

# Seed Source x Environment Interactions in Scotch Pine

## I. Height Growth<sup>1)</sup>

By JAMES P. KING<sup>2)</sup>

(Received for publication December 20, 1964)

### Introduction

Scotch pine (*Pinus sylvestris* L.), one of the most important commercial tree species in Europe, is rapidly becoming an important commercial species in the United States. In 1962 Scotch pine made up 21 percent of the total Christmas tree production in the United States. In Michigan, where this study was carried out, one-fifth to one-third of all stock grown in forest tree nurseries in the past three years was Scotch pine. It is logical that this species should become the subject of a comprehensive tree improvement program.

Tree improvement research relies on the presence of genetic variation. In the past, few estimates of genetic variation have been made in a manner that excludes bias from seed source X environment interaction. Yet unless the magnitude of this interaction is known, the tree breeder can neither make a realistic estimate of the rate of improvement, nor determine the range of environments to which his results will apply.

A replicated seed source test performed in a single location confounds seed source X environment interaction variation with seed source variation, while an unreplicated seed source test repeated at several locations confounds the seed source X environment interaction variation with the within-seed-source variation.

The majority of tests designed to measure interaction (replicated within location and repeated at more than one location) have not been reported in sufficient detail to allow a complete analysis of the interaction variance. But even a look at the general trends can be revealing. For while a constant ranking of seed sources among plantations does not preclude the existence of an interaction, it does indicate that the seed source component of variance is much greater than the interaction component.

Thus, while estimates of genetic variation from a given test may not be free of interaction bias, the effect of this bias may not be great. This seems to be the case in most forest tree species reported thus far.

### Literature Review

RYCROFT and WICHT (1947) reported the ten-year results of a seven-origin test of maritime pine (*P. pinaster* AIT.) at eight test sites in western and southern South Africa. The data showed no seed source-plantation interaction. The Portuguese source was best at all sites and the ranking of the remaining origins remained constant from site to site.

WAKELEY (1961) reported on the mean five-year height of eight sources of loblolly pine (*P. taeda* L.) grown in two plantings in the southeastern United States. This test is part of the Southwide Pine Seed Source Study. The southernmost planting was in Mississippi (latitude 30° 44' N) and the northernmost planting was in Maryland (latitude 36° 35' N). The latitude of the seed sources ranged from

30° N to 38° N. The correlation of five-year height with seed source latitude showed a significant positive relationship ( $r = .92$  with 6 degrees of freedom) at the northern planting and a negative, but non-significant, relationship ( $r = -.48$  with 6 degrees of freedom) at the southern planting. These results suggest an interaction due to the relatively better height growth of the southern origins at the southern planting.

Five-year height of shortleaf pine (*P. echinata* MILL.) shows the same trend. Using seven seedlots whose source ranged from 31° N to 40° N latitude and grown in plantings in Louisiana (30° 58' N) and Tennessee (36° 00' N), there was a significant negative correlation ( $r = -.97$  with 6 degrees of freedom) between height and seed source latitude at the Louisiana planting, but a non-significant correlation ( $r = .34$  with 6 degrees of freedom) in the northern planting.

Three-year height growth of shortleaf pine at plantings in Louisiana (30° 42' N), Tennessee (36° 13' N), and New Jersey (39° 36' N) also bears out the trend toward increased height growth of southern seed sources in southern plantations. Using seven seed sources whose source latitude ranged from 31° to 40° N, the correlation between three-year height and seed source latitude were significant and negative in the southern plantings (Louisiana  $r = -.88$  and Tennessee  $r = -.82$ , with 5 degrees of freedom), but significant and positive in the New Jersey plantation ( $r = .94$  with 5 degrees of freedom).

Incidence of fusiform rust (*Cronartium fusiforme* HEDGE. and HUNT) in the Southwide Pine Seed Source Study was reported by HENRY (1959). Comparing slash pine (*P. elliottii* ENGELM. var. *elliottii*) seed sources from Florida, South Carolina, Alabama, Louisiana, and Mississippi in five-year old plantations in the same five states, significant differences between sources appeared only in the South Carolina planting where the Florida source was significantly higher in infection than the other four sources.

Incidence of fusiform rust on loblolly pine in plantings in Louisiana, Mississippi, Alabama, and North Carolina were also discussed by HENRY (1959). The Texas, Maryland, Arkansas, and Louisiana sources fell into a relatively low susceptibility group as compared with the North Carolina, South Carolina, Georgia, Alabama and Mississippi sources. The Tennessee source was intermediate. One marked exception to this relationship was the high infection of the Texas source and the low infection of the Onslow County, North Carolina source in the Talladega County, Alabama, planting.

SNYDER and ALLEN (1963) reported on ten-year height growth of four sources (two from Alabama; two from Mississippi) of longleaf pine (*P. palustris* MILL.). Seed collected from these sources in three successive years (1947, 1948, and 1949) were sown in two nurseries in Alabama and Mississippi and then planted at two locations in Alabama and two in Mississippi. Their analysis of variance showed a highly significant seed source X plantation interaction. The nature of the interaction was not stated, however.

Five-year results of a 29-origin Lake States jack pine (*P. banksiana* LAMB.) test have been reported by AREND et al.

<sup>1)</sup> This paper is part of a dissertation submitted to the Graduate School of Michigan State University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

<sup>2)</sup> Geneticist, Institute of Forest Genetics, Lake States Forest Experiment Station, Forest Service, U.S. Dept. of Agriculture, Rhinelander, Wisconsin.

(1961). Seed was collected from 29 jack pine stands in Minnesota, Wisconsin and Michigan and outplanted in a 4-replicated randomized block design at 17 locations in the 3 states. AREND's report covered measurements of the three plantations in Lower Michigan. The data showed a non-significant seed source  $\times$  plantation interaction for height growth and incidence of white pine weevil (*Pissodes strobi* PECK) in the three plantations studied. Seed sources from Lower Michigan made the best height growth as a group and the sources from Upper Michigan the least. Seed source differences in weevil incidence were not related to geography.

In the same Lake States jack pine test RUDOLPH (1964) studied lammas growth, prolepsis and long bud formation in 10 selected origins at six plantations for a two-year period. The origins were selected to cover the entire range of jack pine in Minnesota, Wisconsin, and Michigan. Four of the plantations were located in Minnesota and two in Wisconsin. The data showed a significant seed source  $\times$  plantation interaction for lammas growth and long buds, but none for prolepsis. The data also indicated a significant seed source  $\times$  plantation  $\times$  year interaction for lammas growth. Several sources behaved differently between several plantings. There appeared to be no relation between interaction, location of source or location of planting.

In two plantations of this same test, the present author found a significant seed source  $\times$  plantation interaction in susceptibility to jack pine needle cast (*Hypodermella ampla* DEARN.). One planting was located in the western portion of Michigan's Upper Peninsula and the other planting was located about 100 miles to the south in central Wisconsin. Sources from northeast Minnesota showed the highest susceptibility to this disease and sources from Lower Michigan the least. Only one source showed any great difference between plantings. This source, from Lower Michigan, showed a much lower susceptibility in Upper Michigan than in central Wisconsin.

Three-year height growth of six seed origins of eastern white pine (*P. strobus* L.) common to replicated plantings in North Carolina, Georgia and Virginia were described by SLUDER (1963). The source from Georgia made the best growth at all plantings; the Nova Scotia, Ontario, and Minnesota sources were the three poorest at all plantings. The West Virginia and Pennsylvania sources were not significantly different in the Virginia planting; the West Virginia origin was significantly better than the Pennsylvania origin in the Georgia planting; and the Pennsylvania origin was significantly better than the West Virginia origin at the North Carolina planting. Thus, the performance of the West Virginia and Pennsylvania provenances in the three plantings indicates a significant seed source  $\times$  plantation interaction.

Another range-wide provenance test of fifteen sources of eastern white pine has been reported by WRIGHT *et al.* (1963). At two plantings in southern Michigan there was no significant seed source  $\times$  plantation interaction for mortality, color and six-year height. The source from Tennessee was the fastest growing at both plantations and was followed by sources from Georgia and Pennsylvania. The two slowest growing sources were from Nova Scotia and Minnesota. WRIGHT *et al.* compared their results with ten sources in common with a New Jersey test reported by SANTAMOUR (1960). Their comparison shows a non-significant interaction for height growth.

