Geographic Variation in Scotch Pine

Results of a 3-Year Michigan Study[1]

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Introduction

Scotch pine (Pinus sylvestris L.) is the most important timber tree of northern Europe and Asia. It was introduced into the United States in early colonial times.

This is a controversial tree to American foresters. Some regard it as a weed. Others think of it as very promising. Whatever its potential role in American forest economy, it has been planted in large numbers and is as common in some northeastern states as are many native species. For that reason it is due to receive increased attention from forest geneticists and other forest researchers.

Its names. — "Scotch pine" (America) and "Scots pine" (Great Britain) are the preferred English-language common names. These names are somewhat misnomers because the tree is much more common on the continent than in Scotland. There are references in the 17th century Scottish literature to “fir” or “firre” woods when speaking of Scotch pine forests. The lumber is frequently imported into British Commonwealth countries as “deal”, and often enters the United States as "pine", "whitepine", or "yellow pine".

On the continent the common names reflect the tree's importance. In northern Europe it is the only pine species and has a simple name — furu (Norway), tall (Sweden), sosna (Russia), or Kiefer (Germany). Its common names (pino sylvestro in Italy, pin sylvestre in France) are direct translations of the scientific name in countries in which it is relatively unimportant. .

The correct scientific name is Pinus sylvestris L. That is the name and spelling given by LINNAEUS in the second volume of his Species Plantarum. The use of LINNAEUS' spelling is mandatory under the rules included in the International Code of Nomenclature. Notes on LINNAEUS' original specimens indicate that they were collected in Germany. Hence the German population should be considered as the type (P. sylvestris var. sylvestris or P. sylvestris subsp. sylvestris) if subspecific categories are recognized.

Distribution. — Scotch pine's natural range extends from west-central Spain through France and northern Italy to Turkey, north to Scotland and northern Finland, and eastward across Siberia to the vicinity of Lake Baikal (figures 1 and 2).

The natural range is continuous over large areas of Scandinavia, northern Russia, and Siberia. In these countries Scotch pine is common on sandy, well-drained soils at low and medium elevations. It is absent in the far north (north of 70° in Sweden and Norway, of 67° in European Russia, and north of 65° in Siberia) and on high mountains because of low temperature. Its distribution on the fertile lowland sites is limited because of competition from other species. In these northern countries extensive forest planting is a recent phenomenon and has not extended the natural range greatly. Therefore most references to pine forests can be interpreted as applicable to natural stands.

Scotch pine is a true native in a few scattered locations in northern Scotland and has been planted extensively for several hundred years elsewhere in the British Isles. The native pinewoods are located on well- drained, infertile sites in protected valleys (STEVEN and CARLISLE, 1959).

Scotch pine has an extensive natural distribution on sandy soils in the lowlands of the Baltic countries and at medium elevations in the mountains of southern Poland, southern Germany, and Czechoslovakia. In these regions the range is esentially continuous over large areas. There is allong history of planting in these countries, and there is an element of doubt as to the history of any particular stand. Only in the rockiest mountains can the indigenous character of individual stands be certified. The pine forests of Denmark, Belgium, the Netherlands, and most of northwestern Germany are of planted origin (there are two native areas in northwestern Germany). Records by which the ultimate origin of the plantations could be traced are usually lacking.

This species occupies four widely separated natural distribution areas in France — the Vosges Mountains bordering Germany, the Alps bordering Switzerland and Italy, the Central Massif around Auvergne, and the Pyrenees. Most planting has taken place at elevations lower than those occupied by the natural stands.

Scotch pine is an uncommon tree, found only in scattered stands in high mountains in the countries bordering the Mediterranean Sea. In these countries exploitation rather than planting has been the rule, and the native origin of most stands can be guaranteed.

There are extensive Scotch pine plantings in northeastern United States. The majority originated in the 1950's and were made by Christmas tree growers on light, sandy soils. A few of the recent ones are of known geographic origin.

Botanical description. — Scotch pine can be distinguished from all other pine species by the following combination of characters: Needles 2 per cluster, 1 to $3^1/_2$ inches (25 to 80 mm.) long, $^1/_{25}$ to $^1/_{12}$ inch (1 to 2 mm.) broad, stiff, sharp-pointed, twisted, gray-green, with persistent needle sheaths; Female Flowers $^1/_4$ inch (6 mm.) long, ovoid, red to brown, without prickles, borne on strongly reflexed stalks about $^1/_2$ inch (12 mm.) long, borne one to three per branchlet; Cones $1^1/_2$ to $2^1/_2$ inches (4 to 6 cm.) long, 2 to 3 times as long as broad, conic with a rounded base, yellow to grayish or greenish brown, with long angular apophyses on basal scales, opening in December or January and not long persistent after ripening; Seeds dark brown to nearly white, $^1/_8$ to $^3/_{16}$ inch (3.5 to 5.5 mm.) long, Seed Wings tan to yellow-red, $^3/_5$ to $^4/_5$ inch (15 to 20 mm.) long; Male Catkins yellow (more rarely red), $^1/_8$ to $^1/_4$ inch

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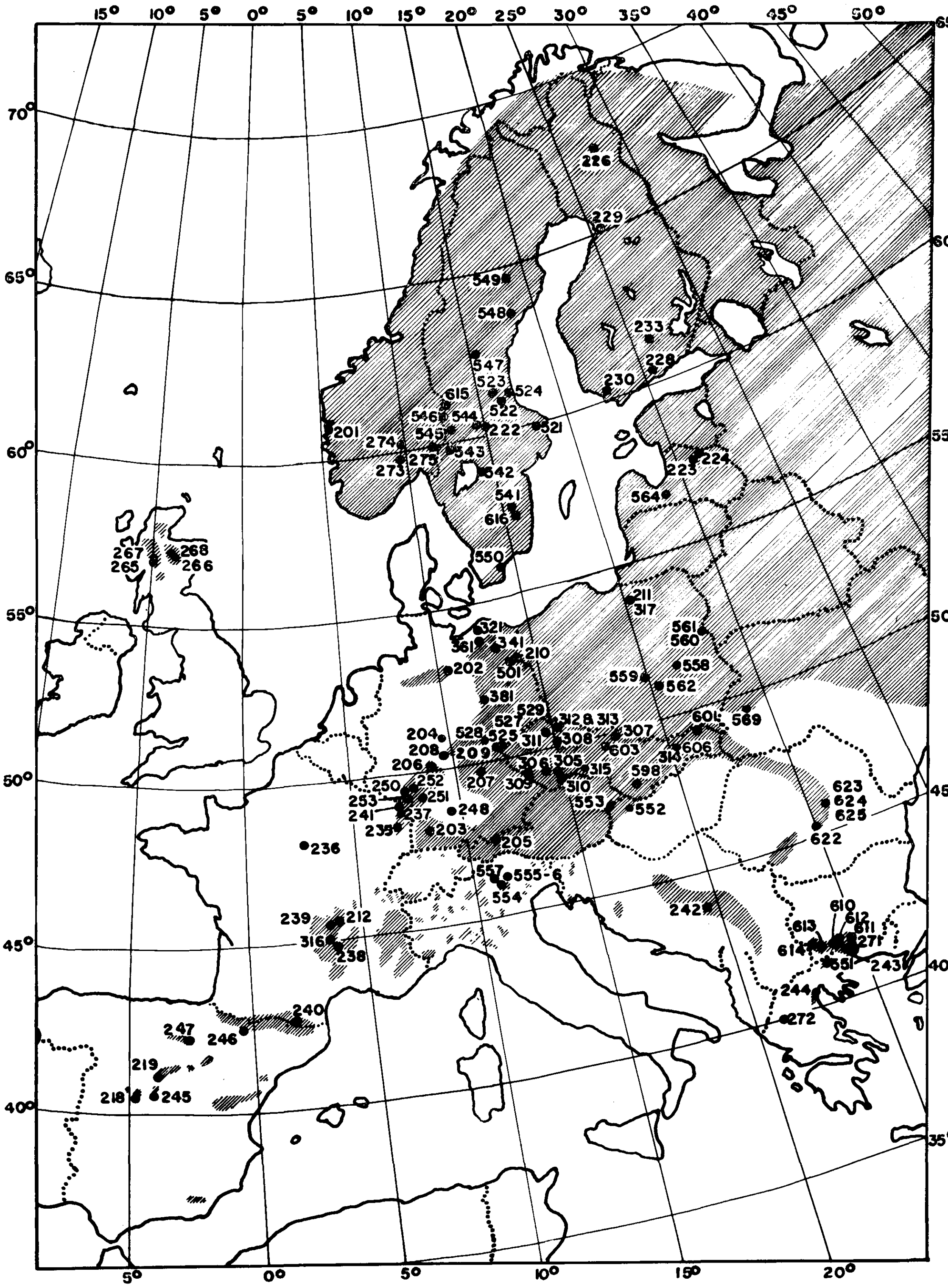

Figure 1. — Natural distribution of Scotch pine in Europe (shaded) and provenances included in this experiment (numbered dots).

(3 to 6 mm.) long before anthesis; Bark scaly, dark brown or black at first but changing to yellow or reddish on large branches and on the lower boles of large trees.

The short, gray-green needles and the strongly reflexed cones are the tree's most distinctive features. The yellow bark on old trees is also a useful diagnostic feature, but can be mistaken for that of the longer needled Japanese red pine (*P. densiflora* Sieb. & Zucc.). (The parts of the description not based on personal observation are taken from Rehder, 1940.)

Form, growth, and wood characters. — In native European stands Scotch pine is straight-trunked and small-branched if grown under good management practices. Pictures of good native Scottish, German, or Swedish stands show many trees which would delight any forester's eye. The maximum heights achieved in these countries vary considerably. The veterans in the Scottish woods are flat-topped and only 50 or 60 feet tall whereas spire-crowned trees 100 to 120 feet tall are common in old German and Scandinavian forests. In Europe the species is

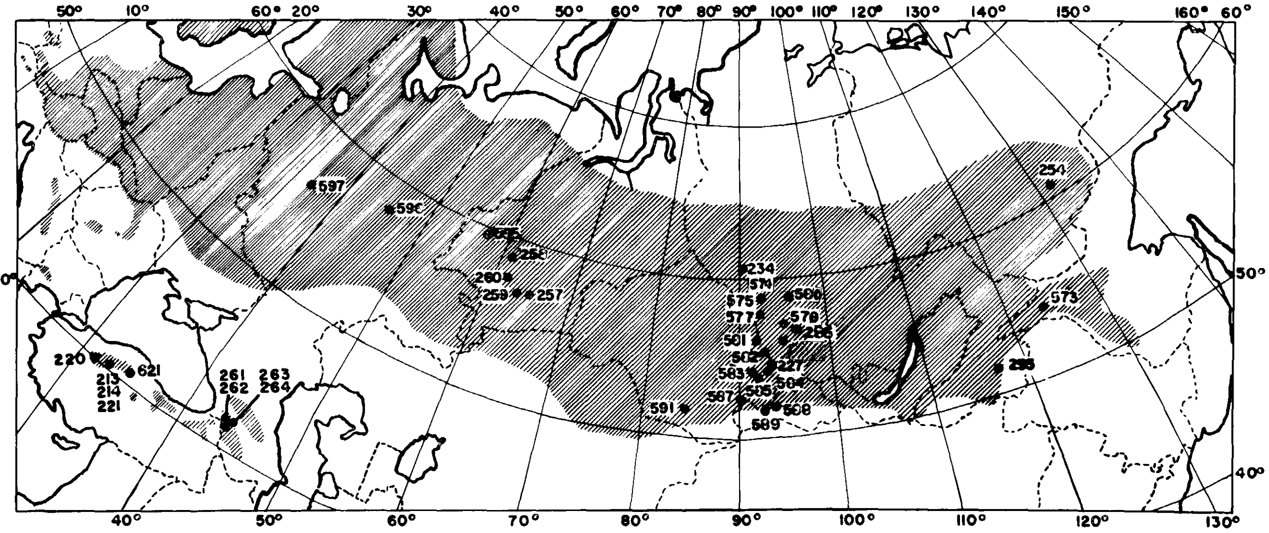

Figure 2. — Natural distribution of Scotch pine in Asia (shaded) and provenances included in this experiment (numbered dots).

subject to many minor pests but to none which causes heavy mortality over large areas.

The majority of the older stands in New York and New England are of presumed German or north French origin and are full of trees with crooked boles, basal sweep, or flat tops. Their growth rate is good, however — about equal to that of other fast growing conifers. A good many of the growth deficiencies are traceable to inherent reactions to various types of damage rather than inherent tendencies to grow crooked. This and the absence of certain types of snow or pest damage may explain why some Michigan plantings of supposed central European origin exhibit good form. The few plantings of undoubted Latvian or Scandinavian origin have moderate growth rates, straight boles, and sharp crowns wherever found.

Scotch pine nursery stock is relatively immune to damping off and has a fibrous, easy-to-transplant root system. It is most commonly distributed as 2-0 stock. The tops are commonly sheared early in the second year in order to obtain a better root-shoot ratio. The shearing is almost always followed by the setting of buds which grow normally the next year.

Fully stocked Scotch pines cast a lighter shade and offer less competition to ground vegetation than most other northern conifers. Advance reproduction of hardwoods is very common in 30- and 40-year-old stands.

Young trees respond to shearing during June or early July by setting numerous buds in the middle of the 2-leaved clusters. Thus a grower can easily obtain trees with crown of any desired shape or density. This trait, together with the ease of handling and rapid growth, is reponsible for the high favor in which small nurserymen and Christmas tree growers hold Scotch pine.

The wood is soft and easily worked, and can be used for many of the same purposes as a white pine. It does not have the strenght or density of the American southern pines. In Europe as well as in Michigan and other northeastern states it is being pulped satisfactorily by the sulphate process. Discrimination against it is due almost entirely to poor form.

Previous Provenance Work in Scotch Pine

The first provenance test on Scotch pine or any species was started in 1820 in France by a seedsman, Vilmorin. It showed the presence of large differences between seedlings from different regions. The results were published in 1857. Since that time many such tests have been conducted in Europe and America. Most were unreplicated and are of historical interest only.

The first large series of provenance tests was the one started in 1907 by the International Union of Forest Research Organizations *(IUFRO)*. It included 13 origins and 16 outplantings in Sweden, Germany, Belgium, Hungary, and the Netherlands. Each origin was represented by 0 or 1 plot per planting. With this design it was possible to obtain reliable information on the large differences common to all plantings. Wiedemann (1930) summarized the separate published reports for the entire experiment as follows: *North Swedish* trees — very slow growth, straight stems; *Latvian* trees — moderately fast growth, straight stems, pointed crowns; *North Polish* trees — similar to Latvian trees but with slightly more crooks; *German* trees — fast growth, crooked stems, pointed crowns, variable; *Scottish* trees — slow growth, variable, many forked and a few crooked stems; *Siberian* trees — very slow growth, variable in form; *South French* trees — slow growth, variable in form; *Belgian* trees — crooked stems, large branches, very fast growth (the tallest seedlot in 10 of the 16 plantings). The correlation between early and late height growth appeared strong for the plantings for which growth data from successive years were available.

During the period 1912—1916 a series of provenance tests was started at Chernigov, Ukrainian S. S. R. (data published in Russian by Samofal in 1926, summarized in detail by Wiedemann, 1930). The series included 102 plots of 54 Polish and Russian provenances. The planting followed an irregular design and the data can not be subjected to precise statistical analysis. Trees from Poland and adjacent parts of European Russia grew fastest *(table 1)*. Those from the Ural Mountains, northern Russia, and Siberia grew slowest. Trees form southern outliers on the Russian steppes were intermediate.

In the early 1930's Langlet conducted a large nursery test with seedlings from 582 Swedish stands. Each stand was represented by a single plot, for which the percent dry weight at age 2 was determined. With this design it was possible to determine the significance of differences from different regions but not among progenies from dif-

Table 1. — Relative growth rates of Russian and Polish origins of Scotch pine growing near Chernigov, Ukrainian S. S. R.*)

Regions of origin	Latitudes of origin	Longitudes of origin	Relative height growth
	° North	*° East*	*Percent of plantation mean*
Eastern Siberia	51—53	70—80	48
Northwest European Russia	61	37—42	61
Central, northern Ural Mts.	56—60	57	64
Latvia, Leningrad region	57—59	22—50	101
E. Poland, White Russian S.S.R., Bashkir A.S.S.R. Gorki and Kazak Areas, northern Ukrainian S.S.R.	51—57	20—56	113
Kuibishev, Middle Volga Terr.	53—54	48—49	80
Eastern Ukrainian S. S. R. (Kiew and Kharkov)	49	31—34	85

*) The data are from Samofal, 1926, quoted by Wiedemann, 1930. The actual mean heights in the various plantings varied from 4 to 15 feet at ages 7 to 11.

ferent stands within the same region. Seedlings from southern Sweden were much more succulent (dry weight percent = 33) than those from northern Sweden (dry weight percent = 38) (Langlet, 1936). The variation pattern was continous.

In another part of his work Langlet obtained data on needle size and color (19 origins) and 2-year height (10 origins) of Swedish provenances grown in three different Swedish nurseries. Each origin was represented by one plot per nursery. This design permitted the detection of differences common to all nurseries. Needle length and height were almost twice as great for southern as for northern provenances. The southern trees were greenest during the winter. The differences between regions were highly significant. There were apparent discontinuities between regions.

In 1938 a new series of IUFRO tests was started. The series included 55 provenances from Scotland to Latvia and from Germany to northern Scandinavia. Each cooperator established one or more plots of as many origins as he chose to include. One of the cooperators included all 55 origins; most included the 20 or 30 closest to the planting site. Spacing was 4 × 4 feet (1.3 × 1.3 meters)in all plantings and all cooperators used complete randomization (Veen, 1952).

With the experimental design used in these later IUFRO plantings it was possible to detect the significance of differences among regional and stand-progeny means. Because of the complete randomization and the 200 tree plots the statistical precision was relatively low. There has been no attempt at an overall summary but there are published reports on three individual plantings.

The most complete and best replicated (all 55 origins, 2 to 7 plots per origin) of the 1938 IUFRO plantings is that established by H. I. Baldwin at the Caroline A. Fox Research Forest, Hillsboro, New Hampshire. This was summarized in a series of reports by Baldwin (1955, 1956), Wright and Baldwin (1957), Echols (1958), and Gerhold (1959). The growth data are summarized in *table 2*. The ecotype delimінations for that table were based on analyses of variance of the 17-year heights. Among the significant findings not included in the table are the facts that the species is composed of broad geographic ecotypes within which variation is more or less random, there was a high correlation (r = 0.85) between juvenile and 17-year height, and growth data from linear and large square plots were practically equivalent over a wide range of growth rates.

Echols' report covered wood quality aspects of some origins in the New Hampshire test. He found that slow growing Scandinavian trees produced the densest wood but that cellulose production per acre was much greater with fast growing origins from Germany and Belgium. Gerhold's report covered the detailed physiology of autumnal color in six different origins. He showed that two Scandinavian seedlots were significantly high (1 or 5 percent levels) in foliar nitrogen in August, in foliar boron (both August and February), and in carotenoids. They were significantly low in foliar iron and in autumnal chlorophyll. The differences in autumnal color were genetic and not influenced by any of 10 liquid fertilizers.

The 1938 Czechoslovakian IUFRO test was reported upon by Vincent and Polnar (1953). It includes one to

Table 2. — Performance of 17-year-old Scotch pine provenances in the 1938 New Hampshire IUFRO study (after Baldwin, 1956 and Wright and Baldwin, 1957).

Region	Autumn foliage color¹)	Mean height	D.b.h.	Branch Diameter	Trees with					
					Basal sweep	Lean	Crooks		Porcupine damage	Fruit
							Total	large		
		Feet	*Inches*				*Percent*			
A Scandinavia	7.0^{d}	5.60^{f}	.40	.15	0	0^{b}	54^{a}	1^{f}	0^{b}	9^{ab}
B Scandinavia	$6,5^{d}$	9.61^{e}	1.30	.39	0^{d}	0^{b}	65	11^{c}	$(T)^{b}$	13^{ab}
C Scandinavia	5.9^{c}	13.11^{d}	2.21	.54	3^{c}	$(T)^{b}$	59	15^{c}	1^{b}	5^{ab}
D Scandinavia	5.0^{c}	$15\ 47^{c}$	2 81	.72	2^{c}	$(T)^{b}$	54^{ab}	26^{b}	3	(T)
E Scotland	1.0^{c}	14.68^{b}	2.66	.47	2^{c}	2	49	15^{b}	0^{b}	9
F Latvia	2.8^{d}	18.45^{b}	3 10	.69	7^{b}	2	63	27^{b}	5	1
G Germany etc.	3.6^{d}	19.74	3.45	.80	21^{a}	5^{a}	68	40^{a}	5	1
H Belgium	1.0^{bd}	22.47^{b}	3.80	.84	43^{b}	13^{b}	69	46^{c}	10	9^{b}
I Rumania	3.1^{e}	17.90^{b}	2.88	.69	15^{d}	2	44^{b}	26^{b}	7	4
J Italy	$4\ 5^{e}$	17.40^{b}	3.42	.72	20^{d}	0	69	33^{d}	0	6

¹) Scored on a basis of 1 = blue-green to 7 = yellow. Low numbers best Christmas trees.

