, Norwegian Forest Research Institute, Vollebekk.

MSFG 285 to 294. Achel, Limburg, Belgium. 51^0 17' N. latitude, 5^0 30' E. longitude. 35 meters elevation. 10 parent trees. Stand planted, of unknown (probably Vosges Mountains, France) origin, 38 years old, on a boggy soil over sandy substratum. Seed sent by Alan de Jamblinne, Centrum voor Bosbiologie in de Limburgse Kempen, Bokrijk-Genk, Belgium.

MSFG 295 to 304. Hechtel, Limburg. Belgium. 51^0 7' N. latitude, 5^0 21' E. longitude, elevation 65 meters. 10 parent trees. Stand 35- to 50-year old natural regeneration from a nearby 100-year-old planted stand of unknown (prob–

ably Vosges Mountains, France) origin; soil iron podzol over sand. Seed sent by Jamblinne.

MSFG 321 to 340. Rövershagen, Meyershausstelle Forest District, East Germany. 54^0 11' N. latitude, 12^0 15' E. longitude, 20 parent trees. Stand native, level, 104 years old. Seed sent by Otto Schröck, Forest Research Branch at Waldsieversdorf, Institute for Forest Science, German Academy of Agricultural Science of Berlin, Eberswalde, East Germany.

MSFG 341 to 360. Neustrelitz, Wilhelminenhof d. Oberförsterei Zinnow Forest District (stands 27d and 28d), East Germany. 53^0 22' N. latitude, 13^0 5' E. longitude, 80 meters elevation. 20 parent trees. Stand native, 110 years old, on coarse sand at base of terminal moraine. Seed sent by Schröck.

MSFG 361 to 380. Güstrow, Kluess Forest District (Sect. 20), East Germany. 53^0 48' latitude, 12^0 11' E. longitude, 20 meters elevation. Stand native, 97 years old, level, on coarse sand. Seed send by Schröck.

MSFG 381 to 400. Nedlitz, Döbritz Forest District (Sect. 539 B), East Germany. 52^0 5' N. iatitude, 12^0 15' E. longitude, 94 meters elevation. 20 parent trees. Stand probably planted, level, on a site covered with Hypnum and Calamagrostis. Seed sent by Schröck.

MSFG 501 to 520. Joachimsthal, East Germany. 52^0 58' N. latitude, 13^0 46' E. longitude. 20 parent trees. Stand native. Seed sent by Schröck.

MSFG 531 to 540. Crown Forest of Pijnven, Campine, Belgium. 60 meters elevation. 10 parent trees. Stand planted in 1914 of unknown origin (north French?). Soil sandy, poor, wind-eroded, Wiedemann site class III. Seed sent by Andre Galoux, Research Station for Waters and Forests, Groenendaal-Hoellaart, Belgium.

Nursery care. — The seedlings were grown in MSU's forest tree nursery, E. Lansing. The soil is a clay loam which had been maintained in a high state of fertility for several years. The seedbed areas were treated with methyl bromide the autumn prior to sowing, in order to kill weeds and damping off fungi.

The seeds were sown May 11 to 13, 1959, and germinated in about two weeks. They were sown in 4-foot rows, the rows being 6 inches apart. Each row was a plot and received about 100 seeds. The plots were thinned to a density of 50 seedlings per row (25 per square foot) early in the first growing season and to 20 per row (10 per square foot) at the start of the third growing season. The thinnings may bave affected the amount of within-plot genetic variability, but probably had no measurable effect on between-family differences.

The seedlings were watered, weeded with mineral spirits, and sprayed with insecticide as needed. During the first winter a ½-inch sawdust mulch was applied to eliminate frost heaving. These measures proved effective in maintaining the experiment in a fully stocked and weed free condition.

Experimental design. — A modified complete block design was used. There were four replicates, each containing one plot of each of the 140 half-sib progenies. Within replicates the 10 or 20 progenies from a single stand were kept together. The groups from single stands were randomized within replicates, and the progenies were randomized within groups. This arrangement resulted in maximum precision as regards detection of within-stand variation but caused a slight under-estimation of differences between stands.

Removal of stock for outplanting reduced the number of usable replicates during the third growing season to three for the East German and Belgian progenies.

This experiment was actually intermingled with the geographic origin test mentioned previously. That arrangement does not affect the interpretation of either test. It is mentioned only because it permits comparisons between the two.