Evidence that a seed source  $\times$  plantation interaction in ponderosa pine (*P. ponderosa* LAWS.) may develop as the

trees mature comes from two reports by MIROV *et al.* (1952) and CALLAHAM and LIDDICOET (1961). Both reports concern the same ponderosa pine individual-tree progeny test. In this test seed was collected from 89 trees along a narrow east-west transect on the west slope of California's Sierra Nevada mountains. The elevation of the 89 trees ranged from 125 to 6919 feet above sea level. The progenies were grown at three planting sites — 960, 2730, and 5650 feet above sea level.

At the end of 12 year's growth, MIROV *et al.* reported that sources from 1500 to 3500 feet in elevation made the best growth at all planting sites, i. e., no major interaction.

At the end of 20 years, however, CALLAHAM and LIDDICOET reported a distinct change from the 12-year trends. At the two lower plantings the progenies from the lower elevations made the best height growth and progenies from high elevations the least. At the high elevation planting site, however, there were no significant differences between progenies.

CALLAHAM and LIDDICOET also reported on 20-year height growth of 21 Jeffrey pine (*P. jeffreyi* GREV. & BALF.) progenies grown at the same planting sites as the preceding ponderosa pine test. The Jeffrey pine show the same pattern as found in the ponderosa pine, i. e., high elevation progenies did relatively better at the high elevation planting than at either lower elevation planting.

Two separate reports on the 1938 International Union of Forest Research Organization Scotch pine test have been issued for a New York and a New Hampshire plantation (WRIGHT and BALDWIN, 1957; SCHREINER, LITTLEFIELD and ELIASON, 1962). The authors published their data in sufficient detail to permit a combined analysis for height of 31 origins common to both plantings. The results of this analysis are shown in Table 1.

The strong differences between plantations is partly due to the fact that the New Hampshire data were from 17-year measurements and the New York data were from 18-year measurements. A careful examination of the data indicated that this age difference did not contribute to the interaction.

The small but significant interaction is probably due to the fact that three of the five south Swedish origins (WRIGHT and BALDWIN's "ecotype D") did better in relation to the overall mean at New Hampshire than at New York, while eleven of the eighteen German origins ("ecotype G") did better at New York than at New Hampshire.

HOLST (1963) recently summarized the results of the International Union of Forest Research Organization Norway spruce (*Picea abies* [L.] KARST.) provenance tests begun in

Table 1. — Combined height growth analysis for thirty-one Scotch pine seed sources grown in New York and New Hampshire.<sup>1)</sup>

Source of Variation	Degrees of freedom	Mean Square	Component of variance as a percent of total variance
Plantation	1	1601.44**	69.07
Rep. within Planting	4	453.25	
Seed Source	30	38.03** <sup>2)</sup>	22.88
Seed Source $\times$ Plantation	30	3.42** <sup>3)</sup>	3.76
Rep. within Seed Source	120	1.07	4.29

\*\* Significant at the one percent level.

<sup>1)</sup> New York data from SCHREINER *et al.* 1962.

New Hampshire data from WRIGHT and BALDWIN, 1957.

<sup>2)</sup> Based upon seed source  $\times$  plantation interaction as error term.

<sup>3)</sup> Based upon seed source  $\times$  replicate-within-planting as error term.

North America in 1938–39. These tests are located in Michigan, Wisconsin, Massachusetts, New Hampshire, Ontario and New Brunswick. Because the number and source of the seedlots varied between plantations a direct measure of seed source  $\times$  plantation interaction is not possible. However, a comparison of the general trends at each planting suggests little interaction. Sources from Poland, White Russia, Czechoslovakia, Yugoslavia and Rumania made better height growth than other European and Scandinavian lots in every planting.

The height growth superiority of east-central European seed sources was also reported by LANGLET (1963) for a 36-origin Norway spruce provenance test in Dönjelt, Sweden. This test was also a part of the 1938 International Union of Forest Research Organization provenance tests.

Although the same trends appeared at both the North American and Swedish Norway spruce tests if seed sources are grouped by general area, the data suggest that some individual seed sources responded differently between countries. For example, the source from Stolpce, White Russia S.S.R., exceeded the plantation average by thirty percent at Harvard Forest in New Hampshire but only equaled the plantation average at Dönjelt, Sweden. The source from Muntele, Rumania, exceeded the plantation average at Dönjelt by twelve percent, but fell twelve percent below the plantation average at Manistee, Michigan. It must be kept in mind, however, that these comparisons are probably biased by the fact that thirty-six origins were represented at Dönjelt while only 13 and 10 origins were in the New Hampshire and Michigan tests respectively.

More detailed analysis of genotype  $\times$  environment interactions have been made in several farm crop plants. GARDNER (1963) has recently reviewed interactions in cross-fertilizing crop plants and MATZINGER (1963) has reviewed interactions in self-fertilizing crop plants. The theory and implications of estimating genotype  $\times$  environment interactions has been discussed by COMSTOCK and MOLL (1963).

Among the most important conclusions from these papers are these:

1. As the genetic diversity of the material increases, the relative magnitude of the interaction decreases.
2. The interaction components vary with the area in the test.
3. The interaction components may be as large or larger than the varietal component.

Item number one above is of special interest to tree breeders. As foresters are presently provenance testing diverse material from natural populations, the size of the interactions should be relatively small. However, as provenance testing continues and narrows down the desirable seed sources to the few best, genotype  $\times$  environment interaction will assume an increasing importance.

### Objectives

This study is 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 United States Department of Agriculture and involves active cooperation by the State Experiment Stations of ten north central states.

The objectives of this study are as follows: (1) determine the magnitude of seed source  $\times$  environment interactions in Scotch pine grown in a variety of conditions in the North Central United States, (2) determine the causes of these in-

teractions and (3) determine the effect of these interactions on a Scotch pine selection and breeding program.

This paper deals with height growth interaction. A later paper will cover needle length and color interactions.

### Methods

#### Material:

Seed was collected from ten average trees in each of 122 stands throughout the natural range of Scotch pine. Within each stand the parents were separated from each other by

Table 2. — Seed source location data — grouped by region.

Region, Country of Origin MSFG No. <sup>1)</sup>	North Lat.	East Long.	Elev. 100's of feet
degrees			
C NOR 201	60.5	3.2	1
SWE 222	60.2	15.0	8
FIN 230	60.5	22.4	1
NOR 273	59.7	9.5	6
NOR 274	60.3	9.9	6
SWE 521	60.0	18.0	1
SWE 523	61.3	16.0	7
SWE 524	61.3	17.9	1
SWE 543	59.9	12.9	7
SWE 544	60.4	14.9	8
SWE 545	60.4	12.9	8
D LAT 223	57.5	25.8	—
LAT 224	57.7	26.3	—
SWE 541	57.0	15.6	5
SWE 542	58.8	14.3	4
SWE 550	55.9	14.1	1
E SIB 227	54.0	94.0	5
URA 253	58.8	60.8	3
F POL 211	53.8	20.3	—
POL 317	53.7	20.5	—
G GER 202	53.0	10.6	4
GER 203	48.2	8.3	—
GER 208	50.6	9.7	—
GER 210	53.2	14.3	—
CZE 305	49.—	14.7	13
CZE 306	49.2	14.—	15
CZE 307	49.9	17.9	8
CZE 308	50.2	15.0	7
CZE 309	49.1	13.3	22
CZE 310	48.7	14.9	18
CZE 311	50.5	14.7	10
CZE 312	50.9	15.1	20
GER 525	50.4	12.2	15
GER 527	50.9	13.7	18
H GER 206	50.2	8.8	—
FRA 241	49.1	7.4	8
GER 251	49.1	8.1	5
GER 253	49.1	7.8	13
BEL 318 <sup>P</sup>	51.2	5.5	—
BEL 530 <sup>P</sup>	50.—	5.—	10
HUN 553	47.7	16.6	10
NY 225 <sup>P</sup>	43.—	75.—	—
J FRA 235	48.2	9.2	22
YUG 242	43.9	19.4	40
K TUR 213	40.5	32.7	49
TUR 220	40.0	31.3	47
TUR 221	40.5	32.7	49
GRE 243	41.5	24.3	49
GRE 271	41.5	24.3	49
GRE 551	41.3	23.2	49
N SPA 218	40.3	—5.2	37
SPA 219	40.8	—4.0	49
SPA 245	40.7	—4.2	49
SPA 246	41.8	—2.8	39
SPA 247	42.3	—0.5	37

<sup>1)</sup> BELgium, CZEchoslovakia, FINland, FRAnce, GERmany, GREece, HUNGary, LATvia, NY New York, NORway, POLand, SIBeria, SPAin, SWEden, YUGoslavia, URAl Mountains.