(T) — Trace less than 0.5 percent.

a — Significant differences within region.

b — Significantly different from Region G (Germany, Poland, Czechoslovakia, Hungary).

c — Significantly different from Region F (Latvia).

d — Significantly different from Region D (Scandinavia).

e — Significantly different from Region C (Scandinavia).

f — Significantly different from Region B (Scandinavia).

²) Large crooks = more than 1.5 inches offset.

three plots of each of 31 origins. The partial replicates are on three different sites. Analysis of variance of their published plot means showed significantly slower growth (at the 5 percent level) for northern than for central European origins.

Rudolf and Slabaugh (1958) reported on the 10-origin replicated Lake States planting of the 1938 IUFRO test. They confirmed earlier European findings as to the general growth superiority of central European sources and form superiority of Latvian and Scandinavian sources. In New York there is an unreplicated series of IUFRO plots which has been measured recently but not reported upon. Published data are also lacking for the remainder of the European IUFRO tests.

In Europe there are a large number of non-experimental plantings in which stock of two to several different origins has been planted in close enough proximity to permit valid conclusions as to the magnitude of differences encountered within a region. Thus, German foresters recognize the existence of large differences in bole form, growth rate, branch size, etc. among provenances collected within Germany.

Objectives

This nursery experiment is a part of a cooperative project entitled „*Tree Improvement through Selection and Breeding of Forest Trees of Known Origin*". This is regional project NC-51 of the U. S. Department of Agriculture and involves active cooperation by the state experiment stations of 10 north central states. The regional project's objectives are as follows: (1) Determine the range and pattern of genetic diversity within selected forest tree species, (2) utilize the genetically most suitable material for breeding purposes, and (3) provide genetically suitable material for reforestation purposes.

This report is concerned with the first and third objectives as they relate to Scotch pine for use in Michigan. Of course a 3-year nursery test is not enough. It must be followed by examination of the trees over a number of years. This will be done in a series of permanent test plantations established from 1961 to 1963 in many parts of the North Central states. These permanent tests will also supply the breeding material by which the second objective can be pursued.

Methods

Seed procurement and handling. — In the summer of 1958 we requested European researchers and dealers to send seed from native Scotch pine stands in their vicinity. They sent seed from 122 stands in 19 Eurasian countries. The 122 samples can be classed as follows: from native stands — 106; from unknown-origin plantations — 11; from dealers — 5. Those form the basis for the 3-year experiment. An additional 64 provenances (56 from native stands and 8 from dealers) were received later and comprise the 1-year experiment. The collection areas are shown in *figures 1 and 2.*

Each stand collection consisted of seed from 10 or more average trees from an area of several acres. All the native-stand and some of the dealer seedlots were accompanied by data on locality, altitude, date of collection, area, soil, age, height, diameter, and hybridization possibilities of parent stand. The most pertinent origin data are summarized in *tables 3 and 5;* the rest are available on request. The general validity of the origin information could be affirmed by the experiment itself. In only five cases was there reason to doubt that the seedlots were not as they were described. Data from those seedlots were disregarded.

Sowing and nursery care. — The nursery occupies a level clay-loam soil which had previously been maintained at a high fertility level by means of cover crops and commercial fertilizers. No fertilizer was added during the experiment. All sowing was done on areas which had been treated with a combination fungicide-weed seed disinfectant (methyl bromide in 1959, "Milon" in 1961) the previous autumn.

Shortly before sowing each seedlot was allotted to numbered packets, one packet per row. The packets were randomized within replicates and the random order was recorded on a nursery map from which nursery stakes were prepared. Two days in early May 1959 and one day in early May 1961 were required for the actual sowing, which consisted of placement of row stakes and packets, checking packet identity against nursery map, hand-planting the seeds $^1/_2$ inch deep in rows exactly 6 inches apart, sprinkling $^1/_2$ inch of sand over the seeds, and covering the seedbeds with wire screen and lath shades. Each plot consisted of one 46-inch row perpendicular to the long axis of the 500-foot seedbeds. (In a fifth, unmeasured replicate the seeds were sown broadcast in various-sized plots.)

The screens and shades were removed at the completion of germination, 3 weeks after sowing. A slight amount of damping off at that time was controlled by the application of "Captan". In mid-July the beds were thinned to a density of about 50 per row (replicates 1 to 4) or 50 per square foot (replicate 5). Periodic applications of Stoddard solvent kept the beds weed-free. The trees were watered as needed to maintain an adequate soil moisture at a 1-inch depth at all times.

A $^1/_2$-inch sawdust mulch applied in November solved the first-year frost heaving problem. This was supplemented by drifting snow which almost covered the seedlings during the winters of 1959-60 and 1961-62. The snow cover was scanty during the 1960-1961 winter. Temperatures below 0° F. (—17.8° C.) were observed in all winters.

In May 1961 the broadcast sown portion of the 1959 experiment was lifted for outplanting. The measured replicates were root-pruned at a 6-inch depth and thinned to a density of 20 trees per row. The root pruning had little effect on subsequent growth. In May 1962 the remainder of the 1959 sowing was lifted and used as a replacement stock. The 1961 sowing remains in place until 1963.

Measurements. — The measurement philosophy was "Measure when differences appear and in whatever (macroscopic) traits they appear." Plot means only were recorded. One trait was measured at a time. Altogether, 36 complete sets of measurements were made for different traits or for the same trait at different times. A plot's identity was always unknown at the time of measurement.

Metrical traits were measured to an accuracy of approximately 1/20th of the range between extremes. Non-metrical traits were scored in terms of the maximum recognizable number of grades. Insofar as possible the grades were defined in standard terms and in such a manner as to eliminate the need for transformation in subsequent analysis. Color was defined in terms of live-tree standards, the extreme grades being duplicated by means of paint on paper.

Table 3. — Three-year growth data for the Scotch pine progenies sown in 1959, summarized by stand-progeny.

Region, Country of origin, MSFG No.	North Lat.	East Long.	Elev.	Age	Seed Wt.	Seed Length	Height Age 1 1959	Height Age 2 1960	Height Age 3 1961	Height ÷ Seed Weight	Foliage color on June 26 1959	Foliage color on Oct. 28 1959	Foliage color on Aug. 10 1960	Foliage color on Dec. 15 1960	Foliage color on Dec. 1 1961	Earliness of leaf color	Bud Color 1960	Bud Formed 1959	Started growth 1960	Branches on terminal 1960	Male fls. 1959	Lammas shoots 1960	Secondary leaf presence Oct. 1959	Leaf length Aug. 1960	Ease of pulling	MSFG No.	Region
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(7/5)	(10)	(11)	(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)	(20)	(21)	(22)	(23)	(24)		
	°	°	100's of Feet	Yrs.	mg.	mm.	mm.	mm.	mm.	mm./mg.	Grade	Grade	Grade	Grade	Grade	Grade	Grade	Day of Year	Day of Year	Per 200 trees	Per 200 trees	Per 200 trees	Grade	mm.	Grade		
A FIN[1] 226	67.5	27.5	8	100	4.2	3.8	38	57	118	9	6	8	5	8	9	1	4	200	113	0	0	0	3	40	15	226	A
FIN 229	65.2	25.5	0	--	3.8	3.8	44	112	192	12	8	6	4	8	7	1	4	200	113	0	0	0	3	54	16	229	
SIB 254	60.8	131.6	25	--	5.2	4.0	41	118	225	8	7	5	6	7	9	1	4	200	113	0	0	0	0	64	18	254	
B SWE 549	64.5	18.7	8	--	2.7	3.6	46	112	323	17	5	8	7	6	8	2	4	219	113	0	0	0	2	56	13	549	B
SWE 548	63.5	18.7	7	--	3.3	3.8	58	151	302	17	5	8	8	9	7	2	6	219	113	2	0	0	4	58	12	548	
SWE 547	62.5	15.7	7	--	4.1	3.8	60	132	300	15	4	8	6	9	10	2	8	219	113	1	0	0	5	58	11	547	
SWE 546	60.9	13.4	15	--	3.4	3.6	54	122	265	16	6	8	7	6	10	2	8	219	113	0	0	0	6	50	12	546	
C FIN 228	60.4	25.4	1	--	5.0	3.6	76	200	335	15	5	9	8	6	9	3	8	219	113	0	0	0	10	56	13	228	C
FIN 230	60.5	22.4	1	--	4.7	3.6	53	153	315	11	5	10	7	13	14	2	8	219	113	0	0	0	19	48	11	230	
FIN 232	60.3	25.4	--	--	4.3	3.7	63	153	302	14	4	8	9	8	13	3	8	219	113	0	0	0	14	64	13	232	
FIN 233	61.5	26.0	--	--	5.0	3.8	79	207	380	16	5	10	8	9	7	2	8	219	113	0	0	0	17	58	11	233	
SWE 222	60.2	15.0	8	--	3.2	3.7	69	234	428	22	7	10	9	6	9	3	8	219	113	0	0	0	13	62	14	222	
SWE 521	60.0	18.0	1	120	4.4	3.8	76	220	390	17	4	8	9	8	9	3	12	219	114	0	0	0	22	56	13	521	
SWE 522	60.9	16.5	7	80	4.4	3.6	81	217	372	18	4	10	9	10	12	2	10	219	113	0	0	0	15	58	14	522	
SWE 523	61.3	16.0	7	150	4.5	3.6	64	189	338	14	4	10	9	9	10	2	8	219	113	0	0	0	10	56	12	523	
SWE 524	61.3	17.9	1	60	5.0	3.8	75	228	392	15	6	10	9	9	9	2	12	219	113	0	0	0	16	56	11	524	
SWE 543	59.9	12.9	7	--	4.3	3.7	69	196	342	16	4	8	7	9	13	2	10	219	113	1	0	0	9	56	12	543	
SWE 544	60.4	14.9	8	--	4.3	3.6	84	228	395	20	5	10	10	8	8	2	10	219	113	1	0	0	10	56	12	544	
SWE 545	60.4	12.9	8	--	3.7	2.8	63	181	313	17	5	11	10	8	9	2	8	219	113	2	0	0	16	56	13	545	
NOR 273	59.7	9.5	6	--	3.4	3.8	55	152	278	16	5	10	7	13	14	1	10	219	113	0	0	0	9	56	9	273	
NOR 274	60.3	9.9	6	--	5.2	3.7	62	185	315	12	6	8	6	11	9	2	8	219	113	0	0	0	9	56	14	274	
NOR 275	59.8	11.6	7	--	4.5	3.7	67	192	272	15	4	9	8	8	6	2	12	219	113	0	0	0	17	56	14	275	
NOR 201	60.5	3.2	1	--	5.6	4.2	81	224	400	14	6	11	9	7	13	2	12	219	113	0	0	0	22	50	14	201	
D SWE 542	58.8	14.3	4	--	5.2	3.8	83	231	425	16	4	9	9	11	5	2	12	219	113	0	0	0	26	56	12	542	D
SWE 541	57.	15.6	5	--	3.6	4.2	82	260	469	26	5	12	10	9	12	2	6	239	114	1	0	0	21	62	11	541	
SWE 550	55.9	14.1	1	--	4.9	4.0	88	257	442	17	4	12	12	11	17	2	7	239	114	0	0	0	27	60	14	550	
LAT 223	57.5	25.8	--	120	6.8	4.0	91	273	468	13	4	18	14	6	11	3	10	239	114	0	0	0	26	54	10	223	
LAT 224	57.7	26.3	--	120	4.6	4.1	90	263	458	20	4	10	9	20	9	3	7	239	114	0	0	0	25	60	9	224	
E SIB 227	54.0	94.0	5	--	5.4	3.8	92	252	385	17	5	9	10	5	5	2	10	219	113	0	0	0	12	66	12	227	E
SIB 234	56.0	95.0	--	--	6.0	4.2	89	260	440	15	5	8	10	5	5	2	8	219	114	0	1	0	8	74	13	234	
SIB 255	52.4	117.7	20	--	4.5	3.9	68	197	325	15	4	7	10	4	4	1	8	219	113	0	0	0	9	64	13	255	
SIB 256	56.7	96.3	13	--	5.5	4.0	79	244	420	14	4	9	11	4	5	1	8	219	113	0	0	0	3	74	17	256	
URA 257	56.8	65.0	5	--	5.6	3.8	95	278	468	17	4	9	11	4	4	1	10	219	113	0	0	0	17	66	13	257	
URA 258	58.8	60.8	3	--	5.5	3.8	91	246	422	17	4	8	10	4	4	2	12	219	114	0	0	0	11	68	14	258	
URA 259	56.9	63.2	3	--	5.5	3.8	97	274	455	18	4	8	10	4	4	1	8	219	114	0	0	0	13	70	14	259	
URA 260	57.0	61.4	5	--	5.6	4.1	100	292	472	18	4	10	12	4	7	2	10	219	114	0	0	0	21	66	12	260	
F POL 211	53.8	20.3	--	--	6.5	4.1	104	330	538	16	4	15	16	11	15	2	10	242	115	0	0	0	31	76	11	211	F
POL 317	53.7	20.5	--	--	6.0	4.0	100	305	565	17	6	12	15	20	19	3	10	244	115	0	0	0	33	70	10	317	
G GER 202	53.-	10.6	4	--	6.6	4.0	101	314	565	15	4	16	16	19	20	3	10	258	115	0	0	1	31	74	10	202	G
GER 203	48.2	8.3	--	--	5.1	4.0	91	286	498	18	5	15	16	23	28	4	10	245	115	1	0	0	32	64	11	203	
GER 204	50.8	9.7	13	--	5.8	4.1	107	316	608	18	4	13	16	23	21	4	10	240	115	0	0	1	27	72	9	204	
GER 207	49.7	11.2	--	--	6.0	4.3	111	360	612	18	4	16	16	20	23	4	10	253	115	0	0	0	30	70	8	207	
GER 208	50.6	9.7	--	--	6.7	4.1	113	341	618	17	4	15	16	22	23	3	10	247	115	0	1	0	33	70	9	208	
GER 210	53.2	14.3	--	--	7.6	4.3	106	372	602	14	5	15	16	19	22	4	10	253	115	0	0	0	30	76	10	210	
GER 248P	48.5	9.8	--	--	6.8	4.6	114	362	578	17	6	18	17	21	24	4	9	244	115	0	0	0	28	72	9	248P	
GER 321	54.2	12.2	0	104	5.8	3.9	108	324	574	19	4	16	16	20	22	3	10	240	115	1	0	0	31	70	10	321	
GER 341	53.3	13.1	3	110	6.2	4.3	93	317	554	15	4	13	16	19	22	4	10	245	115	1	0	0	32	76	11	341	
GER 361	53.8	12.2	1	97	6.2	4.1	97	321	559	16	4	15	16	24	20	4	10	245	115	1	0	0	32	70	12	361	
GER 381P	52.1	12.2	3	100	7.2	4.3	112	349	641	16	4	16	16	25	20	4	10	247	115	0	1	0	29	76	11	381P	
GER 501	53.0	13.8	--	--	6.9	4.3	105	343	596	15	4	15	16	25	20	4	10	245	115	0	0	1	31	70	11	501	
GER 525	50.4	12.2	15	--	4.8	4.0	98	313	585	20	4	15	16	20	21	3	10	245	115	0	0	0	33	70	9	525	
GER 526	50.4	12.2	17	--	4.6	3.8	103	311	592	22	4	15	16	18	22	3	10	239	115	0	0	1	28	68	9	526	
GER 527	50.9	13.7	18	--	6.8	4.6	102	302	560	15	4	15	14	16	18	3	10	242	115	0	0	1	30	70	12	527	
GER 528	50.6	12.0	15	--	6.3	4.2	112	357	660	18	4	16	17	17	22	2	11	247	115	1	0	0	28	68	10	528	
GER 529	50.9	14.3	10	--	5.4	4.0	101	321	595	15	4	13	16	19	21	4	10	254	115	0	0	0	32	72	10	529	
CZE 305	49.-	14.7	13	--	5.2	3.8	98	316	552	19	5	16	16	21	22	4	10	251	115	2	0	0	29	70	10	305	
CZE 306	49.2	14.-	15	--	5.7	3.8	101	313	500	18	4	16	16	21	22	4	10	247	115	0	0	0	28	70	10	306	
CZE 307	49.9	17.9	8	--	5.7	3.8	113	338	580	20	4	16	16	19	20	4	10	245	115	0	0	0	30	72	11	307	
CZE 308	50.2	15.0	7	--	5.5	3.8	91	308	558	16	4	14	16	20	21	3	10	247	115	1	0	0	31	70	9	308	
CZE 309	49.1	13.3	22	--	5.8	3.9	104	306	530	18	5	16	15	18	19	4	9	245	115	0	0	0	30	64	9	309	
CZE 310	48.7	14.9	18	--	5.4	4.1	100	312	598	19	5	16	16	18	20	4	10	244	115	0	0	0	32	72	11	310	
CZE 311	50.5	14.7	10	--	5.2	3.8	104	329	562	20	4	15	15	21	21	4	9	245	115	0	0	0	32	70	10	311	
CZE 312	50.9	15.1	20	--	5.9	4.9	112	324	590	19	6	17	16	20	23	4	9	244	115	0	0	0	28	70	10	312	
CZE 313	50.7	15.2	16	--	5.8	4.1	94	293	548	16	4	15	15	18	20	4	10	249	115	1	0	0	30	70	10	313	
CZE 314	48.9	20.5	27	--	6.6	4.1	108	326	600	16	4	16	16	16	18	4	9	244	115	0	0	0	31	66	11	314	
CZE 315	49.1	16.8	10	--	8.1	3.8	110	338	568	14	4	15	16	16	20	3	10	239	115	0	0	0	30	70	12	315	
AUS 319[d]	--	--	--	--	5.8	4.0	105	338	625	18	4	16	16	19	22	4	9	244	115	0	0	0	31	68	10	319[d]	

Experimental design and statistical analysis. — A randomized complete block design was used. It included four measured replicates, each containing one plot (= row) of each origin.

Analysis of variance was standard procedure for every characteristic. Plot means were used as items. If an analysis included 122 seedlots the degrees of freedom were 121, 3, 363, and 487 for origin, replicate, error, and total respectively. Each variance analysis was supplemented by DUNCAN's "*multiple range analysis*" to determine "Least Significant Difference" between individual progeny means. Only the standard deviations of the provenance means and the LSD's are presented *(tables 3 and 5)*.

Approximate between-region LSD's *(table 4)* were calculated from *analyses of variance for unequal numbers of items per class*, using progeny means as items. These were supplemented by "*t*" *tests* to differentiate between regions with unusually small or unusually large numbers of progenies.

A *partial binomial expansion analysis* was frequently used to determine the advisability of measurement or to check on the validity of the analysis of variance results. If a character was present in p proportion of the 4n plots (n = number of progenies), the probability of its chance occurrence in all 4 plots of a particular progeny was np^4. If np^4 was less than .05, genetic significance could be inferred. For example, the probability was 122 $(8/488)^4$ = 0.00000887 (approximated in the nursery as 120 $(1/60)^4$ = about 0.00001) that MSFG 530 would be among the two tallest of 122 progenies in each of 4 replicates.

Table 3. — (continued).

