SEED SOURCE X ENVIRONMENT INTERACTIONS IN SCOTCH PINE

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presented by

JAMES PHILLIP KING

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Jonathan W. Wright
Major professor

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ABSTRACT

SEED SOURCE X ENVIRONMENT
INTERACTIONS IN SCOTCH PINE

by James P. King

This study was undertaken to determine the effects of differing Michigan environments on the growth of Scotch pine (*Pinus sylvestris* L.) seed sources.

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 from 50 to 100.

In 1962 following the second growing season after out-planting, one plantation in central Illinois was measured for height growth while in Michigan seven plantings were measured for height growth, five for needle length, and seven for color. In 1963 four Michigan plantations were measured for height growth and needle length. Data from 64 seed sources were used in this study.

Analyses of variance of each character was made for each test plantation using plot totals as items. 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 outgrow the Scandinavian sources as the effects of transplanting dissipated.

The planting sites also showed marked differences in growth rate. They differed in the amount of growth per year and in the change in growth rate with time.

Sources from central Europe had the longest needles and sources from either the northern or southern extremity of the Scotch pine range had the shortest needles. However, this trend differed more by plantation than did height growth. While the Scandinavian sources were relatively short-needled in the northernmost Michigan plantation, they had relatively long needles in the southernmost plantation. The Spanish sources, on the other hand, all had relatively longer needles at the northernmost plantation.

The mean plantation needle length differed sharply with site and year. In 1963 the mean needle length decreased by 25 percent in the southernmost Michigan plantation while it increased by 10 percent at the northernmost planting. It is suggested that this year x plantation interaction was the result of a late frost in May 1963.

The Spanish, Greek-Turkish, and south France sources were the darkest green and sources from the Ural mountains and Scandinavia were the most yellow. Sources from Scandinavia showed more yellowing in central lower Michigan than at any other plantation but were still not as yellow as the Ural mountain sources.

The seed source x 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 or photoperiod.

The component of variance resulting from seed source x 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 1/6 the seed source component for height growth; 1/5 the seed source component for needle length; and about 1/12 the seed source component for color.

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

Under the conditions of pest infestation encountered in this test (very low), the researcher could gain little more than a two or three percent increase in precision by replicating measurements in time and space.

From a practical standpoint this data indicates that the most genetic gain per dollar spent would be obtained by testing an increased number of seed sources in a single planting and then replicating in time and space only a few of the best seed sources.

Data from other tests indicates that these results should also be applicable in mature trees throughout North-central and Northeastern United States and central Europe.

SEED SOURCE X ENVIRONMENT
INTERACTIONS IN SCOTCH PINE

By

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INTRODUCTION

Scotch pine (*Pinus sylvestris* L.) is the most important commercial tree species in Europe. Its natural range extends from Spain and Turkey in the south to Scotland and northern Finland in the north, and eastward across Russia almost to the Pacific Ocean. In the southern part of the range it is found in isolated stands on cool moist mountain slopes. Toward the north its occurrence is continuous over large areas.

Although Scotch pine has been planted and grows well over a wide area of the northeastern United States, American foresters held it in low regard because of its poor form. However, as evidence mounted indicating the poor form was due to improper seed source, interest in the species was renewed. The tree reproduces naturally in many parts of the United States, is easily transplanted, and grows well on a variety of sites. It is a favorite of Christmas tree growers. In the past three years one-fifth to one-third of all stock growing in Michigan forest tree nurseries was Scotch pine. It is logical then 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 if any estimates of genetic variation of forest trees have been made in a manner that excludes bias from seed source x environment interactions. Yet, unless the magnitude of this bias is known, a realistic estimate of the rate of improvement is not possible. Furthermore, the magnitude of the seed source x environment interaction determines the extent of the area to which test results will apply and provides a measure of the profit of breeding for specific locations.

Review of Literature

Provenance Tests

A single replicated seed source test gives a valid estimate of the error variance necessary for testing the significance of seed source differences, but confounds variance due to seed source with variance due to seed source x environment interaction. Tests of this nature have been common with forest tree species since about 1930. Results of such tests have been summarized by Wright (1962).

Unreplicated seed source tests repeated at several locations confound seed source x plantation interaction with within-seed-source variation. Thus the magnitude of the interaction cannot be determined and conclusions from such tests cannot be applied to specific environments. Tests in this category have been conducted with Scotch pine (Wiedemann, 1930; Kalela, 1937), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Munger and Morris, 1936), ponderosa pine (*Pinus ponderosa* Laws.) (Munger, 1947; Squillace and Silene, 1962), and Norway spruce (*Picea abies* (L.) Karst.) (Rubner, 1957; Schönbach, 1957).

Thus far only a few seed source tests designed to measure interaction have been reported. These include maritime pine (*Pinus pinaster* Ait.), loblolly pine (*P. taeda* L.), slash pine (*P. elliottii* Engelm. var. *elliottii*), shortleaf pine (*P. echinata* Mill.), longleaf pine (*P. palustris* Mill.), jack pine (*P. banksiana* Lamb.), eastern white pine (*P. strobus* L.), ponderosa pine, Scotch pine, Norway spruce, and European larch (*Larix decidua* Mill.).

The majority of these tests 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 sources between plantings does not preclude the existence of interaction, it does indicate that the seed source component of variance is much greater than the interaction component.

Thus while the estimates of genetic variation from a single 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.

Rycroft and Wicht (1947) reported the ten-year results of a seven-origin test of maritime pine at eight test sites in western and southern South Africa. The data showed no seed source x 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 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 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 the 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 fusiform Hedge. and Hunt) in the Southwide Pine Seed Source Study was reported by Henry (1959). Comparing slash pine 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. Seedscollected 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 Missi-ssippi. Their analysis of variance showed a highly significant seed source x plantation interaction. The nature of the interaction was not stated.

Five-year results of a 29-origin Lake States jack pine test have been reported by Arend et al. (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 x 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 (1962) 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 x plantation interaction for lammas growth and long buds, but none for prolepsis. The data also indicated a significant seed source x plantation x 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 Wisconsin plantations of this same test, the present author found a significant seed source x 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 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 x 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 x plantation interaction for mortality, color and six-year height. The source from Tennessee was the fastest growing at both plantings 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.

Height and diameter growth of one- and two-year old ponderosa pine seedlings was recently described by Baron and Schubert (1963). The seed in this test was collected from five seed collection zones and grown in four California nurseries. The collection zones were: (1) northern east side Sierra (high elevation, 4000 to 6000 feet above sea level); (2) northern west side Sierra (low elevation, 2000 to 4000 feet above sea level); (3) northern west side Sierra (high elevation); (4) southern west side Sierra (low elevation); and (5) southern west side Sierra (high elevation). The four nurseries range in elevation from 226 to 3252 feet above sea level and in latitude from 37°N. to 41°N.

At all four nurseries seed from zone four made the best two-year height growth and was not significantly exceeded in diameter growth by any other seed collection. Zone one stock was poorest at all nurseries.

Evidence that a seed source x plantation interaction in ponderosa pine 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 years' 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 (1961) also reported on 20-year height growth of 21 Jeffrey pine (*Pinus jeffreyi*, Grev. and 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 are 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.

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

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**2/	22.88
Seed Source X Plantation	30	3.42**3/	3.76
Rep. within seed Source	120	1.07	4.29

** Significant at the one percent level.

1/ New York data from Schreiner et al. 1962.
New Hampshire data from Wright and Baldwin, 1957.

2/ Based upon seed source x plantation interaction as error term.

3/ Based upon seed source x replicate-within-planting as error term.

Holst (1963) recently summarized the results of the International Union of Forest Research Organization Norway spruce provenance tests begun in 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 x 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 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.

Vins (1963) reported on diameter growth of twenty-two provenances of Norway spruce at two plantings in Czechoslovakia. These plantings were located at 340 and 850 meters above sea level. The trend noted in height growth was also noted in diameter growth, i.e. sources from east-central Europe were best and sources from northern Europe poorest. The low correlation between provenances at various ages in two plantings (1949 r = .57; 1958 r = .71; 1962 r = .61) suggests that there was a seed source x plantation interaction between these two plantations.

Genys (1960) showed high correlations in height growth of European larch seed sources between United States and European plantations. His correlations were based on 12-year height in New York and New Hampshire and: (1) 9-year height in Scotland (r = .83 with 13 degrees of freedom); (2) 10-year height in northeast Germany (r = .93 with 6 degrees of freedom); and 11-year height in northern Italy (r = .87 with 12 degrees of freedom).

Agronomy Tests

More detailed analysis of genotype x 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 x 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 x environment interaction will assume an increasing importance.

Controlled Environment Tests

Numerous studies under controlled environment conditions have shown interactions between seed source and specific factors of the environment. Photoperiodic response has been the object of the largest number of studies.

Vaartaja (1954) collected Scotch pine seed from several trees in two Finnish stands located at 65° N. latitude and at 60°30' N. latitude. These two seed sources were given two photoperiodic treatments; one limited to two hours of natural light, and the other treatment ten hours of natural light plus continuous (24 hour) low intensity light. The northern origin seedlings grew better than the southern origin under continuous light, but under short days the southern origin made the best growth. These growth differences were measured by needle number and dry weight.

Wassink and Wiersma (1955) collected Scotch pine seed from Sweden (66° N.) and the "Massif Central" of France (45°30'). They tested the seedling growth under two photoperiods, one a 12-hour day and the other a 12-hour day plus continuous weak light. The seed from northern Sweden made only slightly less growth under long days, but much less under short days.

Vaartaja (1959) tested Scotch pine seed from Finland (60° N.) and Spain (41° N.). In this test Vaartaja simulated four different daylengths by varying the length of the period of continuous dark period. All plants received light from 6:00 a.m. to 5:00 p.m. Then, for example, the very long day treatment would receive one hour of light from 11:00 p.m. to 12:00 p.m. This limited the dark period to six hours and was considered equivalent to an eighteen hour day. With this method Vaartaja could hold the amount of light constant and vary only the length of photoperiod. Daylengths of 12, 14, 16, and 18 hours were simulated. As in the previous tests northern origins grew for a longer period and made better growth relative to the southern origins under the long photoperiod.

Vaartaja (1959) has also reviewed the evidence for "photoperiodic ecotypes" in other tree species. In general, the results agree with those of Scotch pine. That is, seed origins from northern latitudes show a greater response to change in photoperiod than southern origins.

Karschon (1949) studied the photoperiodic response of Scotch pine seed from different elevations in Switzerland. He used a short day treatment consisting of natural light only and long day (15 hours) treatment with artificial light. Using seed from five stands ranging in elevation from 385 meters to 1770 meters, he found a statistically significant interaction between seed source and treatment in height growth. The lower the elevation of the seed source, the greater was the growth under short days.

Callaham (1962), using ponderosa pine progenies from 26 localities throughout the ponderosa pine range, measured growth under nine combinations of three day temperatures (30°, 23°, and 17° C.) and three night temperatures (22°, 14°, and 7° C.) with a constant daylength of sixteen hours. The results showed that seedlings from east of the Rocky Mountains need high night temperatures for best growth; seedlings from the southwestern United States did best with cool days and hot nights; and Pacific coast seedlings grew reasonably well at lower night temperatures.

Perry (1962) reported an interaction of day and night temperatures in red maple (*Acer rubrum* L.). Using seed collected from three or four widely separated trees at six locations from Florida to Ontario and Minnesota, the seedlings were grown for 34 days with a constant day temperature of 23° C. and night temperatures ranging from 7° C. to 26° C. Northern origins made their best growth with a night temperature of about 17° while the southern origins did best with a night temperature of about 20° C. Using only two origins (Vermont and Florida), Perry grew the plants under a constant night temperature of 17° C. at different day temperatures of 17°, 20°, 23°, 26°, and 30°C. Again tree growth of the two seed sources varied with temperature. The Vermont seedlings made their best growth with a day temperature of 26° while the Florida seedlings showed increasing growth with increasing temperature. Perry's data also indicated the presence of a seed source x temperature x photoperiod interaction in red maple. This same type second-order interaction was also suggested by Irgens-Moller with Douglas-fir (1962).