<sup>P</sup> Seeds obtained from planted stands.

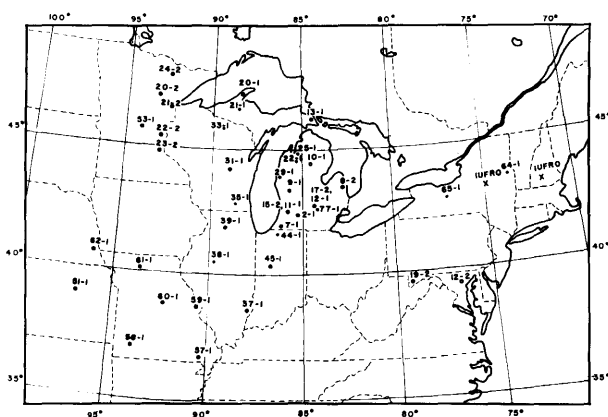


Figure 1. — Location of the test plantations used in the regional study.

100 feet or more. Origin data for the sources used in this study are given in Table 2.

Part of the seed was sown in a 4-replicated randomized block design to provide data on genetic variation in seedling performance. The remainder of the seed was broadcast sown in large rectangular plots. Results of the seedling study as well as a detailed description of nursery procedures have been reported by WRIGHT and BULL (1963).

In the spring of 1961, 2-0 seedlings from the broadcast-sown seed were used to establish 41 permanent test planta-

tions throughout Michigan and the Central States. The locations of these plantings are shown in Figure 1. The plantings in this study followed a randomized block design with seven to ten replications (Table 3).

Replacement stock was planted in the spring of 1962 to fill gaps left by first-year mortality. These replacements were easy to identify in the fall of 1962 by the stunted growth characteristic of Scotch pine in the first season following transplanting. None of the replacements were measured for this study. The trees planted in the spring of 1961 all made apparently normal growth in 1962 and 1963.

Climatic data for the eight plantings used in this study are shown in Table 4.

In general the soils are coarse-textured ranging from sands to clays. The Allegan planting has by far the coarsest-textured soil and is the most moisture deficient site. The Edwards County, Illinois, and the Russ Forest, Michigan plantings have the finest textured soil.

#### Measurement:

Height growth was measured at eight plantations in the fall of 1962 and four plantations in 1963. Average height growth for all living trees on the plot was measured and recorded to the nearest centimeter.

#### Analysis:

The number of seed sources used in the analyses was determined by the number of seed sources the plantations

Table 3. — Summary of plantation location, size, and method of establishment.

Map No.	Name	County, State	North Lat. Degrees	West Long. Degrees	Seed Sources	Replications Number	Trees Plot	Planting Method
2-61	Kellogg Forest	Kalamazoo, Michigan	42.3	85.3	108	10	4	FH <sup>1)</sup>
7-61	Russ Forest	Cass, Michigan	42.0	85.9	105	10	4	CH
9-61	Newaygo	Newaygo, Michigan	43.4	85.8	108	10	4	FM
10-61	Higgins Lake	Crawford, Michigan	44.5	84.7	72	7	4	FM
11-61	Allegan	Allegan, Michigan	42.5	86.0	72	10	4	M
12-61	Rose Lake	Shiawassee, Michigan	42.8	84.3	70	8	4	M
20-61	Houghton	Houghton, Michigan	47.1	88.4	80	8	4	FH
37-61	Edwards	Edwards, Illinois	38.5	88.0	101	13	2	SH

<sup>1)</sup> Furrowed, Hand planted, Machine planted, Scalped, Chemical weed control.

Table 4. — Plantation climatic data.<sup>1)</sup>

	Kellogg Forest	Higgins Lake	Allegan	Houghton	Newaygo	Rose Lake	Russ Forest	Edwards
Temperature:								
degrees F.								
April, 1962	46.0	41.2	47.9	34.7	42.8	46.6	48.4	53.5
May, 1962	63.6	58.9	65.1	52.7	60.2	64.1	66.0	72.5
June, 1962	68.4	63.2	68.9	58.0	64.6	67.6	69.0	73.4
April, 1963	49.0	43.9	50.0	38.7	—	—	—	—
May, 1963	55.9	51.3	57.2	48.1	—	—	—	—
June, 1963	68.9	65.2	69.2	69.2	—	—	—	—
Annual mean, 1962	47.7	42.8	48.4	39.0	44.7	47.2	48.3	—
Period between days with minima of:								
days								
32° F. (1962)	154	110	154	134	135	135	153	—
24° F. (1962)	204	188	266	188	191	193	189	—
32° F. (1963)	134	111	143	113	—	—	—	—
Precipitation:								
inches								
1961 Annual	29.87	40.10	34.93	28.86	34.22	25.11	38.68	54.55
1962 Annual	24.49	32.45	26.44	25.05	23.15	20.44	32.44	—
April-June 1961	8.73	9.34	6.60	7.89	10.04	6.76	—	24.33
April-June 1962	8.75	8.89	6.68	7.83	5.68	7.61	9.80	9.23
April-June 1963	8.07	13.76	8.49	9.15	—	—	—	—

<sup>1)</sup> Nearest U. S. Weather Bureau Station used: Kellogg Forest-Gull Lake Exp. Farm; Higgins Lake-Higgins Lake; Allegan-Allegan Sewage Plant; Houghton-Houghton FAA Airport; Newaygo-Newaygo Hardy Dam; Rose Lake-East Lansing Hort. Farm; Russ Forest-Dowagiac; Edwards-Olney, Ill.

Table 5. — Analysis of variance form used for the combined analysis of yearly results.

Source of variation	Degrees of freedom	Parameters estimated by mean squares
Years	(y—1)	$\sigma_e^2 + \bar{r}\sigma_{yps}^2 + \frac{\sum r_p\sigma_{ys}^2}{p} + \bar{r}s\sigma_{yp}^2 + \frac{\sum r_p s\sigma_y^2}{p}$
Plantations	(p—1)	$\sigma_e^2 + \bar{r}\sigma_{yps}^2 + \bar{r}y\sigma_{ps}^2 + \bar{r}s\sigma_{yp}^2 + r_{ys}\sigma_p^2$
Seed sources	(s—1)	$\sigma_e^2 + \bar{r}\sigma_{yps}^2 + \bar{r}y\sigma_{ps}^2 + \frac{\sum r_p\sigma_{ys}^2}{p} + \frac{\sum r_p y\sigma_s^2}{p}$
Years $\times$ Plantations	(y—1) (p—1)	$\sigma_e^2 + \bar{r}\sigma_{yps}^2 + \bar{r}s\sigma_{yp}^2$
Seed sources $\times$ Years	(s—1) (y—1)	$\sigma_e^2 + \bar{r}\sigma_{yps}^2 + \frac{\sum r_p\sigma_{ys}^2}{p}$
Seed sources $\times$ Plantations	(s—1) (p—1)	$\sigma_e^2 + \bar{r}\sigma_{yps}^2 + \bar{r}y\sigma_{ps}^2$
Seed sources $\times$ Plantations $\times$ Years	(s—1) (p—1) (y—1)	$\sigma_e^2 + \bar{r}\sigma_{yps}^2$
Error	$[\sum(r_p-1)] (s-1)$	$\sigma_e^2$

y = number of years; p = number of plantations; s = number of seed sources;

$r_p$  = number of replications per plantation;  $\bar{r} = \sum r_p^2 / \sum r_p$

$\sigma_e^2$  is the component of variance due to random variations within plots within plantations.

$\sigma_y^2$  is the component of variance due to differences between years.

$\sigma_p^2$  is the component of variance due to differences among plantations.

$\sigma_s^2$  is the component of variance due to differences among seed sources.

$\sigma_{yp}^2$  is the component of variance due to interaction of years and plantations.

