The 1938 International Union Scotch Pine Provenance Test in New Hampshire

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Introduction

Scotch pine (Pinus sylvestris L.) was the first forest tree species to be studied for racial variation. Between 1823 and 1850 DE VILMORIN (1862) established Scotch pine plantings of known geographic origin at his estate at Les Barres, France. By showing that the plantings from different countries differed in several important growth characteristics, he laid the foundation for future racial studies in this and other species.

Following DE VILMORIN's lead, foresters in other European countries established Scotch pine provenance tests in the latter part of the 19th century. These were scattered independent plantings, each with a different design. Among the published reports on these early tests are those of SCHOTTE (1905) and DENGLER (1908). In 1907 the International Union of Forest Research Organizations undertook a series of coordinated racial tests in several European countries. The results of these 1907 tests were summarized by WIEDEMANN (1930) and KALELA (1937).

In 1936 the Congress of the International Union of Forest Research Organizations[2]) meeting in Hungary, proposed a new series of provenance tests for Scotch pine (and other species). These new tests were to be conducted simultaneously in several different countries and were to follow a prescribed experimental design. VEEN (1952) gives the location of these IUFRO tests. The plantings that are the subject of this report are part of these experiments proposed in 1936. Their establishment has been previously reported on by BALDWIN (1953).

Although the unreplicated experiments that were started in the last century and the early years of the present century provided practical information for the localities in which they were conducted, they are mainly of historical interest now. A critical survey of all these papers would involve repetitious criticism of the experimental methods used. Hence we cite in detail only a few of the recent papers that are based on relatively precise experimentation.

Methods

Collection and Distribution of Seed

Cone collections were made in the fall of 1937 from the localities shown in table 1 and figure 1. In most cases (as far as the records show) the cones were collected from several trees of native stock. The cones were forwarded to Eberswalde, Germany, where the seeds were extracted and cleaned. Each seedlot, with accompanying data on origin, was distributed to several cooperating agencies in Europe and to the Fox State Forest in Hillsboro, New Hampshire, USA.

A few additional non-IUFRO seedlots (given F-numbers) that were received directly from foreign experiment stations were also included in the provenance tests. Certain deficiencies in the data supplied with the original seedlots were later corrected by VEEN (1952), who made an extensive tour of the parent stands and European test plantations and prepared a report containing recommendations for the measiirement and analysis of the data. A more complete history of the IUFRO series of experiments and the New Hampshire plantations has been reported by BALDWIN (1953).

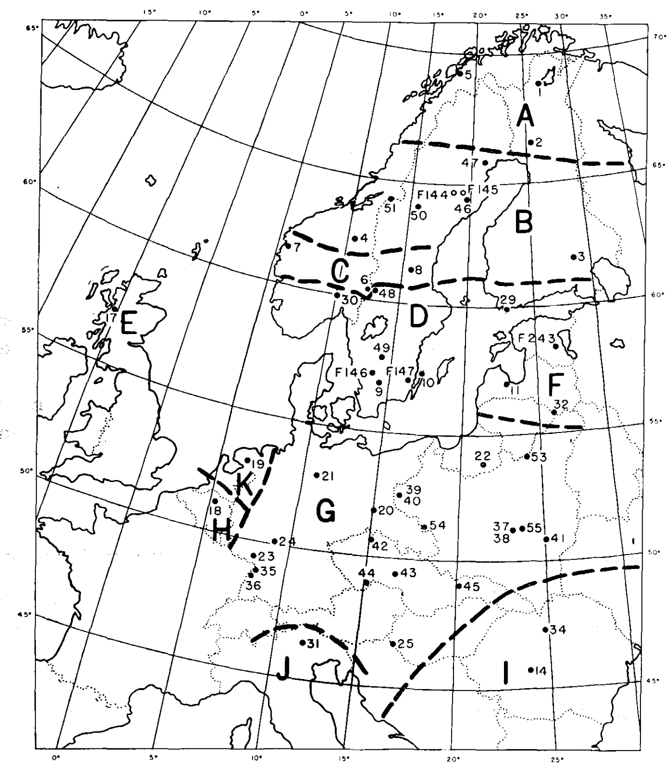

Figure 1. — Geographic distribution of the provenances studied in the New Hampshire IUFRO provenance study of Scotch pine.

Nursery Procedure

Location *and* soil. — All seedlings were grown on the Fox State Forest, Hillsboro, New Hampshire. The nursery soil was a Marlow loam artificially mixed with clean cement sand.

Spacing and replication. — Approximately equal numbers of seeds were sown for each seedlot. The seeds were spaced 3 to 4 millimeters apart in rows 10 centimeters apart. The transplants were spaced 5 centimeters apart in rows 15 centimeters apart. There was no replication.

Age *of* stock. — The stock was grown 2 years in the seedbeds and 2 years in transplant beds.

Maintenance of identity. — The nursery was mappad,

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[2]) For brevity, the International Union of Forest Research Organizations is abbreviated to IUFRO elsewhere in this paper. Unless otherwise qualified, any reference to IUFRO refers specifically to the present test or to other Scotch pine provenance tests proposed by the 1936 Congress.

Table 1. — *Data on origin of seedlots used in the IUFRO Scotch pine provenance test at Hillsboro and Deering, New Hampshire* (All seeds from native stands unless otherwise specified. F-numbers apply to seedlots not received from IUFRO.)

Region	IUFRO No. (and Fox No.)	Country, District, Town	North Latitude	East Longitude	Altitude	Average temperatur: Annual	Average temperatur: Summer	Average annual precipitation
					Meters	°C.	°C.	*Inches*
A	1	Finland, Lappi, Inari	68°55'	27°00'	140	—1.5	10.6	18
	5	Norway, Troms, Malselv	69°10'	18°40'	75	2.7	11.4	23
	2	Finland, Oulu, Rovaniemi	68°30'	25°45'	250	— .1	12.6	17
B	4	Norway, Hedmark, Tynset	62°18'	10°44'	550	.1	—	16
	46	Sweden, Västerbotten, Vindeln	64°12'	19°50'	155	—	—	—
	47	Sweden, Norbotten, Brännberg	65°47'	21°15'	100	—	—	—
	50	Sweden, Jämtland, Strömsund	63°50'	15°35'	300	—	—	—
	51	Sweden, Jämtland, Svenskådalen	64°02'	13°05'	—	—	—	—
	(F-144)	Sweden, Västerbotten, Knaftensby	64°30'	18°19'	250	—	—	—
	(F-145)	Sweden, Västerbotten, Norsjövallensby	64°31'	19°20'	250	—	—	—
C	7	Norway, Sogn og Fjord, Svanöy	61°29'	5°07'	50	—	13.1	83
	3	Finland, Mikkeli, Sääminki	61°53'	28°45'	85	2.5	14.2	22
	6	Norway, Hedmark, Åsnes (Solar)	60°30'	12°10'	230	3.0	13.5	24
	8	Sweden, Gäfleborg, Voxana	61°20'	13°30'	200—300	—	15.3	20
D	9	Sweden, Halland, Tönnersjöheden	56°40'	13°50'	50—100	—	—	—
	10	Sweden, Kalmar, Böda	57°15'	17°00'	10	—	—	—
	29	Finland, Uusimaa, Bromarv	59°58'	23°00'	15	5.1	14.7	23
	30	Norway, Buskerud, Modum	59°56'	10°01'	300	3.7	14.7	27
	48	Sweden, Värmland, Hvitsand	60°20'	13°00'	150—300	—	13.7	27
	49	Sweden, Jönköping, Axamo	57°46'	14°03'	225	—	13.4	27
	(F-146)	Sweden, Halland	57°	13°30'	150	—	—	—
	(F-147)	Sweden, Kalmar, Berga	57°15'	16°15'	250—350	—	—	—
	(F-259)	Finland (Seed dealer)	—	—	—	—	—	—
E	17	*Scotland, W. Invernessshire, Glengarry	57°09'	4°55' W	150	7.4	12.7	65
	(F-261)	*Scotland, (Seed dealer)	—	—	—	—	—	—
F	11	Latvia (USSR), Latvija, Vecmocas	57°00'	23°07'	65	—	13.7	24
	32	Latvia (USSR), Latvija, Griva	55°50'	26°25'	160	6.2	17.8	26
	(F-243)	Esthonia (USSR), Tartu	58°	27°	—	5.0	15.0	25
G	53	Poland (USSR), Ukraina, Mustjeki	54°08'	24°25'	130	—	15.0	24
	55	Poland (USSR), Ukraina, Luboml	51°15'	24°05'	180	—	15.9	23
	37	Poland (USSR), Bialistok, Suprasl IA	51°13'	23°22'	160	—	—	—
	38	Poland (USSR), Bialistok, Suprasl IB	51°13'	23°22'	160	—	—	—
	39	Poland, Poznan, Bolewice IIA	52°24'	16°10'	90	—	—	—
	40	Poland, Poznan, Bolewice IIB	52°24'	16°10'	90	—	—	—
	41	Poland (USSR), Ukraina, Susk IIIA	50°55'	25°27'	180	—	16.1	23
	54	Poland, Poznan, Rychtal A	51°09'	17°52'	190	—	—	—
	22	Poland, Mazury, Rudczany	53°40'	21°29'	130	6.5	16.5	24
	20	Poland, Slask-Dolny, Pförten	51°47'	14°46'	85	8.7	17.8	23
	21	Germany, Hannover, Göddenstedt	52°58'	10°47'	75	8.3	16.4	22
	23	Germany, Rheinland-Pfalz, Elmstein	49°22'	7°57'	325	8.6	16.8	27
	24	Germany, Hessen, Zellhausen	50°01'	9°00'	120	9.2	17.8	21
	35	Germany, Württemberg-Baden, Langensteinbach	48°55'	8°30'	260	9.7	18.2	29
	36	Germany, Baden, Langenbrand	48°42'	8°22'	525	8.5	16.8	30
	42	Czechoslovakia, Liberecky, Kurivody	50°36'	14°43'	300	—	15.2	27
	43	Czechoslovakia, Brennensky, Tisnov	49°21'	16°23'	300—450	—	16.2	22
	44	Czechoslovakia, Ceskobudejovicky	49°00'	14°45'	400—450	—	—	—
	45	Czechoslovakia, Kosicky, Vysoké Tatry	49°09'	20°13'	600—700	—	13.6	38
	25	Hungary, Zala, Lenti	46°38'	16°33'	200	—	—	—
	(F-232)	Hungary	—	—	—	—	—	—
H	18	*Belgium, Antwerp, Herselt	51°03'	4°56'	20	9.3	16.4	35
	(F-246)	*Belgium	—	—	—	—	—	—
I	14	Rumania, Sibiu, Talmaciu	45°40'	24°15'	500—700	9.0	18.9	28
	34	Rumania, Campulung, Tinoava	47°14'	25°18'	910	—	—	—
J	31	Italy, Trento, Val de Fiemme	46°18'	11°20'	1100	8.6	17.3	34
K	19	*Netherlands, Drente, Diever	52°51'	6°21'	10	8.5	15.5	28