Measurements. — The test was measured or scored 36 times, whenever possibly significant differences were visible to the naked eye. Metric traits were measured to an accuracy of approximately 5 percent of the range between extremes. In the case of non-metrical traits the scoring units were as small as could be detected — usually about 10 percent of the range between extremes for the species as a whole. The measurement units were always so defined as to eliminate the use of decimals and the need for transformation prior to analysis.

The characteristics were measured one at a time by an observer who did not know a plot's identity. Only plot means were recorded because of the practical impossibility

Table 1. — One-, two-, and three-year performance data for Scotch pine seedlings from nine stands.

Country and stand of origin	Height			Foliage color on								Date buds formed	Presence of		Leaf length
	Age 1	Age 2	Age 3	June 26	Sep. 20	Oct. 28	Aug. 10	Oct. 5	Nov. 3	Dec. 15	Nov. 29		Secondary leaves Oct.	Primary leaves May	Aug.
	1959	1960	1961	1959	1959	1959	1960	1960	1960	1960	1961	1959	1959	1960	1960
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)
	mm.			grade								day of year	grade		mm.
NORWAY															
275—284	67	192	332	4	10	9	8	12	7	8	6	219	17	0	56
BELGIUM															
285—294	110	346	642	4	16	15	16	24	29	23	23	256	31	8	70
295—304	114	328	600	4	17	15	15	24	28	23	23	258	32	8	71
531—540	117	376	685	4	16	16	12	24	27	24	22	257	32	9	71
EAST GERMANY															
321—340	108	324	574	4	17	16	16	24	20	21	22	240	31	5	70
341—360	93	317	554	4	16	13	16	24	24	19	20	245	32	5	74
361—380	97	321	559	4	16	15	16	24	25	20	20	245	32	5	70
381—400	112	358	641	4	17	16	16	24	25	22	20	247	29	6	75
501—520	105	339	596	4	16	15	16	24	26	20	20	245	31	6	71

Key to Characters

Character No. and description	Lowest grade scored was	Highest grade scored was
(4) Color, June 26, 1959	4 = yellow green	8 = green
(5,6) Color, autumn 1959	8 = slightly red	20 = green
(7) Color, Aug. 10, 1960	8 = dark green	16 = green
(8-11) Color, autumn 1960, 1961	4 = yellow green	32 = dark green
(13) Secondary leaf presence	16 = secondary needles on 51-75% of trees	32 = secondary needles on 6-15% of trees
(14) Primary leaf presence	0 = no primary leaves on new growth	12 = 3 inches of primary leaves at base of new growth

Table 2. — Presence (+) or absence (—) of statistically demonstrable differences among half-sib Scotch pine progenies from the same stand.

Country and stand of origin	Height			Foliage color on								Date buds formed	Presence of		Leaf length
	Age 1	Age 2	Age 3	June 26	Sep. 20	Oct. 28	Aug. 10	Oct. 5	Nov. 3	Dec. 15	Nov. 29		Secondary leaves	Primary leaves	
	1959	1960	1961	1959	1959	1959	1960	1960	1960	1960	1961	1959	Oct. 1959	May 1960	Aug. 1960
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)
NORWAY															
275—284	+	+	+	+	—	+	+	—	+	—	—	—	+	—	+
BELGIUM															
285—294	—	—	—	—	—	+	—	—	—	+	+	+	+	+	+
295—304	+	+	—	+	—	+	+	+	+	—	+	+	+	+	+
531—540	+	+	—	—	—	+	—	—	—	—	—	—	+	—	—
EAST GERMANY															
321—340	+	+	+	—	—	+	+	—	—	+	+	+	+	+	—
341—360	+	+	+	—	—	+	—	—	—	+	+	+	+	+	+
361—380	+	+	—	—	+	+	+	—	—	+	—	+	+	+	—
381—400	+	+	—	—	+	+	—	—	—	—	—	+	+	+	—
501—520	+	+	—	—	—	+	—	+	+	+	—	+	+	—	+

of separating within-plot variance into environmental and genetic components.

Statistical analysis. — The data for each trait and each stand were subjected to a separate variance and multiple-range (Duncan's) analysis. For a 20-family stand the degrees of freedom were as follows: between families — 19, between replicates — 3, error — 57, total — 79. A combined all-German or all-Belgian variance analysis was also made for each trait. For an analysis of the data from the 100 East German progenies the degrees of freedom were as follows: between families within stands — 95, between stands — 4, between replicates — 3, replicate × stand interaction (= error when testing between-stand differences) — 12, family × replicate interaction (= error when testing family-within-stand differences) — 285, total — 399.

