GEOGRAPHIC VARIATION IN FOREST TREES

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Geographic variation in trees has been the subject of experimentation for about 140 years. During the time scores of provenance tests have been established and have given sound evidence of the presence of genetic differences associated with the geographic origin of the seed in over 30 species.

These differences are important from the practical standpoint. The Christmas tree grower who uses the wrong kind of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) or Scotch pine (*Pinus sylvestris* L.) seed will find that his trees grow too slowly or develop an undesirable color in the autumn. The pulpwood planter who plants Upper Michigan jack pine (*Pinus bansiana* Lamb.) in Lower Michigan may lose about 25 percent of his possible growth rate. Geographic variation is also important to the forest geneticist who is breeding trees for the future. A selective breeding program which is based on the wrong ecotype may not produce anything as good as trees already available in nature, even though continued for a century.

Rather than discuss geographic variation in general, I would like to talk about specific experiments under way at Michigan State University as part of a cooperative program (NC-51, financed in part by the U. S. Department of Agriculture) with other states in the North Central Region. The experiments are only one to five years old and include 10 different conifers. They do not yet provide growth data on mature trees. They incorporate many new ideas in design and analysis. Hence, they are giving and should continue to give many types of data not available from older tests.

Scotch Pine Provenance Trial

Methodology

In mid-1958 we asked European tree breeders to send an ounce or two of seed from eight or 10 trees in each of one or two native Scotch pine stands in their vicinity. They responded magnificently and sent a total of 253 different seedlots (plus 70 late arrivals to be included in another test). The collections sampled 122 stands in about 20 different countries all the way from Spain and Scotland on the west to Turkey and eastern Siberia on the east. Our cooperators also sent good information, even including pictures of some of the parent trees.

As the seeds arrived, the data concerning each lot were entered in an accession record, which has been mimeographed for distribution to all those who will cooperate on permanent outplantings. Samples were weighed and mounted on herbarium specimens. In the spring of 1959 we prepared for sowing by placing enough seed for 1,265 different plots into separate numbered envelopes, randomizing the envelopes within replicates, and preparing the nursery labels and map. This preparation took about a week but enabled us to complete the sowing without a hitch in two days, May 11 and 12.

The nursery test follows a four-replicated, randomized complete block design. Each replicate contained one 4-foot row (plot) of each seedlot. The rows were 6 inches apart. The rows were thinned to about 50 seedlings per row during the first summer. An additional set of unmeasured, rectangular plots were seeded solely for growing large numbers of trees for outplantjng.

There was evident variation in so many important characteristics that the *use* of orthodox measurement and analysis techniques would have been an almost interminable task. Therefore, we used several shortcuts such as (1) scoring one character at a time; (2) recording only the plot means; (3) determining plot mean heights from the four tallest trees; (4) disregarding card standards when scoring color, using certain nursery rows as standards instead; (5) determining plot means by summing the deviations from an assumed mean; and (6) recording only numerical grades. The validity of these shortcuts will be covered in a separate paper. Their efficiency is attested by the fact that one man-day per week during the growing season was more than ample to keep ahead of the measurement, summarization, and statistical analysis work, even though we attempted to cover every character in which there were differences visible to the naked eye.

One precaution was always observed in order to eliminate observer bias. The observer had to do his work without knowing a plot's identity.

"Mistic," Michigan State's tape-input electronic computer, was used for the statistical computations. Data for each character were subjected to 12 different analyses of variance--three to determine the significance of differences among provenance or regional means and nine to determine the significance of differences among individual-tree progenies within stands.

Broad Geographic Trends

The broad geographic trends are summarized in the table. The most obvious thing is the extreme variability of Scotch pine. There are 3 to 1 differences in one- and two-year heights, 3 to 2 differences in leaf ' length, 2-month differences in time of first-year bud set, and yellow to blue-green differences in autumn color.