* Planted stands.

and each pine seedlot was separated from the next by rows of spruce. Each seedlot was dug separately.

Outplanting Procedure

Time of establishment. — All outplantings were made in the spring of 1942. Although replacement of dead trees was planned, none was made because of the shortage of labor due to the war.

Location of outplantings. — Blocks I, II, and III were on a nearly level hilltop at an elevation of 1,100 feet on the Vincent State Forest, Deering, New Hampshire, 10 miles from Hillsboro. Blocks I and II are contigous, and block III is about one-fourth mile distant. Block IV is located on a lower east slope at an elevation of 800 feet on the Fox State Forest at Hillsboro.

Plot shape, size, and spacing. — The plots in blocks I, II, and III were rectangular, 55 feet by 63 feet (16.9×19.5 meters), and were planted with about 200 trees each. To eliminate possible border effects no trees in the outer rows of the plots were measured. The plots in block IV were single rows planted to 15 trees each. As recommended by the International Union of Forest Research Organizations, all trees were planted on a spacing of 4.2×4.2 feet (1.3×1.3 meters).

Replication. — Each provenance was represented by 1, 2, 3, 4, 5, 6, 7 measured plots (6, 8, 11, 20, 6, 3, and 1 provenances respectively). As the provenances were completely randomized (recommended by the International Union of Forest Research Organizations) at the time of planting, each provenance was represented by 0, 1, 2, or 3 measured plots in a block. Blocks I and IV were the most complete. This complete randomization and the resultant unequal numbers of plots per block made the statistical analyses difficult but not impossible.

Soil and previous history. — The soil on the outplanting areas was a brown podsol, Paxton loam. From the surface downward the soil had an incipient A_2 layer, a yellow-brown transition layer with a tendency to blocky structure, and an almost impermeable layer of parent material at a depth of 16 inches on the highest points and at a depth of 30 inches on the lower slopes. The parent material was compacted and gray (olivegreen when wet). There were few boulders or rock out-crops, and the soil was remarkably uniform over the entire area except as regards depth to parent material. It is probable that, for their size, the planting sites were about as uniform as is available for forest planting anywhere in the Northeast.

The planting sites were once hayfields and had been grazed until 1941. At that time they were in grass, with scattered shrubs or small trees — mostly common juniper (*Juniperus communis* L.), hardhack (*Spiraea tomentosa* L.), blueberry (*Vaccinium* spp.), and gray birch (*Betula populifolia* Marsh.). The pines were planted in the bottoms of single furrows plowed in the autumn of 1941.

Care of the plantations. — Block IV (at Hillsboro) was kept continually free of shrubby or tree competition after its planting, and was pruned to a height of 6 feet in 1951. Blocks I and II were lightly weeded (all that was necessary to maintain them in pure pine) in 1951 and 1955, and the border rows were pruned to a height of 6 feet in 1955 to facilitate measurement. Block III was weeded in 1955. Except in a few plots that are not included in this study the competing vegetation was not dense enough to affect the growth of the planted trees appreciably.

Measurements and Scorings

November 1938. — (1-year seedlings.) Each provenance was scored for needle color (reported by Baldwin, 1956).

November 1941. — (2-2 transplants.) On 50 seedlings of each provenance, measurements were made of 1940 height, 1941 height, and average needle length (table 2 and figure 2).

February 1955. — (17 years from seed, 13 years from outplanting.) Each plot was scored for needle color (reported by Baldwin, 1955 and 1956).

June 1955. — (17 years from seed and 13 years from outplanting for height measurements; 18 years from seed and 14 years from outplanting for other measurements and scoring.) Total height (to the end of the 1954 growth), diameter at breast height, and diameter of the largest branch immediately below breast height were measured on 36 trees in each plot in blocks I, II and III, and on all trees in block IV. The 36 measured trees were distributed in 9 groups of 4 trees each (trees 3 and 4, 7 and 8, 11 and 12 in rows 3 and 4, 7 and 8, 11 and 12 for each plot). Thus, no border trees were measured. If one of the designated trees was missing, the nearest tree in the row was substituted. The heights were measured with an extension pole to the nearest foot. (One of every four trees was climbed to insure that the pole was even with the tip of the 1954 growth.) The diameter measurements were made with steel calipers to the nearest tenth inch.

Table 2. — *Average needle length of the 1940 shoots (measured in the autumn of 1941) of Scotch pine of the same provenances included in figure 2*
(Each provenance mean was based on the average of 50 trees)

Region	Provenances	Regional average	Range in provenance means
	No.	*Cm.*	*Cm.*
A (Scandinavia)	3	3.5	2.7 to 4.5
B (Scandinavia)	7	3.5	2.9 to 4.5
C (Scandinavia)	4	5.0	4.5 to 5.6
D (Scandinavia)	6	5.0	4.2 to 5.3
E (Scotland)	1	4.1	4.1
F (Latvia, Lithuania)	3	3.6	3.0 to 4 4
G (Germany, etc.)	21	5,4	4.9 to 6.3
H (Belgium)	2	5.7	5.6 to 5.9
I (Rumania)	2	4.0	3.7 to 4.4
J (Italy)	1	4.0	4 0

All trees in all measured plots were scored as living or dead. They were also scored for the presence or absence of basal sweep, lean, slight crook, more than one slight crook per tree, crook resulting in more than 1½ inches (offset the 1½ inches was estimated), porcupine damage, and cones. Scoring was done independently for each characteristic, and only the total number of trees in each class was recorded for each plot.

Statistical Analyses

Veen (1952) recommended the use of the standard errors of the plot means for determining the significance of provenance differences in these IUFRO tests of Scotch pine. Accordingly, standard errors were calculated for each plot for all measurements made in 1941 and 1955. However, there were too many cases in which the difference between the means of two plots of the same provenance exceeded twice the standard error of the plot means (table 3) to permit placing much reliance on the standard errors alone.

In determining the significance of differences between provenance and regional means, most reliance was placed on analyses of variance (table 5) and on Chi-square analyses. Altogether 37 different analyses of variance were necessary for the 1955 height data to make the grouping of provenances into homogeneous regions as objective as possible. Each of these analyses included all the provenances present in certain blocks. Most provenances were included in more than one analysis. In cases where there was doubt as to the correct placement of an intermediate provenance, that provenance was alternately included with one region and then with another for purposes of analysis.

The trees were originally planted on a close spacing and (except for the northern provenances) are now very crowded. In the past few years this crowding has slowed down diameter and branch growth to such an extent that it would be difficult to determine genetic differences in these characteristics. Therefore they were not subjected to statistical analysis although the regional means are included in table 4 for descriptive purposes.

Chi-square analyses were used to establish the significance of differences between plots, provenances, and regions in basal sweep, lean, slight crook, crook resulting in more than 1½ inches offset, porcupine damage, and fruiting. Many separate analyses were made for each characteristic. In general, differences between provenances from the same region were not admitted as statistically significant if there was overlapping between the provenances and significant difference between plots of the same provenance. Likewise, differences between regions were not admitted as statistically significant if there was considerable overlapping between the regions and especially where there were significant differences between provenances from the same region. Because of these precautions some possibly significant differences between provenances from the same region have probably been overlooked.

Observed plot means were used in all calculations of significance. However, for the calculation of the regional height means given in table 3, the plot means for blocks II and III were adjusted by adding 1.26 and 1.09 feet, the amounts by which the average height of block I exceeded those of blocks II and III respectively. This adjustment was necessary because of the unequal numbers of plots of different provenances in the different blocks, and because blocks II and III were significantly slower growing than blocks I and IV.

Personnel and Acknowledgements

H. I. Baldwin initiated the experiment and did or personally supervised all the seed sowing, lifting, planting, mapping, maintenance, and early measurement work. He assisted in the June 1955 measurements.

J. W. Wright supervised and assisted in the June 1955 measurements and performed the June 1955 scoring and the statistical analyses.

George M. Hopkins assisted with the seed sowing. Thomas M. Gaylord and Michael McArdle assisted with the June 1955 measurements and with the compilation of plot means. Employees of the Works Progress Administration performed some of the manual labor in the nursery. The outplanting was done by H. I. Baldwin with local labor.