Simple correlation analyses, using progeny means as items, were made to determine the significance of inter-character relationships within stands. There were 8 or 18 degrees of freedom respectively for 10- or 20-progeny stands.

Many of the analyses were performed by MISTIC, the MSU computer.

Future plans. — The future development of the 140 progenies will be watched in five permanent outplantings located in Michigan, Minnesota, and Illinois. These permanent tests were established in the spring of 1961 with excess stock raised in this experiment. Each test consists of 5 or 10 replicates and follows a 4-tree-per-plot randomized block design.

Performance and Variability of the Progenies

The average performance of each of the nine stands is summarized in *table 1*. That table includes data on those traits for which there was statistical evidence of the presence of within-stand genetic variation. Such evidence is summarized in *table 2*, in which genetically variable traits are marked with a plus (+) sign and those without measurable genetic variability are marked with a minus (—) sign. The evidence is further summarized in *table 3*, which gives the between- and within-stand F values for the German and Belgian populations. Such a comparison was not possible for the Norwegian population, represented by progenies from only one stand.

Variation among Norwegian progenies. — As compared with the German and Belgian seedlings the progenies from the Norwegian stand were much slower growing, had much yellower autumn foliage, formed first-year buds and secondary needles earlier, and had shorter needles *(table 1)*. In none of these traits was there overlapping between Norwegian and continental seedlings. In the geographic origin test also, Norwegian and continental populations were genetically distinct (1).

Height growth differences among the 10 Norwegian half-sib families were marked *(table 2)*. Family 279 (26 percent taller than the stand mean) was outstandingly tall. So were families 277 and 280 (9 and 8 percent taller than stand mean respectively). At the other extreme was family 275 (18 percent shorter than stand mean). Untrained observers who were shown 275 and 279 in one replicate could easily identify them in the other three.

Between-family differences were present also in foliage color, time of formation of secondary leaves, and leaf length *(tables 2 and 3)*. The differences in autumnal color amounted to twice the least recognizable color difference

Table 3. — F values showing the significance of within- and between-stand genetic variation in the Belgian and East German populations.

Characteristic	Belgian progenies		East German progenies	
	Within stand	Between stand	Within stand	Between stand
(1) Height, age 1	3.06**	1.15	5.45**	4.10**
(2) Height, age 2	5.08**	1.55	9.08**	2.06
(4) Color, June 26, 1959	2.04**	0.62	1.28	0.51
(5) Color, Sept. 20, 1959	1.28	1.21	2.03**	1.09
(6) Color, Oct. 28, 1959	5.41**	0.12	4.71**	2.00
(7) Color, Aug. 10, 1960	2.82**	2.72	2.15**	5.76**
(8) Color, Oct. 5, 1960	1.48	0.68	1.50*	1.71
(9) Color, Nov. 3, 1960	3.27**	3 37*	3.66**	3.39*
(10) Color, Dec. 15, 1960	1.73*	0.85	3.68**	2.76*
(11) Color, Nov. 29, 1961	3.84**	0.00	1.80**	2.47
(12) Date buds formed, 1959	5.21**	1.71	5.07**	9.85**
(13) Secondary leaf presence, Oct. 1959	3.29**	0.47	4.07**	0.77
(14) Primary leaf presence, May 1960	1.88*	1.28	2.41**	1 33
(15) Leaf length, Aug. 1960	2.25**	0.04	2.04**	39.76**
Degrees of freedom for Greater mean square	27	2	95	4
Lesser mean square	81	27	285	95
F values needed for significance at				
5 percent level	1.62	3 36	1.39	2.48
1 percent level	2.00	5.50	1.58	3.55

* Significant at 5 percent level
** Significant at 1 percent level

Table 4. — Summary of inter-character correlations of possible biological significance. Correlations are based on within-stand comparisons. Relations not significant at the 2 percent level are omitted.

Families which were taller at age 3 were greener in October 1959 in stands 275—284 (r = .82**) and 341—360 (r = .52*).

Families which formed buds early formed secondary leaves early in stands 285—294 (r = .76**) and 381—400 (r = .60**).

Families which formed buds early had few primary needles at the base of the second-year growth in stands 321—340 (r = .63**), 361—380 (r = .67**), 381—400 (r = .61**), and 501—520 (r = .52*).

Families which formed secondary leaves early had few primary leaves at the base of the second year's growth in stands 321—340 (r = .68***) and 381—400 (r = .85***).