$\sigma_{ys}^2$  is the component of variance due to interaction of years and seed sources

$\sigma_{ps}^2$  is the component of variance due to interaction of plantations and seed sources.

$\sigma_{yps}^2$  is the component of variance due to interaction of years, plantations, and seed sources.

had in common. There were 42 seed sources common to the 8 plantations measured in 1962, and 55 sources common to the four Michigan plantations measured in 1962 and 1963.

Data for each plantation were subjected to analysis of variance using plot means. Plantation analyses were then grouped in various combined analyses as described by COCHRAN and COX (1957). The Edwards County, Illinois plantation was not included in any combined analysis because this was the only planting with two-tree plots.

Components of variance were determined by setting the computed mean squares equal to their expected mean squares (Table 5) and solving for the components.

### Results

Sources from western West Germany and Belgium (Group H) made the best height growth throughout all the plantations. This group made nearly twenty percent more height growth than the average tree in the planting (Table 6).

The Southern East Germany and Czechoslovakian sources (Group G) made the next best height growth over all plantations. This group grew from ten to fifteen percent faster than the plantation average.

Group F was slightly behind Group G in overall growth. This group, probably because it was represented by only two Polish sources, showed much variation between plantings. The differences in height growth between Groups F and G are probably not real.

The percentage by which Groups H and G exceeded the plantation average remained nearly constant for all plantations and years of measurement.

The Spanish sources (Group N) made the least growth over all the plantations measured in 1962, the second year after planting. These sources were the slowest growing group in every planting except Russ Forest. At Russ Forest the Spanish sources made 25 percent less growth than the plantation average but were equaled in slow growth by sources from southern Scandinavia (Group C).

In 1963 the picture began to change. Both the Spanish sources and the Greek-Turkish sources (Group K) did better relative to the plantation mean at every planting in 1963. At the same time the southern Scandinavian group and the two sources from western Siberia (Group E) all did relatively poorer in 1963. At Kellogg Forest the growth of the southern Scandinavian and Spanish groups were equal, while at Houghton (the northernmost planting) the Spanish sources outgrew the southern Scandinavian sources. That this change is real is indicated by the significant seed source  $\times$  year interaction term in Table 7.

Kellogg Forest, Russ Forest, and the Houghton County plantations made better growth in 1963 than in 1962, and while all plantings made better growth in 1963 than in 1962, this yearly acceleration in height growth was not the same for all plantations. Kellogg Forest made 1.8 times as much growth in 1963 as in 1962, Higgins Lake and Houghton both grew about 1.6 times the 1962 growth, and Allegan grew about 1.3 times the 1962 growth. That these differences in growth acceleration are real is shown by the highly significant year  $\times$  plantation interaction in Table 7.

The Edwards County, Illinois plantation was not included in the combined analyses. An examination of the data, however, suggests that ecotypes did not behave markedly different at that plantation. The means of Groups C (a northern group), H (a central European group), and N (a

Table 6. Height growth of Scotch pine seed sources.

Region, Country of origin, MSFG No.	Kellogg Forest		Allegan		Higgins Lake		Houghton		Russ Forest	Newaygo	Rose Lake	Edwards
	1962	1963	1962	1963	1962	1963	1962	1963	1962	1962	1962	1962
-----Percent of plantation mean-----												
C NOR 201	70.3	74.1	76.9	82.2	64.4	75.7	72.2	72.0	64.3	67.4	82.7	63.5
	95.3	86.2	89.9	94.6	83.6	87.0	104.7	92.9	77.8	90.1	88.1	86.3
	69.9	57.2	68.5	61.6	67.4	53.8	49.2	64.0	--	--	--	--
	75.3	66.8	90.1	92.0	80.6	79.5	93.1	89.8	68.0	100.0	76.3	90.7
	95.1	77.7	71.6	71.2	88.4	71.9	92.6	87.3	59.8	98.5	74.3	107.1
	92.7	90.7	79.8	89.0	120.2	103.0	107.2	88.6	86.4	102.5	96.5	96.5
	90.6	84.5	91.1	88.5	113.9	97.0	90.8	88.1	80.0	91.9	102.6	88.7
	96.2	90.0	94.1	93.7	92.3	85.5	89.8	86.9	77.2	96.5	97.4	90.7
	78.7	79.1	74.5	73.2	106.1	98.9	90.3	87.0	87.5	83.0	101.4	103.3
	93.1	93.4	89.1	91.0	96.5	86.6	90.3	82.7	80.8	104.3	87.3	81.9
	82.4	67.6	79.0	82.8	100.9	81.0	58.0	62.8	--	--	--	--
Average	85.4	78.8	82.2	83.6	92.2	83.6	85.3	82.0	75.8	92.7	89.6	89.8
D LAT 223	97.2	95.8	90.1	87.7	107.2	103.8	114.3	106.0	112.1	86.6	99.1	121.2
	83.6	78.9	90.7	91.4	94.1	97.6	101.7	87.6	83.2	94.4	91.0	111.5
	114.7	106.0	99.6	100.0	138.2	116.7	118.8	95.8	109.3	98.2	107.2	115.9
	116.7	98.1	89.6	86.9	116.0	105.6	93.1	101.5	93.5	99.8	105.1	92.6
	98.7	111.4	90.4	89.6	85.1	86.1	87.3	94.6	--	--	--	--
Average	102.1	98.0	92.1	91.1	108.1	102.0	103.0	97.1	99.5	94.8	100.8	110.3
E SIB 227	94.6	83.3	89.6	82.0	118.7	87.4	105.7	83.5	--	--	--	--
	101.3	85.3	111.3	105.3	110.9	91.7	114.6	98.3	106.1	107.4	91.9	108.6
	98.0	84.3	100.5	93.7	114.8	89.6	110.2	90.9	106.1	107.4	91.9	108.6
F POL 211	114.3	110.0	116.3	116.4	96.2	110.7	112.0	111.6	112.8	111.1	123.3	115.4
	112.1	105.8	130.8	119.2	113.9	112.7	103.7	110.5	120.3	121.0	117.2	127.5
	113.2	107.9	123.6	117.8	105.1	111.7	107.9	111.1	116.5	116.1	120.3	121.5
G GER 202	117.5	119.4	96.2	108.2	100.7	106.9	109.8	112.7	104.9	118.2	103.7	107.6
	95.5	100.5	93.0	95.3	89.0	103.0	94.9	95.1	100.3	86.8	97.9	82.4
	122.0	116.4	117.9	122.7	108.8	120.7	108.5	107.3	--	--	--	--
	126.1	119.8	115.2	120.0	106.4	101.0	116.1	109.0	116.6	108.1	124.2	94.0
	118.6	123.1	128.2	125.6	102.1	103.2	109.3	105.9	--	--	--	--
	95.7	108.4	126.3	108.8	91.4	104.1	117.6	120.9	106.1	110.1	112.9	92.1
	117.3	113.9	144.8	135.2	119.6	111.3	107.2	107.6	--	--	--	--
	103.3	111.8	136.9	139.7	129.5	111.6	90.3	114.1	--	--	--	--
	113.0	113.8	96.7	97.8	95.9	105.2	113.5	106.3	116.6	105.6	101.5	90.2
	130.2	133.4	114.7	112.7	143.6	126.4	121.9	113.3	135.3	115.9	105.7	98.4
	121.6	113.3	117.6	119.4	90.5	107.6	120.1	115.8	--	--	--	--
	131.6	117.6	126.3	127.6	114.5	130.0	114.8	108.8	110.9	126.1	117.2	119.3
	108.0	116.4	122.1	119.4	136.7	126.8	120.1	112.4	104.9	113.7	108.9	130.4
	108.7	108.8	140.1	131.7	126.8	128.6	118.1	125.7	131.4	102.3	134.5	111.0
	115.1	115.5	119.7	118.9	111.1	113.3	111.6	111.1	114.1	109.6	111.8	102.8
H GER 206	106.3	109.5	93.6	102.5	79.7	111.1	102.4	116.1	119.4	84.1	103.4	102.3
	118.2	131.9	119.7	119.0	131.9	128.4	119.4	110.8	--	--	--	--
	126.3	131.1	125.0	119.6	146.6	130.0	150.1	126.1	164.3	135.2	135.7	110.5
	116.2	134.2	133.7	126.4	123.8	120.0	109.3	115.5	122.7	138.7	133.3	108.1
	125.5	135.5	132.2	130.1	121.4	128.2	133.7	125.0	132.7	160.0	123.2	139.1
	132.4	125.9	119.7	127.6	89.3	104.9	117.7	134.8	136.7	117.5	157.6	146.4
	114.5	98.7	119.5	114.1	130.2	116.2	128.2	133.5	--	--	--	--
	100.6	98.1	108.4	107.8	127.7	104.3	112.3	104.5	131.0	94.2	97.7	106.2
	117.5	120.6	119.0	118.4	118.8	117.9	121.6	120.8	134.5	121.6	125.2	118.8
	94.7	127.4	110.7	113.3	96.8	94.7	97.7	111.1	93.3	119.0	114.9	121.3
J FRA 235	98.5	104.6	100.7	83.8	87.8	98.7	92.6	96.4	110.9	123.8	115.2	98.9
	96.6	116.0	105.7	98.6	92.3	96.7	95.2	103.8	102.1	121.4	115.1	110.1
K TUR 213	86.9	88.6	89.3	89.0	83.3	89.2	73.4	83.9	75.7	86.8	89.3	88.7
	84.1	85.4	85.6	88.3	77.6	84.6	86.6	100.0	101.6	88.1	84.9	81.4
	74.6	92.6	81.1	84.2	53.1	76.4	83.5	78.2	91.8	77.2	102.8	101.8
	83.0	89.2	71.7	87.3	79.1	85.7	62.3	76.8	92.6	106.9	76.7	100.8
	91.8	92.0	103.1	100.6	104.6	109.6	117.6	112.7	--	--	--	--
	89.9	102.0	79.6	81.6	80.6	85.4	91.6	96.0	--	--	--	--
Average	85.1	91.6	85.0	88.5	79.7	88.5	85.8	91.3	90.4	89.7	88.4	93.2
N SPA 218	73.1	83.9	72.9	82.0	92.9	98.7	78.5	95.5	86.6	71.4	73.7	81.4
	76.6	83.4	65.5	82.0	62.6	77.7	85.8	98.1	85.6	69.4	64.5	85.3
	70.5	79.9	73.5	74.2	55.7	72.0	74.4	91.0	61.3	64.3	67.7	64.0
	61.7	67.3	60.0	62.8	55.2	77.3	71.7	82.4	68.0	61.0	57.6	67.9
	73.3	79.7	65.3	71.2	74.9	79.3	60.1	61.6	77.8	63.8	53.6	69.3
Average	71.0	78.8	67.4	74.4	68.3	81.0	74.1	85.7	75.9	66.0	63.4	73.6
Mean plantation height growth (centimeters)												
	13.41	23.74	9.46	12.48	11.67	19.58	12.39	20.22	13.35	9.88	10.85	7.94
Standard error of seed source means as a percent of plantation mean												
	6.94	5.98	6.24	4.81	9.17	6.33	8.56	8.01	8.16	7.39	8.11	9.32