Grateful acknowledgment is made to all these workers. The office and laboratory space provided for the Northeastern Forest Experiment Station by the Morris Arboretum of the University of Pennsylvania for the compilations and preparation of the manuscript is also deeply appreciated. Acknowledgment is also made to J. M. Fogg, Jr., H. L. Li, and R. A. Howard for help in preparing the taxonomic section; and to E. J. Schreiner, F. I. Righter, P. C. Wakeley, J. W. Duffield, Francois Mergen, and Robert Callaham for critical reading of the manuscript.

Results

Nursery Measurements

In 1940 there was a range in provenance means of the 2-1 transplants from 3.1 centimeters (IUFRO 1, Finland) to 24.5 centimeters (F-246, Belgium). In 1941 there was a range in provenance means of the 2-2 transplants from 6.7 to 55.3 centimeters. In 1940, 1941, and 1954 the same provenances were respectively smallest and largest. The 1940, 1941, and 1954 height data are plotted logarithmically in figure 2. The relationships between juvenile and 17-year growth are discussed in a later section.

The data on average needle length on 1940 shoots (measured in 1941) are presented in table 2. There was considerable overlap between regions in needle length. The provenances from regions A and B (northern Scandinavia), F (Latvia and Lithuania), and I (Rumania) had shorter needles than did the provenances from regions C and D (southern Scandinavia), region G (Germany, Poland, Czechoslovakia, and Hungary) or region H (Belgium).

General Appearance of the Plantings in 1955

When measured in 1955 the trees were 17 years old from seed (13 years old from outplanting) as regards height growth (measured to the tip of the 1954 growth) and 18 years old from seed as regards other characteristics.

In a typical 200-tree plot of continental origin the dominants were thrifty and 22 to 25 feet tall (nearly 30 feet tall on some of the Belgian plots), and the suppressed trees were spindly and 12 to 15 feet tall. Few suppressed trees had died, although many looked as if they would survive only a year or two more. On most trees the branches on the lower third or half of the bole were dead but had not yet dropped off. This made it difficult to traverse the plots rapidly. Except for an occasional opening caused by a weed tree that was not removed until 1951, the forest floor was almost devoid of shrubby or herbaceous vegetation.

There was no noticeable border effect where plots of continental provenance adjoin. Even where a plot of continental provenance bordered a plot of slow-growing trees from northern Scandinavia, the noticeable border effect was confined to the outermost row of trees in each plot (none of which were measured). In such cases the trees in the border rows differed from those in the centers of the plots considerably in diameter and branch size but little in height.

In the slower-growing 200-tree plots of central and southern Scandinavian provenance (regions C and D), crown closure took place in the past 2 or 3 years, and there has been little differentiation into dominants, codominants, and intermediates. Most of the branches were still alive, and the plots were very difficult to traverse. Some of the shrubby vegetation was still alive.

In the 200-tree plots of northern Scandinavian provenance (regions A and B), the crowns had not yet closed and the plots were very brushy. Almost every one of these plots had examples of thrifty 2- to 3-foot-tall trees that had survived for years in the light shade of hardhack or gray birch, which suggests a high degree of tolerance.

The differences between provenances were pronounced enough that a casual visitor to the 200-tree plots could tell at a glance whether a plot was of continental or Scandinavian origin. The differences between the various continental provenances were less pronounced, but an observer who was familiar with Scotch pine could distinguish between plots of Latvian, Belgian, or German provenance.

The 15-tree row plots on the Fox State Forest were free of weeds and had been pruned head-high. The various provenances maintained about the same rates of height growth (but not of diameter growth) on these row plots as on the large rectangular plots in spite of the fact that slow- and fast-growing provenances had often been planted side by side and that the fast-growing provenances seemed to be overshadowing the slow-growing ones. Differences between provenances were even easier to see in these row plots than in the rectangular plots because of the pruning and the closeness of the rows.

Because of the close initial spacing, the trees in these plantings have better form than is usual in Scotch pine plantings in the Northeast. This is unfortunate. However, it probably does not invalidate the results of the experiment unless there should prove to be no relation between the performance of a tree on a 4.2×4.2 foot spacing and the performance of the same tree on a 6×6 foot or 8×8 foot spacing.

1955 Measurements and Scorings

The results of the 1955 measurements and scorings are summarized in tables 3 and 4. The analyses of variance by which the provenances were grouped into regions are summarized in table 5. This grouping is such that provenances from the same region differ less from each other than they do from provenances from other regions. There are a few exceptions as noted below:

Basal sweep. — IUFRO Nos. 36, 37, 38, 44, and 45 (G, Poland and Germany) had as low percentages of trees with basal sweep as do the Latvian (F) provenances.

Total crooks. — IUFRO No. 49 (D, Sweden) had as high a percentage of trees with crooks as the German (G) population.

Large crooks. — IUFRO No. 50 (B, Sweden) had almost as high a percentage of trees with large crooks as the straightest Latvian (F) provenance (F-243).

Damage by Canada porcupine (Evethizon dorsatum L.). — IUFRO No. 3 (C, Finland) had as high a percentage of porcupine-damaged trees as many of the German (G) provenances.

Lean. — IUFRO Nos. 21, 23, and 24 (region G, Germany) have as high a percentage of leaning trees as does IUFRO 18 (H, Belgium).

Table 3. — *Summary of height data, by plots, for the IUFRO Scotch pine provenance test at the Fox and Vincent State Forests, Hillsboro and Deering, New Hampshire; all measurements in feet*

Region	IUFRO No. (Fox No.)	Mean heights of trees in block				Standard errors of mean plot heights in block			
		I	II	III	IV	I	II	III	IV
A	1	4.5	5.4	—	5.2	0.31	0.27	—	1.19
	5	5.8	—	—	5.3	0.32	—	—	0.94
	2	[1]6.9	—	—	5.5	[1]0.26	—	—	0.35
B	4	8.7	8.5	—	[1]10.8	0.50	0.60	—	[1]0.53
	46	9.1	10.2	10.3	10.6	0.38	0.26	0.41	0.71
	47	8.7	9.6	9.7	[1]9.1	0.40	0.37	0.60	[1]0.58
	50	10.8	11.6	10.4	7.5	0.50	0.40	0.36	0.55
	(F—144)	—	—	—	10.8	—	—	—	0.73
	(F—145)	—	6,0	—	11.2	—	0.72	—	0.60
	51	—	[1]9 8	—	8.7	—	[1]0.37	—	1.07
C	7	13.2	11.8	12.7	12.6	0.52	0.73	0.34	0.54
	3	[1]13.4	12.4	[1]13.4	12.7	[1]0.38	0.31	[1]0.23	0.63
	6	13.2	[1]12.8	14.0	14.9	0.45	[1]0.54	0.30	0.64
	8	13.7	13.4	—	13.0	0.62	0.54	—	1.04
D	9	[1]14.6	—	14.6	16.4	[1]0.39	—	0.61	0.51
	10	—	—	—	17,2	—	—	—	0.50
	29	16.3	—	12.8	[1]15.6	0.33	—	0.52	[1]0.48
	30	14.6	13.8	15.3	16.2	0.36	0.50	0.59	0.87
	48	14.9	15.9	13.9	15.3	0.44	0.48	0.53	0.39
	49	—	[1]15.5	—	[1]16.7	—	[1]0.45	—	[1]0.45
	(F—146)	—	—	—	16.7	—	—	—	0.64
	(F—147)	—	—	—	16.6	—	—	—	0.83
	(F—259)	—	—	—	16.4	—	—	—	0.91
E	17	16.6	14.4	—	12.4	0.57	0.37	—	0.72
	(F—261)	—	—	—	[1]13.8	—	—	—	[1]1.05
F	11	[2]17.5	[1]17.2	—	18.0	[2]0.32	[1]0.42	—	0.79
	32	[1]19.2	[1]18.3	—	18.6	[1]0.32	[1]0.38	—	0.93
	(F—243)	[1]17.6	—	18.9	20.2	[1]0.28	—	0.32	0.67
G	53	—	19.3	17.6	[1]20.7	—	0.51	0.31	[1]0.59
	55	[1]19.8	15.9	17.0	18.6	[1]0.41	0.42	0.47	0.62
	37	[1]19.4	—	18.0	19.7	[1]0.34	—	0.43	0.58
	38	19.9	19.5	—	19.6	0.54	0.43	—	0.67
	39	20.8	19.1	18.4	18.8	0.43	0.54	0.47	0.14
	40	[1]19.7	18.7	17.7	20.7	[1]0.32	0.47	0.45	0.49
	41	20.0	—	—	19.7	0.63	—	—	0.85
	54	20.2	—	—	19.7	0.49	—	—	0.76
	22	19.7	[1]18.7	—	18.7	0.48	[1]0.37	—	0.55
	20	[2]20.9	[1]18.6	19.2	18.9	[2]0.27	[1]0.45	0.56	0.93
	21	[1]19.8	[1]18.4	—	18.2	[1]0.35	[1]0.33	—	0.85
	23	19.7	18.3	—	18.9	0.62	0.40	—	0.75
	24	19.0	—	16.6	20.1	0.38	—	0.98	1.25
	35	[1]20.0	—	—	19.7	[1]0.37	—	—	0 60
	36	[1]20.6	—	19.1	19.2	[1]0.35	—	0.47	0.70
	42	19.3	19.5	—	20.2	0.48	0.57	—	0.51
	43	20.0	—	19.4	18.0	0.50	—	0.70	0.38
	44	21.5	20.8	17.4	19.7	0.37	0.52	0.54	0.71
	45	19.7	19.3	17.5	17.8	0.54	0.44	0.34	0.60
	25	20.2	18.6	—	[1]18.1	0.41	0.54	—	[1]0.86
	(F—232)	—	—	—	19.9	—	—	—	0.64
H	18	22.9	19.9	20.9	23.8	0.40	0.78	0 40	0.73
	(F—246)	—	21.6	—	22.2	—	0.49	—	0.76
I	14	18.0	[1]15.8	[1]18.4	17.6	0.63	[1]0.34	[1]0-30	1.14
	34	18.4	16.0	17.0	14.3	0.59	0.52	0.35	1.08
J	31	16.6	—	—	18.2	0.52	—	—	0.86
K	19	19.8	—	—	17.5	0.55	—	—	0.76

[1]) Based on two plots in the same block. [2]) Based on three plots in the same block.