Kriebel and Wang (1962) reported an interaction between seed source and amount of pre-chilling. They subjected four provenances of sugar maple (*Acer saccharum* Marsh.) to seven durations of outdoor chilling in northern Ohio and observed the frequency and timing of bud burst. The sugar maple of southern origin broke dormancy with less outdoor chilling than did the northern sources. The time between the end of the chilling period and the time of bud break was reduced more in the northern origins than in the southern origins.

The preceding tests should suffice to demonstrate why it is so difficult to determine the cause of a particular seed source interaction in a natural environment. For not only do the seed sources interact with several factors of the environment, but the environmental factors themselves may interact with each other in their effect on the genotype.

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 regional project's objectives are as follows: (1) Determine the range and pattern of genetic diversity within selected forest tree species, (2) utilize the genetically most suitable material for breeding purposes, and (3) provide genetically suitable material for reforestation purposes.

The objectives of this study are as follows: (1) determine the magnitude of seed source x environment interactions over a variety of conditions in the North Central United States, (2) determine the causes of these interactions, and (3) determine the effect of these interactions on a Scotch pine selection and breeding program.

METHODS

Material

Seed collected from ten average trees in each of 122 stands throughout the natural range of Scotch pine was sown in the forest nursery at East Lansing, Michigan in the spring of 1959. Within each stand the parents were separated from each other by 100 feet or more. The collection areas are shown in Figures 1 and 2. Origin data are given in Table 2 for the 64 sources used in the present study.

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 plantations throughout Michigan and the central states. The locations of these plantings are shown on Figure 3. Most plantings followed a randomized block design with from 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

Figure 1. Natural distribution of Scotch pine in Europe (shaded) and provenances in this study (numbered dots). (Wright and Bull, 1963)

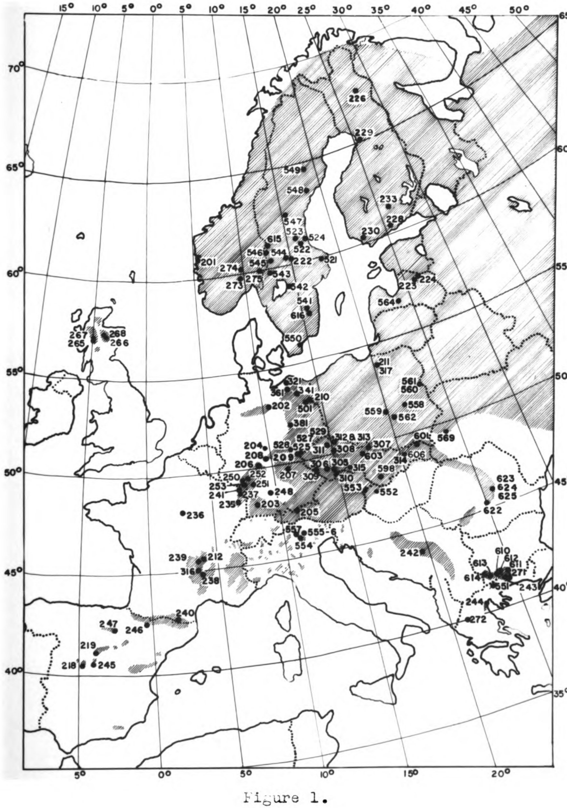
15° 10° 5° 0° 5° 10° 15° 20° 25° 30° 35° 40° 45° 50°
65° 60° 55° 50° 45° 40° 35°
70° 65° 60° 55° 50° 45° 40°
5° 0° 5° 10° 15° 20°
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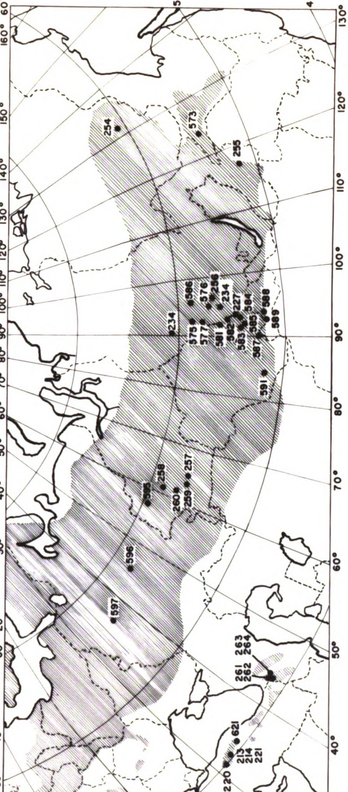
Figure 1.

Figure 2. Natural distribution of Scotch pine in Asia (shaded) and provenances included in this experiment (numbered dots). (Wright and Bull, 1963)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80°
90°
100°
110°
120°
130°
140°
150°
160°

Figure 2.

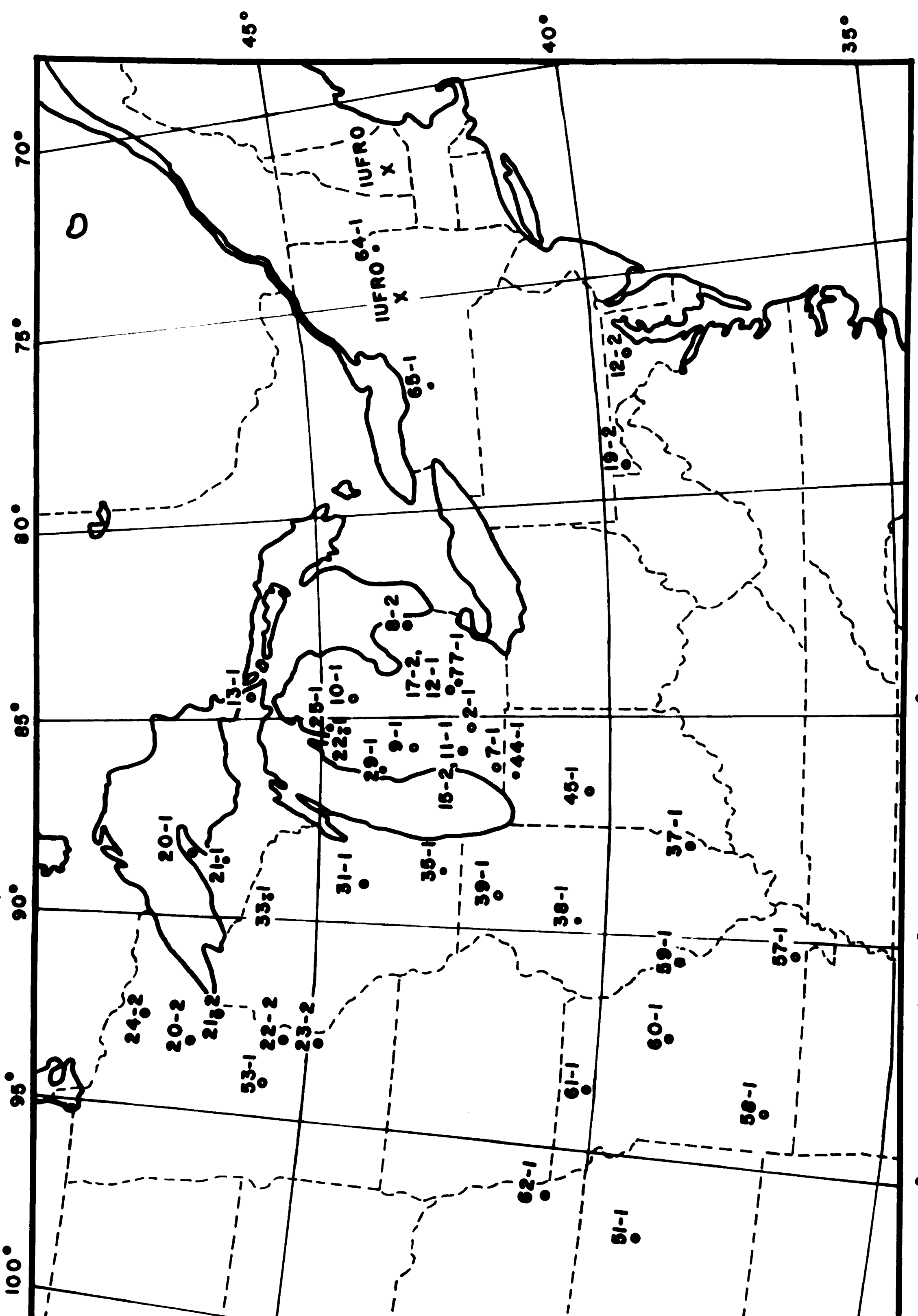
Table 2. Seed source location data - grouped by region.

Region	Country of origin	MSFG No.	North Lat.	East Long.	Elev.
			—degrees—		100's of feet
A	SIB[1]	254	60.8	131.6	25
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	522	60.9	16.5	7
	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	56.8	14.3	4
	SWE	550	55.9	14.1	1
E	SIB	227	54.0	94.0	5
	SIB	255	52.4	117.7	20
	SIB	256	56.7	96.3	13
	URA	258	56.8	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	207	49.7	11.2	—
	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	6.8	—
	FRA	241	49.1	7.4	8
	GER	251	49.1	8.1	5
	GER	252	49.3	7.9	13
	GER	253	49.1	7.8	13
	BEL	316P	51.2	5.5	—
	BEL	530P	50.-	5.-	10
	HUN	553	47.7	16.6	10
	NY	225P	43.-	75.-	—
J	FRA	235	48.2	0.2	22
	YUG	242	43.8	19.4	40
K	TUR	213	40.5	32.7	40
	TUR	220	40.0	31.3	47
	TUR	221	40.5	32.7	40
	GRE	243	41.5	24.3	40
	GRE	244	40.2	22.1	55
	GRE	271	41.5	24.3	40
	GRE	551	41.3	23.2	40
M	FRA	238	44.7	3.8	31
	FRA	239	45.3	3.7	33
N	SPA	218	40.3	-6.2	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

[1] BELgium, CZEchoslovakia, FINland, FRAnce, GERmany, GREece, HUNgary, LATvia, NY New York, NORway, POLand, SIBeria, SPAin, SWEden, YUGoslavia, URAl Mountains.

P Seeds obtained from planted stands.

Figure 3. Location of Scotch pine test plantations used in the regional study.



45°
40°
35°
70°
75°
80°
85°
90°
95°
100°
IUFRO
X
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65-1
12-2
19-2
8-2
17-2
12-1
77-1
2-1
10-1
13-1
9-1
29-1
11-1
7-1
44-1
15-2
45-1
37-1
20-1
21-1
31-1
36-1
39-1
38-1
59-1
57-1
24-2
20-2
22-2
23-2
53-1
60-1
61-1
56-1
62-1
51-1

Figure 3.

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

Map Number	Name	County, State	North Lat.	West Long.	Seed Sources	Replications	Trees/Plot	Planting Method
			Degrees		Number			
2-61	Kellogg Forest	Kalamazoo, Michigan	42.3	85.3	108	10	4	FH1/
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	M
10-61	Higgins Lake	Crawford, Michigan	44.5	84.7	72	7	4	M
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	HS

1/ Furrowed, Hand planted, Machine planted, Scalped, Chemical weed control.

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 loamy sands. The Allegan planting has by far the coarsest-textured soil and is the most moisture deficient site. The Edwards County, Illinois planting, on the other hand, has the finest-textured soil.