1/

BELgium, CZEchoslovakia, FINland, FRANCE, GERmany, GREEce, HUNGary, LATvia, NORway, POLand, SIBeria, SPAin, SWEDen, YUGoslavia, URAL Mountains.

Table 7. — Combined analysis of variance results of 1962 and 1963 height growth for 55 Scotch pine seed sources from 4 Michigan plantations.

Source of Variation	Degrees of freedom	Mean Square	Component of variance as a percent of total variance
Years	1	726951.43**	8.17
Plantations	3	171244.05**	28.27
Seed Sources	54	7653.02**	31.33
Years × Seed Sources	54	500.27** <sup>1)</sup>	1.61
Years × Plantations	3	4920.85** <sup>1)</sup>	2.88
Seed Sources × Plantations	162	499.56** <sup>1)</sup>	0.74
Seed Sources × Years × Plantations	162	191.47** <sup>2)</sup>	0.58
Error	3294	160.32	26.42

\* Significant at the five percent level.

\*\* Significant at the one percent level.

<sup>1)</sup> Based upon seed sources × years × plantations interaction as error term.

<sup>2)</sup> Based upon seed source × replication-within-plantation as error term.

southern group) are identical at Edwards and Houghton, two plantings which are about 575 miles apart in a north-south direction.

Group G, from southern East Germany and Czechoslovakia, seems to differ markedly at Edwards. This group grew about 10 percent less at Edwards than at any other planting. There is no obvious explanation of why several of the sources in this group did so poorly while Groups H and F, also from central Europe, did as well at Edwards as at any other planting.

The individual seed source × plantation interactions were random. That is, there was no relation between location and elevation of the seed source and its performance in a given plantation. For example, sources MSFG 243 and MSFG 271 are both from Greece and from the same latitude, longitude, and elevation. They made almost identical growth at Kellogg Forest in both 1962 and 1963. But at Allegan, Higgins Lake, and Houghton MSFG 271 outgrew 243 in both years from 15 to 45 percent.

Sources MSFG 307 and 308 both from the same elevation in northern Czechoslovakia exceeded the Allegan plantation average by 35 percent in 1962 and 1963. But at Kellogg, Higgins Lake and Houghton they seldom exceeded the plantation average by more than fifteen percent.

Source MSFG 545, a high elevation source from central Sweden, made its poorest showing in both years at the northernmost plantation — Houghton County.

In 1962, between-seed-source differences accounted for 28 percent of the total variation encountered in the Michigan plantings (Table 8). This dropped to 19 percent in 1963 as differences between plantings became more pronounced.

If the variance component due to plantation differences is not considered, the seed source component consistently accounted for between 32 and 44 percent of the remaining variance in both years.

The differences in growth acceleration greatly increased the percent of variance due to plantation differences in 1963. For the four plantings measured in both years the percentage of total variance due to site differences increased from 20 percent in 1962 to 52 percent in 1963.

The plantations were grouped into a number of combined analyses. This was done to determine whether any particular plantation was responsible for most of the interaction. Such was not the case. The seed source × plantation interaction for the 42 sources measured at the seven Michigan plantings in 1962 was significant for any combination of three or more plantings (Table 9). For example, neither the combined analysis for the Kellogg Forest — Allegan plantings nor for the Kellogg Forest — Russ Forest plantings gave a significant interaction. But when these three plantations were combined a significant interaction was found. Furthermore, the percent of total variation due to interaction was the same for these three closely situated plantings as for all seven Michigan plantings.

As may be seen from Table 10, which shows correlations between 1962 seed source totals for all combinations of plantings, there is no relation between size of correlation coefficient and size of interaction. The highest correlation

Table 8. — 1962 and 1963 Components of height growth variance as a percent of total variance — from 55 seed sources.

Plantations in combined analysis	Variance Component							
	$\sigma_p^2$		$\sigma_s^2$		$\sigma_{ps}^2$		$\sigma_e^2$	
	1962	1963	1962	1963	1962	1963	1962	1963
Percent of total variance								
Kellogg Forest Higgins Lake Allegan Houghton	20.8**	51.6**	28.4**	18.8**	5.1**	3.4**	46.4	26.2
Kellogg Forest Higgins Lake Houghton	3.8NS	14.5**	32.8**	33.5**	5.1**	4.1**	58.3	47.9
Kellogg Forest Higgins Lake	6.6NS	21.7**	30.7**	34.7**	7.4**	5.0**	55.3	38.5
Higgins Lake Houghton	0.5NS	0.7NS	33.7**	35.7**	6.3**	1.4NS	59.5	62.3
Kellogg Forest Houghton	3.8NS	15.1**	33.5**	31.8**	2.5*	4.6*	60.2	48.5

$\sigma_p^2$ ,  $\sigma_s^2$ ,  $\sigma_{ps}^2$ , and  $\sigma_e^2$  are the components of variance due to differences between plantations, differences between seed sources, seed source × plantation interaction, and random variation between plots within plantings respectively.

NS = Non-significant.

\* = Significant at the five percent level.

\*\* = Significant at the one percent level.