Provenances from the extreme northern parts of Finland and Siberia are at one extreme in most characters. The location of the other extreme is variable. The tallest trees come from Belgium and the Vosges Mountains of France; the bluest, from Spain, central France, and Scotland; the yellowest from the Urals; the trees with the most branched buds, from Scotland; and those with the shortest needles, from Spain, central France, Scotland, and northern Finland.

The 122 provenances representing stand collections are grouped by region of origin or ecotype in the table. These ecotypes are more or less distinct entities and not arbitrary subdivisions of a continuously varying population. In France the Vosges Mountains (Region M) are separated from the mountains of Auvergne (Region S) by about 150 miles, but the two ecotypes are easily distinguishable in growth rate, leaf length, and leaf color. In Sweden there is an abrupt change at about latitude 62° N. from slow-growing (125 to 150 mm. in two years) northern provenances to fast-growing (190 to 215 mm. in two years) provenances from Region C. The Ural ecotype (Region E) is distinguished by its moderate growth and yellow fall color.

Climate played an important role in the development of these ecotypes. Over the millenia, natural selection in cold northern Finland favored trees which set buds early and resulted in a type which always sets buds early. The favorable growth conditions of the Vosges Mountains favored types which grew rapidly. And the dry summers of Spain favored seedlings which could get their root systems into the soil in a hurry, resulting in an ecotype which is hard to pull as a first-year seedling.

Population structure also played an important role in ecotype development. Over most of Germany and Czechoslovakia, the population is continuous. Here pollen and seed migration quickly transferred genes from one place to another so that the effects of natural selection were quickly swamped. On the other hand, the 150-mile gap between the Vosges and Auvergne Mountains in France was quite sufficient to enable differences in selection pressure to operate continuously for millenia.

There are also indications that small population size and genetic drift were responsible for many of the characters we now observe. There is no obvious reason why the presence of branched buds on two-year seedlings should be almost limited to the Scottish population. Nor is there an obvious reason why northern sources formed secondary needles sooner than the southern sources.

The two-year height data from the present experiment are strongly correlated with the height data from a 17-year-old experiment on Scotch pine ecotypes performed in New Hampshire (see Silvae Genetics 6: 2-14. 1957). Thus, there is good reason to believe that these nursery performance data give reliable clues to mature performance in other characters as well. Of course, the material must be outplanted and followed for perhaps 50 years. These outplantings will bear usable results long before the 50 years are up.

Local Variation Patterns

The variation pattern within any one of the large regions indicated in the table is very different from the pattern for the species as a whole.

Within each of the regions there were significant genetic differences in several traits, but the range of variation was nowhere near as