Table 4. — *Summary of growth data of the Scotch pine racial test (IUFRO) at the Fox and Vincent State Forests, New Hampshire*

Region	Origins	Plots	Trees: Living	Trees: Dead	Average height	Average D. b. h.	Average branch diam.	Trees with — Basal sweep	Lean	Crooks	Large crooks	Porcupine damage	Fruit
	No.	*No.*	*No.*	*Percent*	*Feet*	*In.*	*In.*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
A Scandinavia	3	8	631	38	[6]) 5.60	0.40	0.15	0	[2]) 0	[1])54	[6]) 1	[2]) 0	[1, 2]) 9
B Scandinavia	7	23	1849	32	[5]) 9.61	1.30	.39	[4]) 0	[2]) 0	65	[3])11	[2])(T)	[1, 2])13
C Scandinavia	4	18	2083	22	[4])13.11	2.21	.54	[3]) 3	[2]) (T)	59	[3])15	[2]) 1	[1, 2]) 5
D Scandinavia	9	24	2160	19	[3])15.47	2.81	.72	[3]) 2	[2]) (T)	[1, 2])54	[2])26	3	(T)
E Scotland	2	5	312	28	[2])14.68	2.66	.47	[3]) 2	2	49	[2])15	[2]) 0	9
F Latvia	3	15	1875	24	[2])18.45	3.10	.69	[2]) 7	2	63	[2])27	5	1
G Germany, etc.	21	76	8253	26	19.74	3.45	.80	[1])21	[1]) 5	68	[1])40	5	1
H Belgium	2	6	521	32	[2])22.47	3.80	.84	[2])43	[2])13	69	[3])46	10	[2]) 9
I Rumania	2	10	1055	30	[2])17.90	2.88	.69	[4])15	2	[2])44	[2])26	7	4
J Italy	1	2	148	20	[2])17.40	3.42	.72	[4])20	0	69	[4])33	0	6
K Netherlands	1	2	361	11	[4])18.63	3.33	.85	[4])30	7	67	[4])38	8	6

(T) — Trace, less than 0.5 percent.
[1]) — Significant differences within region.
[2]) — Significantly different from Region G (Germany, Poland, Czechoslovakia, Hungary).
[3]) — Significantly different from Region F (Latvia).
[4]) — Significantly different from Region D (Scandinavia).
[5]) — Significantly different from Region C (Scandinavia).
[6]) — Significantly different from Region B (Scandinavia).

Most of the dividing lines between groups of provenances run roughly east-west (figure 1). This indicates that temperature, day-length, or other factors that normally vary from north to south have caused more genetic differentiation than have rainfall, soil, or other factors that might vary in an east-west direction. Some of the discontinuities between regions correspond to range discontinuites such as the Baltic Sea. There are no significant differences between provenances from different altitudes in the same region. As pointed out in a later section, both population structure and selection pressure seem to have played large parts in regulating the pattern of genetic differentiation.

Surprisingly, the slow-growing Scandinavian provenances maintained their height growth (but not their diameter growth) as well in the 15-tree row plots (Block IV) as in the 200-tree rectangular plots (tables 3 and 5). This was true even though many of the Scandinavian row plots were overtopped by plots of continental provenances in the 15-tree row plots.

There are more significant differences between provenances in height than in any of the other characters that were scored as present or absent. This may indicate more genetic differentiation in growth rate than in other characteristics. Or it may be merely a consequence of the fact that quantitative characters ar susceptible to more precise statistical analysis than qualitative characters.

Two types of off-vertical growth were recognized in the plantations — basal sweep involving the lowermost one or two feet of the bole, and lean involving almost the entire bole. Winter observations made at various times during the life of the plantings indicated that most of the off-vertical growth was due to snow pressure. In certain sections of the plantings the lean was very pronounced. This resulted in a contagious distribution for the data on lean: in the border rows adjacent to susceptible provenances there were sometimes leaning trees in the resistant provenances. The Scandinavian and Latvian provenances were less subject to basal sweep and lean than were most of the continental provenances.

The measurements show that the Italian plots are finer-branched than the German plots. This is contrary to the general impression gained while climbing and measuring the trees. This discrepancy indicates that the expression

Table 5. — *Summary of analyses of variance made on mean heights of plots*

Analysis includes plots from: Regions	Blocks	Significance attached to variance due to — Block	Region	Provenance within region
Analyses Including Scandinavian Provenances				
A, B, C, D, E,	I, II	0	**	—
B, C, D	I, III	0	*	0
B, C, D	I, III	0	**	0
C, D, F	I, II, III, IV	—	**	0
A, B	I, II, III, IV	—	**	0
A, B	I, IV	0	**	0
B, C	I, II, III, IV	0	**	0
C, D	I, II, III, IV	0	**	0
C, D	I, II, III, IV	—	*	0
C, D	I, II, III, IV	0	**	0
[1]C, D	I, II, III, IV	—	0	0
[1]C, D	I, II, III, IV	0	0	0
D, F	I, II, III, IV	0	**	0
A	I, IV	0	—	0
A	I, II, IV	—	—	0
B	I, II, III, IV	—	—	0
Analyses Including Continental Provenances				
E, F, G, H, I	I, II	**	**	0
F, G, H, I	I, III	*	*	0
B, C, F, G, I	II	0	0	0
D, F, G	I	0	**	—
D, F, G	I	0	**	0
F, G, H	I, II	**	**	—
F, G	I, II	*	**	0
F, G	I, IV	*	**	0
F, G	I	0	*	0
[2]F, G	I, II, IV	0	0	0
[2]F, G	I, II, IV	0	0	0
F, I	I, II, IV	0	0	0
F	I, II, IV	0	—	0
G, H	I, IV	0	**	0
G, I	I, III	**	*	0
G, I	I, II, III, IV	**	*	0
G, J	I, IV	0	**	0
G	I, IV	0	—	0
G	I	0	—	0
G	I, III, IV	0	—	0
[3]G	I, III, IV	*	—	0

* Significant at the 5-percent level.
** Significant at the 1-percent level.
[1]) IUFRO Nos. 9 and 29 were grouped with region C in these analyses to determine whether they properly belong with region C or region D.
[2]) These analyses included IUFRO 55 from region G as well as provenances from region F.
[3]) This analysis includes only IUFRO Nos. 37, 39, and 55.

(number of branches per whorl) × (average branch size) would have given more useful information than did diameter of the largest branch immediately below breast height.

Nearly all the crooks occurred at nodes and were due to removal of the terminal bud by some external agency. Field observations made in several years by H. I. BALDWIN indicate that the eastern evening grosbeak *(Hesperiphona vespertina)*, pine grosbeak *(Pinicola enucleator)*, and the eastern red squirrel *(Sciurus hudsonicus)* were the culprits in most cases.

Even the smallest crooks (often with only 1/4 inch offset) were counted in scoring the trees for crook. Of course it was difficult to see all the crooks on the larger trees. For that reason the apparently larger numbers of crooks in the northern Scandinavian provenances (Region B) may be an artifact. However, the fact that the southern Scandinavian (region D) and Rumanian (Region I) provenances have significantly fewer trees with small crooks than do the taller German (Region G) provenances is not an artifact. It may indicate that squirrels and grosbeaks prefer the German provenances. On the same plots there were no apparent differences between large and small trees in the percentage of trees with small crooks, but leaning trees seemed to have fewer small crooks than upright trees.

There were larger differences between regions in the percentage of trees having large crooks (more than 1½ inches offset) than in the percentage of trees with crooks of any size (table 4). The continental provenances from regions G and H had the highest percentages of trees with large crooks. Observations made in the tree tops indicated that these large crooks resulted from damage to the terminal and several lateral buds on the leader. When this happened the leader remained alive but lost its dominance. Its place was taken by the uppermost lateral branch, and a large crook resulted.

Porcupine damage was usually localized (contagious distribution). Also, it was usually limited to the largest trees on a plot. The contagious distribution and the large plot size made it difficult to detect significant differences between continental provenances. The significantly smaller amount of damage to the plots of Scandinavian provenance may be due more to the small size of those trees than to any taste preference for the continental provenances.

The porcupines unwittingly made beautiful demonstrations of the value of girdling as a fruit-induction measure in certain parts of the plantings. Generally, complete girdling was followed by a reduction in needle length, some slowing down of height growth, a swelling above the girdle (often of more than one inch), moderate to heavy fruit production, and ultimately (after 4 or 5 years) by death of the tree above the girdle. The heaviest fruit production seemed to take place 2 or 3 years after the girdling.

In scoring the trees for fruit production, no distinction was made as to whether the fruiting trees had or had not suffered porcupine damage. This does not account for the heavy fruiting of the Scandinavian and Belgian provenances, for in these cases the heavy fruiting occurred on plots that had not been porcupine-damaged. Thus the significantly greater amount of fruiting on those provenances (table 4) can be regarded as due to inherent differences in early flower or fruit production under New Hampshire conditions.

The fruiting behavior pattern is more complex than can be explained simply on the basis of day length or growth rate. At present no explanation can be offered as to why the heaviest fruiting occurred on the slowest growing provenances from northern latitudes (regions A and B) and also on the fastest growing provenances from Belgium (region H.).