Measurement

In the fall of 1962 height growth was measured on eight plantations and needle length on five. In the fall of 1963 height growth and needle length were measured on four plantings. Color was scored in six plantings in 1962 and none in 1963.

Height growth was measured to the nearest centimeter. Total height growth for all four trees on the plot was recorded. If less than four trees were present, the height growth was converted to a four-tree basis before recording. In 1962 the height of the fastest growing tree on each plot was also recorded.

One needle fascicle from the middle of the current terminal growth was removed from each tree and measured to the nearest millimeter. The total length of the four fascicles was recorded. If less than four trees were present, the total length was converted to a four-tree basis.

Table 4. Plantation climatic data. 1/

	Plantation							
	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	66.1	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	60.2	—	—	—	—
Annual mean, 1962	47.7	42.8	48.4	39.0	44.7	47.2	48.3	—
Period between days with minimum of:	days							
32°F. (1962)	154	110	154	134	135	138	153	—
24°F. (1962)	204	188	266	188	191	193	189	—
32°F. (1963)	131+2/	112	131+2/	113	—	—	—	—
Precipitation:	inches							
1961 Annual	30.87	40.10	34.98	28.86	34.22	28.11	38.68	54.55
1962 Annual	24.49	33.45	26.44	28.05	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	6.66	7.83	5.68	7.61	9.80	9.23
April-June 1963	8.07	13.76	8.49	9.15	—	—	—	—

1/ 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.

2/ Date of first 1963 fall frost not available.

Large samples of ten to fifteen fascicles per tree were collected at several plantings in 1962 for comparison with results of the single fascicle measurement. This comparison showed that a single fascicle per tree gave almost identical results as obtained with a larger sample of fascicles (See Appendix A). This was due to the small within-tree variation in needle length.

Color was scored on the basis of ten color grades--grade 1 being the yellowest in the planting and grade 10 the bluest. This scoring system permits within-planting analysis but may bias between-planting comparisons. To determine the constancy of color grades between plantings, several samples were scored in the field and then brought immediately into the office for comparison with Munsell color charts. The following tabulation shows the entire range of Munsell color grades and the field score of the selected samples.

Munsell Color	Plantation and date sample taken: Higgins Lake October 20, 1962	Newaygo October 22, 1962	Russ Forest November 13, 1962
	Field Score 1/		
2.5 Y		1	1
5.0 Y	1		
7.5 Y			
10.0 Y	2		2
2.5 GY			
5.0 GY		6	6
7.5 GY	5		
10.0 GY		9	
2.5 G	9		9
5.0 G			

1/ 1 = yellowest; 10 = darkest green.

There is good general agreement between plantings among the greener shades. However, there are indications that the observer recognized fewer shades of yellow than of green.

The color scorings were made over a fairly wide range of dates. However, subsequent analyses showed that the date of scoring was relatively unimportant. Because of a heavy snowstorm in early December it was not possible to score the plantings when color differences would be at their peak--about mid-December.

One special color scoring was made the first week of December. This scoring was designed to provide precise between-planting comparisons with the effect of date of scoring held constant. Samples of nineteen sources common to three plantings were collected. The needles were removed from each tree, stapled onto a wide card with plot identification on the back, and then brought into the laboratory for direct comparison under uniform light. Collection and scoring were completed within two days. Using this system it was possible to recognize nineteen color grades.

<u>Analysis</u>

The number of seed sources used in the analyses was determined by the number of seed sources the measured plantations had in common. There were 42 seed sources common to all 7 plantings measured in 1962; 55 seed sources common to the 4 Michigan plantings measured in 1962 and 1963; and 57 sources common to the six plantations scored for color.

Data for each characteristic and plantation were individually subjected to analysis of variance using plot totals. Plantation analyses were then grouped in various combinations and tested for treatment differences and seed source x plantation interaction.

Such combined analyses may be open to question because of possible heterogenity of error and interaction variances. Thus the Edwards County, Illinois, plantation was not included in the combined analyses. This plantation had two-tree plots whereas all the other plantings had four-tree plots.

Excluding the Edwards County planting, treatment differences in the combined analyses were so much greater than the interactions that there is no doubt as to their significance.

The "conservative" approach of Cochran and Cox (1957) was used to test the significance of interactions. That is, if one of the plantings had a much higher error variance than any of the others, the tabular F-value used was that with (s-1) and n' degrees of freedom--where s is the number of seed sources and n' the number of error degrees of freedom in the plantation with the highest error variance. There were no instances in the entire study, however, where this conservative approach changed any conclusions as to significance of interactions.

Significance of differences between plantations was determined by the "t-test" since the combined analyses do not provide a valid error term for comparison of plantation means.

Components of variance were determined by setting the computed mean squares equal to their expected mean squares (Tables 5 and 6) and solving for the components.

Correlations between plantations, using seed source totals as items, were made to determine the degree of similarity between plantings.

Table 5. Analysis of variance form used for the combined analysis of a single year's results.

Source of variation	Degrees of freedom	Parameters estimated by mean square
Plantation	$(p-1)$	$\sigma_e^2 + \bar{r}\sigma_{ps}^2 + \bar{r}s\sigma_p^2$
Seed sources	$(s-1)$	$\sigma_e^2 + \bar{r}\sigma_{ps}^2 + \sum_p r_p \sigma_s^2$
Plantations X Seed sources	$(p-1)(s-1)$	$\sigma_e^2 + \bar{r}\sigma_{ps}^2$
Error	$\left[\sum_p (r_p-1)\right](s-1)$	σ_e^2

p = number of plantations; s = number of seed sources; r_p = number of replications per plantation; $\bar{r} = \Sigma r_p^2/\Sigma r_p$

σ_e^2 is the component of variance due to random variations within plots within plantations.

σ_p^2 is the component of variance due to differences between plantations.

σ_s^2 is the component of variance due to differences between seed sources.

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

Table 6. Analysis of variance form used for the combined analysis of yearly results.

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

y = number of years; p = number of plantations; s = number of seed sources; r_p = number of replications per plantation; $\bar{r} = \Sigma r_p^2 / \Sigma r_p$

σ_e^2 is the component of variance due to random variations within plots within plantations.

σ_y^2 is the component of variance due to differences between years.

σ_p^2 is the component of variance due to differences among plantations.

σ_s^2 is the component of variance due to differences among seed sources.

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

σ_{ys}^2 is the component of variance due to interaction of years and seed sources.

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

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

RESULTS

In the presentation of results the seed sources are grouped according to the geographic ecotypes delineated by the three-year nursery measurements of Wright and Bull (1963). It should be pointed out that these ecotypes were determined on the basis of a multi-character analysis. Thus these groups may not conform exactly to a grouping based on height growth, needle length, or color alone.

Height Growth

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 7).

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 group 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

Table 7. --Height growth of Scotch pine seed sources.

Region	Country of origin, MSFG No.	Kellogg Forest 1962	Kellogg Forest 1963	Allegan 1962	Allegan 1963	Higgins Lake 1962	Higgins Lake 1963	Houghton 1962	Houghton 1963	Russ Forest 1962	Newaygo 1962	Rose Lake 1962	Edwards 1962
		Percent of plantation mean											
C	NOR[1] 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
	SWE 222	95.3	86.2	89.9	94.6	83.6	87.0	104.7	92.9	77.8	90.1	88.1	86.3
	FIN 230	69.9	57.2	68.5	61.6	67.4	53.8	49.2	64.0	—	—	—	—
	NOR 273	75.3	66.8	90.1	92.0	80.6	79.5	93.1	89.8	68.0	100.0	76.3	90.7
	NOR 274	95.1	77.7	71.6	71.2	88.4	71.9	92.6	87.3	59.8	96.5	74.3	107.1
	SWE 521	92.7	90.7	79.8	89.0	120.2	103.0	107.2	88.6	86.4	103.5	96.5	96.5
	SWE 523	90.6	84.5	91.1	88.5	113.9	97.0	90.8	88.1	80.0	91.9	102.6	88.7
	SWE 524	96.2	90.0	94.1	93.7	92.3	86.5	89.8	86.9	77.2	96.5	97.4	90.7
	SWE 543	78.7	79.1	74.5	73.2	106.1	98.9	90.3	87.0	87.5	83.0	101.4	103.3
	SWE 544	93.1	93.4	89.1	91.0	96.5	86.6	90.3	82.7	80.8	104.3	87.3	81.9
	SWE 545	82.4	67.6	79.0	82.8	100.9	81.0	58.0	63.8	—	—	—	—
	Average	85.4	78.8	82.2	83.6	93.2	83.6	86.3	83.0	75.8	93.7	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
	LAT 224	83.6	78.9	90.7	91.4	94.1	97.6	101.7	87.6	83.2	94.4	91.0	111.5
	SWE 541	114.7	106.0	99.6	100.0	138.2	116.7	118.8	95.8	109.3	98.2	107.2	115.9
	SWE 542	116.7	98.1	89.6	86.9	116.0	105.6	93.1	101.5	93.5	99.8	106.1	92.6
	SWE 550	98.7	111.4	90.4	89.6	86.1	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	—	—	—	—
	URA 258	101.3	85.3	111.3	105.3	110.9	91.7	114.6	98.3	106.1	107.4	91.9	108.6
	Average	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
	POL 317	112.1	105.8	130.8	119.2	113.9	112.7	103.7	110.5	120.3	121.0	117.2	127.5
	Average	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
	GER 203	95.5	100.5	93.0	95.3	89.0	103.0	94.9	96.1	100.3	86.8	97.9	82.4
	GER 208	122.0	116.4	117.9	122.7	108.8	120.7	108.5	107.3	—	—	—	—
	GER 210	126.1	119.8	115.2	120.0	106.4	101.0	116.1	109.0	116.6	108.1	124.2	94.0
	CZE 305	118.6	123.1	128.2	125.6	102.1	103.2	109.3	105.9	—	—	—	—
	CZE 306	95.7	108.4	126.3	108.8	91.4	104.1	117.6	120.9	106.1	110.1	112.9	92.1
	CZE 307	117.3	113.9	144.8	135.2	119.6	111.3	107.2	107.6	—	—	—	—
	CZE 308	103.3	111.8	136.9	139.7	129.5	111.6	90.3	114.1	—	—	—	—
	CZE 309	113.0	113.8	96.7	97.8	95.9	105.2	113.5	106.3	116.6	105.6	101.4	90.2
	CZE 310	130.2	133.4	114.7	112.7	143.6	126.4	121.9	113.3	135.3	115.9	105.7	98.4
	CZE 311	121.6	113.3	117.6	119.4	90.5	107.6	120.1	115.8	—	—	—	—
	CZE 312	131.6	117.6	126.3	127.6	114.5	130.0	114.8	108.8	110.9	126.1	117.2	119.3
	GER 525	110.0	116.4	122.1	119.4	136.7	126.8	120.1	112.4	104.9	113.7	108.9	130.4
	GER 527	108.7	108.8	140.1	131.7	126.8	128.6	118.1	125.7	131.4	102.3	134.5	111.0
	Average	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
	FRA 241	118.2	131.9	119.7	119.0	131.9	128.4	119.4	110.8	—	—	—	—
	GER 251	126.3	131.1	125.0	119.6	146.6	130.0	150.1	126.1	164.3	135.2	135.7	110.5
	GER 253	116.2	134.2	133.7	126.4	123.8	120.0	109.3	115.5	122.7	138.7	133.3	108.1
	BEL 318	125.5	135.5	132.2	130.1	121.4	128.2	133.7	125.0	132.7	160.0	123.2	139.1
	BEL 530	132.4	125.9	119.7	127.6	89.3	104.9	117.7	134.8	136.7	117.5	157.6	146.4
	HUN 553	114.5	98.7	119.5	114.1	130.2	116.2	128.2	133.5	—	—	—	—
	NY 225	100.6	98.1	108.4	107.8	127.7	104.3	112.3	104.5	131.0	94.2	97.7	106.2
	Average	117.5	120.6	119.0	118.4	118.8	117.9	121.6	120.8	134.5	121.6	125.2	118.8
J	FRA 235	94.7	127.4	110.7	113.3	96.8	94.7	97.7	111.1	93.3	119.0	114.9	121.3
	YUG 242	98.5	104.6	100.7	83.8	87.8	98.7	92.6	96.4	110.9	123.8	115.2	98.9
	Average	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
	TUR 220	84.1	85.4	85.6	88.3	77.6	84.6	86.6	100.0	101.6	88.1	84.9	81.4
	TUR 221	74.6	92.6	81.1	84.2	53.1	76.4	83.5	78.2	91.8	77.2	102.8	101.8
	GRE 243	83.0	89.2	71.1	87.3	79.1	85.7	62.3	76.8	92.6	106.9	76.7	100.8
	GRE 271	91.8	92.0	103.1	100.6	104.6	109.6	117.6	112.7	—	—	—	—
	GRE 551	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
M	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
	SPA 219	76.6	83.4	65.5	82.0	62.6	77.7	85.8	98.1	85.6	69.4	64.5	85.3
	SPA 245	70.5	79.9	73.5	74.2	55.7	72.0	74.4	91.0	61.3	64.3	67.7	64.0
	SPA 246	61.7	67.3	60.0	62.8	55.2	77.3	71.7	82.4	68.0	61.0	57.6	67.9
	SPA 247	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	22.74	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.