Table 9. — 1962 Components of height growth variance expressed as a percent of the total variance of 42 seed sources.†)

Plantations in combined analysis	Variance component			
	$\sigma_p^2$	$\sigma_s^2$	$\sigma_{ps}^2$	$\sigma_e^2$
Percent of total variance				
Kellogg Forest	16.67**	28.17**	4.61**	50.55
Russ Forest				
Allegan				
Newaygo				
Higgins Lake				
Rose Lake				
Houghton				
Kellogg Forest	22.90**	27.74**	4.77**	44.59
Russ Forest				
Newaygo				
Allegan				
Houghton				
Kellogg Forest	21.83**	28.73**	4.14**	45.30
Russ Forest				
Allegan				
Houghton				
Kellogg Forest	28.16**	26.42**	4.99**	40.43
Allegan				
Russ Forest				
Kellogg Forest	3.90NS	35.38**	4.29**	56.43
Higgins Lake				
Houghton				
Kellogg Forest	43.10**	25.70**	0.00NS	31.20
Allegan				
Kellogg Forest	18.09**	25.97**	8.48**	47.46
Rose Lake				
Kellogg Forest	3.02NS	38.58**	2.09NS	56.31
Russ Forest				
Kellogg Forest	2.40NS	35.90**	1.72NS	59.98
Houghton				
Kellogg Forest	7.09**	33.74**	6.76**	52.41
Higgins Lake				
Kellogg Forest	19.69**	30.13**	3.20**	46.98
Newaygo				

$\sigma_p^2$ ,  $\sigma_s^2$ ,  $\sigma_{ps}^2$ , and  $\sigma_e^2$  are the components of variance due to differences between plantations, differences between seed sources, seed source  $\times$  plantation interaction, and random variations between plots within plantings respectively.

NS — Non-significant.

\* — Significant at the five percent level.

\*\* — Significant at the one percent level.

Table 10. — Between-plantation correlation coefficients using the mean 1962 seed source height growth.

	Kellogg Forest	Russ Forest	Al- legan	New- aygo	Higgins Lake	Hough- ton	Rose Lake	Ed- wards
Kellogg Forest	1.00							
Russ Forest	.78	1.00						
Allegan	.80	.77	1.00					
Newaygo	.81	.66	.80	1.00				
Higgins Lake	.72	.67	.68	.65	1.00			
Houghton	.81	.80	.80	.72	.77	1.00		
Rose Lake	.82	.78	.85	.74	.59	.75	1.00	
Edwards	.70	.63	.67	.72	.57	.68	.73	1.00

All values are significant at the 0.1 percent level where  $r = .33$  with 40 degrees of freedom.

coefficient shown (.82) is between the two plantings with the highest interaction component — Kellogg Forest and Rose Lake. The coefficient of determination between Kellogg Forest and Rose Lake is (.82)<sup>2</sup> or .67. This leaves 33 percent of the variance to be divided among interaction and experimental error. Whether a significant amount of interaction is present depends upon the size of the experimental error.

## Applicability of Results to Other Areas

Results of other Scotch pine tests indicate that the results of this test, although based on very young trees, may apply well beyond the confines of this study.

Seventeen-year results in New Hampshire (WRIGHT and BALDWIN, 1957) and eighteen-year results in New York (SCHREINER *et al.*, 1962) show that height growth superiority of the German and Belgium sources continues in this area as the trees mature. WIEDEMANN'S (1930) summary of the 1907 International Union of Forest Research Organizations test based on unreplicated Scotch pine planting in Germany, Belgium, Sweden and the Netherlands also indicate the height growth superiority of the central European sources throughout central Europe.

The New Hampshire and New York plantations, which had thirty-one sources in common, when subjected to a combined analysis (Table 1), showed a seed source  $\times$  plantation interaction component that accounted for about four percent of the total variation or about one-sixth of the variation due to seed source differences. Thus, even the size of the height growth interaction estimates may apply to mature trees in the northeastern United States.

However, there is evidence that the interactions become more severe under extreme conditions of latitude and climate. The effect of a severe winter on 27 Scotch pine seed sources growing in northeastern Minnesota has been described by RUDOLF (1949). These sources, obtained partly from foreign sources and partly from local plantations, include one source from Manchuria, seven sources of known or supposed northern European origin (Norway, Sweden, Finland, and Latvia), and nineteen sources of known or supposed central European origin (Hungary, France and Germany). After 16 years in the field (18 years from seed) the central European seedlots were making the best height growth and producing the most volume per acre. However, during the extremely unfavorable winter of 1947–48, the central European sources suffered more severe foliage damage than the northern European sources. The central European sources also showed a much lower degree of recovery (as measured by new growth initiation) than the northern European sources. As a result, the central European sources were no longer considered suitable for northeastern Minnesota.

JOHNSON (1955) reported on the 15-year growth of progeny from 79 trees located in 24 stands in Sweden and grown at 3 widely separated Swedish locations. The latitude of the seed sources ranged from 57° 35' north to 65° 39' north, and the three plantings were located at Boxholm (58° 10' N. Lat.) Dalfors (61° 18' N. Lat.) and Rorstrom (64° 13' N. Lat.). The southern Scandinavian sources were the fastest growing in the southernmost planting, but did not retain their superiority in either northern planting.

Thus, while the trees in this study are too young to supply reliable information for seed source recommendations, the variance components and general trends shown in this study can be used in planning Scotch pine provenance tests throughout the northeastern United States and central Europe.

## Discussion

There was no indication that poor planting practice affected the performance of individual seedlots at individual plantings. Using first-year mortality as a measure of planting technique, seed sources with an abnormally low growth



rate (for their geographic group) were compared with mortality figures (not shown) for the same planting. There was no apparent relationship.

Transplanting effects probably contributed to the seed source  $\times$  years height growth interaction. WRIGHT and BULL (1963) noted at the time of lifting and transplanting that the Spanish sources were noticeably more tap-rooted. The improved height growth of the Spanish sources in 1963 is probably due to the fact that their root systems were relatively more damaged in transplanting and, therefore, the effects of transplanting dissipate more slowly in these sources.

It should be kept in mind that the seed source  $\times$  year interaction in this study differs somewhat in definition from the seed source (or family)  $\times$  year interaction of the agronomy literature. In this study the measurements were repeated on the same trees. Thus, a combination of yearly climatic fluctuations, physiological maturation of the plant, and among-origin differences in transplanting recovery rate all contribute to this interaction. It is expected then that this component will diminish as the trees mature and recover from transplanting.

In 1962 a combined analysis of the Higgins Lake and Houghton data showed that six percent of the height growth variance was accounted for by the seed source  $\times$  plantation interaction. However, in 1963 the same analyses showed a non-significant interaction in height growth. Other combined analyses show similar fluctuations in the seed source  $\times$  plantation interaction. This suggests that soil type and photoperiod (which obviously remain constant from year to year) are not causal factors in the height growth interactions.

This does not imply that photoperiod *per se* could not cause seed source  $\times$  plantation interactions. It only indicates that the range of photoperiods covered by these sites produced no interaction. This is not surprising since the difference in maximum daylength between the northernmost and southernmost Michigan plantations is only about thirty-five minutes. Furthermore, as indicated by the controlled environment tests of PERRY (1962) and IRGENS-MOLLER (1962), temperature may mask the effects of photoperiod.

The relatively small size of the interaction in this study is not unexpected. The seed sources herein represent a very high degree of genetic diversity. Thus, while the interaction may represent only about 5 percent of the total genetic variance, it is 5 percent of a large amount. As was pointed out earlier in this paper, the interaction will become more important as the base of genetic variance is reduced.

The lack of relationship between seed source location, plantation location, and height growth indicates that, within the area covered by this study, one cannot use the simple relationships discovered by early authors to predict the performance of a seed source at a particular site on the basis of the latitude or average temperature of the seed source. The relationships are more complex.

### Practical Implications of Results

There is no direct way of equating the size of the interaction variance with the advantages of testing at several locations rather than a single one. However, the following examples show the practical consequences of this interaction.

Considering 1963 height growth at Higgins Lake and Kellogg Forest, the seed source  $\times$  plantation interaction is about 5 percent of the total variance, and the seed source com-

ponent is about 35 percent of the total. Both components are statistically significant. If one wanted to breed a faster growing Scotch pine for Higgins Lake but had data only from Kellogg Forest, he would necessarily choose seed sources 241, 251, 253, 310, and 318 because they are the fastest growing at Kellogg. At Higgins Lake those sources grew 126 percent as fast as the plantation mean, compared with 128 percent for the 5 sources that were fastest growing at Higgins Lake.