Region	Country of origin, MSFG No.	North Lat. (1) °	East Long. (2) °	Elev. (3) 100's of Feet	Age (4) Yrs.	Seed Wt. (5) mg.	Seed Length (6) mm.	Height Age 1 1959 (7) mm.	Height Age 2 1960 (8) mm.	Height Age 3 1961 (9) mm.	Height ÷ Seed weight (7/5) mm./mg.	Foliage color on June 26 1959 (10) Grade	Foliage color on Oct. 28 1959 (11) Grade	Foliage color on Aug. 10 1960 (12) Grade	Foliage color on Dec. 15 1960 (13) Grade	Foliage color on Dec. 1 1961 (14) Grade	Earliness of leaf color (15)	Bud Color 1960 (16)	Bud Formed 1959 (17) Day of Year	Bud Started growth 1960 (18) Day of Year	Branches on terminal bud 1960 (19) Per 200 trees	Male fls. 1959 (20) Per 200 trees	Lammas shoots 1960 (21) Per 200 trees	Secondary leaf presence Oct. 1959 (22) Grade	Leaf length Aug. 1960 (23) mm.	Ease of pulling (24) Grade	MSFG No.	Region
H	GER[1] 206	50.2	8.8	--	--	6.5	4.2	119	364	652	18	4	16	16	22	25	4	10	247	115	0	0	0	28	74	11	206	H
	GER 250	49.4	7.6	13	--	7.3	4.4	116	372	675	16	4	16	16	20	23	4	11	250	115	0	0	0	32	78	10	250	
	GER 251	49.1	8.1	5	--	7.2	4.2	107	335	608	15	4	18	16	24	26	4	10	260	115	0	0	0	33	72	9	251	
	GER 252	49.3	7.9	13	--	6.0	4.1	108	332	590	18	4	17	16	28	24	5	10	261	115	0	0	0	33	74	10	252	
	GER 253	49.1	7.8	13	--	7.7	4.1	120	346	615	18	4	18	16	24	25	4	10	257	115	0	0	0	31	78	9	253	
	FRA 236[P]	43.0	2.8	5	150	7.2	4.2	121	380	630	17	4	18	16	26	24	4	10	254	115	0	0	0	31	74	10	236	
	FRA 237	43.8	7.8	5	150	6.2	4.1	120	380	635	19	4	19	16	28	25	5	9	258	115	2	0	3	30	72	10	237	
	FRA 241	49.1	7.4	8	150	6.0	4.3	124	350	612	21	4	18	16	26	25	5	3	261	115	0	0	1	33	76	9	241	
	HUN 552	47.3	17.8	8	80	6.3	4.8	102	343	618	16	4	16	16	21	22	3	10	257	115	0	0	0	31	72	9	552	
	HUN 553	47.7	16.6	10	60	5.7	4.8	112	362	618	20	4	16	16	21	22	3	10	253	115	0	0	0	30	72	9	553	
	ITA 554	46.0	11.2	25	--	6.4	4.5	101	316	565	16	4	19	16	23	25	4	9	267	115	0	0	0	33	68	10	554	
	ITA 555	46.3	11.3	31	--	7.0	4.4	110	312	588	16	6	17	17	21	25	4	10	261	115	1	0	1	34	68	11	555	
	ITA 556	46.3	11.3	33	--	6.6	4.2	112	340	610	17	6	18	16	21	25	3	9	263	115	1	0	0	35	70	10	556	
	ITA 557	46.3	11.0	26	--	5.8	4.7	101	336	582	17	4	19	15	22	25	4	8	263	115	0	0	1	35	70	10	557	
	BEL 285[P]	51.3	5.5	1	38	5.7	4.0	110	346	642	19	4	15	16	23	24	4	10	256	115	0	1	0	30	70	11	285[P]	
	BEL 295[P]	51.1	5.4	2	100	5.1	3.9	114	328	600	22	4	15	16	23	24	4	10	258	115	0	2	0	32	70	10	295[P]	
	BEL 318[P]	51.2	5.5	--	--	6.4	3.7	112	378	620	18	4	18	16	19	23	4	9	250	115	0	0	0	32	72	8	318[P]	
	BEL 531[P]	51.-	5.-	2	55	7.5	4.1	117	383	685	16	4	16	16	24	22	4	10	257	115	0	1	0	32	72	9	531[P]	
	BEL 530[P]	50.-	5.-	10	40	9.0	4.9	140	429	708	16	5	19	16	21	25	4	10	242	115	1	2	0	28	74	10	530[P]	
	NY 225[P]	43.-	75.-	--	--	7.8	4.1	88	271	560	11	10	19	14	31	28	5	9	260	115	0	0	0	33	64	14	225[P]	
I	ENG 269[P]	51.2	0.8	7	80	8.8	4.2	126	340	568	14	8	20	20	26	32	5	10	240	115	0	0	0	32	64	11	269[P]	I
	ENG 270[P]	51.2	0.8	7	80	7.4	4.7	122	332	550	16	7	19	18	28	23	5	9	245	115	5	0	6	36	62	11	270[P]	
J	FRA 235	48.2	9.2	22	50	5.2	4.2	91	278	488	18	6	16	13	24	28	4	8	257	115	1	0	3	32	60	10	235	J
	YUG 242	43.9	19.4	40	--	8.5	4.2	103	313	508	12	4	18	13	25	23	4	9	251	115	0	0	0	32	64	13	242	
	AUS 205	47.2	11.3	30	--	5.7	3.9	98	292	500	17	4	19	12	18	29	4	10	246	115	1	1	0	33	60	10	205	
	GER 209	50.3	12.2	62	--	3.9	4.1	91	292	540	23	4	12	13	19	21	4	8	239	115	0	0	0	32	60	9	209	
K	GRE 243	41.5	24.3	49	--	7.5	4.8	84	274	470	11	7	17	9	28	30	5	10	253	115	0	0	3	34	52	10	243	K
	GRE 244	40.2	22.1	55	--	7.5	4.7	86	284	472	11	5	20	11	28	27	5	10	249	115	0	0	0	31	62	14	244	
	GRE 271	41.5	24.3	49	--	6.7	4.5	93	292	555	14	4	19	11	26	34	5	10	253	115	0	0	6	32	62	13	271	
	GRE 272	39.9	21.2	45	--	9.8	4.8	100	270	458	10	4	19	9	29	24	5	8	239	115	3	0	1	27	56	12	272	
	GRE 551	41.3	23.2	49	--	6.1	4.4	100	290	512	16	4	18	16	26	29	5	10	251	115	0	0	8	32	60	14	551	
	GEO 261	41.7	42.7	36	--	8.8	4.7	84	240	440	10	4	18	9	26	29	5	8	253	115	1	0	6	35	58	10	261	
	GEO 262	41.7	43.0	39	--	8.4	4.7	104	253	468	12	4	20	8	30	30	5	10	261	115	0	0	9	35	66	10	262	
	GEO 263	41.8	43.4	37	--	8.7	5.0	101	295	480	12	4	20	10	30	29	5	10	265	115	1	0	0	32	62	12	263	
	GEO 264	41.8	43.5	52	--	8.8	5.0	100	278	518	11	6	20	10	32	31	5	9	256	115	0	0	6	34	62	13	264	
	TUR 213	40.5	32.7	49	55	10.7	5.7	94	257	448	10	7	20	8	32	32	5	9	253	115	0	0	3	33	52	14	213	
	TUR 214	40.5	32.7	49	55	12.2	5.7	98	285	462	12	7	20	10	28	33	5	10	251	115	1	0	10	33	60	14	214	
	TUR 220	40.0	31.3	47	170	10.0	4.7	91	268	440	11	7	20	9	32	29	5	10	259	115	1	0	0	31	64	13	220	
	TUR 221	40.5	32.7	49	100	--	5.1	96	282	498	--	5	20	9	30	35	5	10	251	115	0	0	7	31	56	11	221	
L	SCO 265	57.1	-4.9	6	120	6.9	4.7	94	254	440	14	4	16	20	31	32	5	8	231	115	0	0	1	30	52	14	265	L
	SCO 266	57.2	-3.7	8	120	7.0	4.7	102	303	528	15	4	17	22	31	37	5	10	229	115	14	0	5	29	48	11	266	
	SCO 267	57.2	-4.8	9	200	6.0	5.0	86	276	398	13	6	14	24	28	37	4	9	229	115	4	0	1	32	46	9	267	
	SCO 268	57.2	-3.8	--	150	8.8	5.0	85	273	400	14	6	16	20	29	34	5	10	229	115	5	0	3	32	48	13	268	
M	FRA 212	45.-	4.-	--	--	7.7	4.6	109	319	510	14	11	19	23	34	40	5	10	249	115	0	0	2	30	60	11	212	M
	FRA 238	44.7	3.8	31	100	5.4	4.6	78	246	475	14	8	19	23	36	40	5	9	254	116	3	0	4	34	50	10	238	
	FRA 239	45.3	3.7	33	100	6.0	4.2	80	257	448	13	10	19	22	34	34	5	10	251	115	0	0	8	35	50	11	239	
	FRA 240	42.6	2.1	50	150	7.2	4.6	74	211	348	16	12	20	21	36	40	5	8	254	115	0	0	7	32	42	14	240	
	AUS? 249[d]	--	--	--	--	6.7	4.8	81	248	428	12	12	20	21	38	39	5	10	244	115	0	0	2	35	46	13	249[d]	
	FRA 316[d]	45.1	3.5	35	--	6.4	4.0	83	263	482	13	10	20	21	36	37	5	8	249	115	0	0	4	33	52	12	316[d]	
	FRA 320[d]	45.-	4.-	30	--	5.2	4.2	86	251	432	16	10	20	22	35	39	5	8	245	116	0	0	0	34	52	14	320[d]	
N	SPA 218	40.3	-5.2	37	--	10.0	5.5	104	314	480	10	12	18	21	36	37	5	10	267	116	1	0	20	30	50	15	218	N
	SPA 219	40.8	-4.0	49	--	10.9	5.2	94	276	485	12	10	19	20	36	36	5	10	265	116	4	0	12	35	62	14	219	
	SPA 245	40.7	-4.2	49	--	11.8	5.0	100	284	458	12	12	20	20	36	39	5	10	260	116	0	0	14	36	44	14	245	
	SPA 246	41.8	-2.8	39	--	9.1	5.1	99	290	422	11	12	20	20	36	37	5	9	267	116	0	0	15	33	50	12	246	
	SPA 247	42.3	-0.5	37	--	9.0	5.2	83	258	445	9	12	20	20	36	37	5	9	269	116	1	0	8	32	48	15	247	
	Standard deviation of a provenance mean							4.9	10.5	21.0	--	.48	.83	.83	1.37	1.50	--	.58	3.06	.59	.62	--	1.74	2.38	3.33	1.67		
	L.S.D.$_{.05}$ of a provenance mean							17	36	72	--	2.9	2.8	2.8	4.7	4.9	--	2.2	10.4	2.0	2.1	--	6.0	8.2	11.4	5.7		
	L.S.D.$_{.01}$ of a provenance mean							22	46	92	--	3.7	3.6	3.6	6.0	6.2	--	2.6	13.5	--	2.7	--	7.7	10.6	15.0	7.5		
	Character	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(7/5)	(10)	(11)	(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)	(20)	(21)	(22)	(23)	(24)		

KEY TO COLOR GRADES

Character	(10)	(11)	(12)	(13-14)	(16)
Grade 4	Yellow-green	Maroon	Dark Green	Yellow	Green
Grade 8	Green	Intermediate	Intermediate	Intermediate	Intermediate
Grade 12	Blue-green	Intermediate	Intermediate	Intermediate	Green-tan
Grade 16	--	Intermediate	Green	Intermediate	Tan
Grade 20	--	Green	Intermediate	Intermediate	Tan-brown
Grade 24	--	--	Blue-green	Green	Brown
Grade 28	--	--	--	Intermediate	--
Grade 32	--	--	--	Dark Green	--
Grade 36	--	--	--	Blue-green	--
Grade 40	--	--	--	Blue-green	--

KEY TO Earliness of Fall coloration (Character 15)

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

Character	(22) Trees with mature needles on Oct. 1, 1959	(24) Ease of pulling July, 1959
	Percent	
Grade 0	91-100	- -
Grade 8	76-90	Easy
Grade 16	51-75	Difficult
Grade 24	16-50	- -
Grade 32	6-15	- -
Grade 40	0-5	- -

[1] AUStria, BELgium, CZEchoslovakia, ENGland, FINland, FRAnce, GEOrgian SSR, GERmany, GREece, HUNgary, ITAly, LATvian SSR., NORway, POLand, SCOtland SIBeria, SPAin, SWEden, YUGoslavia, URAl Mountains.

[P] Seeds obtained from planted stands.

[d] Seeds obtained from a commercial dealer.

Simple correlation analysis, using progeny means as items, were used to determine the significance of intercharacter relationships within ecotypes or groups of ecotypes and also to determine whether a correction for seed weight was desirable. Data from 16 traits were used.

A new technique, used previously only by the authors, was used to determine the general degree of similarity among progenies with regard to 12 unrelated characters. This is called the *summation-of-difference analysis*. For the first trait the differences between progenies 201 and 202, 201 and 203, 202 and 203, etc. were calculated. From these differences the LSD$_{.05}$ was subtracted in order to eliminate the necessity of considering differences due to chance. The (Difference — LSD$_{.05}$) was multiplied by a weighting factor, 4/LSD$_{.05}$. The choice of the *figure 4* was one of convenience to eliminate decimals. Division by

Table 4. — Three-year growth data for the Scotch pine progenies sown in 1959, summarized by ecotype.

Region	Countries of origin[1]	Progenies	Seed Wt.	Seed Length	Height Age 1 1959	Height Age 2 1960	Height Age 3 1961	Height ÷ Seed Weight	Foliage color on June 26 1959	Foliage color on Oct. 28 1959	Foliage color on Aug. 10 1960	Foliage color on Dec. 15 1960	Foliage color on Dec. 1 1961	Earliness of leaf color	Bud Color May 1960	Bud Formed 1959	Started growth 1960	Branches on terminal bud 1960	Male fls. 1959	Lammas shoots 1960	Secondary leaf presence Oct. 1959	Leaf length Aug. 1960	Ease of pulling
			(5)	(6)	(7)	(8)	(9)	(7/5)	(10)	(11)	(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)	(20)	(21)	(22)	(23)	(24)
		No.	mg.	mm.	mm.	mm.	mm.	mm. / mg.	Grade							Day of Year		Per 200 trees			Grade	mm.	Grade
A	FIN SIB	3	4.4	3.9	41	96	178	10	7	6	5	8	8	1	4	200	113	0.0	0.0	0.0	2	53	16
B	SWE	4	3.4	3.7	57	129	274	16	5	8	7	8	9	2	6	219	113	1.5	.0	.0	4	56	12
C	FIN SWE NOR	16	4.6	3.7	70	198	348	16	5	8	8	8	10	2	10	219	113	.2	.0	.0	14	56	12
D	SWE LAT	5	5.0	4.0	87	257	450	18	5	12	11	11	11	2	8	235	114	.2	.0	.0	25	58	11
E	SIB URA	8	5.4	3.9	88	255	423	16	4	8	10	4	5	1	9	219	114	.0	.1	.0	12	69	13
F	POL	2	6.2	4.0	102	318	542	16	5	14	16	16	17	3	10	243	115	.0	.0	.0	32	73	10
G	GER CZE	29	6.1	4.0	105	325	578	18	4	15	16	19	20	4	10	246	115	.3	.1	.2	32	71	10
H	BEL FRA GER HUN ITA NY	20	6.7	4.3	113	350	621	17	4	17	16	23	25	4	9	257	115	.2	.2	.3	32	72	10
I	ENG	2	8.1	4.4	124	336	559	15	8	20	19	27	30	5	10	242	115	2.5	.0	3.0	34	63	11
J	AUS FRA GER YUG	4	5.8	4.0	96	294	509	18	4	16	13	22	25	4	9	248	115	.5	.2	.8	32	61	11
K	GEO GRE TUR	13	8.8	4.9	95	275	479	12	5	19	10	29	30	5	10	253	115	.4	.0	4.2	32	59	12
L	SCO	4	7.2	4.8	92	276	442	14	5	16	22	30	35	5	9	229	115	5.8	.0	2.5	31	49	12
M	FRA	7	6.5	4.4	84	256	446	14	10	20	23	35	38	5	9	249	115	.4	.0	3.9	33	50	12
N	SPA	5	11.6	5.2	96	283	459	11	12	19	20	36	37	5	10	266	116	1.2	.0	14.8	33	51	14
Approximate $LSD_{.01}$ between ecotypes					10	30	50	--	3	2	3	3	3	1	2	10	1.5	2	n.s.	2	5	5	2

KEY TO COLOR GRADES

Character	(10)	(11)	(12)	(13-14)	(16)
Grade 4	Yellow-green	Maroon	Dark Green	Yellow	Green
Grade 8	Green	Intermediate	Intermediate	Intermediate	Intermediate
Grade 12	Blue-green	Intermediate	Intermediate	Intermediate	Green-tan
Grade 16	--	Intermediate	Green	Intermediate	Tan
Grade 20	--	Green	Intermediate	Intermediate	Tan-brown
Grade 24	--	--	Blue-green	Green	Brown
Grade 28	--	--	--	Intermediate	--
Grade 32	--	--	--	Dark Green	--
Grade 36	--	--	--	Blue-green	--
Grade 40	--	--	--	Blue-green	

KEY TO Earliness of Fall coloration (Character 15)

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

Character	(22) Trees with mature needles on Oct. 1, 1959	(24) Ease of pulling July, 1959
	Percent	
Grade 0	91-100	- -
Grade 8	76-90	Easy
Grade 16	51-75	Difficult
Grade 24	16-50	- -
Grade 32	6-15	- -
Grade 40	0-5	- -

[1] AUStria, BELgium, CZEchoslovakia, ENGland, FINland, FRAnce, GEOrgian SSR, GERmany, GREece, HUNgary, ITAly, LATvian SSR, NORway, POLand, SCOtland, SIBeria, SPAin, SWEden, URAl Mountains, YUGoslavia.

$LSD_{.05}$ is mathematically equivalent to weighting inversely to the square root of the error variance. The entire procedure was then repeated for the second trait, the third trait, etc. Finally, the weighted differences for all 12 traits were summed for each progeny-pair. Each summation amounted to

$$4\frac{(\text{Difference} - \text{LSD}_{.05})}{\text{LSD}_{.05}}$$

The entire operation involved 42,504 separate comparisons and 3,542 summations. These are summarized in *table 7, 8, and 9*.

A summation-value of 0 means that two progenies did not differ significantly in any of the 12 traits. A value of 1 means that they differed in one trait. A value of 2 means that they differed slightly in two traits or a little more in one trait. A value of 5 usually means that they differed considerable in just one. A value of 15 or greater usually means large differences in a number of traits.

The summation-of-difference analysis gave a quantitative estimate of the totality of difference between progenies so that one could say, "This is more different from that than from the other". Three other types of analysis could have been used. The discriminant function would have given more precise statements of differences, but is very laborious. Calculation of an index of similarity to a particular type (widely used in taxonomy) is easily done but requires assignment of a direction of variation to each trait; thus progenies which are high and low in the first trait but are low and high in the second trait might be given the same numerical rating even though they were different. The third method would involve the calculation of inter-progeny correlations. This method was not used because of difficulties in interpretation of preliminary results.

Most of the variance and correlation analyses were performed on Michigan State University's digital computer "MISTIC".

General Description of the Experiments

Three-year experiment. — Germination started May 25, 1959, 2 weeks after seed sowing. It was practically complete in all seedlots four days later. By mid-July, when the first thinning was done, the roots were 4 to 5 inches long and slightly branched; the tops barely touched each other. At that time the "pullability" (ease with which thinning could be accomplished) scoring was done. By the end of the first growing season practically all plots appeared fully stocked and the taller ones shaded the ground for a distance of 2 inches to either side of the row. By that time all trees were very firmly rooted.

Table 5. — One-year growth data for the Scotch pine progenies sown in 1961.