over all the plantations measured in 1962, the second year following planting. These sources were the slowest growing group in every planting except Russ Forest. At Russ Forest the Spanish sources made twenty-five 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 x year interaction term in Table 8.

Kellogg Forest, Russ Forest, and the Houghton County plantations made the best overall growth 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 x plantation interaction in Table 8.

Table 8. Combined analysis of variance results of 1962 and 1963 height growth for 55 Scotch pine seed sources from four 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 x Seed Sources	54	500.27**1/	1.61
Years x Plantations	3	4920.85**1/	2.88
Seed Sources x Plantations	162	499.56**1/	0.74
Seed Sources x Years x Plantations	162	191.47*2/	0.58
Error	3294	160.32	26.42

* Significant at the five percent level.
** Significant at the one percent level.

1/ Based upon seed sources x years x plantations interaction as error term.
2/ Based upon seed source x replication-within-plantation as error term.

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 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 ten percent less at Edwards than at any other planting. There seems to be no 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 x 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 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 9). 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 x 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 10). 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.

Table 9. 1962 and 1963 components of height growth variance as a percent of total variance--from 55 seed sources.[1/]

Plantations in combined analysis	σ^2_p 1962	σ^2_p 1963	σ^2_s 1962	σ^2_s 1963	σ^2_{ps} 1962	σ^2_{ps} 1963	σ^2_E 1962	σ^2_E 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

σ^2_p is the component of variance due to differences between planting sites.

σ^2_s is the component of variance due to differences between seed sources.

σ^2_{ps} is the component of variance resulting from the interaction of seed sources and plantings.

σ^2_E is the component of variance due to random variations between plots within plantings.

NS - Non-significant

* - Significant at the five percent level.

** - Significant at the one percent level.

1/ Mean squares used to determine percentages shown in Appendix B, Tables B=1 and B-2.

Table 10. 1962 components of height growth variance expressed as a percent of the total variance of 42 seed sources.1/

Plantations in Combined Analysis	σ^2_p	σ^2_s	σ^2_{ps}	σ^2_E
	Percent of Total Variance			
Kellogg Forest Russ Forest Allegan Newaygo Higgins Lake Rose Lake Houghton	16.67**	28.17**	4.61**	50.55
Kellogg Forest Russ Forest Newaygo Allegan Houghton	22.90**	27.74**	4.77**	44.59
Kellogg Forest Russ Forest Allegan Houghton	21.83**	28.73**	4.14**	45.30
Kellogg Forest Allegan Russ Forest	28.16**	26.42**	4.99**	40.43
Kellogg Forest Higgins Lake Houghton	3.90NS	35.38**	4.29**	56.43
Kellogg Forest Allegan	43.10**	25.70**	0.00NS	31.20
Kellogg Forest Rose Lake	18.09**	25.97**	8.48**	47.46
Kellogg Forest Russ Forest	3.02NS	38.58**	2.09NS	56.31
Kellogg Forest Houghton	2.40NS	35.90**	1.72NS	59.98
Kellogg Forest Higgins Lake	7.09**	33.74**	6.76**	52.41

Continued

Table 10. (Continued)

Plantations in Combined Analysis	Variance Component			
	σ_p^2	σ_s^2	σ_{ps}^2	σ_E^2
Kellogg Forest Newaygo	19.69**	30.13**	3.20**	46.98

σ_p^2 is the component of variance due to differences between planting sites.

σ_s^2 is the component of variance due to differences between seed sources.

σ_{ps}^2 is the component of variance resulting from the interaction of seed sources and plantations.

σ_E^2 is the component of variance due to random variation within plots within plantations.

NS - Non-significant.
* - Significant at the five percent level.
** - Significant at the one percent level.

1/ - Mean squares used to determine percentages shown in Appendix B, Table B-3.

As may be seen from Table 11, 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 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 $(.82)^2$, or .67. This leaves 33 percent of the variance to be divided amongst interaction and experimental error. Whether a significant amount of interaction is present depends upon the size of the experimental error.

Needle Length

Sources from central Europe (Groups F, G, and H) had the longest needles and sources from the southern extremes of the Scotch pine range had the shortest needles (Table 12).

Group C, from southern Norway and central Sweden had relatively longer needles in 1963 than in 1962 (note significant seed source x year interaction in Table 13). However, these sources still averaged intermediate in needle length for both years.

At the Houghton plantation the Spanish sources consistently had longer needles than at any other planting. The Scandinavian sources, on the other hand, tended to have relatively shorter needles at Houghton. As a result, in 1962 the Spanish sources were longer needled than the Scandinavian sources at Houghton while in 1963 the Spanish,

Table 11. Between-planatation correlation coefficients using the mean 1962 seed source height growth.

	Kellogg Forest	Russ Forest	Allegan	Newaygo	Higgins Lake	Houghton	Rose Lake	Edwards
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 = .36 with 40 degrees of freedom.

Table 12. —Needle length of Scotch pine seed sources.

Region, Country of origin, MSFG No.	Kellogg Forest 1962	Kellogg Forest 1968	Allegan 1962	Allegan 1968	Higgins Lake 1962	Higgins Lake 1968	Houghton 1962	Houghton 1968	Rose Lake 1968
	Percent of plantation mean								
C NOR 201 [1]	86.9	94.0	94.6	94.0	83.5	88.3	86.7	90.6	88.3
SWE 222	96.9	90.6	90.3	105.0	93.9	88.3	92.5	98.8	88.3
FIN 230	77.7	80.5	79.6	80.0	76.6	80.1	80.0	81.2	—
NOR 373	96.0	105.6	91.9	102.7	94.6	96.0	88.9	98.5	86.7
NOR 374	86.4	90.1	85.1	91.8	88.3	96.5	79.3	94.5	84.8
SWE 521	91.5	101.1	93.2	104.0	96.1	90.4	88.9	90.7	87.9
SWE 523	91.5	105.0	80.1	104.6	88.3	98.0	88.9	93.8	79.8
SWE 534	92.8	100.4	100.7	90.0	91.1	92.8	87.4	88.5	88.6
SWE 543	92.4	110.7	88.5	90.3	96.7	91.3	88.7	101.7	89.8
SWE 544	96.7	108.8	91.2	97.3	96.0	96.0	86.7	96.1	84.2
SWE 545	85.9	93.2	86.4	100.5	86.2	86.1	81.5	89.2	—
Average	90.5	100.7	90.9	99.0	90.5	91.3	84.6	92.8	86.3
D LAT 223	93.7	94.0	92.5	94.3	106.4	96.0	104.3	90.7	94.8
LAT 224	96.0	90.1	90.5	95.8	96.0	92.8	90.1	101.1	90.5
SWE 541	104.1	109.4	106.5	106.3	109.2	104.6	101.4	103.0	101.8
SWE 542	99.7	116.5	100.0	102.6	96.7	112.8	99.1	103.7	98.3
SWE 580	96.0	103.0	104.1	102.8	94.6	96.5	100.0	107.0	—
Average	98.1	102.6	98.5	100.4	100.6	100.9	100.8	102.9	94.9
E SIB 227	102.3	119.1	108.2	112.8	110.6	90.4	119.7	108.3	—
URA 258	98.9	120.4	102.7	109.8	96.0	103.1	97.7	99.7	98.0
Average	100.6	119.8	105.5	111.8	103.3	101.3	108.7	104.0	98.0
F POL 211	113.6	108.8	123.8	110.7	106.0	110.6	109.4	104.4	121.2
POL 317	112.7	101.7	110.2	104.0	100.8	115.0	102.8	114.3	125.6
Average	113.2	105.3	117.0	107.4	103.9	112.8	106.1	109.4	123.4
G GER 202	117.9	104.3	108.2	109.6	107.1	122.4	100.6	104.4	119.2
GER 203	101.5	95.3	104.8	102.6	103.9	98.7	102.8	90.1	94.8
GER 208	114.9	101.7	106.8	104.0	109.2	106.9	110.2	105.3	—
GER 210	124.8	109.4	112.3	113.8	109.9	122.4	127.1	116.2	128.1
CZE 305	111.4	112.6	112.3	106.3	102.2	111.3	96.5	101.7	—
CZE 306	108.4	101.7	102.1	105.3	99.5	104.6	118.2	105.0	109.0
CZE 307	114.4	108.1	117.0	116.6	105.7	113.5	110.9	108.0	—
CZE 308	106.2	103.0	117.0	106.9	112.7	113.5	110.9	108.3	—
CZE 309	104.5	104.3	107.5	96.0	100.8	104.6	102.8	104.4	100.5
CZE 310	113.1	106.1	108.2	102.1	113.4	115.8	96.2	108.4	111.8
CZE 311	113.1	102.3	109.6	96.6	110.6	109.1	107.2	106.3	—
CZE 312	114.0	110.7	109.6	108.2	113.4	105.7	109.4	105.7	118.7
GER 525	98.9	97.2	102.1	97.5	104.3	103.1	110.2	109.3	104.9
GER 527	90.3	97.8	103.4	100.2	118.2	103.9	96.2	101.1	99.9
Average	110.2	103.9	108.6	104.8	107.9	109.7	107.0	106.2	108.5
H GER 206	117.4	104.0	118.4	110.0	121.0	106.1	121.2	107.7	117.5
FRA 241	122.2	120.4	108.2	110.8	100.9	116.5	113.1	107.7	—
GER 251	117.0	102.4	113.6	117.6	111.3	122.4	126.3	110.3	130.6
GER 253	119.2	112.7	109.6	111.5	118.9	106.9	117.5	119.6	137.6
BEL 318	121.3	108.8	120.4	113.1	115.5	115.8	118.2	111.6	127.5
BEL 530	125.5	114.6	116.4	115.1	112.0	111.3	117.5	110.3	136.9
HUN 553	107.5	97.1	107.5	100.3	114.1	111.3	116.8	109.0	—
NY 225	103.8	96.6	100.0	98.7	111.3	102.4	106.7	103.7	—
Average	116.8	107.1	111.8	110.9	114.3	111.6	117.4	110.0	130.0
J FRA 235	102.3	100.7	100.7	95.8	96.3	92.0	112.4	103.7	99.8
YUG 242	106.6	98.5	102.7	87.9	106.4	106.4	105.8	100.4	110.5
Average	104.5	99.6	101.7	91.9	100.9	98.7	109.1	102.1	105.2
K TUR 213	86.4	77.3	91.2	84.2	93.2	98.5	90.3	86.5	98.0
TUR 220	89.4	95.3	96.3	92.3	93.9	87.6	106.5	90.1	94.2
TUR 221	86.9	84.3	87.1	83.9	86.3	76.4	80.8	93.9	98.0
GRE 243	84.2	81.1	89.7	78.0	86.5	87.6	80.0	78.6	79.8
GRE 271	77.3	86.9	83.0	87.0	87.6	88.3	85.2	91.1	—
GRE 581	82.9	79.2	86.1	82.7	81.4	78.0	77.8	89.8	—
Average	84.5	84.0	87.6	84.7	88.3	86.2	84.9	88.1	91.0
M SPA 218	77.7	77.2	86.4	86.1	86.2	86.1	93.3	93.8	77.9
SPA 219	79.9	83.7	85.7	83.0	81.4	77.2	107.2	94.5	74.7
SPA 245	85.9	75.3	83.7	86.0	82.8	83.1	89.6	89.8	80.4
SPA 246	80.5	76.0	77.6	80.4	79.3	77.2	91.1	88.9	74.1
SPA 247	82.9	76.0	86.4	88.5	94.6	78.7	80.1	87.9	81.7
Average	79.2	77.6	84.0	85.0	84.9	80.5	84.1	90.4	77.8
Mean plantation needle length (millimeters)	37.91	42.92	45.98	37.64	31.36	48.03	42.84	47.30	48.81
Standard error of seed source mean as a percent of plantation mean	4.00	4.17	4.03	3.16	4.38	4.02	5.83	4.06	4.68