* = Significant at 2 percent level
** = Significant at 1 percent level
*** = Significant at 0.1 percent level

or to 20 percent of the range found in the geographic origin study. The range in leaf length was 35 percent of the mean. The correlation between height at age 3 and first-year autumnal color was statistically significant; other inter-character relationships were not *(table 4)*.

The Norwegian progenies offered several opportunities for improvement in one trait, a limited opportunity for simultaneous improvement in two traits, and no opportunity for simultaneous improvement in three or more traits. The tallest family (279) was greener than average the first autumn and average in other respects. The next-to-tallest family (277) had significantly long needles and was average in other respects. Concentration on needle length through the selection of family 277 rather than 279 would have meant a 17 percent loss in growth rate.

Within- and between-stand variation in the Belgian population. — Of the three ecotypes which were repre-

sented in the experiment, the Belgian population was the fastest growing, greenest in the autumn, and the last to form first-year terminal buds (table 1). According to the geographic origin study this ecotype consists of the Belgian trees as well as native stands in the Vosges Mountains of France and in the Pfalz Land of West Germany. It shows some genetic overlap with the ecotype occupying the remainder of Germany (1).

Each Belgian stand was found to be genetically variable in one or more traits but the variability pattern was not the same for any two stands (tables 2 and 3). The within-stand differences were less than the differences among Norwegian progenies. Among the progenies from stands 295—304 and 531—540 the tallest half-sib families exceeded the stand averages by 9 and 7 percent respectively. The within-stand range of variation in color was approximately equal to the least recognizable difference. The range of variation in leaf length was about 25 percent of the mean.

In this experiment between-stand differences were small and not significant. In the geographic origin study, where more stands were represented, between-stand differences were significant in several traits. It is worth noting that the three tallest half-sib families in this experiment (532, 538, 539) were from a single forest near Pijnven. They were 7 percent taller than the average of all seedlings from that forest, and 15 percent taller than the all-Belgian average.

The only significant inter-character correlation was between time of bud formation and time of secondary leaf formation in stand 285—294. A breeder working with that stand could obtain earliness in either trait by selecting families 286 and 290. The only other possibility for simultaneous 2-character selection involved height and first-year autumnal color. Family 539 was 13 percent above the Belgian average in height and slightly (½ the least recognizable color difference) greener than average on October 28, 1959. The use of family 539 would result in less improvement in height growth than would be the case if family 532 (19 percent above the Belgian average) were selected.

Within- and between-stand variation in the East German population. — The 100 East German half-sib progenies are representatives of a geographic ecotype which covers most of Germany and Czechoslovakia (1). They offered the best opportunity to study within- and between-stand variation.

In each of the five East German stands there was a large amount of variation among half-sib progenies in height growth (table 2). Differences among stands were also large (tables 1 and 3). In the second and third years all families from stand 381—400 near Nedlitz were taller than any family from stand 341—360 near Neustrelitz. In fact the Nedlitz stand yielded the four tallest (385, 390, 392, 395) East German families. These were 8 percent taller than the stand average and 16 percent taller than the all-German average.

Large between-stand differences were also evident in leaf length, autumnal foliage color, and time of first-year bud formation. Within-stand variation was small (but significant) in the first-named trait, and considerable in the last two. Within-stand differences were significant but between-stand differences were not in two other traits (presence of secondary and primary leaves on certain dates).

A breeder interested in increased height and longer needles could obtain improvement in both respects by selecting families 385, 390, 392, and 395 from the Nedlitz stand. He could achieve an increase (over the all-German average) of 16 and 7 percents in the two traits respectively. A breeder interested in increased height growth and decreased needle length could achieve selection differentials of 7 and 7 percent in the two traits respectively by selecting families 323, 330, and 514. A breeder interested in earlier bud formation and in yellower autumnal foliage could achieve his goal by selecting families 365, 381, and 502. However, no families were outstanding with respect to early bud formation and green autumnal foliage. There were several other possibilities for simultaneous 2-character selection but few of the possibilities would be of economic interest. (See table 4.)

Improvement in growth rate, color in August 1960, bud formation date, and leaf length would proceed more rapidly by testing a few progenies from each of many different stands than by testing many progenies from each of a few stands (note high between-stand F values for traits 1, 7, 12, and 15 in table 3).