Region, Country of origin MSFG No.			North Lat.	East Long.	Elev.	Germination Date June 1961	Height Age 1 Oct. 9 1961	Primary needle length Oct. 10 1961	Trees with secondary needles Oct. 9 1961	Trees with terminal buds Oct. 9 1961	Foliage color Oct. 10 1961
			(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
			°	°	Feet	Day in June	mm.	mm.	Grade	Grade	Grade
B	SWE[1]	549	64.5	18.7	800	--	--	--	0	4	4
	SWE	615	60.6	12.3	--	12	26	16	4	4	11
	KRA	576	--	--	--	11	19	13	1	4	5
C	SWE	222	60.2	15.0	800	--	--	--	12	4	12
	SWE	544	60.4	14.9	800	--	--	--	4	4	8
D	LAT	564	56.-	23.7	--	7	50	22	24	4	10
	SWE	616	57.5	16.0	--	10	36	17	15	4	11
	RUS	597	56.1	36.7	--	13	33	17	16	5	11
E	AMU	573	54.0	124.0	2500	8	34	19	4	4	4
	KRA	574	60.2	90.0	200	8	34	18	4	4	6
	KRA	575	58.5	92.0	200	8	30	16	4	4	7
	KRA	577	57.5	92.0	800	8	33	18	3	4	5
	KRA	578	57.0	95.0	800	7	33	17	5	4	5
	KRA	580	58.5	96.0	800	9	32	17	6	4	6
	KRA	581	56.0	91.0	800	10	32	17	4	4	6
	KRA	582	55.2	92.0	800	9	34	19	4	4	7
EE	KRA	583	54.2	91.0	1300	9	42	18	6	4	8
	KRA	584	54.2	93.0	1300	12	39	19	6	4	7
	KRA	585	53.7	92.0	1300	9	40	19	5	5	9
	KHA	586	53.0	90.5	800	8	38	18	4	4	7
	KHA	587	52.7	90.0	1300	9	40	21	5	4	8
	TUV	588	52.0	93.7	2000	10	38	20	6	4	9
	TUV	589	51.5	93.0	800	10	45	20	5	4	9
	MOL	595	59.5	57.5	500	10	43	19	4	4	8
	KOS	596	58.0	45.0	500	9	43	18	5	4	7
	ALT	591	52.0	84.0	800	10	49	20	12	4	10
F	POL	558	51.5	21.5	--	5	48	20	24	4	13
	POL	559	51.4	19.9	--	5	58	29	30	18	15
	POL	560	52.4	23.8	--	5	51	23	30	6	15
	POL	561	52.4	23.8	--	5	55	25	30	5	15
	POL	562	51.1	20.8	--	5	69	29	30	10	16
G	CZE	306	49.2	14.-	1500	--	--	--	32	16	16
	CZE	309	49.1	13.3	2200	--	--	--	32	8	16
	CZE	312	50.9	15.1	2000	6	60	27	30	14	18
	CZE	568[d]	--	--	--	10	43	23	30	14	16
	CZE	572[d]	--	--	--	10	43	24	32	14	16
	CZE	598	48.4	17.3	2000	11	50	30	32	17	17
	CZE	599	50.2	15.0	1300	11	44	25	32	14	14
	CZE	600	49.9	13.2	2000	11	44	26	31	14	14
	CZE	601	49.3	21.7	500	9	50	28	32	15	15
	CZE	602	50.2	16.1	1300	13	44	24	32	15	13
	CZE	603	49.7	17.1	800	13	40	22	32	13	16
	CZE	604	50.2	16.1	800	12	42	27	32	16	14
	CZE	605	50.2	12.7	2000	11	38	20	31	10	17
	CZE	606	48.8	20.5	1300	9	44	22	32	11	16
	CZE	607	49.2	14.5	800	11	49	27	32	15	16
	CZE	608	48.5	14.1	2600	10	40	22	31	11	15
	CZE	609	48.9	14.9	2600	8	54	26	32	14	16
	GER	529	50.9	14.3	1000	9	48	26	32	11	15
	GER	571[d]	50.-	11.-	--	10	47	26	31	11	16
	RUM	622	26.-	46.-	2700	--	--	--	32	14	16
	RUM	623	27.-	46.-	2200	--	--	--	32	14	16
	RUM	624	27.-	46.-	2600	--	--	--	32	14	16
	RUM	625	27.-	46.-	2600	--	--	--	32	14	16
	UKR	569[d]	--	--	--	6	66	30	31	8	15
H	GER	566[d]	49.-	8.-	--	7	60	27	31	15	20
	FRA	236	48.0	2.8	500	--	--	--	32	16	16
K	TUR	213	40.5	32.7	4900	--	--	--	32	16	20
	TUR	220	40.0	31.3	4700	--	--	--	32	16	20
	TUR	221	40.5	32.7	4900	7	56	28	30	15	23
	TUR	621	41.5	34.5	3900	5	55	26	32	14	21
	BUL	610	41.5	24.1	--	12	38	22	31	15	19
	BUL	611	41.3	24.9	--	10	41	23	32	15	19
	BUL	612	41.7	24.3	--	10	39	22	31	12	17
	BUL	613	41.9	23.5	--	8	51	26	31	14	21
	BUL	614	42.2	23.4	--	9	52	26	29	16	19
M	FRA	619	45.-	4.-	--	10	46	22	30	15	19
	FRA	563[d]	45.-	4.-	--	6	45	22	31	16	22
	FRA	567[d]	45.-	4.-	--	6	44	22	31	15	22
N	SPA	246	41.8	-2.8	3900	--	--	--	32	20	24
	SPA	247	42.3	-0.5	3700	7	58	26	29	20	25
	POR	565[d]	--	--	--	10	44	26	31	19	20
Standard deviation of a provenance mean						0.75	2.57	1.17	0.99	0.93	1.05
LSD$_{.05}$ of a provenance mean						2.5	8.5	4.0	3.3	3.1	3.4
LSD$_{.01}$ of a provenance mean						3.2	10.5	5.0	4.3	4.1	4.5

[1] ALTai Region USSR, AMUr Prov. USSR, BULgaria, CZEchoslovakia, FRAnce, GERmany, KHAkasskaya Aut. Prov. USSR, KRAsnoyarski Region USSR, KOStromskaya Prov. USSR, LATvian SSR, MOLotovskaya Prov. USSR, PORtugal (planted stand), RUMania, RUSsian SSR, SPAin, SWEden, TURkey, TUVinskaya Oblat, USSR, UKRaine SSR.

[d] Seeds obtained from dealers.

KEY TO GRADES

Character	(7) Trees with secondary needles Oct. 9 1961	(8) Trees with terminal buds Oct. 9 1961	(9) Foliage color Oct. 10 1961
	Percent	Percent	
Grade 0	100	--	--
Grade 4	96-99	96-100	Red-tipped
Grade 8	86-95	76-95	Intermediate
Grade 12	66-85	26-75	Intermediate
Grade 16	36-65	6-25	Intermediate
Grade 20	16-35	0-5	Slightly red-tipped
Grade 24	6-15	--	Green
Grade 28	1-5	--	Blue-green
Grade 32	0	--	--

By the end of the first year the seedlings were more than twice as large (both diameter and height) as ordinary non-experimental stock. This excellent growth continued in later seasons. Intra-plot competition, which was slight the first year, became serious the second season but was reduced to a moderate amount during the third year by the second thinning. This competition was such that the shortest trees in each plot averaged 60 percent as tall as the largest ones. This percentage was one of the few characteristics that did not differ significantly among progenies or among regions.

Differences in root systems were evident at both thinnings and at the time of lifting. They may have been as pronounced as those in above-ground characters. Only casual observations were made, however, because intensive study would have disrupted the long-term aspects of the experiment.

The three most northern origins (MSFG 226, 229, 254) ceased height growth and set terminal buds in mid-July of the first growing season. They started to form 2-needled fascicles at the same time. In contrast, southern origins continued height growth until late October. They did not form secondary needles until the second year. The growth cycle in the second and third years was very different from that in the first. In 1960 and 1961 there was only a few days difference in start and stop of growth between the most extreme provenances. All started growth in early May and formed terminal buds by mid-June.

Differences in summer foliage color became evident 2 weeks after germination. At that time trees from the far north and from southeastern Europe were dark green, those from western Europe were blue-green, and those from central Europe were medium green. These summer colors tended to remain constant in later years.

The autumnal coloration pattern changed between the first and second years. Northern 1-year-old seedlings became red whereas northern 2- and 3-year-old seedlings became yellow. The major 1- and 2-year geographic trends were similar although there were differences in detail. Autumnal color started to appear first in late September in the Ural Mountain provenances and reached full intensity in early December. It remained fairly constant from then until early April, when there was a return to summer conditions. During the period of active growth in the spring there were no noticeable color differences.

Damage from damping off, pests, winter cold, or growing season frosts (there was a severe one on May 25, 1961) was almost non-existent. Hence there was no opportunity to study differences in resistance to these factors. Nor was there an opportunity to study differences in form — all trees were straight.

The initial decision to use a single row as a plot was based on efficiency and statistical considerations. Some progenies were in direct competition with very dissimilar ones to either side. If anything this practice reduced the differences among progenies. The very slow growing trees from northern Scandinavia grew almost twice as tall in the row plots as in the broadcast-sown fifth replicate. This is partly traceable to differences in first-year frost heaving. None occurred in the row plots whereas considerable occurred where small trees were grown with no side protection. Leaves in full sunlight developed more intense autumnal coloration than did shaded leaves. Hence, a northern origin closely bordered by very fast-growing progenies did not become so yellow as when grown by itself. Among the Scottish progenies trees with branched buds were more common in the rectangular, broadcast-sown plots than in the row plots. Trees with branched buds were rare in all plots of other progenies.

One-year experiment. — The seed sown in 1961 required about 4 weeks to germinate. As compared with the 3-year experiment germination was less complete, one-third fewer plots were fully stocked, height growth was reduced about 50 percent, but the development of other traits proceeded similarly. There were no noticeable differences between the rows and the broadcast-sown plots.

Major Geographic Trends

Several adaptive geographic trends were evident. Most were from north to south but a few were from east to west or from the center to the outside of the species' range. Even in the most clearcut of these trends the correlation between the environment at the place of origin and the progenies' characteristics was imperfect. Evidently selection pressure played a large role in the differentiation into ecotypes but on occasion other factors could be more important.

Growth rate was greatest in the progenies from Belgium, northern France, northern Italy, and western Germany. Trees from cooler climates to the north and east, or from drier climates to the south and west grew more slowly. The slowest growth was found in trees from northern Scandinavia and Siberia. Most major features of the growth rate pattern are explainable in terms of adaptation — the more favourable the parental climate the more rapid the growth. However, the resemblance of the Italian progenies to those from northern France and adjacent Germany seems better explained in terms of a common Pleistocene ancestry and lack of differentiation.

The needle-length trend (character 23 in *tables 3 and 4,* character 5 in *table 5)* was similar to that in height. The needles were longest in trees from central Europe and shortest in trees to the north and south. The Spanish and south French trees had the shortest needles. There were many discrepancies in the leaf length-growth rate relationship and it is best to assume no direct casual relationship between the two traits.

The trend in seed weight (character 5 in *tables 3 and 4)* was from northern Scandinavia (smallest) to Spain and Turkey (largest). The seed size differences probably represent adaptations to soil moisture at germination time. Seeds falling on a dry Spanish soil would need large food reserves and rapid root penetration to survive. If we consider the population from Germany south seed size and height were inversely correlated. This indicates that the causal relationship, if any, between the two characters is weak.

The most pronounced north-south trend was in date of first-year bud set (character 17 in *tables 3 and 4,* character 8 in *table 5).* The three most northerly origins formed dormant winter buds in mid-July 1959 whereas growth continued until late October in trees from Turkey and Spain. There was a strong relation between time of bud set and latitude. This indicates adaptation to photoperiod, as WAREING (1951) and VAARTAJA (1954) have suggested. However, the photoperiodic adaptation was not complete. Trees from the same latitudes in Turkey and Spain differed by up to 18 days in date of bud set.

A similar north-south trend was found in time of secondary leaf formation (character 22 in *tables 3 and 4,* character 7 in *table 5)*. Two-needled clusters appeared first (August of the first year) on the smallest seedlings from the extreme north. They appeared later on ecotypes from Germany and last (early the second year) on trees from southern Europe. Inasmuch as Wells (1962) found almost the opposite pattern in ponderosa pine *(Pinus ponderosa* Laws.) no adaptation can be assumed.

The Lammas shoot (character 21 in *tables 3 and 4)* differentiation pattern is explainable partly in terms of adaptation and partly in terms of ancestry. The percentage of trees forming Lammas shoots was highest in the Spanish progenies. It was moderately high in progenies from southern France, Scotland, Greece, Turkey, and Georgia. The ability to form Lammas shoots (midsummer growth from previously dormant buds) is a characteristic common to southern ecotypes of several species and probably results from selection for late maturation. However, this can not explain the high incidence of Lammas shoots in Scottish trees. That is better interpreted in terms of a common Pleistocene ancestry of the Scottish, south French, and Spanish populations.

Northern seedlots turned red (first year) or yellow (second and later years) whereas southern seedlots retained nearly the same color throughout the year. There were very important exceptions to this general trend. The most extreme yellow color occurred in progenies from intermediate latitudes (54^0 to 57^0)N. in the Ural Mountains and Siberia. The equally northern Scottish ecotype remained nearly green throughout the year whereas trees from similar latitudes in maritime parts of southern Scandinavia became moderately yellow. Much of this autumnal color trend is probably adaptive to some part of the light environment although the evolutionary mechanism is not clear. Hacskaylo and Goslin's (1957) and Gerhold's (1959) work showed that development of the yellow pigments in single plants is under the control of light quality; trees exposed to full sunlight changed color but shaded ones did not. Historical factors seem to have influenced the trend also. As already noted, the green Scottish trees probably descended from a pre-Pleistocene green Iberian type and the yellow Ural trees may have descended from a very northern pre-Pleistocene type.

The summer color trend (characters 10 and 12 in *tables 3 and 4)* was from dark green in Scandinavia and southeastern Europe to medium green in central Europe to blue-green in southern France, Spain, and Scotland. This pattern does not parallel that found in *Pinus nigra* Arn. from southern Europe (Wright and Bull, 1962) and has no obvious environmental explanation. An historical explanation fits the pattern very well however, if we postulate that the present populations were descended with relatively little change from pre-Pleistocene remnants in the Pyrenees, Alps, Scandinavia, southeastern Europe, and Siberia.

Trees from the extreme north and from dry parts of southern Europe were harder to pull from the ground the first growing season than were much taller trees from central Europe (character 24, *tables 3 and 4)*. There is a ready explanation for the exceptional performance of the southern types — they are large-seeded types capable of rapid early root growth into soils which become dry in early summer. Upon lifting these southern trees proved to have many fibrous roots and very long taproots. The difficulty with which the most northern seedlots could be pulled is harder to explain. Upon lifting they proved to have shallow but very much branched root systems which would not seem to offer as much resistance to pulling as the deeper fibrous root systems of the central European progenies. Perhaps the hard "pullability" of the first-year seedlings is of selective advantage to trees growing in cold, relatively snow-free habitats where frost heaving could be a serious cause of early mortality.

The presence of branched terminal buds was practically limited to the Scottish origins. These have no obvious adaptive significance, and possibly arose as a result of genetic drift.

Ten of the Scotch pines produced male flowers at the start of the second growing season. Six of these were from seed collected in Belgium, suggesting a concentration of early flowering ability in the planted stands of that country.

Trends in stem form are not yet evident in the present experiments. They are present in many older European provenance tests, in the 17-year-old plantations in New Hampshire (Wright and Baldwin, 1957), and in the 18-year-old plantations in New York (Schreiner, Littlefield, and Eliason, 1962). Progenies from Scotland, Scandinavia, and Latvia have generally been straight whereas fast growing trees from Germany, Belgium, and Italy have often been very crooked. Little is known as to the comparative forms of ecotypes from Turkey, Greece, southern France, and Spain.

Correlations Between Characters

All possible correlations were calculated between latitude of origin, seed weight, and 14 progeny traits. The correlations were calculated separately for four groups of ecotypes and five single ecotypes. The ecotypes chosen were those in which the most progenies were available. Progeny means were used in the analyses, which are therefore applicable to variation among progenies. Data for the 45 most meaningful character-combinations are presented in *table 6*. In that table coefficients are starred which are statistically significant at the 5, 1, and 0.1 percent levels. Those significant at only the 5 percent level are suspect because they occurred with no greater frequency than would have been expected with random numbers.

Correlations involving physiologically unrelated characters. — All relationship save those between seed weight and height, height and height, and color and color are assumed to be between physiologically unrelated characters.

If the means of all progenies from ecotypes G, H, M, and N were used in the calculations, 29 of the 33 possible correlations were found to be significant at the 1 percent level. If the calculations were limited to ecotypes G and H, 6 of the 33 possible correlations were significant at the 1 percent level. If they were limited to G and H separately, only 4 of 66 possible correlations were significant at the 1 percent level.

When the means of all Scandinavian progenies (ecotypes A, B, C, D, and E) were considered together there many significant inter-character correlations. But when ecotypes C or E were considered separately there were no significant correlations among physiologically unrelated characters.

Biologically these results mean that variation within a major geographic ecotype was more or less random. The major geographic trends wihch are so evident when considering all Scotch pine from Scandinavia to Spain or Scotland to Siberia do not apply when considering the

Table 6. — Inter-character correlations in different ecotypes and groups of ecotypes. — Combinations which were not significant in any ecotype are omitted. — Note that the within-ecotype and between-ecotype relations are usually very different.

Characters to which correlation applies		Correlation coefficients applicable to progenies from Ecotype --								
		A,B,C D,E	G,H,M N	G,H	K,M,N	C	E	G	H	K
		Correlation coefficients								
(1) Latitude	(5) Seed weight	-.57***	-.63***	.02	-.66***	.05	.67	.32	.25	-.50
	(9) Height age 3	-.73***	.64***	-.06	-.03	-.01	.79*	.18	.59*	.41
	(14) Autumn color age 3	.10	-.84***	-.49**	.50*	-.12	.09	-.15	-.05	.23
	(17) Bud formation date	-.59**	-.67***	-.55***	-.05	.00	.00	.12	-.54	.57*
	(21) Lammas shoots	.00	-.79***	-.05	-.09	.00	.00	.25	.05	.37
	(23) Leaf length	-.71***	.78***	.24	-.25	-.01	.39	.54**	.85***	.14
	(24) Pullability	.18	-.60***	.20	-.46*	-.29	.32	.14	-.44	-.42
(5) Seed weight	(7) Height age 1	.66***	.02	.48**	.45*	.30	.72*	.44*	.31	.16
	(8) Height age 2	.64***	-.18	.44**	.20	.06	.78*	.47*	.07	-.25
	(9) Height age 3	.58***	-.37**	.40**	-.12	.02	.82**	.32	.36	-.56*
	(14) Autumn color age 3	-.10	.59***	.06	-.03	.13	.33	-.26	.26	.18
	(17) Bud formation date	.21	.52***	.23	.24	.00	.00	.07	-.30	-.08
	(21) Lammas shoots	.00	.75***	-.01	.31	.00	.00	.05	-.30	.05
	(23) Leaf length	.44**	-.48***	.42**	.07	-.51*	.62	.37*	.37	-.05
	(24) Pullability	.04	.71***	.27	.40	-.19	.04	.45*	.08	.11
(7) Height age 1	(8) Height age 2	.96***	.89***	.81***	.75***	.83***	.94***	.81***	.66**	.26
	(9) Height age 3	.94***	.77***	.72***	.49*	.71**	.84***	.71***	.60*	.28
(8) Height age 2	(9) Height age 3	.97***	.89***	.81***	.68***	.86***	.95***	.78***	.83***	.65**
(9) Height age 3	(14) Autumn color age 3	.02	-.73***	.17	-.16	.00	.34	-.03	-.41	.43
	(17) Bud formation date	.73***	-.27	.21	-.13	.00	.00	.05	-.87***	.02
	(19) Branched terminal bud	-.08	-.43**	-.17	-.10	-.14	.00	-.30	.11	.17
	(21) Lammas shoots	.00	-.68***	.13	-.08	.00	.00	.04	.07	.32
	(22) Secondary leaf presence	.69***	-.33*	-.06	-.08	.27	.50	-.24	-.62*	.00
	(23) Leaf length	.61***	.87***	.51***	.56*	.06	.33	.38*	.68*	.18
	(24) Pullability	-.33*	-.65***	-.20	-.08	-.12	.01	-.10	-.18	.20
(10) Summer color age 1	(11) Autumn color age 1	-.07	.69***	.17	.10	.40	.00	.37*	-.05	.12
	(13) Autumn color age 2	.04	.87***	-.07	.88***	-.04	.00	.10	-.39	.49
	(14) Autumn color age 3	-.16	.91***	.23	.80***	-.14	.15	.28	.25	.28
(11) Autumn color age 1	(13) Autumn color age 2	.34	.78***	.54***	.29	-.02	.00	-.12	.46	.65*
	(14) Autumn color age 3	.52*	.77***	.56***	.13	-.04	.75*	.02	.80***	.20
(13) Autumn color age 2	(14) Autumn color age 3	.67***	.95***	.72***	.75***	.25	.15	.66***	.36	.05
(14) Autumn color age 3	(17) Bud formation date	.41*	.55***	.59***	.38	.00	.00	.10	.64*	.30
	(19) Branched terminal bud	.04	.46***	.19	.09	-.06	.00	.25	.29	-.46
	(21) Lammas shoots	.00	.77***	.12	.50	.00	.00	-.25	.32	.57*
	(23) Leaf length	-.34*	-.84***	.12	-.57**	-.26	.04	-.07	-.21	.00
	(24) Pullability	-.29	.59***	-.27	.13	-.07	-.26	-.21	.24	.04
(17) Bud formation date	(21) Lammas shoots	.00	.53***	.18	.54***	.00	.00	-.14	.12	.01
	(22) Secondary leaf presence	.70***	.56***	.60***	.34	.00	.00	.15	.78**	.60*
	(24) Pullability	-.54**	.30*	-.29*	.29	.00	.00	-.25	.24	-.19
(19) Branched terminal bud	(23) Leaf length	-.10	-.39**	-.21	-.02	-.03	.00	-.15	.16	-.34
	(24) Pullability	-.16	.39**	.16	.11	-.08	.00	.07	.00	.47
(21) Lammas shoots	(23) Leaf length	.00	-.79***	.01	-.35	.00	.00	.05	-.16	.23
	(24) Pullability	.00	.74***	.02	.33	.00	.00	.00	.28	-.10
(22) Secondary leaf presence	(24) Pullability	-.47**	.23	.01	-.21	-.18	-.71*	.11	.44	-.32
(23) Leaf length	(24) Pullability	.13	-.67***	-.07	-.14	.24	.65	.15	-.46	.20
Number of progenies included in analysis		37	50	41	22	16	8	28	13	13
Value of r needed for significance at 5 percent level		.33	.28	.31	.42	.50	.71	.37	.55	.55
Value of r needed for significance at 1 percent level		.43	.36	.40	.54	.62	.83	.48	.68	.68
Value of r needed for significance at .1 percent level		.54	.45	.50	.65	.74	.92	.59	.80	.80

(a) High latitude, heavy seeds, tall seedlings, blue color, late bud formation date, many branched terminal buds, many Lammas shoots, late appearance of secondary leaves, long leaves, and hard-to-pull root systems would be positively correlated.