Region	Countries of origin[1]	Provenances	Seed Wt. (5)	Seed Length (6)	Height Age 1 (7)	Height Age 2 (8)	Height / Seed Wt. (7/5)	Foliage color on Jun 26 1959 (9)	Jul 22 1959 (10)	Sep 30 1959 (11)	Oct 28 1959 (12)	Aug 10 1960 (13)	Oct 6 1960 (14)	Nov 3 1960 (15)	Dec 15 1960 (16)	Earliness of leaf color (17)	Bud Color April 1960 (18)	Bud Set 1959 (19)	Bud Grew 1960 (20)	Diam. April 1960 (21)	Branches on terminal bud 1959 (22)	Branches on terminal bud 1960 (23)	Male fls. (24)	Lammas shoots (25)	Primary lvs. on 1960 growth (26)	Secondary leaf presence Sep 21 1959 (27)	Secondary leaf presence Oct 1 1959 (28)	Leaf length, Aug. 1960 (29)	Pullability, July 1959 (30)	Region
		No.	Mg.	Mm.	Mm.	Mm.		Grade	Grade	Grade	Grade	Grade	Grade	Grade	Grade	Grade	Grade	Day of year	Day of year	Mm.	Per 200 trees	Per 200 trees	Per 200 trees	Per 200 trees	Grade	Grade	Grade	Mm.	Grade	
A	FI	1	4.2	3.8	38	57	9	6.0	7.0	8.0	8.0	5.0	9.0	9.0	8.0	1.0	4.0	200	113	2	0.0	0.0	0.0	0.0	0.0	0.0	3.0	40	15	A
B	FI SI	2	4.5	3.9	42	115	10	7.5	7.5	7.5	5.5	5.5	5.5	6.0	7.5	1.0	4.0	200	113	2	1.5	.0	.0	.0	.0	.0	1.5	59	17	B
C	SW	4	3.4	3.7	57	129	16	5.0	6.8	9.8	8.0	7.0	12.2	7.5	7.5	2.0	6.5	219	113	3	1.5	1.5	.0	.0	.2	2.2	2.0	55	12	C
D	FI SW NO	16	4.6	3.7	72	203	16	4.9	4.2	10.0	9.4	8.5	13.4	10.4	8.5	2.2	9.6	219	113	3	2.0	.2	.0	.0	.2	9.1	6.2	56	13	D
E	NO	1	3.4	3.8	55	152	16	5.0	6.0	10.0	10.0	7.0	16.0	15.0	18.0	1.5	10.0	219	113	3	.0	.0	.0	.0	.0	6.0	3.0	56	9	E
F	SI	8	5.4	3.9	88	255	16	4.2	4.0	10.8	8.5	10.5	6.0	4.0	4.2	1.5	9.2	219	114	3	1.2	.0	.1	.0	.9	7.4	4.5	68	14	F
G	SW LA	4	5.0	4.0	88	264	19	4.2	4.0	10.8	11.0	12.2	15.5	12.8	8.5	2.5	7.5	234	114	3	2.5	.8	.0	.0	1.5	12.8	11.5	59	11	G
H	PO	1	6.5	4.1	104	330	16	4.0	4.0	16.0	15.0	16.0	10.0	13.0	11.0	3.0	10.0	242	115	4	1.0	.0	.0	.0	7.0	15.0	16.0	76	11	H
I	GE CZ	27	6.0	4.0	104	323	18	4.3	4.0	16.4	15.2	15.9	23.7	23.7	19.4	3.7	9.9	246	115	4	1.2	.3	.1	.2	6.1	15.1	15.8	70	10	I
I[P]	GE	4	6.5	4.2	108	335	17	4.8	4.0	16.4	14.8	16.0	24.2	24.2	19.6	3.8	9.8	248	115	4	.8	.0	.2	.0	6.0	16.0	15.8	71	10	I[P]
J	FR GE HU IT	12	6.8	4.4	111	337	18	4.3	4.0	16.2	17.5	16.0	24.0	28.0	24.7	4.0	9.5	259	115	4	1.5	.3	.0	.2	8.3	15.3	17.2	72	10	J
J[P]	GE BE	5	6.4	4.2	115	359	18	4.0	4.0	16.6	16.4	16.0	24.0	28.2	23.0	4.0	9.8	255	115	4	.8	.0	.8	.0	8.4	15.6	15.8	72	10	J[P]
K[P]	BE	1	9.0	4.9	140	429	16	5.0	4.0	18.0	19.0	16.0	24.0	27.0	21.0	4.0	10.0	242	115	4	.0	1.0	2.0	.0	6.0	16.0	12.0	74	10	K[P]
L	FR GE AU YU	4	5.8	4.0	96	294	18	4.5	4.2	20.2	16.2	12.8	24.5	26.8	21.5	4.0	8.8	248	115	4	.2	.5	.2	.8	4.5	16.0	16.2	61	10	L
M[P]	EN	2	8.1	4.5	124	336	15	7.5	4.0	19.0	19.5	19.0	26.0	26.0	27.0	5.0	9.5	242	115	5	1.5	2.5	.0	3.0	5.5	16.0	18.0	63	11	M[P]
N	GR RU TU	13	8.8	4.9	95	275	12	5.1	4.0	20.7	19.4	9.9	26.3	30.0	29.1	5.0	9.6	253	115	4	.7	.4	.0	4.2	5.2	14.7	17.4	60	12	N
O[P]	NT	1	7.8	4.1	88	271	11	10.0	8.0	23.0	19.0	14.0	24.0	28.0	31.0	5.0	9.0	260	117	4	1.0	.0	.0	.0	8.0	15.0	17.0	64	14	O[P]
P	SC	4	7.2	4.8	92	276	14	5.0	4.5	15.0	15.8	21.5	31.2	31.2	29.8	4.8	9.2	229	115	4	1.5	5.8	.0	2.5	2.5	15.2	15.2	48	12	P
Q	FR	4	6.6	4.5	85	258	14	10.2	11.2	25.0	19.2	22.2	31.8	35.8	35.0	5.0	9.2	252	115	4	.8	.8	.0	5.2	6.8	15.8	17.0	50	12	Q
Q[P]	FR	3	6.4	4.3	83	254	14	10.7	11.7	27.0	20.2	21.3	31.7	35.7	35.7	5.0	8.7	246	116	4	.0	.0	.0	2.0	4.0	15.7	18.3	50	12	Q[P]
R	SP	5	11.6	5.2	96	283	11	11.6	12.0	28.0	19.4	20.2	31.4	35.0	36.0	5.0	9.6	266	116	4	.4	1.2	.0	14.8	6.2	15.0	18.2	49	14	R
Standard Deviation of a provenance mean		—	—		4.9	10.6	--	.86	.48	1.19	.83	.83	1.15	1.36	1.37	--	.58	3.1	.59	.21	1.32	.62	n.s.	1.75	1.13	1.05	1.33	3.33	1.67	
Approximate L.S.D.$_{.01}$ between regions					10	30		3	2	4	2	3	3	3	3	1	2	10	1.5	.8	n.s.	2	n.s.	2	1.5	2	3	5.2	2	