1/ BElgium, CZEchoslovakia, FINland, FRAnce, GERmany, GREece, HUNgary, LATvia, NORway, POLand, SIBeria, SPAin, SWEden, YUGoslavia, URAl Mountains.

Table 13. Combined analysis of variance for 1962 and 1963 needle length of 55 Scotch pine seed sources grown in four Michigan plantations.

Source of Variation	Degrees of Freedom	Mean Square	Component of Variance as a percent of total Variance
Years	1	6518.83**	7.94
Plantations	3	3185.03**	7.27
Seed Sources	54	273.93**	12.78
Years x Seed Sources	54	16.19**1/	.73
Years x Plantations	3	2170.14**1/	31.06
Seed Sources x Plantations	162	12.40*1/	1.36
Seed Sources x Years x Plantations	162	8.88**2/	2.78
Error	3186	5.36	36.08

** Significant at the one percent level.
* Significant at the five percent level.

1/ Based upon seed sources x years x plantations interaction as error term.

2/ Based upon seed sources x replication-within-plantation as error term.

Greek-Turkish, and Scandinavian groups did not differ in needle length.

At the Kellogg plantation, however, the opposite trend was observed. While in 1962 the Scandinavian sources were intermediate in needle length, in 1963 these sources were nearly equal to the long-needled German-Belgium-Czechoslovakian sources.

Thus there was a tendency in both years for sources from the southern part of the range to have relatively longer needles in the northernmost plantation, while sources from the northern part of the range had longer needles at the southernmost plantation.

There were large year to year changes in the mean plantation needle length. Houghton, which had the lowest mean needle length in 1962, had, with Higgins Lake, the highest mean needle length in 1962. While the mean needle length increased at Houghton in 1963, it decreased at all the other plantations. The ratio of mean 1963 needle length to mean 1962 needle length was .74 for Kellogg Forest; .82 for Allegan; .94 for Higgins Lake; and 1.11 for Houghton. That the differences in these ratios are real is shown by the significant plantation x year interaction (Table 13).

The amount of variation due to seed source x plantation interaction (Table 14) in 1962 was small compared to the variation due to seed source differences. However, this interaction component showed a definite increase between

Table 14. 1962 and 1963 components of needle length variance as a percent of total variance--from 55 seed sources.1/

Plantations in combined analysis	σ^2_p 1962	σ^2_p 1963	σ^2_s 1962	σ^2_s 1963	σ^2_{ps} 1962	σ^2_{ps} 1963	σ^2_E 1962	σ^2_E 1963
	Percent of total variance							
Kellogg Forest, Higgins Lake, Allegan, Houghton	37.4**	34.3**	25.7**	25.4**	3.3**	5.0**	33.6	35.3
Kellogg Forest, Allegan	44.3**	26.7**	26.6**	30.3**	1.4*	3.3**	27.7	39.7
Kellogg Forest, Higgins Lake	17.5**	18.8**	38.8**	32.7**	2.0*	8.2**	41.7	40.3
Kellogg Forest, Houghton	52.6**	16.3**	18.1**	26.2**	3.9**	7.1**	25.4	50.4
Houghton, Higgins Lake	33.7**	0.2NS	24.9**	43.2**	2.1*	6.6**	39.3	50.0

σ^2_p is the component of variance due to differences between planting sites.

σ^2_s is the component of variance due to differences between seed sources.

σ^2_{ps} is the component of variance resulting from the interaction of seed sources and plantings.

σ^2_E is the component of variance due to random variations within plots within plantings.

NS Non-significant.

* Significant at the five percent level.

** Significant at the one percent level.

1/ Mean squares used to determine percentages are shown in Appendix B, Tables B-4 and B-5.

1962 and 1963 (Table 13--note significant seed source x plantation x years interaction). Although never accounting for more than eight percent of the total variance, in some instances the interaction component was more than one-quarter the seed source component in 1963.

As with height growth, the interactions of individual seed sources within groups showed no relation between location of seed source and location of planting.

The lower Michigan plantations were all very similar in 1962 seed source needle length (Table 15). The Houghton plantation, however, showed the lowest degree of similarity with the other Michigan plantations.

Color

Field Measurements.--The color differences between seed sources closely followed the results reported by Wright and Bull (1963) as well as the 1961 plantation scorings[1/] (Tables 16 and 17).

Northern seed sources were the yellowest and southern seed sources the most blue-green. This trend was not completely related to latitude however. Group E, from the Ural Mountains of Russia--an area of intermediate latitude--was the yellowest in all plantations. Sources from Spain (Group N) and southern France (Group M) were the darkest green in all plantations.

The plantings at Higgins Lake and Newaygo--the two

1/ The 1961 color scorings were made by J. W. Wright.

Table 15. Between plantation correlation coefficients using the mean 1962 seed source needle length.

	Kellogg Forest	Higgins Lake	Allegan	Rose Lake	Houghton
Kellogg Forest	1.00				
Higgins Lake	.88	1.00			
Allegan	.92	.83	1.00		
Rose Lake	.92	.83	.88	1.00	
Houghton	.74	.70	.75	.76	1.00

All values are significant at the 0.1 percent level where r = .36 with 40 degrees of freedom.

Table 16. Color grades and date of scoring Scotch pine seed sources.

Region, Country of origin, MSFG No.		Rose Lake	Higgins Lake	Newaygo	Kellogg Forest	Allegan	Russ Forest
		Date of scoring					
		Oct. 10	Oct. 20	Oct. 22	Oct. 31	Nov. 6	Nov. 13
		Percent of plantation mean					
A	SIB[1/] 254	41	33	23	44	52	38
C	NOR 201	74	64	72	88	81	71
	SWE 222	74	50	47	62	84	57
	NOR 273	83	59	76	79	89	68
	NOR 274	83	50	40	64	84	50
	SWE 521	67	33	70	54	84	50
	SWE 522	63	42	52	51	81	47
	SWE 523	52	39	56	39	71	46
	SWE 524	63	42	49	58	71	52
	SWE 543	80	53	43	64	87	57
	SWE 544	70	56	54	62	87	57
	SWE 545	70	56	68	64	86	51
	Average	70.8	49.5	57.8	62.1	82.3	55.8
D	LAT 223	72	43	70	61	83	57
	LAT 224	80	47	60	78	81	63
	SWE 541	87	73	93	76	87	71
	SWE 542	67	53	51	54	76	54
	Average	76.5	54.0	68.5	67.3	81.8	61.3
E	SIB 255	37	26	21	34	45	37
	URA 258	46	36	33	37	65	35
	Average	41.5	36.0	27.0	35.5	55.0	36.0
F	POL 211	100	92	99	91	89	91
	POL 317	102	81	107	95	94	96
	Average	101.0	86.5	103.0	93.0	91.5	93.5
G	GER 202	91	98	130	106	110	104
	GER 203	117	103	130	118	110	118
	GER 207	115	95	134	113	109	120
	GER 208	111	111	113	115	109	117
	GER 210	109	95	103	103	107	96
	CZE 305	115	86	113	99	99	110
	CZE 306	120	106	144	101	106	110
	CZE 308	102	111	115	105	102	111
	CZE 309	106	103	126	110	99	96
	CZE 310	106	103	117	105	102	108
	CZE 311	111	98	124	99	107	111
	CZE 312	106	81	113	99	104	113
	GER 525	104	106	146	113	104	115
	GER 527	93	95	107	86	102	96
	Average	107.6	99.4	122.5	105.1	104.0	109.1
H	GER 206	109	120	122	113	110	120
	HUN 225	115	114	142	135	115	131
	FRA 241	117	137	136	113	115	129
	GER 251	117	134	147	128	107	127
	GER 252	115	117	134	124	107	125
	GER 253	111	125	132	126	109	115
	BEL 318	117	126	151	115	109	116
	BEL 530	120	111	138	117	107	122
	[illegible]	106	109	[illegible]	113	104	103
	Average	114.1	121.3	136.0	120.4	109.2	120.9
J	FRA 235	122	131	146	122	113	139
	YUG 242	120	122	124	115	105	122
	Average	121.0	126.5	135.0	118.5	109.0	130.5
K	TUR 213	[illegible]	167	151	138	117	134
	TUR 220	117	167	134	128	112	127
	TUR 221	128	151	130	133	113	141
	GRE 243	115	139	146	121	112	120
	GRE 244	116	111	132	120	109	123
	Average	119.4	147.0	138.6	128.0	112.6	129.0
M	FRA 238	135	164	163	145	133	141
	FRA 239	122	159	175	149	125	151
	Average	128.5	161.5	169.0	147.0	129.0	146.0
N	SPA 218	137	176	175	149	131	157
	SPA 219	132	176	157	147	123	148
	SPA 245	132	176	175	149	130	150
	SPA 246	[illegible]	164	151	128	118	137
	SPA 247	135	173	167	145	125	139
	Average	131.6	173.0	165.0	143.6	125.4	146.2
Mean plantation color grade[2/]		5.75	5.13	5.66	5.92	6.17	5.75
Standard error of seed source mean as a percent of plantation mean		5.39	6.19	7.06	5.57	3.57	4.70

[1/] BELgium, CZEchoslovakia, FRAnce, GERmany, GREece, HUNgary, LATvia, NORway, POLand, SIBeria, SPAin, SWEden, YUGoslavia, URAl Mountains.

[2/] Color grades: 1 = yellowest; 10 = darkest green.

Table 17.. Between-plantation correlation coefficients using the mean seed source color grade for the 1961 and 1962 measurements.