Repeatability of Height and Color Data

The relative heights of seedlings from different regions and from different stands changed little from year to year. Belgian seedlings were tallest at all ages. Families from stands 531—540 and 381—400 were the tallest of the Belgian and East German populations respectively at ages 1, 2, and 3.

The repeatability of height differences among families from the same stand was also high in most cases. Families which ranked in the upper 10 percent in one year usually ranked in the upper 20 percent in other years (table 5). Presumably the nursery data give valid estimates of relative heights for the next several years.

Belgian seedlings were slightly greener than the East German and much greener than the Norwegian seedlings in all three autumns. The latter became red the first year and yellow in succeeding years.

As regards within-stand variation in color, there were several reversals in trend between the first and second autumns. For example, progenies 331, 341, and 348 changed from significantly redder than average on Oct. 28, 1959 to significantly greener than average on Dec. 15, 1960. On the other hand progenies 355, 379, and 380 were significantly greener than average on both dates. There were also reversals in trend between summer and autumn.

There were no reversals in trend between the second and third autumns although differences recognizable at one time were not always noted at succeeding times.

Table 5. — Repeatability (= r = correlation coefficient) of within-stand differences in height.

Correlation between heights at ages —	Size of correlation coefficient in stand —						
	275—284	295—304	321—340	341—360	361—380	381—400	501—520
1 and 2	.85***	.95****	.55**	.59***	.60***	.80****	.79****
2 and 3	.80***	.78***	.47*	.44*	.44*	64***	.76***
1 and 3	.93****	.71**	.61***	.11	.17	.42	.57***

* Significant at 5 percent level
** Significant at 2 percent level
*** Significant at 1 percent level
**** Significant at 0.1 percent level

Presumably different genes control red first-year color and yellow second-year color. Also, different genes seem to control summer and winter foliage color.

Estimates of Variance Components and Stand Heritabilities

Family-within-stand (σ^2_F) and stand (σ^2_S) variances were calculated for the Belgian and East German populations according to the following scheme. The letters f, s, and r designate numbers of families-per-stand, stands, and replicates respectively.

Source o variation	Degrees of freedom	Expectation mean squares
Replication	r—1	
Stands	s—1	$\sigma^2e + r\,\sigma^2F + f\,\sigma^2RS + rf\,\sigma^2S$
Families-within-stands	s (f—1)	$\sigma^2e + r\,\sigma^2F$
Replication × Stand	(r—1)(s—1)	$\sigma^2e + r\,\sigma^2F + f\,\sigma^2RS$
Replication × Families-within-stands	s (r—1)(f—1)	σ^2e

The variances in five traits are presented in *table 6*. For all five traits family-with-stand variance was appreciable and improvement by family selection would be productive in either the Belgian or East German population. On the other hand, between-stand variance was appreciable for only four traits in the East German population (none in the Belgian population). Stand selection would be a productive way of improving those four traits in the East German population.

Table 6. — Within-stand (σ^2_F) and between-stand (σ^2_S) variances, expressed as percents of the Family × Replicate interaction (σ^2_e), for the Belgian and East German populations.

Characteristic	Belgian population		East German population	
	σ^2F	σ^2S	σ^2F	σ^2S
	percent of σ^2e			
(2) Height, age 2	102	22	111	58
(9) Color, Nov. 3, 1960	52	5	67	46
(12) Date buds formed, 1959	105	3	102	39
(13) Secondary leaf presence, Oct. 1959	52	0	76	0
(15) Leaf length, Aug. 1960	31	0	26	29

The nursery results give actual improvement rates in juvenile traits in the present generation. To forecast improvement during the next generation heritability estimates are needed. From this experiment it was possible to calculate family heritabilities, applicable to family selection. Very small plots, replicated many times, would have been needed to calculate heritabilities applicable to single plants.

The formula used to calculate family heritability agrees in essential respects with the formulas suggested by LERNER and FALCONER (2). Some seeming discrepancies should be explained. Only ¼ of the additive genetic variance is recovered in a half-sib progeny test. Therefore, the numerator should properly contain the quantity $(4\sigma^2_F)$ rather than (σ^2_F). But in that case the heritability estimate must be divided by 4 to be applicable to the next generation. It is easiest to omit the 4 altogether. The use of the quantity (σ^2_e/r) in the denominator makes the estimates applicable to selection based upon family means. If the quantity (σ^2_e) were used the estimates would apply to selection based on plot means. (Note that the use of $[\sigma^2_e]$ would result in

a lower heritability but a lower selection differential. The estimate of gain is similar whichever quantity is used.)