KEY TO COLOR GRADES

Character	(9-10)	(11)	(12)	(13)	(14)	(15-16)	(18)
Grade 4	YE-GR	RE-GR	MA	DGR	YE-GR	YE	GR
Grade 8	GR	INT	INT	INT	INT	INT	INT
Grade 12	BL-GR	INT	INT	INT	INT	INT	GR-TA
Grade 16	—	GR	INT	GR	INT	INT	TA
Grade 20	—	INT	GR	INT	INT	INT	TA-BR
Grade 24	--	INT	—	BL-GR	GR	INT	BR
Grade 28	—	BL-GR	—	—	INT	GR	—
Grade 32	--	--	—	--	BL-GR	INT	--
Grade 36	--	—	—	—	—	BL-GR	--

BL = BLue, BR = BRown, DGR = Dark GReen, GR = GReen, INT = INTermediate, MA = MAroon, RE = REd. TA = TAn, YE = YEllow

KEY TO Earliness of Fall coloration (Character 17)

Grade	Fall color evident by
1	Oct. 6
2	Nov. 3
3	Dec. 1
4	Dec. 15
5	No change by December 15

KEY TO OTHER CHARACTERS

Grade	(26) 1960 stem covered by primary needles	(27) Trees with mature needles on Sep 21 1959	(28) Trees with mature needles on Oct 1 1959	(30) Ease of pulling July 1959
	Inches	Percent	Percent	
0	0	51-100	91-100	—
4	1	16-50	76-90	—
8	2	6-15	51-75	Easy
12	3	1-5	16-50	Medium
16	--	0	6-15	Difficult
20	--	--	0-5	

[1] AUstria, BElgium, CZechoslovakia, ENgland, FInland, FRance, GErmany, GReece, HUngary, ITaly, LAtvia, NOrway, POland, RUssia (specifically Georgian S. R. R.), SCotland, SPain, SIberia (Asiatic U. S. S. R.), SWeden, YUgoslavia.