	1961 Measurements Kellogg Forest	Russ Forest	Newaygo	Higgins Lake	Michigan State nursery	1962 Measurements Kellogg Forest	Russ Forest	Newaygo	Higgins Lake	Allegan	Rose Lake
1961 Measurements											
Kellogg Forest	1.00										
Russ Forest	.91	1.00									
Newaygo	.92	.91	1.00								
Higgins Lake	.90	.86	.88	1.00							
Michigan State nursery	.91	.88	.93	.82	1.00						
1962 Measurements											
Kellogg Forest	.96	.92	.94	.87	.95	1.00					
Russ Forest	.95	.94	.95	.87	.95	.97	1.00				
Newaygo	.95	.90	.95	.89	.93	.96	.97	1.00			
Higgins Lake	.91	.89	.94	.82	.96	.95	.95	.93	1.00		
Allegan	.95	.88	.93	.89	.93	.94	.94	.94	.91	1.00	
Rose Lake	.95	.91	.93	.89	.92	.96	.96	.95	.91	.95	1.00

All values are significant at the 0.1 percent level where r = .31 with 55 degrees of freedom.

northernmost plantations scored for color--showed the greatest color differentiation. These plantation means were lower and they show the greatest range in plot means. Allegan--the next northernmost plantation--showed the least differentiation. Since Allegan was one of the last plantations measured this suggests that the plantation itself is a more important source of color variation than the date of scoring.

There was a small but significant seed source x plantation interaction among the plantings. But this interaction never accounted for more than six percent of the total variation and was very small in relation to the variation due to seed source differences.

Sources from southern Scandinavia (Group C) were much more yellow at Higgins Lake than at any other planting. Source MSFG 521 from southern Sweden was about 1 1/2 grades yellower at Higgins Lake than at any other planting. The Spanish sources appeared bluer at Higgins Lake than anywhere else, but this was probably a result of the scoring method.

Laboratory Measurements.--As mentioned previously (See Methods--measurement) a special color scoring was made in the laboratory under uniform lighting conditions. This was done to eliminate observer bias when evaluating color at different times and places.

The results of this laboratory test (Table 19) strongly confirm the conclusions from the plantation measurements. There are real differences between plantations. Southern

Table 18. 1962 components of color variance as a percent of total color variance--from 57 seed sources.[1/]

Plantations in Combined Analysis	Variance Component			
	σ^2_p	σ^2_s	σ^2_{ps}	σ^2_E
Russ Forest, Allegan, Kellogg Forest, Newaygo, Higgins Lake, Rose Lake	3.18**	69.15**	5.73**	21.94
Russ Forest, Allegan, Kellogg Forest, Newaygo, Higgins Lake	3.34**	69.43**	5.84**	21.39
Russ Forest, Allegan, Kellogg Forest, Newaygo, Rose Lake	2.28**	69.42**	5.68**	22.67
Newaygo, Rose Lake, Higgins	2.22**	68.48**	5.59**	23.71
Kellogg Forest, Newaygo, Russ Forest	0.25NS	77.05**	0.80*	21.90
Kellogg Forest, Russ Forest	0.21NS	80.04**	0.22NS	19.53

σ^2_p is the component of variance due to differences between planting sites.

σ^2_s is the component of variance due to differences between seed sources.

σ^2_{ps} is the component of variance resulting from the interaction of seed sources and planting sites.

σ^2_E is the component of variance due to random variations within plots within plantings.

NS Non-significant.
* Significant at the five percent level.
** Significant at the one percent level.

1/ Mean squares used to determine percentages shown in Appendix B, Table B-6.

Table 19. Results and analysis of laboratory color measurement.

Region, Country of origin, MSFG No.			Plantation		
			Nevaygo	Higgins Lake	Rose Lake
			Mean color grade 1/		
C	NOR 2/	201	6.6	6.2	7.8
	NOR	273	7.0	5.2	11.6
	SWE	521	5.8	3.8	8.6
D	LAT	223	9.6	3.8	8.0
E	SIB	256	3.4	6.2	4.6
	URA	258	3.8	3.8	3.8
G	GER	202	10.8	10.8	12.4
	GER	208	10.6	13.2	14.8
	CZE	310	11.0	12.2	13.2
H	FRA	241	13.0	13.6	15.6
	GER	251	15.2	15.2	15.0
	BEL	530	14.4	12.4	16.2
	HUN	553	12.0	13.2	13.6
J	YUG	242	12.6	14.8	14.6
K	TUR	213	15.4	14.4	16.4
	TUR	221	17.2	17.6	17.6
M	FRA	239	17.0	17.6	16.0
N	SPA	218	18.2	18.0	17.6
	SPA	219	17.2	17.6	15.6
Plantation mean			11.36	11.25	12.68

Analysis of variance

Source of variation	Degrees of freedom	Mean square	Component of variance as a percent of total variance
Plantation	2	60.48** 3/	2.1
Seed source	18	283.92** 4/	70.9
Seed source X Plantation	36	10.65** 5/	3.6
Error	216	6.00	23.4

** - Significant at the one percent level.

1/ 1 = yellowest; 19 = darkest green.

2/ BELgium, CZEchoslovakia, FRAnce, GERmany, HUNgary, LATvia, NORway, TURkey, URAl Mountains, SIBeria, SPAin, SWEden, YUGoslavia.

3/ Significance established by t-test.

4/ Based on seed source X plantation interaction as error term.

5/ Based on seed source X replicate within-plantation as error term.

Scandinavian sources are more yellow at Higgins Lake than at any other plantation. Source MSFG 521 from southern Sweden does show a distinctly different color at Higgins Lake.

Furthermore, the components of variance expressed as a percent of total variance differ by less than two percent between the laboratory scoring and the combined plantation analyses of the same three plantation scorings.

APPLICABILITY OF RESULTS TO OTHER AREAS

Results of other Scotch pine provenance tests indicate that the results of this study, although based on very young trees, are applicable over a large part of north-central and northeastern United States as well as central Europe and southern Sweden.

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 plantings 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 (see page 11), showed a seed source x plantation interaction component that acoounted for about four percent of the total variation or about one-sixth 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.

Needle length measurements made on four-year-old trees of the New Hampshire study are also in general agreement with the results of this study. Sources from Belgium and Germany had the longest needles while sources from southern Sweden were slightly shorter. Although there were no needle length measurements of northern Scandinavian sources in this present study, both the three-year Michigan nursery study (Wright and Bull, 1963) and the New Hampshire study indicated that sources from northern Sweden had shorter needles than sources from southern Sweden.

Color results are probably applicable over the widest range of sites and regions. The present study, the Michigan nursery study (Wright and Bull, 1963) and the New Hampshire study (Wright and Baldwin, 1957) all reported the same pattern of color differences. Moreover, both the New Hampshire study and a Swedish study (Langlet, 1936--see below) reported the same differences between sources from northern and southern Sweden.

Further evidence of the constancy of Scotch pine seed source color may be inferred from advertisements of tree seed dealers. Many dealers have long advertised "French green" or "golden yellow" strains of Scotch pine in nationally distributed publications. Such advertising would not be profitable for very long unless the seed produced the color advertised wherever the buyer grew them.

However, there is evidence that seed source x plantation interactions become more severe at the extreme northern portion of the species range.

Johnsson (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.

Langlet (1936) reported on 26 Swedish Scotch pine seed sources ranging in latitude from 56°07' N. to 70°0' N. The sources were grown at three Swedish locations: Tönnersjöheden (56°40' N. Lat.); Kulbacksliden (64°10' N. Lat.); and Gaillivare (67°8' N. Lat.). At the southernmost plantation the northern sources all had much shorter needles than the southern sources. At Kulbacksliden, the intermediate site, there were only slight differences in needle length between all seed sources, while at the northernmost planting the northern sources had the longest needles.

Thus while these results may apply over a wide area of intermediate latitudes, the height growth and needle length results probably do not apply north of about 60° N. latitude.

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 years x seed source 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.

In 1962 a combined analysis of the Higgins Lake and Houghton data showed that six percent of the height growth variance and two percent of the needle length variance was accounted for by the seed source x plantation interaction. However, in 1963 the same analyses showed a non-significant interaction in height growth while the needle length interaction jumped to 6.6 percent of the total variance. Other combined analyses show similar fluctuations (Tables 9 and

14) in the seed source x plantation interaction. This suggests that soil and photoperiod (which obviously remain constant from year to year) are not causal factors in the height growth and needle length interactions.

This does not imply that photoperiod could not cause seed source x 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 lack of correlation between seed source location, plantation location, and 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 from its latitude or average temperature. The relationships are more complex.

It should be kept in mind that the seed source x year interaction in this study differs somewhat in definition from the seed source (or family) x 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.

The year x plantation height growth interaction agrees with what is commonly observed on standard forest tree site index curves. These curves show that for many tree species both growth rate and change in growth rate with time vary from site to site.

An exceptionally large portion of the total needle length variance was due to the years x plantation interaction. There was a late spring frost in 1963. All four Michigan plantations had below freezing temperatures on May 23. This suggests the following explanation for the large year x plantation needle length interaction.

Wright and Bull (1963) reported that all sources began growth together in early May at East Lansing. If we assume the southernmost plantation would begin growth first and the northernmost plantation begin last, then there would be large between-plantation, but little within-plantation (among-seed source) variation in foliage condition at the time of the late frost. The needles at the southernmost plantation would be elongating and exposed while the needle fascicles at the northern plantation would still be protected by the bud scales. As a result there would be little effect on among-seed-source needle reduction, large between-planting differences in needle reduction, and the amount of needle length reduction would decrease as we move north.

This is exactly the pattern that was found. The seed source interactions show little variation between plantings while Kellogg Forest (the southernmost plantation) shows the greatest needle length reduction, Allegan the next greatest reduction, Higgins Lake next, and Houghton (the northernmost plantation) shows no reduction in needle length.

The amount of interaction was about the same (five percent of the total) for all three traits. It is expected that for the same variety of seed sources the interaction would be of the same relative magnitude for other complex traits--diameter growth, form, wood density, etc.

Replication in time and space seems to offer little increase in precision of estimates of genetic variance. A researcher studying genetic variation in Scotch pine could make very reliable conclusions regarding ecotypes or clines on the basis of only a single set of test conditions.

PRACTICAL APPLICATION OF RESULTS

There is no direct way of equating the size of the interaction variance and 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 x plantation interaction is about 5 percent of the total variance, and the seed source component 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.

The ten fastest growing seed sources at Kellogg Forest, Higgins Lake, and Houghton are all in groups G and H (Belgium-Germany-Czechoslovakia). This indicates that in the present study height growth measurements of individual seed sources should be confined to those sources in groups G and H.

In tests of other species, the tree breeder should establish only a single large outplanting, measure it for two or three years, and then replicate in space only those ecotypes, or portions of clines, that do best in the large planting. Such a procedure would also allow the tree breeder to test a larger number of seed sources with the same amount of effort thus increasing the amount of genetic gain per dollar spent.

That there was a significant amount of seed source x plantation interaction would have little practical significance in a breeding program designed to obtain a tree with darker green foliage because the interaction involved only the medium and yellower sources. If one selected the greenest seed sources in table 15, he would choose sources 218, 219, 238, 239, 245, and 247. In other words, one could select for color almost any place in Michigan for planting at almost any other place.

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 from 50 to 100.

In 1962 following the second growing season after outplanting, one plantation in central Illinois was measured for height growth while in Michigan seven plantings were measured for height growth, five for needle length, and seven for color. In 1963 four Michigan plantations were measured for height growth and needle length.

Analyses of variance of each character was made for each test plantation using plot totals as items. 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 outgrow the Scandinavian sources as the effects of transplanting dissipated.

The planting sites also showed marked differences in growth rate. They differed in the amount of growth per year and in the change in growth rate with time.

Sources from central Europe had the longest needles and sources from either the northern or southern extremity of the Scotch pine range had the shortest needles. However, this trend differed more by plantation than did height growth. While the Scandinavian sources were relatively short-needled in the northernmost Michigan plantation, they had relatively long needles in the southernmost plantation. The Spanish sources on the other hand all had relatively longer needles at the northernmost plantation.