* = correlation significant at 5 percent level
** = correlation significant at 1 percent level
*** = correlation significant at 0.1 percent level

Scotch pine from a limited area such as Scotland, Germany, or Spain.

Mathematically the results show that caution should be used in stating and interpreting correlations. It would be very misleading to make the word statment "Leaf length and the presence of Lammas shoots are inversely correlated" on the basis of the r = .79 for the G-H-M-N group of ecotypes. Rather, one should say, "Ecotypes M and N have more Lammas shoots and shorter needles than do ecotypes G and H; within these ecotypes there is no significant relationship between the two characters."

Height-height correlations. — Heights at ages 1, 2, and 3 are causally related. This is reflected by the high degree of correlation within groups of ecotypes and within single ecotypes. The correlations were strongest for the northern progenies. They were surprisingly low for southern Ecotype K (Greece, Turkey, Georgia). This may reflect hidden winter damage — sufficient to cause growth irregularities but not great enough to be seen in the nursery.

Seed weight-height correlations. — Seed weight and height were positively and significantly correlated within the A-B-C-D-E and G-H groups of ecotypes. The correlation was barely significant in Ecotype E (Siberia, Ural Mountains) and nil or reversed in direction in other cases. This pattern indicates that the cause-and-effect relationship is nil or very tenuous.

Why the seeming independence of seed weight and seedling height? Large seeds should give trees a good start and a good finish. The performance of albino seedlings gives a clue. These depend on seed reserves for their total growth. In Scotch pine they grow to the cotyledon stage and no further. Within 10 days of germination time they are surpassed in size by normal seedlings as the result of photosynthesis. After that growth is governed by the external environment and genetic factors. Hence the percentage of the first-year growth under the sole control of seed size is relatively small.

The results are such as to indicate that it is not necessary or desirable to attempt a seed weight correction to most Scotch pine growth data.

Color-color correlations. — The summer color-autumn color correlations were highly significant when all data from the G-H-M-N and K-M-N groups of ecotypes were considered. They were nil in others cases. This is the expected pattern if ecotypes differ but there is no relationship within ecotype.

The correlations between autumn color at age 1 and autumn color at later dates were high for the G-H and G-H-M-N groups of ecotypes and for some ecotypes conidered singly. They were moderate for the A-B-C-D-E group of ecotypes. In other cases they were nil. This indicates that first-year red color and later yellow color may be under the control of different genes. A few instances in which there were significant reversals in trend lend further support to this hypothesis. In ecotype D for example progeny 550 was significantly less green than 223 at age 1 but significantly more green at ages 2 and 3.

Autumn colors at ages 2 and 3 are presumably under control of the same genes. The age 2-age 3 correlations were significant within all the ecotype-groups and within ecotype G considered singly. They were very low in other ecotypes considered singly. Much of this lack of significance is probably a mathematical consequence of the small range of within-ecotype variability. In any event the repeatability of the within-ecotype autumnal color observations must be considered low. More time will be needed to choose the particular stand-progenies with a many-year superiority to the ecotype average.

Within-Plot Variability

At ages 2 and 3 the four tallest and the four shortest trees in each plot were measured. Then the height of the shortest trees was converted to a percent of the height of the tallest trees. These percentages were subjected to analysis of variance. These provided simple estimates of within-plot variability.

There were no significant differences in height variability among progenies or among ecotypes. Even more sur-

Table 7. — Summary of the genetic discontinuities between adjacent ecotypes of Scotch pine.

If comparison is between		Is there a discontinuity in this character?							
This ecotype and	This ecotype	Height	Summer foliage color	Autumnal foliage color	Time of 1-year bud set	Time of secondary leaf formation	Branched terminal buds	Leaf length	Lammas shoots
A FIN SIB[1]	B SWE[1]	No	No	No	Yes	No	No	No	No
	E SIB URA	Yes	Yes	Yes	Yes	No	No	Yes	No
B SWE	C FIN SWE NOR	Yes	Yes	No	No	Yes	No	No	No
	E SIB URA	Yes	Yes	Yes	No	Yes	No	Yes	No
C FIN SWE NOR	D SWE LAT	Yes	No	No	Yes	No	No	No	No
	E SIB URA	Yes	No	Yes	No	No	No	Yes	No
	F POL	Yes	Yes	Yes	Yes	Yes	No	Yes	No
	L SCO	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
D SWE LAT	E SIB URA	No	No	Yes	Yes	Yes	No	Yes	No
	F POL	Yes	Yes	Yes	No	Yes	No	Yes	No
	G GER CZE	Yes	Yes	Yes	Yes	Yes	No	Yes	No
	L SCO	No	Yes	Yes	No	No	Yes	Yes	Yes
E SIB URA	K GEO GRE TUR	No	No	Yes	Yes	No	No	Yes	No
F POL	G GER CZE	No	No	No	No	No	No	No	No
G GER CZE	H GER FRA ITA HUN	No	No	No	Yes	No	No	No	No
	K GEO GRE TUR	Yes	Yes	Yes	No	No	No	Yes	No
	L SCO	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
H FRA GER ITA HUN	K GEO GRE TUR	Yes	Yes	Yes	No	No	No	Yes	No
	L SCO	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No
	M FRA	Yes	Yes	Yes	No	No	No	Yes	Yes
L SCO	M FRA	No	Yes	Yes	Yes	No	No	No	No
M FRA	N SPA	No	No	No	Yes	No	No	No	No

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[1] CZEchoslovakia, FINland, FRAnce, GEOrgian SSR, GERmany, GREece, HUNgary, ITAly, LATvian SSR, NORway, POLand, SCOtland, SIBeria, SWEden, TURkey, URAl Mountains.

prising, there was no difference in within-plot variability between 140 single-tree progenies grown in a concurrent experiment and the 122 stand progenies grown in this one. In all cases the smallest trees were 55 to 60 percent as tall as the largest trees in the same plots. Visual estimates of within-plot variability in other traits indicate that the story would have been the same.

These results may have been influenced by the presence of an appreciable amount of intra-plot competition. Thus, they should not be interpreted as proof of the similarity of genetic variability throughout Scotch pine. However, they tend to support the validity of such measurement shortcuts as estimation of plot means from the four tallest trees, the trees with the longest needles, or the trees which set buds earliest.

Nature of the Scotch Pine Ecotypes

Scotch pine is here considered as a group of geographic ecotypes, each inhabiting a definite region and more or less well adapted to that region. The decision to follow the ecotype concept was based largely on practical considerations. Theoretical implications of its use with Scotch pine are summarized in a series of papers by WRIGHT and BALDWIN (1957), LANGLET (1959), and BOUVAREL (1959).

Most of the ecotype boundaries are pineless regions — the North Sea, the Baltic Sea, the French lowlands, the Russian steppes, or the lowland areas of southern Europe. Where these boundaries are so broad as to be total barriers to migration the genetic distinctions between ecotypes are sharp. In Scandinavia the ecotype barriers are ill-defined — probably areas of unusually low density which constitute partial migration barriers. In western Germany the boundary between ecotype G to the east and ecotype H to the west and south is a rather narrow pineless region which would have hindered migration for several generations past.

The genetic discreteness of neighboring ecotypes with regard to individual traits is shown in *table 7,* which is based upon *tables 3 and 5.* It should be noted that the number of characteristics in which discontinuities (i. e. at least one $LSD_{.05}$ between the lowest value of the high ecotype and the highest value of the low ecotype) occur vary considerably. For example, Ecotype A from northern Finland and northern Siberia was separable from Ecotype E from southern Siberia and the Ural mountains only on the basis of one character — time of first-year bud set. On the other hand Ecotypes M (southern France) and N (Spain) were separable from each other on seven traits.

Tables 8, 9, 10, and 11 show the degree of discreteness among ecotypes when 12 characters (characters 6, 9, 10, 11, 14, 16, 17, 19, 20, 21, 23, and 24 in *tables 3 and 4)* are considered simultaneously by means of the summation-of-difference analyses. When considered in this manner ecotypes B and C, C and E, D and F, G and H, H and J, and

Table 8. — Degree of similarity (small numbers) or difference (large numbers) among 3-year-old Scotch pine progenies from northern Europe.

Ecotype, progeny, country	Total difference (in summation-units[1]) between progeny listed below and progeny on left																																			
A 226 FIN	226																																			
229 FIN	2	229																																		
254 SIB	8	0	254																																	
B 549 SWE	9	6	6	549																																
548 SWE	16	10	8	1	548																															
547 SWE	15	8	8	1	0	547																														
546 SWE	10	7	8	0	0	0	546																													
C 228 FIN				3	1	1	1	228																												
230 FIN				6	5	3	2	3	230																											
232 FIN				5	3	3	2	0	3	232																										
233 FIN				9	4	3	5	2	2	2	233																									
222 SWE				11	6	6	7	3	6	4	1	222																								
521 SWE	All			13	8	9	9	3	3	3	3	3	521																							
522 SWE	values			6	2	2	2	1	0	1	0	1	1	522																						
523 SWE	greater			4	0	1	1	1	1	1	1	4	4	0	523																					
524 SWE	than			9	4	5	5	1	1	2	0	1	1	0	0	524																				
543 SWE	fifteen			4	1	0	1	1	1	1	1	3	4	0	0	0	543																			
544 SWE				8	2	4	5	1	4	4	1	1	4	0	0	0	1	544																		
545 SWE				7	3	5	3	1	2	2	0	4	3	0	0	1	2	1	545																	
273 NOR				3	3	1	1	3	2	2	6	9	10	2	1	5	1	6	2	273																
274 NOR				1	0	0	0	0	2	1	1	4	5	1	1	2	0	3	3	1	274															
275 NOR				4	5	0	2	1	3	2	3	6	4	2	2	4	2	5	0	4	1	275														
201 NOR				14	9	9	9	4	1	6	1	2	2	0	2	0	4	3	1	7	6	4	201													
D 542 SWE	All			**	10	11	11	7	2	6	1	4	1	1	5	1	6	5	3	10	8	6	0	542												
541 SWE	values			**	**	**	**	12	10	13	6	5	8	5	10	5	13	7	11	**	13	13	4	4	541											
550 SWE	greater			**	**	**	**	**	12	14	9	11	10	5	13	9	**	13	14	**	**	**	4	5	1	550										
223 LAT	than			**	**	**	**	**	**	**	14	3	3	5	10	5	**	14	**	**	**	**	3	3	10	8	223									
224 LAT	fifteen			**	13	12	14	8	7	7	1	2	0	2	8	2	8	5	6	14	9	9	1	1	1	4	10	224								
E 227 SIB	All			All				1	8	5	0	1	3	0	0	0	1	0	0	8	2	3	2	0	9	15	15	5	227							
234 SIB	values			values				6	**	8	3	3	7	2	5	4	6	3	8	**	8	10	7	8	12	**	**	7	0	234						
255 SIB	greater			greater				2	10	6	3	7	6	2	2	3	3	3	3	7	3	2	8	8	**	**	**	13	1	4	255					
256 SIB	than			than				7	**	10	7	4	11	5	5	8	7	4	9	**	9	13	12	12	**	**	**	12	2	1	2	256				
257 URALS	fifteen			fifteen				9	**	12	3	2	4	3	7	3	9	4	7	**	11	11	3	3	9	14	13	4	1	2	6	3	257			
258 URALS								3	11	8	0	2	4	0	2	1	3	1	4	12	5	6	6	5	10	**	**	5	1	0	3	2	1	258		
259 URALS								5	14	11	2	2	3	3	4	1	5	1	6	12	7	8	6	4	12	**	**	6	1	1	4	1	0	1	259	
260 URALS								10	13	9	3	2	3	3	7	2	9	3	5	**	12	10	4	1	5	8	8	1	1	3	10	6	1	1	2	260
F 211 POL	All values greater than fifteen.							All values greater than fifteen.																12	3	3	6	5	**	**	**	**	**	**	**	8
317 POL																								**	8	4	6	12	**	**	**	**	**	**	**	10

[1] Summation-unit = $\sum 4(\text{Actual difference} - LSD_{.05}) / LSD_{.05}$ for 12 different characters.

** Value greater than 15.

Table 9. — Degree of similarity (small numbers) or difference (large numbers) among 3-year-old Scotch pine progenies from central and southeastern Europe.