Relationship between 1940, 1941, and 1954 heights

The logarithm of the 1940, 1941 and adjusted 1954 heights of 50 provenances are plotted in figure 2. This method of plotting was chosen because it emphasizes percentage rather than actual differences. The following tabulation was prepared from figure 2 to show the accuracy with which the 1954 heights could be forecast from the 1940 and 1941 height data.

	Provenances (out of a possible 50) having differencies in height of less than —	
	5 percent	26 percent
(Years)	*(Number)*	*(Number)*
1940 vs. 1941	28	46
1940 vs. 1954	16	38
1941 vs. 1954	30	42

Correlation coefficients that were calculated from the 1940, 1941, and (adjusted) 1954 provenance mean heights are presented in the following tabulation. With 48 degrees of freedom all the correlation coefficients are significant at the 1-percent level:

Correlation by years	*Correlation coefficient (r)*
1940 with 1941	0.860
1940 with 1954	.933
1941 with 1954	.861

These tabulations speak for themselves. The 17-year heights can be forecast with a great deal of accuracy from the nursery measurements. Undoubtedly the accuracy could be increased if the nursery tests as well as the field plantings had been replicated.

Our results confirm those of JOHNSSON (1955) with Scotch pine in Sweden. In a 10-progeny test (involving 6 different provenances) at Boxholm, he found a statistically significant correlation ($r = 0.942$) between 8-year and 17-year height. In another 34-progeny test (involving 10 different provenances) at Boxholm he found a statistically significant corelation ($r = 0.798$) between 8-year height and 17-year stem volume.

Applicability of the New Hampshire Results in other Regions

There are other published reports of American provenance tests with Scotch pine (RUDOLF, 1950, 1951; CRAM and BRACK, 1953; MCGREGOR, COWAN, and SPURR, 1954, VAARTAGE, 1954; HEIMBURGER, 1954), but for one reason or another their results are not considered comparable with the results of the present test. Therefore the general applicability of the results of the present study to other parts of the United States and Canada can be judged best by comparison with the results of some of the European investigators who have had adequate data on seed origin and have studied more than a single plot of each origin (Tables 6 and 7).

However, such comparisons must be made with caution because of the lack of precision in the European experi-

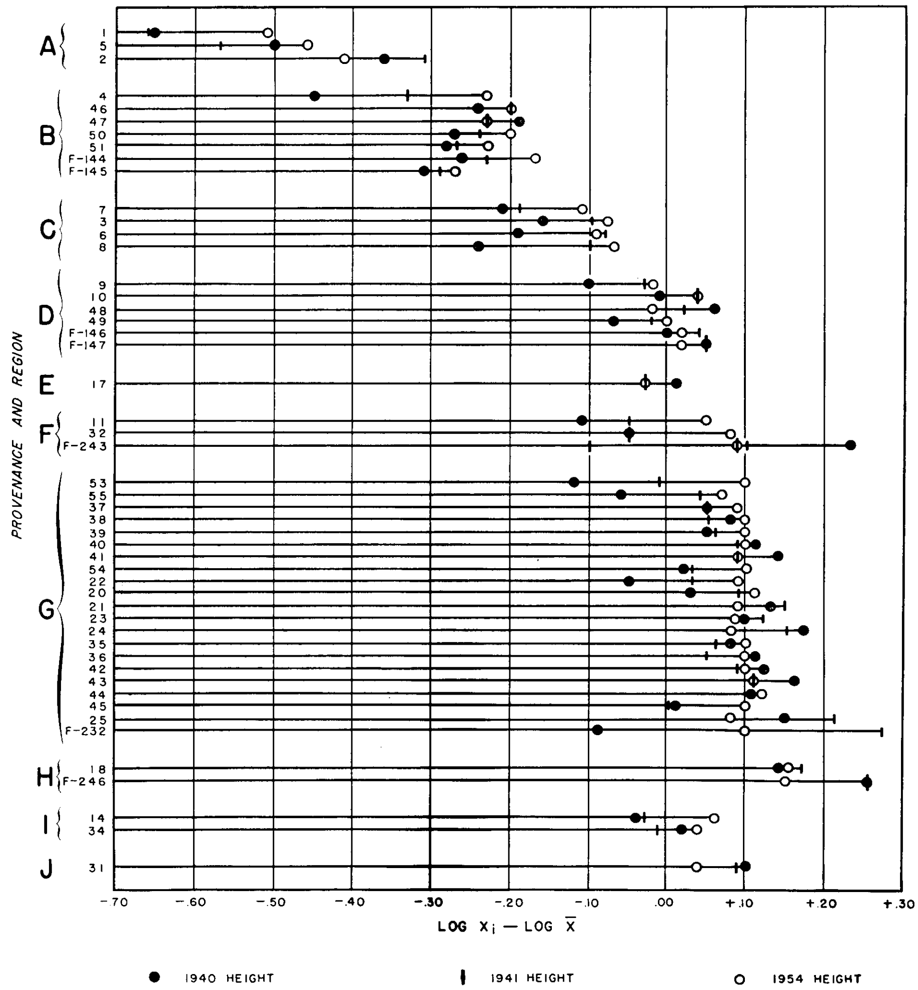

Figure 2. — The relationship between third-year (1940), fourth-year (1941), and seventeenth-year (1954) heights of Scotch pine as shown by plotting the logarithms of the deviations of the provenance means from the mean for the year (log $x_i / \bar{x}$). All heights are expressed in millimeters.

ments cited. Only Vincent and Polnar's (1953) experiment would be considered replicated, and their plots were on such variable sites that analyses of variance (made by the present authors) could show the presence of significant (at the 5-percent level) differences only between the Scandinavian-Latvian and the German-Czechoslovakian-Belgian populations. In Wiedemann's (1930) and Langlet's (1937) experiments, the sets of plots of different provenances were located in different regions. In Johnsson's (1955) experiment several seedlots from the same geographic origin were outplanted in the same locality, and identical seedlots were outplanted more than once in different regions.

The results of the New Hampshire and European tests agree in showing that the Belgian provenances grew fastest, that the German and Latvian provenances grew faster than the Scandinavian provenances, and that the south Scandinavian provenances grew faster than the north Scandinavian provenances (tables 6 and 7). In Johnsson's tests, however, the growth superiority of the south Scandinavian over the north Scandinavian provenances is evident only when the tests were conducted in south Sweden. His data indicate a probable source-site interaction in that the southern provenances do best in a southern locality and the middle provenances do best on an intermediate planting site.

The similarity of results in different regions is also evident in characteristics other than growth rate. The New Hampshire plots can be characterized in much the same words used by Wiedemann (1930). He described the Latvian and Eeast Prussian provenances (our regions F and G) as fine-branched, straight, and slender; the German provenances (our region G) as fine- to coarse-branched, having horizontal branches and crooked stems; the Belgian provenances (our region H) as rather fine-branched, with straight to very crooked boles. Langlet's (1936) data on needle color in Sweden (table 8) agree with Baldwin's (1955, 1956) data on needle color in New Hampshire.

The agreement between the European and American results suggests that, within the limits of experimental error, the results of the present study are probably applicable within a radius of at least 200 or 300 miles of Hills-

Table 6. — *Relative growth rates of Scotch pine provenances tested in various regions*
(All heights expressed as percentage of standard values)

Region	Present study (New Hampshire)	Wiedemann, 1930 (Germany, Belgium, Sweden, Hungary, The Netherlands)	Langlet, 1936 (Sweden)	Vincent and Polnar, 1953 (Czechoslovakia)
	Percent	*Percent*	*Percent*	*Percent*
A (Scandinavia)	30	75	49	—
B (Scandinavia)	52	—	59	—
C (Scandinavia)	71	—	82	76
D (Scandinavia)	84	—	[1]84	91
E (Scotland)	80	93	—	89
F (Lativa, Esthonia)	100	[1]100	—	[1]100
G (Germany, etc.)	107	93	—	97
H (Belgium)	122	120	—	114
I (Rumania)	97	—	—	80
K (Netherlands)	101	—	—	112
	Number	*Number*	*Number*	*Number*
Origins	55	11	11	29

[1]) Standard value (assumed equal to the mean for the same region in the present study) from which all other values in the column were calculated.

Table 7. — *Ranges in heights and average heights (in parenthese) of 15-year-old individual tree progenies of Scotch pine from our regions B, C, and D; data given by Johnsson (1955)*

Outplanting site	Plots	Provenances from region — B	C	D
	Number	*Feet*	*Feet*	*Feet*
Boxholm (58°N.)	54	11.7—16.3 (14.4)	14.7—17.8 (16.9)	16.5—19.5 (17.6)
Dalfors (61°N.)	44	15.7—18.3 (17.0)	15.5—19.9 (17.5)	15.5—18.7 (17.2)
Rörström (64°N.)	52	7.3— 9.6 (8.3)	8.1—10.0 (9.2)	7.2— 9.7 (8.3)

Table 8. — *Needle and plant characteristics of Scotch pine seedlings grown at Tönnersjöheden (columns 1, 3, 5, 6, 9, 10), Kulbacksliden (columns 2,4), Lerje (column 7) and Torsskulla (column 8), Sweden*
(Data were derived from LANGLET [1936, tables 25, 27, 28, and 29]. Underlining signifies a discontinuity between regions.)