The mean needle length for all sources combined differed sharply with site and year. In 1963 the mean needle length decreased by twenty-five percent at Kellogg while it increased by ten percent at Houghton. It is suggested that this year x plantation interaction was the result of a late frost in May 1963.

The Spanish, Greek-Turkish, and south France sources were the darkest green and sources from the Ural mountains and Scandinavia were the most yellow. Sources from Scandinavia showed more yellowing at Higgins Lake than at any other plantation but were still not as yellow as the Ural mountain sources.

The seed source x 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 or photoperiod.

The component of variance resulting from seed source x 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 1/6 the seed source component for height growth; 1/5 the seed source component for needle length; and about 1/12 the seed source component for color.

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

Under the conditions of pest infestation encountered in this test (very low), the researcher could gain little more than a two or three percent gain in precision by replicating measurements in time and space. From a practical standpoint these data indicate that the most genetic gain per dollar spent would be obtained by testing an increased number of seed sources in a single planting and then replicating in time and space only a few of the best sources.

Data from other tests indicates that these results should also be applicable in mature trees throughout the North-central and Northeastern United States and central Europe.

LITERATURE CITED

Arend, J. L., Smith, N. F., Spurr, S. H., and Wright, J. W. 1961. Jack pine geographic variation--five year results from Lower Michigan. Mich. Acad. Sci. Papers 1961. 46:219-38.

Baron, Frank J., and Schubert, Gilbert H. 1963. Seed origin and size of ponderosa pine planting stock grown at several California nurseries. Pacific Northwest Forest and Range Expt. Sta. Res. Note PSW-9. 11 pp.

Callaham, R. Z. and Liddicoet, A. R. 1961. Altitudinal variation at 20 years in ponderosa and Jeffrey pines. J. For. 59: 814-820.

Callaham, R. Z. 1962. Geographic variability in growth, p. 311-325. In T. T. Kozlowski, (ed.), Tree growth. Ronald Press, New York.

Cochran, William G., and Cox, Gertrude M. 1957. Experimental designs. 2nd ed. John Wiley & Sons, New York. 611 pp.

Comstock, R. E. and Moll, R. H. 1963. Genotype-environment interactions, p. 164-196. In W. D. Hanson and H. F. Robinson, (ed.), Statistical genetics and plant breeding. Nat. Acad. Sci. Publ.982.

Gardner, C. O. 1963. 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.

Genys, John B. Variation in European larch. Fox. Res. Forest Bull. 13. 96 pp.

Henry, B. W. 1959. 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.

Holst, M. 1963. Growth of Norway spruce (Picea abies (L.) Karst.) provenances in eastern North America. Canada Dept. of Forestry Publ. 1022. 15 pp.

Irgens-Moller, H. 1962. Genotypic variation in photoperiodic response of douglas-fir seedlings. Forest Sci. 8:360-62.

Johnsson, H. 1955. Utvecklingen i 15- åriga försöksodlingan av tall i relation till proveniens och odlingsort. Svenska SkogsvFören. Tidskr. 53:58-88.

Kalela, A. 1937. Zur Synthese der experimentallen Untersuchungen über Klimarassen der Holzarten. Helsinki. 434 pp.

Karshcon, R. 1949. Untersuchen über die physiologische Variabilität von Fohrenkumlingen antochthoner Populationen. Schweiz. Anstalt forstl. Versuchsw. Mitt. 26: 205-244.

Kriebel, H. B., and Wang, Chi-Wu. 1962. The interaction between provenance and degree of chilling in bud-break of sugar maple. Silvae Genetica, 11:125-130.

Langlet, Olof. 1936. Studier över tallens fysiologiska variabilitet och des samband med klimatet. Meddelanden från Statens Skogsförsöksanstalt 29:219-470.

Langlet, Olof. 1963. The Norway spruce provenance experiments at Dönjelt and Hjuleberg. Stöckholm, 1963 (Mimeographed).

Matzinger, D. F. 1963. 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.

Mirov, N. T., Duffield, J. W., Liddicoet, A. R. 1952. Altitudinal races of Pinus ponderosa--a 12-year progress report. J. Forestry 50:825-831.

Munger, T. T., and Morris, W. G. 1936. Growth of Douglas-fir trees of known seed source. U. S. Dept. Agr. Tech. Bull. 537. 40 p.

Munger, T. T. 1947. Growth of ten regional races of ponderosa pine in six plantations. Pacific Northwest Forest Expt. Sta. Forest Res. Note 39. 4 p.

Perry, Thomas O. 1962. Racial variation in the day and night temperature requirements of red maple and loblolly pine. Forest Sci. 8:336-344.

Rubner, K. 1957. Ergebnisse einer heute 20- Jährigen Fichtenherkunfst-versuches. I. Teil. Die Fläche in

Bayern. Silvae Genetica, 6:65-74.

Rudolph, T. D. 1962. Lammas growth and prolepsis in jack pine in the Lake States. Ph.D. Thesis. Univ. of Minn. (L. C. Card No. Mic 61-5866) 325 p. Univ. Microfilms. Ann Arbor, Mich. (Dissertation Abstr. 22: 2156-2157)

Rycroft, H. B. and Wicht, C. L. 1947. Field trials of geographical races of Pinus pinaster in South Africa. Pretoria, Dept. of Forestry. Brit. Empire Forestry Conf. 12 p.

Santamour, Frank S. Jr. 1960. Seasonal growth in white pine seedlings from different provenances. Northeast. Forest Expt. Sta. Forest Res. Note 105. 4 p.

Schönbach, H. Ergebuisse eine heute 20- jahrigen Fichtenherkunftsversuches. II. Teil Die Flächen in Thuringen und Sachsen. Silvae Genetica 6:74-91.

Schreiner, Ernst J., Littlefield, E. W., and Eliason, E. J. 1962. Results of 1938 IUFRO Scotch pine provenance test in New York. Northeast. Forest Expt. Sta. Pap. 166. 23 p.

Sluder, Earl R. 1963. A white pine provenance study in the southern Appalachians. Southeastern Forest Expt. Sta. Res. Pap. SE-2. 16 p.

Snyder, E. B. and Allen, R. M. 1963. 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. Conf. Publ. 22.

Squillace, A. E., and Silen, Roy R. 1962. Racial variation in ponderosa pine. Forest Sci. Monog. 2. 27 p.

Vaartaja, O. 1954. Photoperiodic ecotypes of trees. Canad. J. Bot. 32:392-399.

Vaartaja, O. 1959. Evidence of photoperiodic ecotypes in trees. Ecol. Monog. 29:91-111.

Vins, B. 1963. Report on the state and preliminary evaluation of Czechoslovak provenance trial plots of Norway spruce in the international series from the year 1938. World Consultation of Forest Genet. and Tree Impr., Stockholm, 1963. (Mimeographed).

Wakeley, Philip C. 1961. Results of the southwide pine seed source study through 1960-1961. South. Conf. on Forest Tree Impr. Proc. 6:10-24.

Wassink, E. C. and Wiersma, J. H. 1955. Daylength responses of some forest trees. Acta Bot. Neerl. 4:657-670.

Wiedemann, Erband. 1930. Die Versuche über den Einfluss der Herkunft des Kiefernsamens aus der preussischen forstlichen Versuchsanstalt. Z. Forst- u. Jagdw., 62: 498-522, 809-836.

Wright, Jonathan W. 1962. Genetics of forest tree improvement. FAO Forestry and Forest Prod. Studies 16, Rome. 399 p.

Wright, Jonathan, W., and Baldwin, Henry J. 1957. The 1938 International Union Scotch pine provenance test in New

Hampshire. Silvae Genetica 6:2-14.

Wright, Jonathan W., and Bull, W. Ira. 1963. Geographic variation in Scotch pine. Silvae Genetica 12:1-25.

Wright, Jonathan W., Lemmien, Walter L., and Bright, John. 1963. Geographic variation in eastern white pine--6-year results. Quart. Bull., Mich. Agr. Expt. Sta., East Lansing. 45:691-697.

APPENDIX A

METHODOLOGY

Height measurement

In the nursery phase of this test Wright and Bull (1963) found no differences between progeny in the amount of within-plot variability. If this constant within-plot variation pattern continues in the field, it should be possible to develop many measurement shortcuts based on measuring only a few extreme individuals within each plot, i.e. the tallest, shortest, longest needled, etc.

In 1962 the fastest growing tree on each plot was recorded separately for comparison with results from the four-tree measurement. The following tabulation shows a comparison of the coefficients of variation between four-tree totals and the tallest tree measurement.

Plantation	Coefficient of Variation: 4-tree total	Coefficient of Variation: Tallest tree
	Percent	
Kellogg Forest	6.9	7.7
Russ Forest	8.1	9.0
Newaygo	7.4	8.2
Higgins Lake	8.9	9.5
Allegan	6.3	7.6
Rose Lake	8.1	9.9
Edwards	9.3 1/	9.7

1/ Based on two-tree total.

Measuring all the trees on the plot reduces the coefficient of variation by about 1.5 percent. With ten replications per planting, an increase in the coefficient of variation of two percent will increase the size of the detectable difference at the one percent significance level about six percent (Cochran and Cox, 1957, Table 2.1).

Moreover, a combined analysis of the tallest-tree-per-plot data for the 42 sources common to Kellogg Forest, Russ Forest, Newaygo, Allegan, Higgins Lake, and Rose Lake shows that 16.8 percent of the total variance is accounted for by plantation differences, 28.2 percent of the variance is due to seed source differences, and 4.6 percent of the variance due to seed source x plantation interaction. These components are all within two percent of the four-tree plot data shown in Table 10.

Thus there seems to be little advantage gained from measuring more than the tallest tree on each plot.

Needle length measurement

The needle length data presented in this study is based on the measurement of one needle fascicle per tree. To determine the increase in precision from measuring more fascicles, ten to fifteen fascicles per tree were removed from nineteen seed sources in five replications of three plantations in 1962. The following tabulation shows the coefficient of variation for: ten to fifteen fascicles measured in five replications; one fascicle per tree measured in the same five replications; and one fascicle per tree measured in all replications.

Plantation	Coefficient of variation: 10-15 fascicles per tree 5 reps.	1 fascicle per tree 5 repls.	1 fascicle per tree all reps.1/
		Percent	
Kellogg Forest	5.8	5.9	4.0
Higgins Lake	5.0	4.7	4.2
Allegan	4.5	5.7	4.5

1/ Kellogg Forest, Higgins Lake, and Allegan had respectively 10, 7, and 8 measured replications.

As the tabulation indicates, measuring one fascicle per tree was as precise as measuring many fascicles at Kellogg Forest and Higgins Lake, but resulted in a small loss of precision at Allegan.

Increasing the number of replications was more important than increasing the number of fascicles.

APPENDIX B

Table B-1. 1962 combined analyses of variance of height growth.

Plantations in combined analysis	Plantation	Source of variation: Seed source	Seed source X plantation	Error
Kellogg Forest		Degrees of freedom		
Higgins Lake	3	54	162	1674
Allegan		Mean square		
Houghton	24483.03**	2665.53**	227.10**	114.05
Kellogg Forest		Degrees of freedom		
Higgins Lake	2	54	108	1188
Houghton		Mean Square		
	4410.54^{ns}	2166.35**	239.68**	137.17
Kellogg Forest		Degrees of freedom		
Higgins Lake	1	54	54	810
		Mean square		
	8029.21^{ns}	1556.87**	290.46**	134.07
Higgins Lake		Degrees of freedom		
Houghton	1	54	54	702
		Mean square		
	7[illegible].[illegible]7^{ns}	1[illegible].54**	244.[illegible]0**	135.98
Kellogg Forest		Degrees of freedom		
Houghton	1	54	54	864
		Mean square		
	4688.07^{ns}	1606.4[illegible]**	104.81*	141.08

ns - Non-significant

* - Significant at the five percent level.