P Seeds obtained from planted stands or from dealers.

great as for the species as a whole. The 30 different provenances from Germany and Czechoslovakia had average two-year heights ranging from 250 to 355 millimeters. These differences are statistically significant, but no German provenance was as slow growing as the average Latvian stock or as fast growing as the average Vosges Mountain stock.

Within one of these ecotypes there was little relation between place of origin and performance of a provenance. As often as not, the fast-growing provenances were from both low and high elevations or from opposite ends of a mountain range. Or a provenance such as 0312 (west central Czechoslovakia) was exceptional with regard to earliness of secondary leaf formation but average in all other respects.

Why this random variation pattern within the ecotypes? Evolution is a slow process, and there is always a considerable lag between a climatic change and the evolutionary adaptation to the changed habitat. Also, evolutionary changes are governed by population structure as well as selection pressure. In northern Scotland, for example, the native Scotch pine woodlands are small and scattered, and each one of them may have been subject to rather intense inbreeding in the past. The environmental differences within the pine area of Scotland are small enough that this inbreeding could have swamped incipient changes due to selection pressure. Hence, it is quite logical to find that much of the relatively minor variation within' ecotypes seems to be slightly out of tune with its environment.

Within-Stand Variation

Although we did not ask for them, some of our European correspondents kept the seed separate by individual trees. Hence, the test included 140 single-tree collections from nine different stands in Belgium, East Germany, and Norway. These half-sib progenies gave us a great deal of useful information, especially for planning future breeding work within ecotypes.

Within each one of these nine stands, there were statistically significant differences among half-sib progenies in at least five different traits. It was pretty much a random variation pattern, and the progeny which excelled in one respect was apt to be average in others. Each of these stands presented a different story, so that heritability estimates made for bud color for the stands from Neusteulitz and Gustrow, Germany, may not be applicable to the other stands.

The variation among half-sib progenies within a stand was about as great as the.variation among stand collections within a region. For example, the individual-tree progenies from one stand near Oslo, Norway, ranged from 150 to 250 millimeters in two-year height. Such large differences--40 percent of the highest value--show that selective breeding within ecotypes will lead to appreciable improvement.

The fact that the differences among progenies of individual trees within the same stand are about as large as the differences among stand-progenies from within the same ecotype has an important bearing on future plans for improving Scotch pine. We already know from theory and from agricultural practice that mass selection is nowhere near as effective as is selection based on the performance records of half-sib (one parent in common) or full-sib (both parents in common) progenies. Once we have determined which of the geographic ecotypes is best suited to a particular area, such as southern Michigan, further testing of many stand-progenies within that ecotype would merely constitute a form of mass selection. Instead, it would be far better to go directly from the broad geographic approach to the individual tree approach. The last approach would entail selecting good individuals from anywhere in the ecotype, testing their progeny, and breeding selected individuals within the progenies.

European Black Pine Provenance Trials

Coincident with the Scotch pine test we started a 29-origin provenance study of European black pine (*Pinus nigra* Arn.). The methodology is thel4ame as that already described for Scotch pine.

The natural range of European black pine consists of isolated areas in Spain, Corsica, Italy, Greece, Yugoslavia, Turkey, the Caucausus, and the Crimea. The range is roughly parallel to but at a lower elevation than the southern range of Scotch pine.

This European black pine was separable into only two ecotypes, Corsican (slow growing, curly needled) and non-Corsican. The differences between these two were of about the same magnitude as the differences between Spanish and central-French Scotch pines. Among the 26 provenances comprising the non-Corsican ecotype, the variation was only about as great as that within a single stand of Scotch pine.

There was no evident parallelism in the genetic differentiation of the Scotch and European black pines. For example, there was very little difference between Spanish and Turkish black pine, whereas Scotch pine were very different. Also, the characters in which differentiation was strongest differed between the two species.