Ecotype, progeny, country			Total difference (in summation-units[1]) between progeny listed below and progeny on left																																																																					
F	211	POL	211
	317	POL	2	317
G	202	GER	5	4	202
	203	GER	10	6	5	203
	204	GER	5	2	5	6	204
	207	GER	8	4	1	5	2	207
	208	GER	6	2	1	6	1	1	208
	210	GER	5	2	1	4	0	0	1	210
	248	GER^{p}	7	7	3	3	5	0	2	1	248
	321	GER	4	2	4	4	2	2	0	2	1	321
	341	GER	5	1	3	1	1	2	2	0	3	2	341
	361	GER	3	2	2	3	1	1	2	0	1	1	0	361
	381	GER^{p}	6	5	3	8	1	0	1	0	0	2	3	2	381
	501	GER	4	2	2	6	0	0	1	0	1	1	0	0	0	501
	525	GER	2	2	1	4	1	1	0	1	1	0	1	1	1	1	525
	526	GER	5	2	6	5	1	3	0	3	1	0	1	1	1	1	0	526
	527	GER	1	3	3	5	1	2	1	1	3	0	1	1	2	1	0	0	527
	528	GER	7	6	4	7	3	2	1	2	2	3	6	5	2	2	2	1	4	528
	529	GER	5	2	2	5	2	1	1	0	3	4	0	0	1	0	0	2	1	3	529
	305	CZE	4	3	1	1	3	1	2	0	0	2	1	0	2	0	1	2	1	5	1	305
	306	CZE	4	3	2	1	6	4	5	3	2	3	1	0	5	3	3	5	1	8	4	0	306
	307	CZE	3	3	2	5	1	0	1	0	0	0	1	0	0	0	1	1	1	3	1	0	0	307
	308	CZE	2	0	1	3	1	1	0	1	3	0	1	0	2	1	0	0	0	3	1	1	1	1	308
	309	CZE	3	3	2	4	3	2	3	2	1	1	2	0	4	1	1	2	1	6	2	0	0	0	1	309
	310	CZE	4	3	3	6	1	0	1	0	0	1	1	0	0	0	1	1	1	2	1	0	3	0	1	1	310
	311	CZE	3	2	2	2	0	0	1	0	1	1	0	0	1	0	1	1	1	2	0	0	0	0	1	0	0	311
	312	CZE	6	4	3	4	3	0	1	0	0	1	2	0	0	0	1	1	2	2	2	0	3	0	2	1	0	0	312
	313	CZE	3	2	1	3	1	1	2	1	1	1	0	0	2	0	1	1	1	5	0	0	0	0	1	0	0	0	0	313
	314	CZE	3	3	3	7	1	1	2	1	1	1	1	0	0	0	1	1	1	2	1	0	3	0	1	1	0	0	1	0	314
	315	CZE	2	1	4	4	1	3	0	3	2	0	1	1	2	1	0	0	0	3	3	2	1	1	0	1	1	1	1	1	1	315
	319	AUS^{p}	8	5	2	6	1	0	1	0	0	2	3	2	0	0	0	0	1	2	1	2	5	0	2	3	0	1	0	2	0	2	319
H	206	GER	10	7	4	7	1	0	1	0	0	3	4	4	1	1	2	1	6	2	1	3	6	2	3	5	1	2	0	4	2	4	0	206
	250	GER	9	5	3	8	2	0	2	0	2	3	4	3	0	1	2	3	5	2	2	3	6	1	4	4	1	3	1	3	2	4	0	0	250
	251	GER	11	10	1	5	6	0	3	1	3	5	5	3	1	3	4	6	5	3	3	0	3	2	4	4	3	3	3	2	5	6	1	1	0	251
	252	GER	10	9	2	5	9	1	4	1	4	7	6	4	3	4	5	7	5	5	3	1	4	4	5	5	4	4	4	2	5	7	2	3	4	1	252
	253	GER	10	8	1	5	7	0	2	1	1	4	4	2	0	2	3	5	4	2	3	0	3	1	3	4	1	2	1	1	4	5	0	0	0	0	1	253
	236	FRA^{p}	9	10	2	5	6	0	2	1	1	3	4	2	0	1	2	4	4	2	3	1	4	0	4	5	0	2	0	2	1	4	0	0	0	0	1	0	236
	237	FRA	14	13	4	9	11	2	5	3	4	7	10	6	3	5	6	8	8	4	6	3	7	4	7	8	4	6	3	4	6	8	2	3	2	1	0	1	1	237
	241	FRA	13	8	2	9	10	1	5	2	4	7	7	5	3	5	6	8	7	5	4	1	6	4	6	3	4	4	4	3	6	8	2	3	1	1	0	1	1	0	241
	552	HUN	6	3	0	6	4	1	0	1	2	3	4	2	1	2	1	3	0	1	2	1	4	2	0	3	2	2	2	1	2	3	1	1	1	1	2	1	2	2	2	552
	553	HUN	5	2	0	5	3	1	0	1	1	2	2	1	1	1	0	2	0	1	2	1	4	1	3	2	1	1	1	1	1	2	1	1	1	1	2	1	2	2	2	0	553
	554	ITA	12	13	2	7	14	3	7	4	5	9	10	7	6	7	8	10	9	8	6	4	5	6	6	7	6	7	5	5	8	10	4	7	6	0	1	0	1	1	1	2	4	554
	555	ITA	10	8	1	4	8	0	3	0	3	6	5	3	2	3	4	6	6	5	2	0	3	3	5	0	3	3	3	1	3	5	1	2	3	0	1	0	0	1	1	1	1	0	555
	556	ITA	12	10	0	9	9	1	4	2	5	6	8	6	4	6	5	7	6	4	4	2	7	5	6	7	5	6	5	4	7	7	3	4	2	1	2	1	1	2	2	0	0	1	1	556
	557	ITA	13	12	2	7	12	1	6	2	4	8	9	6	4	6	7	9	8	6	5	2	5	5	4	6	5	6	4	4	7	9	3	3	4	0	1	0	0	1	1	2	2	0	0	1	557
	285	BEL^{p}	9	5	2	5	4	0	1	0	3	4	2	2	0	1	2	4	3	2	0	1	4	1	2	3	1	2	1	0	2	4	0	0	0	1	1	1	1	3	2	1	2	3	0	2	2	285
	295	BEL^{p}	9	5	1	4	5	0	2	0	3	5	2	2	1	2	3	5	3	3	0	0	3	2	2	3	2	2	2	0	3	5	0	1	0	1	1	1	1	3	2	1	1	2	0	2	2	0	295
	318	BEL^{p}	6	6	1	5	4	0	2	1	0	1	3	1	0	1	2	3	3	2	3	0	3	0	3	1	0	1	0	1	1	3	0	0	0	0	2	0	0	1	2	1	1	3	1	2	1	0	1	318
	531	BEL^{p}	12	7	4	10	6	1	1	1	4	7	6	5	0	3	4	6	5	3	3	4	7	3	5	6	2	5	3	4	2	7	0	0	0	1	3	0	0	1	1	1	1	3	2	1	2	0	1	0	531
	530	BEL^{p}	14	12	10	10	8	3	4	4	4	6	10	8	2	6	6	6	10	2	9	6	9	5	11	8	4	7	3	8	5	8	2	1	1	5	8	4	2	5	7	6	5	10	7	8	8	2	7	2	2	530
	225	NY^{p}	6	11	3	4	11	2	5	4	3	8	9	6	8	9	6	8	10	6	7	2	4	5	7	6	5	12	3	5	7	9	2	3	7	1	0	1	1	1	1	4	4	1	2	0	1	5	3	2	7	9	225
I	269	ENG^{p}	**	**	**	6	**	8	9	11	5	10	14	12	13	12	12	11	12	**	5	9	9	11	14	12	11	12	7	13	12	13	10	8	10	8	9	9	8	8	9	13	11	11	9	11	11	13	11	8	**	10	5	269
	270	ENG^{p}	13	14	8	4	10	5	6	6	2	5	9	6	10	5	5	4	10	9	2	4	5	5	8	8	5	8	4	8	7	7	4	6	9	4	3	5	4	3	3	6	5	6	3	6	5	8	5	3	9	9	2	1	270
J	235	FRA	**	**	**	**	**	**	**	**	14	**	**	**	**	**	**	**	13	**	**	13	13	**	14	**	**	**	**	14	**	**	**	**	12	5	5	8	7	9	8	8	8	3	4	6	3	6	4	7	11	13	3	12	6	235
	242	YUG	11	**	12	**	**	**	**	**	14	**	**	**	**	**	**	**	8	**	**	12	12	14	14	11	**	13	**	13	**	14	**	**	8	3	3	5	5	6	6	5	5	3	3	6	2	6	4	4	8	10	2	11	6	1	242
	205	AUS	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	13	7	8	9	8	9	10	11	10	6	6	9	5	8	7	7	13	12	2	8	7	0	1	205
	209	GER	**	12	**	**	**	**	**	**	**	**	**	**	**	**	**	**	8	**	**	**	14	**	12	13	**	13	**	14	**	13	**	**	11	13	11	13	11	**	**	9	8	14	11	14	12	5	5	9	12	**	3	**	13	5	2	2	209
K	243	GRE	**	**	**	7	**	14	14	**	14	14	**	13	**	**	**	14	12	**	**	11	10	**	13	11	**	11	13	12	**	**	**	**	**	**	**	**	**	**	**	**	**	10	13	**	12	**	14	**	**	**	4	4	1	3	5	2	11	243
	244	GRE	**	**	12	8	**	14	13	14	13	9	**	12	**	**	**	12	12	**	**	10	9	14	13	9	14	10	10	11	13	13	**	**	**	13	12	14	13	12	12	**	**	10	13	14	10	**	13	13	**	**	3	2	2	3	1	1	8	1	244
	271	GRE	**	**	12	7	11	10	11	12	10	12	**	13	**	**	**	12	12	14	14	10	10	12	13	13	12	11	10	13	14	**	**	11	**	7	9	10	11	7	7	12	12	8	9	9	6	14	11	10	**	**	3	3	1	3	7	3	**	1	4	271
	272	GRE	**	**	**	8	**	**	14	**	14	11	**	11	**	**	**	**	9	**	**	10	8	12	12	8	13	10	11	10	12	12	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	10	5	2	8	4	2	10	3	0	8	272
	551	GRE	11	11	5	3	8	6	6	7	6	4	8	6	12	6	4	4	7	8	9	3	3	6	6	6	7	5	4	6	8	7	**	8	13	6	5	10	8	4	5	8	7	3	3	6	2	10	6	8	12	13	4	3	0	2	5	5	12	5	5	4	3	551
	261	GEO	**	**	**	8	**	**	**	**	**	**	**	**	**	**	**	13	**	**	12	9	**	**	12	**	13	14	14	**	**	**	**	**	**	**	**	**	**	**	**	**	12	13	**	11	**	**	**	**	**	7	7	3	3	5	3	**	0	1	4	3	7	261
	262	GEO	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	11	**	**	14	13	**	**	**	**	**	**	14	**	**	**	**	**	**	14	**	**	14	14	**	**	12	**	**	11	**	**	**	**	**	9	9	5	7	6	7	**	3	4	2	6	7	0	262
	263	GEO	**	**	12	12	**	13	**	14	**	**	**	**	**	**	**	14	**	**	11	11	**	**	**	**	13	**	14	**	**	**	**	**	10	11	12	13	10	10	14	11	7	11	11	6	**	13	11	**	**	3	8	6	4	5	5	**	2	3	5	7	9	2	2	263
	264	GEO	**	**	13	10	**	13	14	14	14	**	**	**	**	**	**	12	**	**	11	11	**	**	**	**	12	12	14	**	**	**	**	**	10	11	11	13	9	9	**	**	8	10	11	5	**	13	12	**	**	3	4	1	4	6	2	**	1	1	0	5	5	1	0	0	264
	213	TUR	**	**	**	13	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	8	5	2	7	8	3	**	1	1	3	4	7	0	0	1	0	213
	214	TUR	**	**	**	**	12	**	**	**	**	**	**	**	**	**	**	**	**	**	**	14	**	**	**	**	14	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	12	**	**	**	**	**	7	6	1	6	9	4	**	2	4	1	6	5	0	0	5	0	1	214
	220	TUR	**	**	**	15	12	**	**	**	**	**	**	**	**	**	**	**	**	**	13	11	**	**	**	**	**	**	**	**	**	**	**	**	**	**	14	13	**	**	14	14	**	**	12	**	**	11	**	**	**	**	**	6	8	5	5	5	4	**	2	0	4	5	9	1	0	0	2	0	0	220
	221	TUR	**	**	**	**	13	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	13	**	**	14	**	**	**	**	**	6	3	2	7	9	3	**	2	3	0	7	7	1	1	4	0	0	0	0	221

[1] Summation-unit = $\sum 4(\text{Actual difference} - LSD_{.05}) / LSD_{.05}$ for 12 different characters.

** Value greater than 15.

Table 10. — Degree of similarity (small numbers) or difference (large numbers) among 3-year-old Scotch pine progenies from western Europe.

Ecotype, progeny, country			Total difference (in summation-units[1]) between progeny listed below and progeny on left																																	
			269	270	235	242	205	209	243	244	271	272	551	261	262	263	264	213	214	220	221															
L	265	SCO	7	6	5	11	6	11	5	6	9	3	6	5	13	11	9	8	3	10	7	265														
	266	SCO	5	8	14	**	15	**	9	12	10	9	**	12	**	**	3	11	10	**	8	4	266													
	267	SCO	**	**	14	**	**	**	11	**	**	11	**	13	**	**	**	13	**	**	**	6	5	267												
	268	SCO	13	13	9	**	12	**	**	12	**	7	12	9	**	**	**	11	11	**	11	2	5	3	268											
M	212	FRA	3	11	11	14	9	**	7	9	6	14	12	10	9	13	8	5	4	5	1	3	3	8	8	212										
	238	FRA	8	13	11	**	11	**	7	10	7	**	11	10	9	12	9	5	3	6	1	3	2	7	5	0	238									
	239	FRA	8	6	5	10	4	**	2	7	6	10	7	4	4	8	5	2	0	4	0	3	2	7	3	1	0	239								
	240	FRA	**	**	**	**	**	**	9	11	12	**	**	11	13	**	14	5	8	12	6	7	3	9	5	5	4	2	240							
	249	AUS^{d}	8	9	9	13	7	**	4	8	7	10	11	6	10	12	9	2	4	8	0	3	5	8	4	1	0	1	1	249						
	316	FRA^{d}	3	2	8	11	4	**	4	5	2	8	5	4	5	6	3	2	1	5	0	3	3	9	5	0	4	0	4	0	316					
	320	FRA^{d}	5	8	9	12	6	**	6	8	7	9	10	6	10	5	8	5	4	8	1	3	4	8	4	1	0	2	3	0	0	320				
N	218	SPA	**	**	14	**	**	**	14	**	12	**	11	12	12	**	11	12	8	14	9	**	**	**	**	11	8	7	10	13	10	9	218			
	219	SPA	12	6	7	**	12	**	9	14	6	**	8	7	4	10	6	5	6	8	5	**	11	**	**	9	4	4	7	10	7	11	2	219		
	245	SPA	**	12	14	**	**	**	9	**	9	**	11	8	8	**	10	6	5	14	3	**	12	**	**	7	4	1	4	6	4	8	0	2	245	
	246	SPA	**	13	12	**	**	**	10	**	9	**	9	7	6	11	9	7	4	10	6	**	**	**	**	10	5	4	4	10	6	11	0	2	0	246
	247	SPA	**	12	10	**	13	**	7	13	8	**	8	6	6	7	7	5	5	7	4	**	**	**	**	6	3	3	4	7	4	8	4	0	1	1	247

[1] Summation-unit = $\sum 4(\text{Actual difference} - LSD_{.05}) / LSD_{.05}$ for 12 different characters.

** Value greater than 15.

J and K are found to overlap to such a great extent that it is difficult to assign a given progeny to one or the other without considering its geographic location. In cases like this, breeding programs designed to obtain improved varieties for one region should make use of some progenies from a neighboring region. At the other extreme are pairs of neighboring ecotypes such as D and L, E and G, E and K, G and J, G and L, H and L, H and M, I and J, and L and N. In these cases there was no genetic overlap so that one progeny could be said to be more similar to every other progeny from the same region than to any progeny from the neighboring region.

It has occasionally been maintained that all variation is essentially continuous and that any apparent discreteness among neighboring populations is the result of incomplete sampling. That undoubtedly explains some of the discontinuities in the Scandinavian and Siberian populations. These were very lightly sampled, and it is probable that more intensive study would show the presence of intermediate types. On the other hand, the sampling within the central and western portion of the range was intensive enough that the discovery of a large number of intermediate types is improbable.

There were genetic differences among progenies of different stands within the same ecotype in most characteristics *(tables 3 and 5)*. These differences are large enough to indicate that there are very real possibilities of improving almost any of the ecotypes by selective breeding. However, in nearly all traits the amount of within-ecotype variation was very small compared with the range of variation for the species as a whole. This can be stated another way. According to the analyses of variance of the progeny means the F values

$$\left(= \frac{\text{between-ecotype mean square}}{\text{within-ecotype mean square}} \right)$$

for most traits ranged from 10 to 50; they were as high as 288 for character 10 in *table 4*.

The major geographic trends were not evident within the confines of single ecotypes (note relative scarcity of significant inter-character correlations in *table 6* when the ecotypes were treated singly). Consider the intensively sampled Ecotype G from Germany and Czechoslovakia for example. The variation among progenies was random. There was no evidence for the presence of minor genetic clines, local soil races, or local altitudinal races. Progeny MSFG 314 was extreme in its geographic location (high elevation in eastern Czechoslovakia) but was average genetically. Progeny MSFG 528 was centrally located geographically but extreme in several genetic characteristics. Progeny MSFG 203 was from south west West Germany, close to the region occupied by Ecotype H. It resembled that ecotype in winter color but was very dissimilar in growth rate and leaf length. Similar examples could be cited from each of the other regions.

The existence of a random within-ecotype variation pattern has a profound bearing on tree improvement programs. Suppose that the present experiments succeed in pinpointing a region from which the progenies are well suited for growth in Michigan. The next step will be the selection of superior progenies from stands and single trees within that region. Evidently this next step must be done by means of progeny testing, with little help from data on the location and characteristics of the stands or single trees.

Evolution of the Ecotypes

Northern Europe and northern Asia were extensively glaciated during the Pleistocene. The glaciers obliterated most of the vegetation. Remnants survived south of the ice or in highlands within the glaciated areas. Five Pleistocene refuges may be postulated for Scotch pine — the Pyrenees, the Alps or Carpathians, southeastern Europe, the Scandinavian highlands, and the Urals or a part of Siberia. The pine was probably already well differentiated in pre-Pleistocene times so that these remnants formed distinct races whence came the modern Scotch pine population.

Selection pressure acted on these remnants to cause further differentiation, provided there were pineless areas which acted as migration barriers. Where no such barriers existed, as in the continuously forested areas of Germany and Czechoslovakia, there was a constant gene interchange between neighboring populations. In such areas no differentiation resulted unless selection differentials were very large.

Responses to changes in selection pressure are much slower than the changes themselves. Thus modern Scotch

Table 11. — Comparison of the amount of within- and between-ecotype variation in many characters.

Ecotype	Country of origin[2]	WITHIN-ECOTYPE COMPARISONS The columns below contain the percentage of cases in which difference between provenances is---					BETWEEN-ECOTYPE COMPARISONS						
		Summation-units[1] Percent of comparisons					Comparison is between Ecotypes	The columns below contain the percentage of cases in which difference between provenances is-- Summation-units[1] Percent of comparisons					Degree of overlap
		0-1	2-4	5-8	9-14	15+		0-1	2-4	5-8	9-14	15+	
A	FIN, SIB	33	33	33	0	0	A and B	0	0	57	33	8	11
B	SWE	100	0	0	0	0	B and C	26	29	27	19	1	65
C	FIN, SWE, NOR	49	41	8	2	0	C and D	6	15	25	34	20	32
							C and E	13	35	29	18	5	58
D	SWE, LAT	30	30	20	0	0	D and E	7	8	25	25	35	34
							D and F	0	30	40	20	10	66
							D and G	0	0	9	31	60	8
							D and L	0	0	0	0	100	0
E	SIB	56	33	7	4	0	E and F	0	0	0	6	94	4
							E and G	0	0	0	0	100	0
							E and K	0	0	0	0	100	0
F	POL	0	100	0	0	0	F and G	7	64	27	2	0	42
							F and H	0	5	27	68	0	13
G	GER, CZE	66	28	6	0	0	G and H	23	43	29	5	0	59
							G and I	0	12	38	46	4	18
							G and J	0	0	2	21	77	0
							G and K	0	1	9	54	36	7
							G and L	0	0	0	0	100	0
H	GER, FRA, BEL, ITA, HUN	62	30	7	1	0	H and I	0	20	38	40	2	28
							H and J	19	41	31	9	0	58
							H and K	0	4	8	27	61	13
							H and L	0	0	0	0	100	0
							H and M	0	0	0	0	100	0
I	ENG	100	0	0	0	0	I and J	0	0	50	38	12	0
							I and K	20	42	38	0	0	20
J	GER, FRA, YUG	50	33	17	0	0	J and K	4	33	36	10	17	54
K	GRE, TUR, GEO	50	28	21	1	0	K and L	0	4	18	42	36	23
							K and M	9	17	39	31	4	44
							K and N	0	6	42	37	15	23
L	SCO	0	50	50	0	0	L and M	0	54	39	7	0	48
							L and N	0	0	0	10	90	0
M	FRA	67	28	5	0	0	M and N	3	34	34	29	0	40
N	SPA	70	30	0	0	0							

[1] Summation-unit = $\sum \frac{4(\text{Actual difference} - \text{LSD}_{.05})}{\text{LSD}_{.05}}$ for 12 different characters.

[2] BELgium, CZEchoslovakia, ENGland, FINland, FRAnce, GEOrgian SSR, GERmany, GREece, ITAly, HUNgary, LATvian SSR, NORway, SCOtland, SIBeria, SPAin, SWEden, TURkey.

pine does not show complete adaptation to modern environments. Ecotypes still reflect their Pleistocene ancestry to a considerable extent. The intense autumnal coloration of the Ural Mountain and Siberian population, the blue color and short needles of the three west European ecotypes, and the several traits shared by all Scandinavian progenies are evidences of common ancestries.

The slowness of response to selection pressure also hindered the development of well adapted local races within ecotypes. Suppose that 10 generations ago semi-isolated populations occupied the north and south slopes of a ridge. If the climate warmed slightly 5 generations ago the populations migrated to the ridge top and coalesced. The incipient trends toward the formation of north-slope and south-slope races disappeared. If the climate cooled slightly 5 generations ago the populations migrated to the valley bottoms. The direction of the incipient trends changed. Hence the random nature of the within-ecotype variation patterns.

Genetic drift occurs if a population is reduced to a few score breeding individuals and remains isolated for a few generations. The effects of inbreeding in one generation remain if the number of breeding individuals rise the next generation. Mild inbreeding (if breeding size equals a few score trees) can result in the random fixation of non-adaptive genes or slightly adaptive genes. Intensive inbreeding (if breeding size equals a few trees) can result in the fixation of genes against considerable selection pressure. Genetic drift has apparently occurred in Scotland, Greece, and parts of Spain. In those countries there are several isolated stands which have remained small for several generations because of cutting and lack of suitable micro-sites for Scotch pine.

Some putative *P. sylvestris* × *nigra* hybrids were found in a Turkish progeny. The remainder of the progeny was typical Scotch pine. In Spain, where the ranges of the two species also overlap, no signs of hybridity were found. It is probable that introgression between the two species has not played a significant role in the evolution of either one.

Progeny of three plantations (MSFG 225, 269, 270) were relatively uniform and intermediate between two naturally occurring ecotypes. They offer evidence that hybridization between ecotypes can occur and lead to the production of a stable population within a few generations.

Usefulness of the Ecotypes in Michigan

This section contains generalized textual descriptions of the 14 ecotypes recognized in this paper *(figure 6)*. Additional details on origin and nursery performance are contained in *figures 3 and 4* and in *tables 3, 4 and 5*.

The 1-year and 3-year nursery data were supplemented by information from older provenance tests for which the origin data were satisfactory. Four publications were particularly useful in this respect. WIEDEMANN'S (1930) paper summarized existing information about the many 1907 International Union of Forest Research Organization (IUFRO) plantings in central Europe. Those tests were not replicated and cannot be evaluated singly but they are of considerable value when considered as a whole. LANGLET'S paper is the source of information about 1- and 2-year-old nursery stock of 586 Swedish origins grown in Sweden. The papers by WRIGHT and BALDWIN (1957) and SCHREINER *et al.* (1962) are the source of information about the 17-year-old, 55-origin IUFRO test of north European provenances tested in New Hampshire and the 18-year-old, 43-origin IUFRO test in New York.

Scandinavian, Baltic, and Siberian Ecotypes

The 36 seedlots from the Scandinavian, north Baltic, and Siberian regions were grouped into 5 ecotypes. The ecotype boundaries run more or less east-west and are poorly defined.

As a group the Scandinavian-Siberian seedlots were characterized by small seeds, very slow to medium growth rate; dark green to medium green summer foliage color, intense red (first year) or intense yellow (second year) autumnal color; early autumnal coloration; very early to early bud set and secondary leaf formation; unbranched terminal buds; short to medium-length leaves; absence of male flowers and Lammas shoots; shallow to moderately deep, much branched root systems. Both in native stands and in older provenance studies bole form seems to be excellent.

Except for Ecotype D (southern Sweden and Latvia) the yellow autumn color and slow growth seems to rule out this northern material for either Christmas tree or timber planting in Michigan. Some of the far northern types (especially Ecotypes A and B) would be useful horticulturally as dwarf forms.

Ecotype A. Northern Finland, northeastern Siberia. — This is synonymous with Ecotype A of the New Hampshire test. This ecotype had small seeds, extremely slow growth rate; shallow, hard-to-pull and much branched root systems; very dark green summer foliage; very red (age 1) or very yellow (age 2+) autumn color appearing in early October; very early appearance of first-year buds and secondary leaves; short needles. First-year survival after outplanting was comparatively low.

North Scandinavian trees exhibited exellent bole form but very slow growth (6 feet in 17 years) and yellow autumn color in New Hampshire and New York. In Swedish nursery tests material from above 66⁰ N. latitude had high (37 to 38 percent) dry matter content, short needles, very early needle maturation, slow growth, and very yellow autumn color.