** - Significant at the one percent level.

Table B-[illegible]. 196[illegible] combined analyses of variance of height growth.

Plantations in combined analysis	Plantation	Source of variation: Seed source	Seed source X plantation	Error
Kellogg Forest		Degrees of freedom		
Higgins Lake	[illegible]	54	10[illegible]	1620
Allegan		Mean square		
Houghton	1[illegible]00.[illegible]**	[illegible]559.09**	41[illegible].15**	[illegible]09.77
Kellogg Forest		Degrees of freedom		
Higgins Lake	[illegible]	54	10[illegible]	1134
Houghton		Mean square		
	37008.61**	50[illegible]1.06**	[illegible].83**	[illegible]71.56
Kellogg Forest		Degrees of freedom		
Higgins Lake	1	54	54	756
		Mean square		
	[illegible].80**	[illegible].98**	19[illegible].51**	[illegible]9.13
Higgins Lake		Degrees of freedom		
Houghton	1	5[illegible]	54	70[illegible]
		Mean square		
	[illegible]71.[illegible]^{ns}	44.[illegible]*	[illegible].7[illegible]^{ns}	[illegible].88
Kellogg Forest		Degrees of freedom		
Houghton	1	5[illegible]	54	810
		Mean square		
	[illegible]7[illegible].00**	[illegible].61**	56[illegible].99**	311.10

ns - Non-significant

* - Significant at the five percent level.

** - Significant at the one percent level.

Table B-3. 1962 combined analyses of variance of height growth.

Plantations in combined analysis	Plantation	Source of variation: Seed source	Seed source X plantation	Error
Kellogg Forest		Degrees of freedom		
Russ Forest	6	41	246	2009
Allegan		Mean square		
Newaygo	17076.42**	4900.98**	2[illegible]3.13**	1[illegible]2.86
Higgins Lake				
Rose Lake				
Houghton				
Kellogg Forest		Degrees of freedom		
Russ Forest	4	41	164	1763
Newaygo		Mean square		
Allegan	24917.84**	3771.78**	240.51**	118.27
Houghton				
Kellogg Forest		Degrees of freedom		
Russ Forest	3	41	123	1107
Allegan		Mean square		
Houghton	248[illegible].93**	3302.84**	[illegible]38.35**	127.12
Kellogg Forest		Degrees of freedom		
Russ Forest	2	41	82	1394
Allegan		Mean square		
	[illegible]6983.54**	2732.88**	279.40**	125.15
Kellogg Forest		Degrees of freedom		
Higgins Lake	2	41	82	902
Houghton		Mean square		
	[illegible]425.35^{ns}	[illegible]250.20**	214.10**	129.90
Kellogg Forest		Degrees of freedom		
Allegan	1	41	41	738
		Mean square		
	54[illegible].[illegible]1**	16[illegible].90**	66.00^{ns}	93.74
Kellogg Forest		Degrees of freedom		
Rose Lake	1	41	41	656
		Mean square		
	17520.39**	1472.17**	310.02**	117.97
Kellogg Forest		Degrees of freedom		
Russ Forest	1	41	41	738
		Mean square		
	3843.09^{ns}	24[illegible]1.76**	220.33^{ns}	160.65
Kellogg Forest		Degrees of freedom		
Houghton	1	41	41	656
		Mean square		
	2217.97^{ns}	1610.69**	168.84^{ns}	133.84
Kellogg Forest		Degrees of freedom		
Newaygo	1	41	41	738
		Mean square		
	38665.00**	1585.60**	183.76**	109.28
Kellogg Forest		Degrees of freedom		
Higgins Lake	1	41	41	615
		Mean square		
	6609.76**	1678.80**	273.36**	128.41

ns - Non-significant

* - Significant at the five percent level.

** - Significant at the one percent level.

Table B-4. 1962 combined analyses of variance of needle length.

Plantations in combined analysis		Plantation	Seed source	Seed source X plantation	Error
Kellogg Forest, Higgins Lake, Allegan, Houghton	Degrees of freedom	3	54	162	1568
	Mean square	3565.97**	187.14**	12.87**	6.92
Kellogg Forest, Allegan	Degrees of freedom	1	54	54	864
	Mean square	5610.60**	130.93**	10.10**	6.98
Kellogg Forest, Higgins Lake	Degrees of freedom	1	54	54	810
	Mean square	1555.52**	131.66**	10.84*	7.06
Kellogg Forest, Houghton	Degrees of freedom	1	54	54	864
	Mean square	8829.94**	129.29**	20.47**	8.51
Higgins Lake, Houghton	Degrees of freedom	1	54	54	702
	Mean square	2442.24**	74.54**	9.53*	6.84

ns - Non-significant
* - Significant at the five percent level.
** - Significant at the one percent level.

Table B-5. 1963 combined analyses of variance of needle length.

Plantations in combined analysis		Plantations	Seed source	Seed source X plantation	Error
Kellogg Forest, Higgins Lake, Allegan, Houghton	Degrees of freedom	3	54	162	1620
	Mean square	1789.20**	102.98**	8.66**	3.65
Kellogg Forest, Allegan	Degrees of freedom	1	54	54	918
	Mean square	1196.66**	86.00**	6.06**	3.38
Kellogg Forest, Higgins Lake	Degrees of freedom	1	54	54	756
	Mean square	939.77**	60.45**	11.78**	4.44
Kellogg Forest, Houghton	Degrees of freedom	1	54	54	810
	Mean square	715.65**	51.40**	10.38**	4.06
Higgins Lake, Houghton	Degrees of freedom	1	54	54	702
	Mean square	17.26ns	56.72**	8.82**	4.46

ns - Non significant
* - Significant at the five percent level.
** - Significant at the one percent level.

Table B-6. Combined analyses of variance for color scoring.

Plantations in combined analysis		Plantation	Seed source	Seed source X plantation	Error
Kellogg Forest, Russ Forest, Allegan, Newaygo, Higgins Lake, Rose Lake	Degrees of freedom	5	56	280	2744
	Mean square	78.70**	173.01**	3.36**	0.98
Kellogg Forest, Russ Forest, Allegan, Newaygo, Higgins Lake	Degrees of freedom	4	56	224	2352
	Mean square	89.74**	187.98**	3.65**	1.01
Kellogg Forest, Russ Forest, Allegan, Newaygo, Rose Lake	Degrees of freedom	4	56	224	2408
	Mean square	55.39**	142.27**	3.22**	0.95
Newaygo, Higgins Lake, Rose Lake	Degrees of freedom	2	56	112	1232
	Mean square	59.66**	92.24**	3.69**	1.23
Kellogg Forest, Russ Forest, Newaygo	Degrees of freedom	2	56	112	1512
	Mean square	8.90ns	121.66**	1.56*	1.14
Kellogg Forest, Russ Forest	Degrees of freedom	1	56	56	1008
	Mean square	6.50ns	76.11**	1.02ns	0.92

ns - Non significant
* - Significant at the five percent level.
** - Significant at the one percent level.

Table D-7. Analysis of variance of individual plantation 1962 height growth.

Plantation		Replication	Seed source	Error
		Source of variation		
Kellogg Forest	Degrees of freedom	9	54	486
	Mean square	638.81	992.89**	138.96
Allegan	Degrees of freedom	9	54	486
	Mean square	220.75	701.09**	56.25
Higgins Lake	Degrees of freedom	6	54	324
	Mean square	173.43	843.07**	127.10
Houghton	Degrees of freedom	7	54	378
	Mean square	343.98	798.38**	148.75
Kellogg Forest	Degrees of freedom	9	41	369
	Mean square	435.18	1063.32**	138.33
Allegan	Degrees of freedom	9	41	369
	Mean square	218.79	649.58**	54.15
Higgins Lake	Degrees of freedom	6	41	246
	Mean square	224.66	898.82**	121.03
Houghton	Degrees of freedom	7	41	287
	Mean square	325.87	726.22**	134.49
Russ Forest	Degrees of freedom	9	41	369
	Mean square	1077.02	1568.77**	187.96
Rose Lake	Degrees of freedom	7	41	287
	Mean square	457.60	728.88**	96.23
Newaygo	Degrees of freedom	9	41	369
	Mean square	531.82	715.95**	85.10
Edwards	Degrees of freedom	12	41	492
	Mean square	150.67	118.30**	28.46

** Significant at the one percent level.

Table D-8. Analysis of variance of individual plantation 1963 height growth.

Plantation		Replication	Seed source	Error
		Source of variation		
Kellogg Forest	Degrees of freedom	9	54	486
	Mean square	3030.35	3008.89**	338.94
Allegan	Degrees of freedom	9	54	486
	Mean square	789.11	987.21**	87.97
Higgins Lake	Degrees of freedom	6	54	324
	Mean square	396.62	1844.12**	172.70
Houghton	Degrees of freedom	7	54	378
	Mean square	1089.34	1808.71**	336.42

** Significant at the one percent level.

Table D-9. Analysis of variance of individual plantation 1962 needle length.

Plantation		Replication	Seed source	Error
		Source of variation		
Kellogg Forest	Degrees of freedom	9	54	486
	Mean square	24.96	104.10**	9.01
Allegan	Degrees of freedom	7	54	378
	Mean square	13.56	36.90**	4.36
Higgins Lake	Degrees of freedom	6	54	324
	Mean square	12.28	38.41**	5.88
Houghton	Degrees of freedom	7	54	378
	Mean square	40.84	45.66**	7.87
Kellogg Forest	Degrees of freedom	9	41	369
	Mean square	14.53	100.02**	8.65
Allegan	Degrees of freedom	7	41	287
	Mean square	9.20	34.21**	4.10
Higgins Lake	Degrees of freedom	6	41	246
	Mean square	12.36	36.32**	5.30
Houghton	Degrees of freedom	7	41	287
	Mean square	33.28	41.68**	7.55
Rose Lake	Degrees of freedom	7	41	287
	Mean square	25.06	98.88**	6.94

** Significant at the one percent level.

Table B-10. Analysis of variance of 1962 individual plantation needle length.

Plantation	Source of variation		
	Replication	Seed source	Error
Kellogg Forest	Degrees of freedom		
	8	54	432
	Mean square		
	29.82	37.60**	4.60
Allegan	Degrees of freedom		
	9	54	486
	Mean square		
	10.20	23.50**	2.27
Higgins Lake	Degrees of freedom		
	6	54	384
	Mean square		
	28.38	43.60**	4.15
Houghton	Degrees of freedom		
	7	54	378
	Mean square		
	9.56	24.08**	4.70

** Significant at the one percent level.

Table B-11. 1962 analysis of variance results of plantation color scorings.

Plantation	Source of variation		
	Replication	Seed source	Error
Kellogg Forest	Degrees of freedom		
	9	56	504
	Mean square		
	2.63	36.70**	1.11
Allegan	Degrees of freedom		
	9	56	504
	Mean square		
	0.99	13.10**	0.50
Higgins Lake	Degrees of freedom		
	6	56	336
	Mean square		
	1.49	34.70**	1.21
Russ Forest	Degrees of freedom		
	9	56	504
	Mean square		
	3.28	40.43**	0.72
Newaygo	Degrees of freedom		
	9	56	504
	Mean square		
	0.80	47.65**	1.58
Rose Lake	Degrees of freedom		
	7	56	392
	Mean square		
	6.59	17.26**	0.78

**Significant at the one percent level.

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