Considering 1963 height growth at Kellogg Forest and Houghton, the sizes of the seed source and interaction components are about the same as between Kellogg Forest and Higgins Lake. However, the consequences of selection at Kellogg for planting at Houghton would be much more serious. At Houghton the 5 seed sources growing the fastest at Kellogg grew only 118 percent as fast as the plantation mean, whereas there are 5 sources at Houghton capable of growing 129 percent as fast as the plantation mean.

Similar comparisons using 1962 height growth and the combined 1962 and 1963 height growth indicate that the 5 best selected at Kellogg Forest may be as much as 18 percent lower than the 5 best growing at either Houghton or Higgins Lake.

### Summary

Scotch pine seed, collected from 122 native stands throughout the species range, was sown in the Michigan State University forest tree nursery in the spring of 1959. Each seed lot consisted of seed from about ten trees per stand.

In 1961 two-year-old stock was used to establish permanent test plantations throughout Michigan and the central United States. The plantings follow a randomized block design with seven to ten replications. The number of seed sources per plantation varies approximately from 50 to 100.

In 1962 following the second growing season after out-planting, one plantation in central Illinois and seven plantations in Michigan were measured for height growth. In 1963 height growth was measured in four Michigan plantations.

Analysis of variance of each character was made for each test plantation. The individual plantation analyses were grouped into various combinations and the mean squares used to compute the resulting variance components. These components were then expressed as a percent of the total variance for comparative purposes.

Seed sources from Belgium, Germany and Czechoslovakia made the most height growth at all plantings in 1962 and 1963. Sources from Spain made the least. However in 1963 there were indications that the Spanish sources might out-grow the Scandinavian sources as the effects of transplanting dissipated.

The planting sites also showed marked differences in growth per year.

The seed source  $\times$  plantation interaction of the individual seed sources showed no relation to seed source location or plantation location. Differences in performance of sources between plantations seems more a result of temperature and moisture variations than between-planting differences in soil type or photoperiod.

The component of variance resulting from seed source  $\times$  plantation interaction never accounted for more than six percent of the total variation encountered in all plantings in either 1962 or 1963. This interaction component was about  $\frac{1}{6}$  the seed source component for height growth.

The effect of yearly fluctuations of climate on seed source differences (year  $\times$  seed source interaction) was also very small in relation to the seed source differences.

Despite the relatively small interaction variance and the large between-planting seed source correlations, selection based on only a single test may seriously reduce selection efficiency.

### Zusammenfassung

Titel der Arbeit: *Interaktion von Herkunft  $\times$  Umwelt bei Pinus sylvestris. I. Höhenwachstum.*

Samen von 122 autochthonen Herkünften aus dem gesamten Verbreitungsgebiet der Art wurde im Frühjahr 1959 in der Baumschule der Michigan State University ausgesät. Jede Herkunft bestand aus Samen von etwa 10 Bäumen eines Bestandes.

Das zweijährige Pflanzenmaterial wurde 1961 in Michigan und den mittleren Vereinigten Staaten in Feldversuchen angebaut. An jedem Versuchsort wurde ein randomisierter Blockversuch mit 7 bis 10 Wiederholungen angelegt.

Im Jahre 1962, nach Abschluß der zweiten Wachstumsperiode, wurde das Höhenwachstum an einem Ort in Illinois und an sieben in Michigan gemessen; 1963 folgten vier weitere Messungen in Michigan.

Für jedes Merkmal und jeden Versuchsort wurde eine Varianzanalyse durchgeführt. Die Werte der einzelnen Versuchsorte wurden in verschiedener Weise kombiniert und die Mittelquadrate benutzt, um Varianzkomponenten zu errechnen. Diese Varianzkomponenten wurden dann als Prozent der Gesamtvarianz ausgedrückt, um Vergleiche zu ermöglichen.

Herkünfte aus Belgien, Deutschland und der Tschechoslowakei zeigten 1962 und 1963 das stärkste Wachstum, Herkünfte aus Spanien das schwächste. Jedoch gab es 1963 Anzeichen dafür, daß nach Überwindung des Pflanzschocks die spanischen Herkünfte die skandinavischen überholen könnten.

Auch die Versuchsorte hatten bedeutende Unterschiede im Wachstum pro Jahr.

Die Interaktion Herkunft  $\times$  Versuchsort zeigte bei den einzelnen Herkünften keine Beziehung zum Herkunftsgebiet oder Versuchsort. Die Leistung der Herkünfte auf verschiedenen Versuchsorten schien mehr von der Temperatur und Feuchtigkeit abhängig zu sein als von Bodentypen oder der Photoperiode.

Die aus der Interaktion Herkunft  $\times$  Versuchsort sich ergebende Varianzkomponente überschritt niemals 6% der Gesamtvarianz aller 1962 und 1963 gemessenen Versuchsorte. Diese Interaktion erreichte ungefähr ein Sechstel der Herkunftskomponente für das Höhenwachstum.

Der Einfluß jährlicher Klimaschwankungen auf Herkunftsunterschiede (Interaktion Jahr  $\times$  Herkunft) war im Verhältnis zu den Herkunftsunterschieden ebenfalls sehr klein.

Trotz der verhältnismäßig geringen Interaktionsvarianz und der guten Korrelation der Herkünfte auf verschiedenen Versuchsorten würde eine Auslese, die nur auf den Ergebnissen einer einzigen Versuchsfläche beruht hätte, stark an Wirksamkeit einbüßen.

### Résumé

Titre de l'article: *Interactions provenance  $\times$  environnement chez le pin sylvestre. I. Croissance en hauteur.*

Des graines de pins sylvestres, récoltées sur 122 peuplements autochtones répartis dans toute l'aire de l'espèce, ont été semées dans la pépinière de l'Université de Michigan au printemps de 1959. Chaque lot de graines représentait la récolte sur environ dix arbres.

En 1961, des plants de deux ans ont été utilisés pour établir des plantations comparatives dans le Michigan et la région centrale des Etats-Unis. Le dispositif utilisé était un dispositif en blocs complets avec sept à dix répétitions. Le nombre de provenances par plantation varie de 50 à 100.

En 1962, après la seconde saison de végétation, une plantation dans l'Illinois et sept plantations dans le Michigan ont été mesurées pour la croissance en hauteur. En 1963, la croissance en hauteur a été mesurée dans quatre plantations du Michigan.

L'analyse de variance de chaque caractère a été réalisée pour chaque plantation comparative. Les résultats obtenus pour chaque plantation ont été combinés et les carrés moyens utilisés pour calculer les composantes de la variance. Ces composantes ont été alors exprimées en pourcentage de la variance totale.

Les provenances de Belgique, Allemagne et Tchécoslovaquie ont donné la hauteur la plus forte pour toutes les plantations en 1962 et 1963. Les hauteurs les plus faibles ont été obtenues avec des provenances espagnoles. Cependant en 1963 il est apparu que les provenances espagnoles pourraient dépasser les scandinaves lorsque les effets de la transplantation auraient disparu.

On a constaté également des différences notables entre les diverses stations.

L'interaction provenance  $\times$  plantation de chaque provenance individuelle ne traduit aucune relation avec les conditions du lieu d'origine ou celles du lieu de plantation. Les différences dans la hauteur des diverses provenances suivant les différentes plantations semblent plus un résultat des variations de température et d'état hygrométrique que des différences entre plantations dues au type de sol ou à la photopériode.

La composante de la variance résultant de l'interaction provenance  $\times$  plantation n'intervient jamais pour plus de 6% de la variation totale calculée dans toutes les plantations en 1962 ou 1963. Cette composante représente environ 1/6 de la composante représentant la variation provenance pour la hauteur.

Les effets des fluctuations annuelles du climat sur les différences entre provenances (interaction année  $\times$  provenance) sont également très faibles en comparaison des différences entre provenances.

Malgré le fait que la variance de l'interaction est relativement faible et que les corrélations des diverses provenances entre plantations sont fortes, une sélection basée sur une seule plantation comparative doit réduire de façon sérieuse l'efficacité de la sélection.