Region and provenance	North latitude	(1) Needle length	(2)	(3) Needle weight	(4)	(5) Proportion of mature needle length evident on June 3	(6) Plant height	(7)	(8)	(9) Needle color: Blue-green	(10) Yellow-green
		mm.	*mm.*	*mg.*	*mg.*	*Per-cent*	*cm.*	*cm.*	*cm.*	*Per-cent*	*Per-cent*
A Alta	70°	23.9	45.5	18.8	59.3	50.0	—	—	—	0	96
Övertorneå	69°23'	—	45.0	—	58.2	—	—	—	—	—	—
Tranöy	69°10'	25.5	46.7	25.3	58.0	43.6	20.2	15.2	15.9	0	93
Malselv	69°	25.6	48.9	20.6	62.2	46.9	—	—	—	0	97
Skjomen	68°15'	25.6	50.7	26.3	60.7	37.8	18.7	13.9	14.8	0	87
Storbacken	66°30'	26.6	—	25.3	—	31.9	—	—	—	0	87
Overkalix	66°20'	26.3	—	24.3	58.9	34.2	—	—	—	0	88
Lappträsk	66°02'	27.0	42.7	21.7	54.8	36.0	18.7	14.1	13.0	0	87
B Bodens Revir	65°50'	31.0	46.9	27.8	52.3	27.5	—	—	—	0	[1])88
Hällnäs	64°20'	32.3	48.3	28.9	54.5	25.1	25.7	17.4	15.8	0	69
Vindeln	64°11'	31.8	51.7	27.2	63.6	25.5	—	—	—	0	61
Vindeln	64°11'	31.9	50.5	29.8	60.8	24.7	—	—	—	0	67
C Torp	62°30'	—	46.9	—	49.9	—	—	—	—	—	—
Njurunda	62°16'	—	—	—	—	—	36.7	18.7	24.4	—	—
Gloppen	61°50'	35.3	48.3	28.6	52.9	16.1	34.7	22.6	23.0	12	0
Svanöy	61°33'	40.5	54.2	[1])37.7	64.1	16.5	36.2	24.2	26.3	66	0
Älvdalen	61°25'	37.1	53.4	31.1	65.3	19.7	—	—	—	9	0
Siljansfors	60°55'	37.2	53.8	28.5	59.0	16.8	—	—	—	11	0
Voss	60°40'	38.6	53.1	34.4	61.9	16.9	—	—	—	59	0
D Ruskåsen	60°22'	—	50.1	—	51.7	—	—	—	—	—	—
Koppom	59°43'	—	53.2	—	59.7	—	—	—	—	—	—
Dalarö	59°08'	46.5	53.0	38.0	34.9	11.8	—	—	—	30	2
Grimsten	59°	43.0	50.1	41.0	41.0	13.7	36.9	20.4	21.7	19	1
Karlsby	58°38'	49.0	53.8	43.3	51.3	12.5	—	—	—	68	0
Gyltige	56°46'	48.2	57.2	39.8	53.4	12.9	38.7	24.3	25.9	76	0
Värnanäs	56°30'	43.3	43.8	[1])29.0	27.0	10.9	38.7	21.1	22.8	8	1
Karlsholm	56°07'	25.4	—	37.3	—	9.6	—	—	—	40	0

[1]) An exception to the grouping indicated.

boro — over much of New England and New York. Perhaps farther north — in Quebec — the Scandinavian provenances would show up relatively better than they did at Hillsboro.

Ecotypes, Clines, or Geographic Varieties?

The analyses of variance and Chi-square analyses performed on the authors' data indicate the presence of discontinuous variation in Scotch pine (tables 4 and 5). There are discontinuities in height growth (between regions A and B, B and C, C and D, E and F, F and G, G and H) and in the percentage of trees with large crooks, fruit, or lean (between regions A and B, C and D, G and H) that cannot be explained by incomplete sampling of the range (table 1, figure 1). Thus, Scotch pine may be regarded as being composed of a number of geographic ecotypes. Some of these ecotypes appear to be identical with already named and described geographic varieties (see below).

This interpretation of the variation pattern in Scotch pine is similar to that given by WIEDEMANN (1930), but differs from that given by LANGLET (1936) and LINDQUIST (1946, 1948). Few of the Scotch pine provenance tests of other investigators have been conducted with sufficient replication or precision to warrant drawing conclusions on discontinuous variation.

WIEDEMANN (1930) summarized his conclusions (based on a survey of published reports of the 1907 IUFRO provenance tests, on his own plots, and on observations of non-experimental plots in Germany) as follows:

"*According to the conclusions quoted in Section III, in general there is uniformity of growth characters within the various race regions* so that in most cases the results of the International Experiment and the other race investigations can be carried over to the races concerned *in toto*. In these experiments as well as in practice, the susceptibility of the southern [Scotch] pine to needle cast, the crookedness and susceptibility to snow break of the southwest German pine, and the exceedingly straight narrow form of the East Prussian and Belgian pine are apparent." (Translation by J. W. WRIGHT. Italics are WIEDEMANN'S.)

LANGLET'S (1936) nursery studies are the most extensive Scotch pine provenance tests yet reported in the literature. He measured percent dry weight in 582 Swedish provenances, and other characteristics in 10 to 27 Swedish provenances. From these studies he concluded that most of the variation in Scotch pine in Sweden was continuous from north to south and from low to high altitudes.

LANGLET'S (1936) conclusion that there is north-south variation in Scotch pine in Sweden is indisputable, but his conclusion that this variation is continuous is open to doubt. His data show discontinuities not explainable by incomplete sampling between regions A, B, C, and D in several characteristics such as needle length, needle weight, proportion of mature needle length evident on June 3, plant height, and needle length evident on June 3, plant height, and needle color (table 8). On the other hand, the data for percent dry weight for 582 provenances (LANGLET, 1936, pp. 407—419) do seem to form a continuous north-south gradient; the mean dry-weight percents for seedlings grown in a uniform nursery were respectively 32.9, 32.9, 33.5, 33.7, 34.4, 35.2, 34.9, 35.5, 35.8, 36.4, 37.4, and 38.2 percents for seedlings originating from the twelve 1° intervals from 56°0' N. to 67°59' N. latitude. It should be pointed out, however, that small (2 to 3 percent) discontinuities in this percent dry-weight data may have been masked by the relatively large measurement error and the lack of replication. Each provenance mean (= plot mean) contained a measurement standard error (due to the necessity of making dry-weight determinations at different times of year and correcting for time of year) of about 1 percent mean dry weight (= about 10 percent of the difference between extremes).

Among the most widely quoted seed-collecting recommendations are those given by LINDQUIST (1946, 1948), derived from LANGLET's data. They, too, are based on the clinal hypothesis. For Scotch pine in southern Sweden they call for the collection of seed within 250 kilometers north-south distance or within 300 meters elevation of the planting site.

Most of the evidence from the Hillsboro study indicates that the variation in Scotch pine is discontinuous. Much of the evidence from other studies supports (or at least does not refute) this hypothesis. Therefore one might well revise the standard seed-collecting recommendations to read: "Collect seed from within the boundaries of the geographic ecotype best suited to the planting area." This may permit the safe transfer of seed for several hundred miles or for only a few miles.

The manner in which a discontinuous pattern of genetic differentiation arose in response to continous variation in the environment need not be puzzling if we remember that selection pressure is only one of the factors involved in genetic differentiation of a species. Population structure is often equally important. In a dense continuous population there may be relatively strong selection pressures but relatively little genetic differentiation because of continual gene interchange between distant parts of the population. If, however, this gene interchange is slowed down by small range gaps or areas of light population density, genetic differentiation can proceed in response to differences in selection pressure.

Taxonomy

Taxonomic names are applicable in a wider variety of circumstances than are ecotype names. Thus it is desirable to indentify the geographic ecotypes with previously described taxonomic varieties whenever possible. The following list was compiled from BEISSNER (1891); DALLIMORE and JACKSON (1948); ELWES and HENRY (1908); ROL, POURTET, and DUCHAFOUR (1944); REHDER (1940); and REHDER (1949). Unfortunately the list is incomplete. It does not include such presumably valid geographic varieties as *P. sylvestris* var. *engadinensis* (HEER) HEGI, *P. sylvestris* var. *nevadensis* CHRIST, and *P. sylvestris* var. *uralensis* FISCHER; nor does it correctly dispose of the geographic ecotypes from southern Scandinavia, Rumania, and Italy. We have made no attempt to describe new varieties from the New Hampshire plantings to cover those segments of the population for which no varietal names have been proposed. To do so would require a comprehensive herbarium and field study of the trees as they occur in their native habitats.

The ecotype in region G (Germany, Czechoslovakia, Poland, and Hungary) is tentatively regarded as *P. sylvestris* L. var. *sylvestris*. Photographs of two of LINNAEUS' specimens in the herbarium of the Arnold Arboretum have notations on them indicating Switzerland as the probable locality of origin.[3]) HEER (BEISSNER 1891) evidently followed this same interpretation, as he called the German population *P. sylvestris* a. *genuina* HEER.

The ecotype in region A (northern Scandinavia) is *P. sylvestris* var. *lapponica* (FRIES) HARTMANN. As compared with the type variety it is very slow growing; has a narrower and more pyramidal crown; has shorter, straighter, and stiffer leaves remaining alive for 4 to 7 years; has more resinous buds and redder bark; and has smaller cones with hook-like apophyses.

The ecotyye in region E (Scotland) is *P. sylvestris* var. *scotica* WILLD. As compared with the type variety, it is slower growing, straighter, and shorter needled.

The ecotype in region F (Latvia, Esthonia) is *P. sylvestris* var. *rigensis* LOUDON. As compared with the type variety, it is a little slower growing, has very red bark, and a tall straight stem. Possibly the variety extends eastward into Russia. WIEDEMANN (1930) considered that "there was a great similarity between the Latvian and East Prussian races . . ." However, our tests indicate that the East Prussian material belongs to *P. sylvestris* var. *sylvestris*.