The formula used is as follows. It is illustrated by a numerical example from the East German population.

$$\text{Family heritability} = \frac{\sigma^2F}{\sigma^2e/r + \sigma^2F} = \frac{111}{100/4 + 111}$$

= .816 = family (within stand) heritability for 2-year height in the East German population.

The corresponding family heritability for 2-year height in the Belgian population was .803. For the Belgian and East German populations respectively the heritabilities for Nov. 3, 1960 color were .675 and .728; for bud formation data .808 and .816; for secondary leaf presence .675 and .752; for leaf length .554 and .510.

It seems meaningless to calculate heritabilities for the separate stands. They would vary from zero to very high. Each estimate would be applicable only to the specific stand for which it was calculated. It is hoped that the 10 estimates given above are applicable to moderately large segments of the continental Scotch pine population.

It should be re-emphasized that the family heritability estimates apply to family selection, based on the performance of half-sib families in a well-replicated progeny test. A great over-estimate of genetic gain will result if the family heritabilities are used when the selection is based on the phenotypic performance of individual trees.

Selection for One or Several Traits?

The many pluses in *table 2* and the many significant F values in *table 3* show how easily a single trait can be improved.

Improvement in two or more traits is another matter. A breeder working with the East German population and interested in simultaneous improvement in growth rate and needle length could achieve selection differentials of 16 and 7 percent respectively, by selecting families 385, 390, and 392. However, if he limited himself to material represented in the present experiment, he could not practice effective family selection for growth rate and autumnal greenness because no family was significantly superior in both traits. Selection pressures would also be low if a breeder were trying to increase growth rate and decrease needle length.

A breeder need not limit himself to the material in the present experiment. If he tests $100^2 = 10,000$ half-sib families he can obtain the same amount of improvement in each of two traits as he obtained in one trait with 100 families. If he tests several hundred families he can obtain a reasonable amount of improvement in each of two traits but not in each of three.

The breeder working with the 100 East German families has a third possibility open to him. He could cross families which are best in each of two traits, grow an F_1 population in which there would be no selection, and then grow a segregating F_2 generation. From a medium sized F_2 population it would be possible to obtain segregates with nearly the same amount of superiority in each of the two traits as could be found in one trait among the present 100 families.

The crossing of selected families seems the most economical way to obtain a large amount of improvement in each of two traits and the only way to obtain a large amount of improvement in each of three traits. Such a program involving the production of F_2 and F_3 generations can be accomplished in a reasonable length of time. Already

some 4-year-old trees in this experiment have flowered and it is anticipated that the F_1 generation could be started in another 3 years. It is likely that the F_2 generation could be started in another 10 years.

The answers obtained with the Scotch pine progenies are in agreement with theoretical expectations. They indicate that the practice of selecting 'plus' trees on the basis of 10 or 20 characters can be inefficient. It is probable that in some cases the selection really involves only two or three traits and that the rest could be ignored.

In cases where all characters are actually taken into account there may be such a dilution of effort that the amount of improvement obtained will be negligible for any one.

Summary

In the autumn of 1958 European investigators collected and sent 140 open-pollinated, single-tree seedlots from 9 stands in Norway, Belgium, and East Germany. These were sown in the MSU forest tree nursery at E. Lansing, Michigan in the spring of 1959 and were grown there for 3 years. A modified randomized block design with four replications was used. In genetic terminology the experiment was a series of half-sib progeny tests, with each seedlot representing a half-sib family. Each set of measurements was subjected to analysis of variance.

The mean squares were separated into plot $\times$ replicate interaction ($= \sigma^2_e$), family-within-stand ($= \sigma^2_F$) and between-stand ($= \sigma^2_S$) variances. Family heritabilities were calculated according to the formula:

Family heritability $= \dfrac{\sigma^2_F}{\sigma^2_e/4 + \sigma^2_F}$. Inter-character correlations were calculated separately for each stand, using progeny means as items.

For most of the 9 stands there was a significant amount of between-family variation in growth rate, date of first-year bud formation, and presence of secondary leaves in October 1959. Foliage color on various dates and leaf length were genetically variable traits in which the amount of between-family variation differed considerably among stands. Family heritabilities of the five most variable traits ranged from .5 to .8 in the East German and Belgian populations.

In the East German but not in the Belgian population between-stand differences in several traits were significant. Significant between-stand differences mean that stand selection would be an effective improvement measure.