### Literature Cited

- AREND, J. L., SMITH, N. F., SPURR, S. H., and WRIGHT, J. W.: Jack pine geographic variation — five year results from Lower Michigan. Mich. Acad. Sci. Papers 1961, 46—219—38, 1961. — CALLAHAM, R. S., and LIDDICOET, A. R.: Altitudinal variation at 20 years in ponderosa and Jeffrey pines. J. Forestry 59: 814—820 (1961). — COCHRAN, WILLIAM G., and COX, GERTRUDE M.: Experimental designs. 2nd ed. John Wiley & Sons, New York, 1957, 611 pp. — COMSTOCK, R. E., and MOLL, R. H.: Genotype — environment interactions, p. 164—196. In W. W. HANSON and H. F. ROBINSON, (ed.), Statistical genetics and plant breeding. Nat. Acad. Sci. Publ. 982, 1963. — GARDNER, C. O.: Estimates of genetic parameters in cross-fertilizing plants and their implications in plant breeding, p. 225—252. In W. D. HANSON and H. F. ROBINSON, (ed.), Statistical genetics and

plant breeding. Nat. Acad. Sci. Publ. 982, 1963. — HENRY, B. W.: Disease and insects in the southwide pine seed source study plantations during the first five years. South. Conf. on Forest Tree Impr. Proc. 5: 12–17, 1959. — HOLST, M.: Growth of Norway spruce (*Picea abies* [L.] KARST.) provenances in eastern North America. Canada Dept. of Forestry Publ. 1022, 15 pp., 1963. — IRCENS-MOLLER, H.: Genotypic variation in photoperiodic response of Douglas-fir seedlings. Forest Sci. 8: 360–62 (1962). — JOHNSON, H.: Utvecklingen i 15-åriga försöksodlingen av tall i relation till proveniens och odlingsort. Svenska Skogsv. Fören. Tidskr. 53: 58–88 (1955). — LANGLEY, O.: Studier över tallens fysiologiska variabilitet och dess samband med klimatet. Meddel. Statens Skogsförsöksanst. 29: 219–470 (1936). — LANGLEY, O.: The Norway spruce provenance experiments at Dönjelt and Hjuleberg. Stockholm, 8 pp., Mimeo., 1963. — MATZINGER, D. F.: Experimental estimates of genetic parameters and their applications in self-fertilizing plants, p. 253–279. In W. D. HANSON and H. F. ROBINSON, (ed.), Statistical genetics and plant breeding. Nat. Acad. Sci. Publ. 982, 1963. — MIROV, N. T., DUFFIELD, J. W., and LIDDICOET, A. R.: Altitudinal races of *Pinus ponderosa* — a 12-year progress report. J. Forestry 50: 825–831 (1952). — PERRY, T. O.: Racial variation in the day and night temperature requirements of red maple and loblolly pine. Forest Sci. 8: 336–344 (1962). — RUDOLF, P. O.: Winter damage and seed source of planted pines in northern Minnesota. Minn. Acad. Sci. Proc. 17: 74–79, 1949. — RUDOLPH, T. D.: Lammas growth and prolepsis in jack pine in the Lake States. Forest Sci. Monog. 6., 70 p., 1964. — RYCROFT,

H. B., and WICHT, C. L.: Field trials of geographical races of *Pinus pinaster* in South Africa. Pretoria, Dept. of Forestry. Brit. Empire Forestry Conf. 12 pp., 1947. — SANTAMOUR, F. S., JR.: Seasonal growth in white pine seedlings from different provenances. Northeast. Forest Expt. Sta., Forest Res. Note 105., 4 pp., 1960. — SCHREINER, E. J., LITTLEFIELD, E. W., and ELIASON, E. J.: Results of 1938 IUFRO Scotch pine provenance test in New York. Northeast. Forest Expt. Sta. Pap. 166, 23 pp., 1962. — SLUDER, E. R.: A white pine provenance study in the southern Appalachians. Southeastern Forest Expt. Sta. Res. Pap. SE-2, 16 pp., 1963. — SNYDER, E. R., and ALLEN, R. M.: Sampling, nursery, and year-replication effects in a longleaf pine progeny test, p. 26–27. Proc. Forest Genet. Workshop, Macon, Georgia, Oct. 1962. Southern Forest Tree Impr. Com. Publ. 22, 1963. — WAKELEY, P. C.: Results of the southwide pine seed source study through 1960–1961. South. Conf. on Forest Tree Impr. Proc. 6: 10–24, 1961. — WIEDEMANN, E.: Die Versuche über den Einfluß der Herkunft des Kiefernensamens aus der preußischen forstlichen Versuchsanstalt. Z. Forst- u. Jagdw. 62: 498–522, 809–836 (1930). — WRIGHT, J. W., and BALDWIN, H. J.: The 1938 International Union Scotch pine provenance test in New Hampshire. Silvae Genetica 6: 2–14 (1957). — WRIGHT, J. W., and BULL, W. IRA: Geographic variation in Scotch pine. Silvae Genetica 12: 1–25 (1963). — WRIGHT, J. W., LEMMIEN, W. L., and BRIGHT, J.: Geographic variation in eastern white pine — 6-year results. Quart. Bull., Mich. Agr. Exptl. Sta., East Lansing, 45: 691–697 (1963).

## Assessment of Stem Form in Clones and Progenies of Larch

By H. KEIDING and H. C. OLSEN

Arboretum Hørsholm, and Forest Research Institute, Springforbi, Denmark

(Received for publication December 20, 1964)

### Introduction

As part of a general assessment of clone collections and progeny trials in larch it was desired to study the variation and inheritance of stem form. Beside vigour, straightness of stem plays an important part in the evaluation of parent trees for breeding. Various methods for measuring and scoring stem form have been suggested by different workers, especially in connection with provenance trials. These methods may roughly be divided into 3 groups. Firstly evaluation based solely on measurements: PERRY (14), GENYS (4) and SHELBORNE (15). Secondly evaluation based solely on scoring: GÖHRN (5), LANGNER (9), LITTLEFIELD and ELIASON (11), and SØEGAARD (16) and thirdly an evaluation based on a mixture of measurements and scoring: FISCHER (3).

Stem form is usually assessed by three kinds of deviations from the straight: *Crooks* (sinuosity), *basal sweep* and *lean*. In general it is believed that crookedness is to a considerable extent genetically determined and that basal sweep and lean are mainly the result of factors such as wind and site.

In the current investigations of larch our aim was to find a practical method of assessment, which at one and the same time gave us a sufficiently detailed picture of the variation in stem form, and made it possible to sort out the least desirable parents from the point of view of crookedness. Various means of measuring crooks and basal sweeps have been contemplated but no satisfactory method was found, which would enable us to measure a large number of trees within a reasonable time.

We therefore decided to classify the material into 5 groups, each group being defined and illustrated by type trees. The distribution of trees in the 5 classes was registered for each clone or progeny. These distributions were compared and formed the basis for grading the material.

### Material

Stem form was scored in two clone collections of Japanese larch (*Larix leptolepis*) and in one of European larch (*Larix decidua*). Further scoring was done in a progeny trial of Hybrid larch from controlled crossings between parents from the clone collections.

The clones were all grafted in 1953 and were thus 10 years old at the time of assessment. They represent a selection of plus trees made by Dr. C. SYRACH LARSEN (V-numbers) and by H. BARNER (K-numbers). One of the clone collections of Japanese larch and that of European larch are situated in the same experimental field at the State Forest Plant Breeding Station at Humlebaek. The soil here is of a rather heavy, clayish nature. The second clone collection of Japanese larch and the progeny trial of the hybrids are a few kilometers apart at Viborg State Forest district in the central part of Jutland. The soil here is lighter and more sandy and the climate of a more continental type with heavier frosts and stronger winds than that of Humlebaek. The two clone collections of Japanese larch are duplicates.

The lay-outs of the clone collections and the progeny trial are as follows: —

#### Clone collections:

1. Humlebaek, Birkemarken: Randomized block design with 3 replications and 4 trees per plot. Number of clones is for Japanese larch, 32, and for European larch, 27. Planting distance: 3 × 3 m.
2. Viborg district: Randomized block design with 2 replications and 6 trees per plot. 33 clones and planting distance, 3 × 3 m.

#### Progeny trial, Viborg district:

Randomized block design with 3 replications and 50 trees per plot. 39 progenies of which 5 are replicated twice only. The progenies consist of two groups of halfsibs of 19 and