The type locality for *P. sylvestris* var. *haguenensis* LOUDON is the forest at Hagenau, Alsace, France. ROL, POURTET, and DUCHAFOUR's (1944) description (which we use here) is based on material grown in the arboretum at Les Barres, France, from seed collected at Hagenau, possibly by LOUDON. As compared with the type variety, *P. sylvestris* var. *haguenensis* is faster growing, has a more flexible bole, less red bark, and coarser branches. This description fits our Belgian material (region H) and WIEDEMANN's (1930) material from Campine, Belgium.

Notes on Experimental Design

These plantings can teach us several lessons about experimental design. One is the need for replication. In the majority of provenances at least one difference between plot means exceeded twice the standard error of the plot means (table 3). Thus, even when the planting site is as uniform as in the present experiment, data from unreplicated plots can easily be misinterpreted.

In this, as in other IUFRO tests, the plots were completely randomized. It would have been better if the plots had been randomized in blocks, so that each provenance was represented once in each block. As it is, data from only 12 of the 25 plots of Rumanian and Latvian provenance could be used in a single analysis of variance to settle the important question as to whether the trees from those two regions differ significantly in growth rate.

One of the supposed disadvantages of the use of small row plots is the fact that, as the crowns close, the large provenances tend to crowd out the shorter provenances, causing an accentuation of growth-rate differences. Therefore it is widely accepted that growth data from row plots are unreliable after the crowns close.

The Hillsboro series of plots offered one of the most rigorous possible tests of the importance of this possible accentuation of growth-rate differences. Crown closure took place several years ago because of the close initial spacing, and the slowest growing provenances from northern Scandinavia grew only 25 percent as fast in height as the Belgian provenances. (In very few species would we expect a 4 to 1 ratio in height growth between the tallest and shortest provenances.) The anticipated accentuation of heigh-growth differences did not appear, for there are no significant differences in height growth between the row plots (block IV) and the large rectangular

[3]) R. A. HOWARD, personal communication.

Table 9. — *Comparison of growth-rate data (13 years after outplanting) obtained from 200-tree rectangular plots (block I) and from 15-tree row plots (block IV)*

Region	Block I (Rectangular Plots)			Block IV (row plots) as a percentage of Block I		
	Height	Diameter	Branch diameter	Height	Diameter	Branch diameter
	Feet	*Inches*	*Inches*	*Percent*	*Percent*	*Percent*
A	6.0	—	—	90	—	—
B	9.5	1.9	0.53	104	58	60
C	13.0	2.6	.52	102	69	87
D	15.2	2.8	.67	107	96	106
F	17.2	3.1	.69	110	95	90
G	19.7	3.4	.79	99	100	99
H	21.4	3.3	.80	107	139	117

plots (block I) for any of the provenances (tables 3, 5, and 9.)

There was, however, an accentuation of differences in stem diameter and branch diameter involving the very slow-growing provenances (regions A, B, and C) and the very fast-growing provenances (Belgium, region H). In the moderately fast-growing provenances from regions D, F, and G there was no accentuation of either height- or diameter-growth differences.

It is likely that the row plots in block IV made possible more precise estimates of the differences between provenance means than did the rectangular plots in blocks II and III. This was true in spite of — or perhaps because of — the smaller numbers of trees in the row plots. Especially in block III there was noticeable variation in site (and in resulting hardwood competition) and in frequency of porcupine damage from one end of the block to the other end. A few of the plots had so few live trees that they were not even measured, and others were so variable that it might have been better if they had not been measured.

These findings indicate that, in Scotch pine plantings 17 years old from seed, with a close initial spacing of 4.2 × 4.2 feet, small row plots and large rectangular plots give equally valid data on height growth for provenances 6.0 to 21.4 feet tall, and on stem-diameter and branch-diameter growth for provenances 15.2 to 19.7 feet tall.

Summary

One of a series of International Union of Forest Research Organizations Scotch pine provenance tests was established on the Fox and Vincent State Forests, near Hillsboro, New Hampshire. The seeds were sown in 1938, and the seedlings were outplanted on abandoned fields in 1942. The trees were spaced 4.2 × 4.2 feet in the outplantings. These outplantings covered about 12 acres, and consisted of 117 200-tree rectangular plots and of 72 15-tree row plots. (These figures do not include plots that were not measured because of excessive mortality or excessive hardwood competition.) Light weedings in 1951 and 1955 sufficed to keep the measured plots free of serious condition.

In November 1941 the 3-year height, 4-year height, and needle length of each provenance were measured. In June 1955 height, diameter, and branch diameter were measured on 36 trees in each 200-tree plot and on an average of 11.3 live trees in each 15-tree row plot. Also in 1955 the presence or absence of basal sweep, lean, small crooks, large crooks (more than 1½ inches offset), porcupine damage, and fruit was scored on all trees. All conclusions as to the statistical significance of differences between provenances were based on analyses of variance or on *Chi-square* analyses of the 1955 data.

There were statistically significant correlations ($r = 0.933$ and 0.861 respectively) between 3- or 4-year height and 17-year height.

The statistical analyses indicate that most of the geographic variation in Scotch pine is discontinuous, not clinal. This interpretation of the variation pattern is in harmony with most of the data obtained from the replicated experiments of Wiedemann (1930) and Langlet (1936), but differs from some published interpretations of those data.

The Scotch pine provenances grown in this experiment may be grouped into seven geographic ecotyps: northern Scandinavia, north-central Scandinavia, central Scandinavia, southern Scandinavia, Latvia-Esthonia, Germany-Poland, Czechoslovakia-Hungary (including certain planted Netherlands trees), and Belgium (planted trees, possibly of French provenance).

There was insufficient replication to settle definitely the ecotypic status of the Scottish provenances (similar to provenances from southern Scandinavia), the Rumanian provenances (similar to the Latvian provenances), and the Italian provenances. There are probably additional geographic ecotypes in untested portions of the species' range. With a few exceptions there were no statistically significant differences between provenances assigned to the same geographic ecotype; but there were statistically significant differences between provenances assigned to different geographic ecotypes.

The Latvian-Esthonian ecotype was moderately fast growing (18.5 feet in 17 years from seed) and had satisfactory bole form. It seems to be the most satisfactory for forest planting in New Hampshire. The Belgian ecotype was the fastet growing (22.5 feet tall in 17 years from seed) but had the most basal sweep, lean, large crooks, and porcupine damage. The ecotype from Germany-Poland-Czechoslovakia-Hungary was next fastest growing (19.7 feet tall in 17 years from seed), and had second-most basal crook, lean, large crooks, and porcupine damage. A few provenances in this ecotype were satisfactory in bole form. The Scandinavian ecotypes were slow-growing (5.6, 9.6, 13.1, and 15.5 feet tall respectively in 17 years from seed), but had few bole defects.

Baldwin (1955 and 1956) reported winter foliage color of these plantings in a separate publication. The continental ecotypes, which remain green in the winter, are more satisfactory for Christmas tree growers than the Scandinavian ecotypes, which turn yellow in the winter.

The slow-growing northern Scandinavian and fast-growing Belgian trees fruited most heavily. Fruiting behavior seems too complex to be explained by day length or growth rate alone.

Certain of the geographic ecotypes can be identified with previously described taxonomic varieties: *Pinus sylvestris* L. var. *sylvestris* (Germany-Poland-Czechoslovakia-Hungary), *P. sylvestris* var. *lapponica* (Fries) Hartmann (northern Scandinavia), *P. sylvestris* var. *scotica* Willd. (Scotland), *P. sylvestris* var. *rigensis* Loudon (Latvia-Esthonia), and *P. sylvestris* var. *haguenensis* Loudon (planted Belgian trees).

The experiment yielded much useful information on experimental design. One of the most important findings is that slow- and fast-growing provenances grew in height at the same rate in large rectangular plots as in row plots.

Résumé

Titre de l'article: *l'expérience de l'Union Internationale de 1938 sur les provenances de pin sylvestre en New Hampshire.* —

Une des expériences de provenances de pin sylvestre organisées par l'Union Internationale des Recherches Forestières fut établie dans les forêts d'Etat de Fox et Vincent, près de Hillsboro, New Hampshire. Les graines furent semées en 1938, et les plants mis en place sur des terrains agricoles abandonnées en 1942, à l'espacement de 4,2 × 4,2 feet (1,25 × 1,25 mètres). Ces plantations occupaient environ 12 acres (4,8 hectares) et comprenaient 117 placeaux rectangulaires de 200 arbres chacun et 72 placeaux linéaires de 15 arbres. (Ces chiffres ne comprennent pas les placeaux qui n'ont pas été mesurés en raison d'une mortalité excessive ou d'une très forte concurrence des feuillus). De légers dégagements en 1951 et 1955 ont suffi à garder les placeaux en bonne condition.

En novembre 1941, on a mesuré la hauteur à 3 ans, la hauteur à 4 ans et la longueur des aiguilles de chaque provenance. En juin 1955, la hauteur, le diamètre et le diamètre des branches furent mesurés sur 36 arbres dans chaque placeau de 200 arbres et sur une moyenne de 11.3 arbres restant vivants dans chaque rangée de 15 arbres. En 1955 également, on a noté les arbres courbés à la base, inclinés, présentant des flexuosités minimes ou importantes (flèche de plus de 1½ inches — 3,7 centimètres), les dégâts de porc-épic, la fructification. Toutes les conclusions concernant le degré de signification des différences entre les provenances étaient basées sur les analyses de variance ou de *Chi*² d'après les données de 1955.

On a trouvé des corrélations significatives $r = 0.933$ et $r = 0.861$) entre la hauteur à 3 ou 4 ans et la hauteur à 17 ans.