The repeatability of the relative height differences for countries, stands, and families was high during the 3-year test period. Repeatability estimates were also made from

the eight color determinations. Between countries the color trends did not change appreciably. As regards family-within-stand color differences there were several reversals in trend from the first to the second autumn and from summer to autumn, but none from the second to the third autumn.

Improvement by selection of families which excel in one trait seems relatively simple. Both selection differential and heritability could be high enough to assure detectable progress. Simultaneous selection for two traits is also possible but would usually entail a serious sacrifice in selection differential in one or the other trait. No families were found which deviated significantly from the stand average in three or more traits.

Zusammenfassung

Titel der Arbeit: *Genetische Variation zwischen 140 Halbgeschwisterfamilien der gemeinen Kiefer, deren Mutterbäume aus 9 Beständen stammen.*

Im Herbst 1958 sammelten und übersandten europäische Wissenschaftler 140 windbestäubte Einzelbaumabsaaten aus 9 Beständen in Norwegen, Belgien und Mitteldeutschland. Diese wurden im Frühjahr 1959 im Forstpflanzgarten der Michigan State University in East Lansing, Mich., ausgesät, wo sie für drei Jahre verblieben. Die Anlage erfolgte in modifizierten zufälligen Blocks mit vier Wiederholungen. In genetischen Termini war das Experiment eine Serie von Halbgeschwister-Nachkommenschaftsprüfungen, wobei jede Sorte eine Halbgeschwisterfamilie darstellte. Jede Meßreihe wurde einer Streuungszerlegung unterworfen. Die Mittelquadrate wurden aufgeteilt in die Varianzen der Interaktion Sorten $\times$ Wiederholungen ($= \sigma^2_e$), zwischen Familien gleicher Bestände ($= \sigma^2_F$) und zwischen Beständen ($= \sigma^2_S$). Familienheritabilitäten wurden berechnet nach der Formel:

$$\text{Familienheritabilität} = \frac{\sigma^2_F}{\sigma^2_e/4 + \sigma^2_F}$$

Merkmalskorrelationen der Familienmittel wurden für jeden Bestand getrennt berechnet.

Bei den meisten der 9 Bestände ergab sich ein signifikanter Betrag der Variation zwischen Familien bezüglich Wuchsgeschwindigkeit, Zeitpunkt der Knospenbildung im ersten Jahr und dem Vorhandensein von Sekundärnadeln im Oktober 1959. Die Nadelfärbung zu verschiedenen Zeitpunkten und die Nadellänge zeigten genetische Variation, der Betrag der Variation zwischen Familien war bei den einzelnen Beständen beträchtlich verschieden. Die Familienheritabilitäten der fünf am meisten variablen Merkmale bewegten sich zwischen 0,5 und 0,8 in den mitteldeutschen und belgischen Populationen.

In der mitteldeutschen, nicht aber in der belgischen Population, waren die Unterschiede zwischen Beständen in mehreren Merkmalen signifikant. Signifikante Bestandsunterschiede bedeuten, daß Bestandsauslese eine wirksame Züchtungsmaßnahme wäre.

Die Wiederholbarkeit der relativen Höhenunterschiede für Populationen, Bestände und Famlien war während der dreijährigen Versuchsperiode hoch. Auch für die acht Farbbestimmungen wurde die Wiederholbarkeit geschätzt. Zwischen Populationen wechselten die Farbtrends nicht merklich. Hinsichtlich der Farbunterschiede zwischen Familien gleicher Bestände kehrte sich der Trend verschiedentlich um vom Herbst des ersten zum Herbst des zweiten Jahres und vom Sommer zum Herbst, nicht aber vom Herbst des zweiten zu dem des dritten Jahres.

Züchtung durch Auslese der Familien, die in einem Merkmal besonders hervorragen, erscheint relativ einfach. Sowohl Selektionsdifferential als auch Heritabilität könnten hoch genug sein, um einen meßbaren Fortschritt zu gewährleisten. Gleichzeitige Auslese auf zwei Merkmale ist ebenfalls möglich, würde aber gewöhnlich erhebliche Opfer an Selektionsdifferential in dem einen oder anderen Merkmal mit sich bringen. Keine Familien wurden gefunden, die sich in zwei oder mehr Merkmalen signifikant vom Bestandsmittel abhoben.