Ecotype B. North-central Scandinavia. — This is synonymous with Ecotype B of the New Hampshire test. This differed from Ecotype A in its 40 percent faster growth (the difference was similar in New Hampshire and Sweden); in its 2 week later appearance of autumn color and first-year root systems. First-year survival after outplanting was moderately high. In the Swedish nursery tests trees from this region had longer needles, later needle formation, and smaller percent dry weight than did trees from farther north.

Ecotype C. Southern Norway, south-central Sweden, southern Finland, and adjacent parts of the USSR. — This includes Ecotype C and the northern part of Ecotype D of the New Hampshire test. As compared with the more northerly Ecotype B this was 25 percent faster growing, had lighter summer foliage and browner expanding buds, and formed secondary needles later. In New England trees from this region grew straight and moderately fast (13 to 17 feet in 17 years) but exhibited yellow autumn color. In Sweden trees of this ecotype had longer needles, later needle formation, less autumnal coloration, and greater height growth than did more northern trees.

In both the New Hampshire and Swedish tests it was possible to make a growth rate differentiation between trees from north and south of approximately 60½⁰ N. latitude. Such a differentiation was not possible from the present data.

Ecotype D. Southern Sweden, Latvia, and adjacent parts of the USSR. — This includes Ecotype F and part of Ecotype D of the New Hampshire test, and the 'Riga' type of many authors.

Ecotype D was characterized by moderate growth rate, medium-green summer foliage; yellow autumn foliage; moderately late first-year bud set and change from summer to autumn foliage color; no branched terminal buds, Lammas shoots, or male flowers; and by root systems which were moderately deep and well branched but easy to pull.

In the New Hampshire study there was a significant difference in growth rate between the south Swedish (14 to 17 feet in 17 years) and Latvian (17 to 20 feet in 17 years) trees. The latter grew straight and nearly as fast as the German trees but turned yellow in the autumn. In LANGLET'S nursery experiments the south Swedish stock from 56⁰ to 57⁰ N. latitude exhibited the same characteristics as did trees from slightly farther north.

VILMORIN (1857) was the first to extol the virtues of Latvian or 'Riga' provenances. In his tests they grew perfectly straight but not so fast as trees from farther south. One or more Riga provenances was included in most of the 1907 IUFRO tests and performed well as regards stem form and branch size. In no case did they grow as fast as Belgian (Campine) material but in some plantings they grew as rapidly as German trees.

There are a few older plantings of certain Latvian origin in New Hampshire, New York, and Michigan. These plantings are similar in having straight stems, moderate growth rate, yellow autumn color, and moderate needle length.

At the present time this ecotype must be regarded as the best *proven* form of Scotch pine for timber production in New Hampshire and presumably in Michigan. The picture may change if faster growing provenances show an ability to grow straight.

Ecotype E. Southern and western Siberia. — This is similar to Ecotype C in several respects but differs in having a 25 percent greater growth rate, very yellow autumn foliage (the yellowest of any in the test), and 20 percent longer needles. The Siberian progenies should possibly be considered as differentiated into a slower growing northern and eastern ecotype and a faster growing western and southern one (labelled EE in *table 5).*

In the early Russian trials (quoted by WIEDEMANN) Siberian trees grew much more slowly than did trees from the Ukraine.

Central European Ecotypes

The central European Scotch pine population contains four moderately well defined geographic ecotypes. These are the "average" Scotch pines of most Americans. They are long-needled, green, rapidly growing types which have been planted by the million.

Ecotype F. Northeastern Poland. — This differs slightly from Ecotype G (Germany, Czechoslovakia, Rumania, Ukraine SSR) in its yellower autumn foliage and earlier secondary needle formation. The two were not separable in the New Hampshire test. North Polish ("East Prussian") provenances were included with Latvian origins in some reports of the 1907 IUFRO tests, and with German origins in others.

Ecotype G. Germany, Czechoslovakia, Rumania, and adjacent parts of the Ukraine SSR. — This is synonymous with Ecotype G of the New Hampshire test. It was characterized by rapid growth, medium-green summer foliage; slightly yellow to green autumn foliage; first-year bud set in early September; late formation of secondary needles; long needles; few Lammas shoots; and root systems which were moderately deep and well branched but very easy to pull.

On the basis of the 1-year data the Rumanian and German progenies could not be distinguished. The New Hampshire and New York results indicate that the Rumanian progenies will be slower growing and will have coarser branches in later life.

The German and Czech trees grew rapidly in the northeastern tests. In New Hampshire they averaged 20 feet tall in 17 years and in New York they averaged 26 feet tall in 18 years. Most had green autumnal foliage. As a group they were deficient in form, having many trees with basal sweep and crooked trunks. It is hoped that straight individual progenies will be found.

This is the ecotype which contributed most to the American picture of Scotch pine as a possible timber tree. Comparisons between the older provenance tests and the many unknown-origin plantations indicate that north-central Europe furnished most of the seed used in the United States until recent years.

Ecotype H. Western West Germany, northeastern France (Vosges Mountains), Belgium, western Hungary, and northern Italy. — This includes Ecotypes H and J and a part of Ecotype G of the New Hampshire test. As compared with Ecotype G it grew faster, set first-year buds later, and had greener autumn foliage.

Progeny MSFG 530 was unique in having the most rapid growth rate in the experiment — its average height was significantly greater (5 percent level) than that of all except two others. In addition it differed from other progenies of the same ecotype in its larger seeds, earlier bud set, and earlier presence of secondary leaves. This progeny was grown from seed collected in a 1902 plantation in the Commune d'Auby, Honsart, western Ardennes, Belgium. The origin of the parental plantation is unknown but may be presumed to be northeastern France or western West Germany. It may be that more intensive sampling of the native stands in those regions would uncover other progenies similar to this. Or, it may be that the uniqueness of MSFG 530 shows the effectiveness of the artificial selection practiced by the Belgians during past centuries.

Progeny MSFG 531 from the Campine district of Belgium was second fastest growing. A Campine seedlot (IUFRO 18) grew fastest in the New Hampshire study (15 percent faster than German trees), had desirable autumn color, but was very crooked. IUFRO was also the tallest in the Czech IUFRO provenance trial established in 1938 (VINCENT and POLNAR, 1953). A similar (possibly identical) seed source was tallest in 10 of the 16 IUFRO plantings established in central Europe in 1907. The Campine seedlot was described as very crooked in some of the early IUFRO trials and as straight in others.

Progeny MSFG 225 (the "Booneville" strain of some American planters) was grown from seed collected in a planted stand in Booneville, New York. It had a distinctive combination of characters indicating that it arose as the result of hybridization between Ecotypes H and K (Greece, etc.) The hybridization probably occurred a few generations past; the progeny was as uniform as others in the study.

At MSU's W. K. Kellogg Forest in southwestern Michigan there are several excellent 25-year-old Scotch pine stands of unknown origin. Their growth rate, needle length, and color are suggestive of Ecotype H. Their bole form is as good as that of any native species. These stands give hope that the inherent tendency toward poor bole form is expressed only under certain environmental conditions. Where those conditions are lacking the inherently rapid growth of this ecotype can be used.

Belgian, north French, and west German seed is being used successfully by many Christmas tree growers. After further test some origins may be certified for timber production.

Ecotype I. Surrey, England. — Two seedlots were collected from the natural offspring of planted stands in the vicinity of Frensham, Surrey, England. The parent stands were 2 miles apart. These seedlots were very similar to each other. They did not match any native-stand progenies but had a combination of characters suggestive of a hybrid origin between Ecotypes H (Belgium, France, etc.) and L (Scotland). The within-progeny variation was no greater then in native-stand progenies, indicating that the presumed hybridization occurred a few generations ago.

Seeds from these or other stands in East Englia or Surrey appear regularly on the American Christmas tree market. If all stands are similar to the two which were tested, the stock should be satisfactory as regards growth rate, color, and needle length. However, its stem form under Michigan conditions is unknown.

Ecotype J. Yugoslavia, Austria, Germany, France. — This is an arbitrary group consisting of four seedlots which resemble each other in genetic characteristics but do not have a common geographic range. They are intermediate between Ecotypes G and K.

Southeast European Ecotype

Ecotype K. Greece, Bulgaria, Turkey, Georgian SSR. — As compared with the German-Czechoslovakian-Rumanian Ecotype G, this has 15 percent less growth, darker green foliage both summer and winter, larger seeds, later first-year bud set, more Lammas shoots, and stiffer needles which are 15 percent shorter. This differs sufficiently from other ecotypes to justify the belief that it descended from a separate Pleistocene remnant. It has not been represented in previous range-wide provenance tests.

The dark green winter color, moderate growth rate, and moderately short needles are desirable Christmas tree traits. However, its growth form and hardiness under Michigan conditions are still unknown quantities.

West European Ecotypes

The 14 provenances from Scotland, southern France, and Spain are similar to each other in several respects even though they are from differing climates. They have the following traits in common: moderate growth rate, blue-green foliage with little autumn coloration, late appearance of secondary needles, short needles, deep root systems, and medium to large seeds. They have been planted very little for forestry purposes but are widely used by Christmas tree growers.

Ecotype L. Scotland. — This is synonymous with Ecotype E of the New Hampshire test. As compared with the south French Ecotype M it has slightly less blue-green winter foliage, much earlier first-year bud set, and a higher percentage of branched terminal buds.

Scottish trees in New Hampshire had medium growth rate (15 feet in 17 years), good bole form, and blue winter color. They grew about 90 percent as fast as Latvian stock in the 1907 IUFRO tests. VINCENT and POLNAR (1953) reported moderate growth rate in the 1938 Czech IUFRO plantings.

The Scottish ecotype was distinctive in its high percentage of trees with branched terminal buds (3 percent in the replicated plots, 10 to 20 percent in the broadcast-sown plots). Through the third year these branched buds had no effect on growth form. They may be related to a later tendency to fork which has been noted by several European writers and by some Michigan Christmas tree growers.

The recent book "the Native Pine Woods of Scotland" by Steven and CARLISLE (1959) covers the known history, floristics, silvics, and silviculture of all the native Scotch pine remnants in Scotland. Among other things the authors noted that the trees have good bole form but become flat-topped at 40 to 50 feet and reach a maximum height of slightly over 60 feet.

All characteristics except the forking mark this as a desirable Christmas tree type in Michigan. Its slow growth rate in comparison with continental types and its probable low maximum height make it of little interest for forestry.

Ecotype M. Central Massif of France. — This is not represented in other range-wide provenance tests. In the 1-year study of the south French origins had slightly shorter primary needles and less blue-green foliage than Spanish trees. In the 3-year study the two ecotypes were similar except in time of first-year bud set (earlier in French origins) and percentage of trees with Lammas shoots (fewer in French origins). In the outplantings south French origins withstood transplanting well even though taprooted. In several cases first-year mortality was less than 3 percent.

In recent years 'Auvergne', 'Race noble d'Auvergne', and 'French Blue' seed from this region has appeared on the American Christmas tree market in large quantities. Growers have generally been well satisfied. The timber qualities of trees grown in Michigan are still an unknown quantity. The excellent timber form which is characteristic of native French stands (witness the common name 'Race noble') may or may not be characteristic of trees grown in Michigan.

Ecotype N. Spain. — This differs from the south French ecotype M in its later bud set and higher percentage of trees with Lammas shoots. Its root systems had a most tenacious hold on the ground during the first summer and were noticeably taprooted at lifting time.

Progeny MSFG 218 (Navarredonda, Avila, Sierra de Gredos, lat. 40° N, long. 5° 15' W) was thought to be outstandingly blue in the broadcast-sown plots whereas it was not noticeably different from the other Spanish seedlots in the row plots.

Spanish trees in a University of Wisconsin plantation in the northern part of that state have suffered appreciable needle browning during the winter. There are reports of similar damage in the 'Thumb' area of lower Michigan. Such winter injury was not found in the Lansing nursery or in several commercial nurseries in the southwestern part of the state. (Two erroneous reports of extreme winter injury to Spanish trees were found to be based upon *Pinus pinaster* AIT.)

The outlying population of Scotch pine in southern Spain is represented in the University of Wisconsin test but not in the present one. It became flat-topped at a very early age and should possibly be considered separately from the rest of the Spanish population.

The short needles, excellent autumn color, and good bole form under natural conditions mark this ecotype as an interesting possibility for Christmas tree and timber production in the midwestern states. Several Christmas tree growers are experimenting with it on a large scale. Its hardiness and bole form under plantation conditions will have to be studied further before it can be recommended without reservation.

Seed Procurement Recommendations

Nurserymen wanting average seed from a spencified region can often order directly from the catalogs issued by seed companies. They should ask for a written statement giving the locality in which the seed was collected and a guarantee that the seed was collected from native stands (if a native origin is desired). With three exceptions to be noted later seed ordered in this manner will probably be true to name. Several dealers are able to supply seed from unlisted localities (the U. S. S. R., Czechoslovakia, Rumania, Turkey, Greece, etc.) for which there has been little previous demand. A year's advance notice is desirable for such orders.

Nurserymen wanting seed from a plantation or wanting the best seed from a certain region must specify the exact stand of origin. The specification should be within a quarter-mile and should be based upon the results of adequate progeny tests. It is not sufficient to ask that the seed be from a certain elevational zone or aspect because of the random within-ecotype variation patterns. Nor is it sufficient to ask that the seed be from a phenotypically good stand in Europe — there are many discrepancies between the phenotype of a stand in Europe and the performance of its progeny in America.

'Latvian' or 'Riga' seed commonly can not be guaranteed to be true to name. Confusion arises from the known excellence (for timber production) of true Riga pine and the use of the names in a varietal sense without attempting to standardize the contents of the variety. Some foresters of northeastern United States have recognized only 'Riga' and 'non-Riga' types of Scotch pine and have distributed 'Riga' seed from various unknown-origin plantings. Some European collectors have used the names in a broad sense so that 'Collected in Poland' labels can be found inside 'Riga' seed packets. There are two cures for this confusion: (1) insist on a written guarantee that 'Latvian' seed be collected from native stands in the Latvian S. S. R. or the immediately surrounding area, and (2) convert the very few known-origin American plantings into seed orchards.

Austrian Hill' seed can not be guaranteed either. In this experiment progenies MSFG 205, 249, and 319 were purported to be of Austrian origin but had very diverse characteristics. Many growers have had similar results. Apparently the seed is collected in Austria but from plantations of unknown origin. The same dealer may collect from different stands in different years. There is no immediate cure for this situation unless a grower knows the exact stand from which a particularly good seedlot was collected.

The name 'French green' has been applied to seed collected from at least two different regions. A grower who was satisfied with the short needles and slow growth of the Central Massif trees may be disappointed if he receives Vosges Mountain seed which produces trees with long needles and rapid growth. The cure for this confusion is simple. Order 'Vosges Mountain' or 'Central Massif' rather than 'French green' seed.

The ordering of seed from a specific general area or from a specified stand could eliminate the difficulties encountered with the various "dealer's special" varieties or strains. These usually consist of seed collected from phenotypically good plantations of unknown origin. Nearly always the seed is genetically equivalent to that which could be obtained from one of the natural stands listed in *tables 3 or 5*. In few cases can one of the "special" varieties of Scotch pine be considered as analogous to an improved variety of a crop plant.

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Summary

A 122-origin, 3-year provenance study of Scotch pine (*Pinus sylvestris* L.) was sown in Michigan State University's forest tree nursery, E. Lansing in the spring of 1959. A supplementary 66-origin, 1-year study was sown in the spring of 1961 to cover parts of the range not previously sampled. Each origin consisted of offspring of approximately 10 trees in a single stand. Most of the parental stands were native. Most parts of the native range were sampled. This report covers only nursery performance; all origins have been or will be tested in permanent outplantings.

In both experiments there were four replicates, each replicate containing one 40-tree row of every origin. A flexible measurement schedule was used so that apparently significant macroscopic differences could be evaluated as they occurred. A complete set of measurements on a single character involved the determination of every plot mean to an accuracy of approximately 1/5 to 1/10 (color, etc.) or 1/40 (height, etc.) of the range between extremes. Summaries of 17 such sets (3-year experiment) and 6 such sets (1-year experiment) are presented. Analyses of variance (with plot or progeny means as items) were used to determine the significance of differences among origins and among ecotypes. Simple correlation analyses (with progeny means as items) were used to determine the significance of various trends within and between ecotypes. A newly described 'summation-of-differences' analysis was used to quantify the degree of similarity between progenies with regard to several traits. MSU's "MISTIC" computer was used for most of the computations.

The uniformity of growth conditions was such that genetic differences among progenies accounted for more

than 95 percent of the total variance in some traits. Most plots were fully stocked and growth conditions were generally favorable. The nursery was maintained in a pest-free condition and there was no damage from unusual weather conditions.

The following major geographic trends were recognized. Seed size varied from 4 mg. (northern Scandinavia) to 12 mg. (Turkey and Spain). Three-year height varied from 12 cm. (northern Finland) to 71 cm. (Belgium); in central Europe the trend was reversed and the southern origins were only 50 cm. tall. Summer foliage color varied from medium green (central Europe) to dark green (northern Scandinavia and southeastern Europe) to blue-green (western Europe). Autumn foliage color varied from very yellow (Ural Mountains) to yellow (Baltic countries) to dark green (southeastern Europe) to blue-green (western Europe). Autumnal coloration started in early September (Ural Mountains) and did not appear in southern origins. Date of first-year bud formation varied from mid-July (northern Finland) to early October (Spain); this trait showed the closest relation to latitude of origin. Dates of second-year growth initiation and bud formation varied little. Branched terminal buds were more prevalent on Scottish seedlot but were also found in various south Eureopean progenies. Percentage of trees with Lammas shoots varied from 0 (Poland and northward) to 20 (Spain). Secondary leaves were formed earliest on the smallest northern progenies and latest (early second year) on progenies from Germany southward. Second-year leaf length varied from 50 mm. (western Europe) to 55 mm. (northern Scandinavia) to 78 mm. (western West Germany). Ease of pulling at the age of 6 weeks varied from easy (Germany, Belgium, Czechoslovakia) to difficult (northern Scandinavia, southern Europe). Type of root system at age 3 varied from shallow and fibrous (northern Scandinavia and Siberia) to long and taprooted (Spain). Of the nine 2-year-old trees which produced male flowers six were fast-growing ones from Belgium.

On th basis of the summation-of-difference analyses 14 geographic ecotypes were recognized. These are A — northern Finland and northern Siberia; B — northern Sweden; C — southern Finland, central Sweden and Norway; D — Latvia and southern Sweden (should possibly be subdivided); E — the Ural Mountains and parts of Siberia (should possibly be subdivided); F — northern Poland; G — most of Germany, Czechoslovakia, Rumania; H — Belgium, northeastern France, western West Germany; northern Italy, Hungary (should possibly be subdivided); I — England (planted stands); J — a heterogeneous catchall of 4 central European origins; K — Georgia, Bulgaria, Greece, Turkey; L — Scotland; M — southern France; and N — Spain. In older experiments the Latvian ecotype (good form, moderate growth rate) was found to be best for pulp and sawtimber production in northeastern United States. It must be regarded as the standard for use in Michigan until the form of the faster growing types can be evaluated. For Christmas tree production any of several progenies from central, western, or southern Europe can be considered as ideal, depending on an individual grower's personal preference as to needle length, growth rate, and foliage color. Similarly any of various progenies might be preferred as ornamentals.

Where the ecotype boundaries were sharply defined by broad pineless areas the genetic distinctions between neighboring ecotypes were sharp. In such cases a progeny was more similar in the totality of its characters to other progenies from the same region than to any progeny from another region. Where there was a large opportunity for gene interchange the genetic discontinuities were slight or not present.

A stand-progeny did not differ from about half the other stand-progenies of the same ecotype in any trait and differed from about half in one or two traits. The differences usually amounted to slightly more than the amount needed for significance at the 5 percent level; differences between the most extreme progenies in the species were several times this large. Genetic improvement of most traits through selective breeding appears feasible.

The correlation analyses showed the existence of many significant correlations between one progeny-trait and another or between a progeny-trait and a characteristic of the original environment if progenies from a large part of the species range were considered. These correlations were rarely significant if progenies form only a single ecotype were considered. That is, variation within ecotypes was essentially random. These findings are important to the seed buyer. If he wishes average trees of a particular ecotype he can specify that the seed be collected anywhere within a relatively large region. If he wishes above-average trees he must specify that the seed be collected from a particular stand which is known (trough adequate progeny tests) to produce superior seedlings. Specification of a particular elevational zone or aspect is not sufficient.