L'analyse statistique montre que les variations géographiques du pin sylvestre sont surtout discontinues et non clinales. Cette interprétation du type de variation est en accord avec la plupart des résultats obtenus dans les expériences de Wiedemann (1930) et de Langlet (1936), mais s'écarte de quelques unes des conclusions publiées à partir de ces résultats.

Les provenances de pin sylvestre figurant dans cette expérience peuvent être groupées en sept écotypes géographiques: Nord de la Scandinavie, Centre-Nord de la Scandinavie, Sud de la Scandinavie, Lettonie-Esthonie, Allemagne-Pologne, Tchécoslovaquie-Hongrie (y compris certaines provenances introduites en Hollande), et Belgique (provenances introduites, peut-être de France).

Les répétitions étaient insuffisantes pour qu'il soit possible de définir sûrement le comportement écotypique des provenances écossaises (semblables à celles du Sud de la Scandinavie), roumaines (semblables à celles de Lettonie) et italiennes. Il existe probablement d'autres écotypes géographiques dans les parties de l'aire non représentées dans l'expérience. Sauf quelques exceptions, il n'existe pas de différence significative entre les provenances appartenant au même écotype géographique, alors qu'il en existe entre les provenances appartenant à des écotypes géographiques différents.

L'écotype de Lettonie-Esthonie a une croissance relativement rapide (18,5 feet — 5,6 mètres — en 17 ans depuis le semis) et une forme de fût satisfaisante. Il semble être le meilleur pour les plantations forestières en New Hampshire. L'écotype belge a la croissance la plus rapide (22,5 feet — 6,8 mètres — en 17 ans) mais présente la plus forte proportion de courbures à la base, inclinaisons, courbures importantes du fût, et dégâts de porc-épic. L'écotype d'Allemange-Pologne-Tchécoslovaquie-Hongrie est le second en ce qui concerne la vitesse de croissance (19.7 feet — 5,9 mètres en 17 ans) et de même le second pour l'importance des défauts signalés plus haut. Quelques provenances de cet écotype ont une forme de fût satisfaisante. Les écotypes de Scandinavie ont une croissance faible (5.6, 9.6, 13.1 et 15.5 feet — 1.7, 2.9, 3.9 et 4.7 mètres en 17 ans) mais ont peu de défauts de forme.

Baldwin (1955 et 1956) a étudié dans un autre article la coloration hivernale du feuillage de ces arbres. Les écotypes continentaux, qui restent verts en hiver, conviennent mieux pour les producteurs d'arbres de Noël que les écotypes scandinaves, qui jaunissent en hiver.

Les écotypes à croissance lente du Nord de la Scandinvie et les arbres belges à croissance rapide ont la fructification la plus abondante. Le mécanisme de la fructification semble trop complexe pour être expliqué seulement par le photopériodisme ou la vitesse de croissance.

Certains écotypes géographiques peuvent être identifiés avec des variétés taxonomiques déjà décrites: *P. sylvestris* L. var. *sylvestris* (Allemagne-Pologne-Tchécoslovaqie-Hongrie), *P. sylvestris* var. *lapponica* (Fries) Hartmann (Scandinavie du Nord), *P. sylvestris* var. *scotica* Willd. (Ecosse), *P. sylvestris* var. *rigensis* Loudon (Lettonie-Esthonie), et *P. sylvestris* var. *haguenensis* Loudon (plantations belges).

Cette expérience a permis d'obtenir des renseignements précieux sur le dispositif expérimental. Un des plus importants est que les provenances à croissance rapide et celles à croissance lente ont la même vitesse de croissance en hauteur dans de grands placeaux rectangulaires et dans des placeaux linéaires.

Zusammenfassung

Titel der Arbeit: *Der internationale Kiefern-Provenienzversuch aus dem Jahre 1938 in New Hampshire.* —

Aus der Reihe der *Pinus-silvestris*-Herkunftsversuche der IUFRO wurde einer in den Fox und Vincent State Forests, nahe Hillsboro, New Hampshire angelegt. 1938 gelangte das Material zur Aussaat und 1942 wurde es auf die Freifläche verpflanzt. Man wählte einen Verband von 4,2 × 4,2 feet (ca. 1,3 × 1,3 m). Die Fläche ist etwa 12 acres groß (rund 4,86 ha) und besteht aus 117 rechteckigen Parzellen mit je 200 Pflanzen und aus 72 Einzelreihen mit je 15 Pflanzen. (Die infolge starker Abgänge und übermäßiger Laubholzkonkurrenz nicht ausgewerteten Parzellen sind in diesen Zahlen nicht enthalten.) Eine leichte Unkrautbekämpfung in den Jahren 1951 und 1955 genügte, um die Parzellen vor entsprechenden Schäden zu bewahren.

Im November 1941 wurde die Höhe im dritten Jahr, die Höhe im vierten Jahr und die Nadellängen je Provenienz gemessen. Im Juni 1954 ermittelte man Höhe, Durchmesser und Aststärke von je 36 Stämmen in jeder der 200 Stamm-Parzellen und von durchschnittlich 11,3 Stämmen jeder Reihenparzelle. Im gleichen Jahr wurde jeder Stamm auf Säbelwuchs, Schiefstand, geringe Stammkrümmung, starke Stammkrümmung (mehr als 1½ inches Biegung), Stachelschweinschaden und Fruchten bonitiert. Alle Ergebnisse hinsichtlich der Signifikanz von Unterschieden zwischen den Herkünften wurden auf der Basis der Varianzanalyse oder des *Chi*²-Tests gewonnen.

Statistisch gesicherte Korrelationen ($r = 0{,}933$ bzw. $0{,}861$) ergaben sich zwischen den Höhen im dritten und vierten Jahr und der Höhe im 17. Jahr. Die statistische Analyse weist darauf hin, daß die geographische Variation bei *P. silvestris* unregelmäßig und nicht klinal auftritt. Diese Aussage stimmt mit den meisten von WIEDEMANN (1930) und LANGLET (1936) mitgeteilten Ergebnissen überein, weicht aber auch von einigen veröffentlichten Aussagen ab.

Die in diesem Versuch angebauten *silvestris*-Herkünfte hat man in sieben geographische Ökotypen eingeteilt: Nordskandinavien, nördl. Mittelskandinavien, Mittelskandinavien, Südskandinavien, Lettland-Estland, Deutschland-Polen, Tschechoslowakei-Ungarn (incl. einiger holländischer Bäume) und schließlich Belgien (Ursprung möglicherweise Frankreich).

Es gab zu wenige Wiederholungen, um in gleicher Weise einen Ökotyp der schottischen Provenienz (ähnlich der südskandinavischen) der rumänischen Provenienz (ähnlich der lettischen) und der italienischen Provenienz festzulegen. Vermutlich finden sich außerdem noch andere geographische Ökotypen in unzugänglichen Regionen des Verbreitungsgebietes dieser Art. Mit wenigen Ausnahmen gab es keine gesicherten Unterschiede zwischen den Herkünften innerhalb desselben geographischen Ökotyps, sehr wohl aber zwischen Herkünften verschiedener geographischer Ökotypen.

Der Ökotyp Lettland-Estland war von mäßiger Wuchsleistung (18,5 feet = rd. 5,6 m in 17 Jahren) und befriedigender Stammform. Er scheint für den Anbau in New Hampshire der geeignetste zu sein. Ökotyp Belgien wuchs am schnellsten (22,5 feet = rd. 6,9 m in 17 Jahren), war aber am meisten durch Säbelwuchs, Stammkrümmungen, Schiefstand und Stachelschweinschäden entwertet. Der Ökotyp Deutschland-Polen-Tschechoslowakei-Ungarn war nach diesem am wüchsigsten (19,7 feet = rd. 6,0 m in 17 Jahren), stand aber auch bezüglich des Säbelwuchses, des Schiefstandes, großer Stammkrümmungen und der Stachelschweinschäden an zweiter Stelle. Einige Herkünfte in dieser Gruppe befriedigten in der Stammform. Die skandinavischen Ökotypen wuchsen langsam (5,6 feet = rd. 1,7 m, 9,6 feet = rd. 3,3 m, 13,1 feet = rd. 4,0 m, 15,5 feet = rd. 4,72 m in 17 Jahren), hatten aber nur wenig Stammschäden.

In einer gesonderten Veröffentlichung berichtete BALDWIN (1955 und 1956) über die Winterverfärbung der Nadeln dieses Materials. Die kontinentalen Ökotypen — ihre Nadeln bleiben im Winter grün — sind als Weihnachtsbaum besser geeignet als die skandinavischen, deren Nadeln gelb werden.

Die trägwüchsigen nordskandinavischen und raschwüchsigen belgischen Kiefern fruchteten am stärksten. Jedoch erscheint das Fruchten zu komplex bedingt zu sein, als daß man es nur mit Tageslängen und Wuchskraft erklären könnte.

Einige der geographischen Ökotypen können mit früher beschriebenen taxonomischen Varietäten gleichgesetzt werden: *Pinus sylvestris* L. var. *sylvestris* (= Deutschland-Polen-Tschechoslowakei-Ungarn), *P. sylvestris* var. *lapponica* (FRIES) HARTMANN (= Nordskandinavien), *P. sylvestris* var. *scotica* WILLD. (= Schottland), *P. sylvestris* var. *rigensis* LOUDON (= Lettland-Estland), und *P. sylvestris* var. *haguenensis* LOUDON (= Belgien, angebaut).

Der Versuch erbrachte auch viele nützliche Erkenntnisse für die Versuchsplanung. Eines der wichtigsten Ergebnisse in dieser Richtung war, daß träg- und raschwüchsige Herkünfte in den rechteckigen und in den Reihenparzellen die gleiche Höhenentwicklung aufwiesen.

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