Résumé

Titre de l'article: *Variation génétique dans 140 descendances maternelles de pin sylvestre venant de 9 peuplements.*

A l'automne 1958, des chercheurs européens ont envoyé des graines récoltées sur 9 peuplements en Norvège, Belgique et Allemagne et représentant 140 descendances individuelles par fécondation libre. Elles ont été semées dans la pépinière forestière MSU à East Lansing, Michigan, au printemps de 1959 et y ont été cultivées pendant 3 ans. On a utilisé un dispositif en blocs complets modifié, avec 4 répétitions. Dans la terminologie génétique, cette expérience constituait un test de descendance maternelle, chaque lot de graines représentant une famille «half-sib». Chaque série de mesures a fait l'objet d'une analyse de variance. Les écarts-types ont été répartis entre : interaction parcelle unitaire $\times$ répétition ($= \sigma^2_e$), variance des familles à l'intérieur d'un peuplement ($= \sigma^2_F$) et variance entre peuplements ($= \sigma^2_S$). Les héritabilités des descendances ont été calculées d'après la formule:

$$\text{Héritabilité de la descendance} = \frac{\sigma^2_F}{\sigma^2_e/4 + \sigma^2_F}$$

Les corrélations entre les caractères ont été calculées séparément pour chaque peuplement en utilisant comme bases les moyennes des descendances.

Pour la plupart des 9 peuplements, on trouve une variation significative entre descendances pour la vitesse de croissance, la date de formation du bourgeon la première année et la présence de feuilles secondaires en Octobre 1959. La couleur des aiguilles à différentes dates et leur longueur sont des caractères génétiquement variables pour lesquels la variation entre les descendances diffère de façon considerable suivant les peuplements. Les héritabilités des cinq caractères les plus variables se situent entre 0,5 et 0,8 pour les populations d'Allemagne et de Belgique.

Dans la population d'Allemagne mais non dans celle de Belgique, les différences entre peuplements sont significatives pour plusieurs caractères. L'existence de différences significatives entre les peuplements indique que la sélection des peuplements serait une mesure d'améloration efficace.

Au cours des 3 années, les différences constatées dans la hauteur relative pour les pays, les peuplements et les descendances se sont maintenues. Les estimations de cette constance ont également été faites pour les huit déterminations de couleur. Les tendances à la coloration ne changent pas de façon appréciable entre les pays. En ce qui concerne les différences de couleur entre les descendances du même peuplement, on constate plusieurs changements du classement entre le premier et le second automne et entre l'été et l'automne, mais aucun changement du second au troisième automne.

L'amélioration par sélection des descendances sur un seul caractère semble relativement simple. L'écart de sélection et l'héritabilité paraissent tous les deux assez élevés pour assurer un progrès appréciable. La sélection simultanée pour deux caractères est également possible, mais entraînera un sacrifice sérieux de l'écart de sélection pour l'un ou pour l'autre trait. On n'a trouvé aucune descendance qui s'écarte significativement de la moyenne du peuplement pour trois caractères ou plus.

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Growth stresses in trees

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Growth stresses in trees were observed by MARTLEY about 1928 but received increasing attention after the observations of M. R. JAKOBS (1938—1955). Since then they have been studied by a number of investigators, viz. BOYD, MAYER-WEGELIN, PERKITNY, KÜBLER and others. According to MAYER-WEGELIN, the presence of gelatinous fibres increases these stresses. They can play an important part in timber utilization (as they have to be taken note of), e. g. defect-free seasoning of wood, conditioning of logs for peeling into veneers, etc. They can also be the cause of stresses, etc., in standing trees. A defect known as "water blister" in teak trees has been noticed in the Kerala State (*vide* BAKSHI and BOYCE, 1960). Several discs from a tree suffering from "water blister" were available for examination. They are shown in *fig. 1.* The discs showed evidence of stresses (cracks and splits). It was considered worth while to see whether these were subjected to growth stresses, especially as no data on growth stresses in Indian trees are available. For the authors' work they are of importance in the conditioning of logs for peeling, etc.

For evaluation of the stress intensity and distribution the discs were planed to uniform thickness and three radii at 120° to one another marked on them. The thickness (X) of the disc along these radii at definite intervals was measured with the help of a Hilger Watts microptic machine with an accuracy of $\pm 10^{-5}$ cm. Then radial strips were cut (about 1 cm. in width) along these radii and the measurements (Y) taken at the same places. They were then cut into pieces about 1×1 cm. at the places of measurement and the measurements taken again (Z). It was noticed that X>Y>Z suggesting that tensile stresses along the grain were present in the disc. The length variation

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