A large part of the vegetation of northern Europe and northern Asia was obliterated during the Pleistocene. Scotch pine probably survived in a few locations such as the Pyrenees, the Alps, or Carpathians, southeastern Europe, the Urals or a part of Siberia, and the Scandinavian highlands. The populations entering these refuges were probably already well differentiated. Since the Pleistocene each of these remnants was subjected to natural selection, which caused differentiation provided there were pineless migration barriers. In regions where the pine population was essentially continuous the selection pressure was operative but could not result in appreciable differentiation because of the constant gene interchange. Response to changes in selection pressure is much slower than the actual changes. Hence, modern ecotypes reflect their Pleistocene ancestry and trends toward the development of well adapted local races have been upset by post-Pleistocene climatic fluctuations. Genetic drift occasioned by small population size has been important in a few special situations such as are found in Scotland and Greece.

Zusammenfassung

Titel der Arbeit: *Geographische Variation bei der Gemeinen Kiefer — Ergebnisse eines dreijährigen Versuchs im Staate Michigan.*

Ein jetzt dreijähriger Provenienzversuch mit 122 Herkünften der Gemeinen Kiefer (*Pinus silvestris* L.) wurde im Frühjahr 1959 im Forstpflanzgarten der Michigan State University in East Lansing ausgesät. Ein zusätzlicher, jetzt einjähriger Versuch mit 66 Herkünften wurde im Frühjahr 1961 ausgesät, um bisher unberücksichtigte Teile des Verbreitungsgebiets zu erfassen. Jede Herkunft bestand aus Nachkommen von annähernd 10 Bäumen eines einzelnen Bestandes. Die meisten Elternbestände waren autochthon. Von den meisten Teilen des natürlichen Verbreitungsgebiets wurden Proben genommen. Dieser Bericht umfaßt nur das Verhalten in der Baumschule; alle Herkünfte wurden oder werden noch nach der endgültigen Auspflanzung geprüft.

Beide Versuche waren vierfach wiederholt. Jede Wiederholung enthielt eine Langparzelle mit 40 Bäumen von jeder Herkunft. Ein flexibles Meßschema kam zur Anwendung, so daß scheinbar signifikante makroskopische Unterschiede festgestellt werden konnten, wenn sie auftraten. Ein vollständiger Satz von Messungen eines einzigen Merkmals umschloß die Erhebung der Parzellenmittel mit einer Genauigkeit von annähernd $^1/_5$ oder $^1/_{10}$ (Farbe usf.) oder $^1/_{40}$ (Höhe usf.) der Variationsbreite. Übersichten von 17 (dreijähriger Versuch) bzw. 6 (einjähriger Versuch) solcher Sätze werden wiedergegeben. Zur Bestimmung der Signifikanz der Unterschiede zwischen Herkünften und Ökotypen werden Streuungszerlegungen angewendet (als statistische Einheit dienten die Parzellen- oder Nachkommenschaftsmittel). Anhand einfacher Korrelationsanalysen (Nachkommenschaftsmittel als statistische Einheit) wurde die Signifikanz verschiedener Trends in und zwischen Ökotypen bestimmt. Eine neuerdings beschriebene Analyse der „Summation der Differenzen“ wurde zur Quantifikation des Ähnlichkeitsgrads der Nachkommenschaften hinsichtlich vieler Merkmale benutzt. Die meisten Rechenarbeiten wurden auf der Rechenanlage „MISTIC“ von MSU durchgeführt.

Die Einheitlichkeit der Wachstumsbedingungen war derart, daß genetische Unterschiede zwischen Nachkommenschaften bei einigen Merkmalen mehr als 95% der Totalvarianz betrugen. Nur wenige Parzellen hatten Ausfälle und die Wachstumsbedingungen waren allgemein günstig. Der Pflanzgarten wurde krankheitsfrei gehalten, Schäden durch Witterungsextreme traten nicht auf.

Folgende großräumige geographische Trends waren zu erkennen: Das Korngewicht variierte zwischen 4 mg (nördliches Skandinavien) und 12 mg (Türkei und Spanien). Die Höhe im Alter von 3 Jahren variierte zwischen 12 cm (Nordfinnland) und 71 cm (Belgien); in Mitteleuropa kehrte sich der Trend um, und die südlichen Herkünfte waren nur 50 cm hoch. Die sommerliche Nadelfarbe variierte zwischen einem hellen Grün (Mitteleuropa), Dunkelgrün (nördliches Skandinavien und Südosteuropa) und Blaugrün (Westeuropa). Die Nadelfärbung im Herbst variierte von Hellgelb (Uralgebirge) bis Gelb (Baltenländer), Dunkelgrün (Südosteuropa) und Blaugrün (Westeuropa). Die Herbstverfärbung begann Anfang September (Uralgebirge), sie trat bei südlichen Herkünften nicht auf. Der Zeitpunkt der Knospenbildung im ersten Jahr variierte zwischen Mitte Juli (Nordfinnland) und Anfang Oktober (Spanien); dieses Merkmal zeigte den engsten Zusammenhang zur geographischen Breite des Herkunftsortes. Die Zeitpunkte des Wachstumsbeginns und der Knospenbildung im zweiten Jahr variierte kaum. Verzweigte Terminalknospen herrschten bei den schottischen Herkünften vor, fanden sich aber auch in verschiedenen südeuropäischen Nachkommenschaften. Der prozentuale Anteil der Bäume mit Johannistrieben variierte zwischen 0 (Polen sowie nördlich davon) und 20 (Spanien). Sekundärnadeln bildeten sich zuerst bei den am langsamsten wachsenden nördlichen Nachkommenschaften und zuletzt (erst zu Beginn des zweiten Jahres) bei den Nachkommenschaften aus Deutschland und südlicher liegenden Gebieten. Die Nadellänge im zweiten Jahr variierte zwischen 50 mm (Westeuropa) bis 55 mm (nördliches Skandinavien) und 78 mm (westliches Westdeutschland). Der Widerstand beim Herausziehen im Alter von 6 Wochen variierte zwischen gering (Deutschland, Belgien, Tschechoslowakei) und groß (nördliches Skandinavien, Südosteuropa). Der Bewurzelungstyp im Alter von 3 Jahren variierte zwischen einem flachen Faserwurzelsystem (nördliches Skandinavien und Sibirien) und einer langen Pfahlwurzel (Spanien). Von den 9 zweijährigen Bäumen, die männliche Blüten entwickelten, waren 6 raschwüchsige Individuen aus Belgien.

Auf der Grundlage der Analyse der „Summation der Differenzen“ wurden 14 Ökotypen unterschieden: A — Nordfinnland und Nordsibirien; B — Nordschweden; C — Südfinnland, Mittelschweden, Norwegen; D — Lettland und Südschweden (evtl. zu unterteilen); E — Uralgebirge und Teile von Sibirien (evtl. zu unterteilen); F — Nordpolen; G — größere Teile von Deutschland, Tschechoslowakei, Rumänien; H — Belgien, Nordwestfrankreich, westliches Westdeutschland; Norditalien, Ungarn (evtl. zu unterteilen); I — England (Pflanzbestände); J — eine heterogene Gruppe von 4 mitteleuropäischen Herkünften; K — Georgien, Bulgarien, Griechenland, Türkei; L — Schottland; M — Südfrankreich; N — Spanien. In älteren Versuchen wurde der lettische Ökotyp (gute Form, mäßig rasches Wachstum) als der beste befunden hinsichtlich der Produktion von Faser- und Schnittholz im Nordosten der Vereinigten Staaten. Er ist als Standard in Michigan anzusehen, bis die Form der rascherwüchsigen Ökotypen bewertet werden kann. Zur Erzeugung von Weihnachtsbäumen können beliebige Herkünfte aus Mittel-, West oder Südeuropa als ideal gelten, je nach der Bevorzugung bestimmter Nadellängen, Wuchsgeschwindigkeiten und Nadelfarben durch den Anbauer. In ähnlicher Weise mag beliebigen Herkünften als Zierbäumen der Vorzug gegeben werden.

Wo die Grenzen der Ökotypen durch weite kiefernfreie Gebiete scharf umrissen sind, ist auch die genetische Differenzierung zwischen benachbarten Ökotypen sehr deutlich. In solchen Fällen war eine Nachkommenschaft in der Gesamtheit ihrer Merkmale anderen Nachkommen des gleichen Wuchsgebiets ähnlicher als irgendeiner Nachkommenschaft aus einem andern Wuchsgebiet. Wo Möglichkeit zu Genaustausch auf breiter Basis entstand, waren genetische Diskontinuitäten nur schwach ausgeprägt oder nicht vorhanden.

I. a. unterschied sich eine Bestandsnachkommenschaft in einem Merkmal von etwa der Hälfte der andern Bestandsnachkommenschaften des gleichen Ökotyps nicht, und sie unterschied sich etwa von der Hälfte in einem oder zwei Merkmalen. Die Unterschiede betrugen gewöhnlich geringfügig mehr, als zur Signifikanz bei $P = 0.05$ notwendig war; die Unterschiede zwischen den extremen Nachkommenschaften innerhalb der Species betrugen ein Mehrfaches davon. Die genetische Verbesserung der meisten Merkmale durch Auslesezüchtung erscheint durchführbar.

Die Korrelationsanalysen ergaben viele signifikante Merkmalskorrelationen bei den Nachkommenschaften oder zwischen Merkmalen der Nachkommenschaften und des Milieus des Herkunftsortes, wenn Nachkommenschaften von einem großen Teil des Verbreitungsgebiets der Art betrachtet wurden. Diese Korrelationen waren selten signifikant, wenn Nachkommenschaften nur eines einzigen Ökotyps betrachtet wurden. Das bedeutet, die Variation innerhalb der Ökotypen ist im wesentlichen zufallsmäßig. Diese Befunde sind für den Saatgutkäufer von Bedeutung.

Wünscht er durchschnittliche Bäume eines Ökotyps, kann er Ernte irgendwo in einem relativ großen Gebiet verlangen. Wünscht er überdurchschnittlich gute Bäume, muß er im einzelnen den Erntebestand bestimmen, welcher (auf Grund angemessener Nachkommenschaftsprüfungen) erwiesenermaßen überlegenes Material liefert. Die Spezifizierung eines bestimmten Höhengürtels oder einer bestimmten Exposition ist nicht ausreichend.

Während des Pleistozäns wurde ein Großteil der Vegetation Nordeuropas und Nordasiens vernichtet. Die Kiefer überlebte wahrscheinlich an wenigen Stellen wie etwa in den Pyrenäen, Alpen, Karpathen, in Südosteuropa, im Ural oder in Teilen von Sibirien und in den Hochländern Skandinaviens. Die Populationen waren beim Eintritt in diese Refugien wahrscheinlich schon gut differenziert. Seit dem Pleistozän waren all diese Reste natürlicher Selektion unterworfen, welche eine Differenzierung herbeiführte, sofern kiefernfreie Migrationsbarrieren existierten. In Gebieten mit einer im wesentlichen kontinuierlichen Kiefernpopulation war der Selektionsdruck wohl wirksam, führte aber infolge des ständigen Genaustausches nicht zu merklicher genetischer Differenzierung. Die Antwort auf Wechsel des Selektionsdrucks ist viel langsamer als die tatsächlichen Wechsel. Daher widerspiegeln die rezenten Ökotypen ihre pleistozänen Vorfahren, und Trends in Richtung auf gut adaptierte Lokalrassen wurden durch nachpleistozäne Klimaschwankungen aufgelöst. Genetische Drift infolge geringen Populationsumfangs war von Bedeutung in einzelnen besonderen Situationen wie in Schottland und in Griechenland.

Résumé

Titre de l'article: *Variation géographique du Pin sylvestre — Résultats d'une étude de 3 ans au Michigan.*

Une expérience sur les provenances de Pin sylvestre (*Pinus sylvestris* L.), portant sur 122 origines et prévue pour 3 ans, a été semée au printemps 1959 à la pépinière de l'Université de Michigan, E. Lansing. Une expérience complémentaire prévue pour 1 an a été semée au printemps 1961; elle porte sur 66 provenances originaires des parties de l'aire non représentées dans l'expérience précédente. Chaque origine comprend la descendance d'environ 10 arbres du même peuplement. La plupart de ces peuplements sont autochtones. A peu près toutes les parties de l'aire naturelle sont représentées. Ce compte rendu porte uniquement sur les résultats en pépinière; toutes les origines ont été ou seront essayées dans des plantations permanentes.

Les deux expériences comprennent quatre répétitions, chacune d'entre elles avec une rangée de 40 arbres de chaque origine. Un programme de mesures très souple a été utilisé de manière à pouvoir évaluer, au fur et à mesure de leur manifestation, les différences macroscopiques apparemment significatives. Une série complète de mesures sur un seul caractère comprend la détermination de la moyenne de chaque placeau avec une précision d'environ $^{1}/_{5}$ à $^{1}/_{10}$ (pour la couleur, etc....) ou $^{1}/_{40}$ (pour la hauteur, etc....) de l'étendue de la variation entre les extrêmes. L'article présente les résumés de 17 de ces séries de mesures pour l'expérience de 3 ans et de 6 séries pour l'expérience de 1 an. Les analyses de variance (avec les moyennes des placeaux des descendances comme variables) sont employées pour déterminer les différences significatives entre les origines et entre les écotypes. Des analyses de corrélation simples (avec les moyennes des descendances comme variables) permettent de déterminer la valeur significative des différentes tendances à l'intérieur et entre les écotypes. L'analyse de «sommation des différences» récemment décrite est utilisée pour évaluer le degré de similitude entre les descendances en ce qui concerne plusieurs caractères. Le calculateur «MISTIC» de MSU a été utilisé pour la plupart des calculs.

L'uniformité des conditions de culture était telle que les différences génétiques entre origines représentaient pour certains caractères plus de 95% de la variance totale. La plupart des placeaux étaient complets et la croissance généralement favorable. La pépinière était maintenue dans de bonnes conditions sanitaires et il n'y eut aucun dégât dû à des conditions météorologiques exceptionnelles.

Les grandes caractéristiques géographiques suivantes ont été mises en évidence. Le poids des graines varie de 4 mg (Nord de la Scandinavie) à 12 mg (Turquie et Espagne). La hauteur à 3 ans varie de 12 cm (Nord de la Finlande) à 71 cm (Belgique); en Europe centrale, le gradient est inversé et les origines méridionales ont seulement 50 cm de haut. La couleur des aiguilles en été varie du vert moyen (Europe centrale) au vert foncé (Nord de la Scandinavie et Sud-Est de l'Europe) et au bleu vert (Ouest de l'Europe). La couleur des aiguilles en automne varie du jaune accentué (Ourals) au jaune (pays baltiques), au vert foncé (Sud-Est de l'Europe) et au bleu vert (Ouest de l'Europe). La coloration automnale commence au début Septembre (Ourals) et ne se manifeste pas dans les origines méridionales. La date de formation du bourgeon de la première année varie de la mi-juillet (Nord de la Finlande) au début Octobre (Espagne); ce caractère montre une relation très étroite avec la latitude d'origine. Les dates de débourrage et de formation du bourgeon la seconde année varient peu. Les bourgeons subterminaux sont les plus importants sur les lots d'Ecosse, mais on les trouve aussi dans diverses provenances du Sud de l'Europe. Le pourcentage d'arbres avec des secondes pousses varie de 0 (Pologne et plus au Nord) à 20 (Espagne). Les aiguilles secondaires se forment plus tôt sur les provenances septentrionales à croissance faible et plus tard (au début de la seconde année) sur les provenances d'Allemagne et plus au Sud. La longueur des aiguilles de seconde année varie de 50 mm (Ouest de l'Europe) à 55 mm (Nord de la Scandinavie) et 78 mm (Ouest de l'Allemagne). La facilité d'arrachage à l'âge de 6 semaines est facile pour les provenances d'Allemagne, Belgique et Tchécoslovaquie et difficile pour les provenances du Nord de la Scandinavie et du Sud de l'Europe. Le système radiculaire à 3 ans est superficiel et compact pour le Nord de la Scandinavie et la Sibérie, long et pivotant pour l'Espagne. Sur les 9 plants de 2 ans qui ont produit des fleurs mâles, 6 étaient des plants à croissance rapide de Belgique.

Sur la base des analyses de sommation des différences, on a reconnu 14 écotypes géographiques: A — Nord de la Finlande et Nord de la Sibérie; B — Nord de la Suède; C — Sud de la Finlande, centre de la Suède et de la Norvège; D — Lettonie et Sud de la Suède (pourrait peut-être être subdivisé); E — Ourals et partie de la Sibérie (pourrait peut-être être subdivisé); F — Nord de la Pologne; G — La plus grande partie de l'Allemagne, Tchécoslovaquie, Roumanie; H — Belgique, Nord-Est de la France, Ouest de l'Allemagne, Nord de l'Italie, Hongrie (pourrait peut-être être subdivisé); I — Angleterre (reboisements); J — ensemble hétérogène de 4 provenances d'Europe centrale; K — Géorgie, Bulgarie, Grèce, Turquie; L — Ecosse; M —

Sud de la France; N — Espagne. Dans des expériences plus anciennes, l'écotype de Lettonie (bonne forme, croissance moyenne) s'est révélé le meilleur pour la production de bois à papier et de sciage dans le Nord-Est des Etats-Unis. Il faut le considérer comme tel dans le Michigan jusqu'à ce que l'on ait pu apprécier la forme des types à croissance plus rapide. Pour la production d'arbres de Noël, plusieurs provenances d'Europe du centre, de l'Ouest, du Sud peuvent être considérées comme les meilleures selon la préférence personnelle des producteurs en ce qui concerne la longueur des aiguilles, la vitesse de croissance et la couleur des aiguilles. De même, on peut choisir entre diverses provenances pour la production d'arbres d'ornement.

Là où les limites des écotypes sont nettement définies par de larges régions où le pin n'existe pas, les différences génétiques sont bien déterminées. Dans ce cas, une provenance est plus proche pour la totalité de ces caractères des autres provenances de la même région que de toutes provenances d'une autre région. Là où existent des possibilités de large échange de gènes, les discontinuités génétiques sont faibles ou absentes.

Une provenance comparée aux autres du même écotype ne diffère pas d'environ la moitié de celles-ci pour tous les caractères et diffère d'environ la moitié de celles-ci pour 1 ou 2 caractères. Les différences sont en général légèrement supérieures au seuil de signification au niveau de 5%; les différences entre les provenances extrêmes atteignent plusieurs fois la valeur au seuil de signification. L'amélioration génétique de la plupart des caractères par sélection paraît possible.

Les analyses de corrélation montrent l'existence de nombreuses corrélations significatives entre 2 caractères d'une provenance ou entre un caractère d'une provenance et un facteur praticulier du milieu, si l'on considère les provenances d'une grande partie de l'aire. Ces corrélations sont rarement significatives, si l'on considère les provenances d'un seul écotype dont la variation à l'intérieur des écotypes est dûe essentiellement au hasard. Ces résultats sont importants pour l'acheteur de graines. S'il désire des arbres moyens d'un écotype particulier, il peut spécifier que la graine soit récoltée n'importe où dans une région relativement étendue. S'il veut des arbres au-dessus de la moyenne, il doit spécifier que la graine soit récoltée dans un peuplement particulier, connu par des tests de provenance pour produire des plants de qualité supérieure. La mention d'une zone d'altitude ou d'une exposition donnée n'est pas suffisante.

Une grande partie de la végétation du Nord de l'Europe et de l'Asie a été bouleversée au cours du pléistocène. Le Pin sylvestre a probablement survécu dans quelques stations des Pyrénées, des Alpes, des Carpates, du Sud-Est de l'Europe, de l'Ourals, d'une partie de la Sibérie et des montagnes de Scandinavie. Les populations qui ont colonisé ces refuges étaient déjà probablement bien différenciées. Depuis le pléistocène, chacune d'elles a été soumise à la sélection naturelle qui a causé une différenciation là où existaient des barrières à la migration par interruption géographique de l'aire. Dans les régions où les peuplements de pin étaient continus, la pression de sélection a joué, mais n'a pu aboutir à une différenciation appréciable en raison des échanges de gènes constants. La réponse aux changements dans la pression de sélection est beaucoup plus lente que les changements eux-mêmes. Les écotypes actuels reflètent donc les traits de leurs ancêtres du pléistocène et les tendances pour la formation de races locales bien adaptées ont été boulevérsées par les fluctuations climatiques qui ont suivi le pléistocène. La dérive génétique due au faible effectif de certaines populations a joué un rôle important dans certains cas particuliers en Ecosse et en Grèce.

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