Ceographic Variation in Ponderosa Pine

I. The Ecotypes and Their Distribution [1])

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Introduction

Ponderosa pine (Pinus ponderosa DOUGL. ex LAWS.) is an important timber species of western North America. *Figure* 1 shows the range of the typical variety and the variety *scopulorum* in the United States. A line drawn from southern California to western Montana roughly divides the two varieties. Within this vast area ponderosa pine occurs over an extremely wide range of sites and climatic conditions.

Ponderosa pine has been planted extensively within its natural range. Most of this planting has been within the elevational zone commonly occupied by natural stands. It has also been planted with varying success in many places outside of its natural range. Over 90,000 acres have been planted to ponderosa pine in New Zealand (WESTON, 1957). It has also been used for forest planting in Australia. Small test plantings have been established in many other countries.

Ponderosa pine has been tried as an exotic ornamental and forest tree in many midwestern and northeastern states. Small forest plantings have been established in Nebraska, Iowa, Illinois, Minnesota, Michigan and New York. Those in southern Michigan, and New York have grown well while those in northern Michigan, Minnesota, Iowa, and Illinois have not. In nearly all cases the seed source was unknown.

The present study was begun in order to test planting potential of many seed sources of ponderosa pine in Michigan and to gain insight into the genetic variation pattern of the species. Further abjectives of the study were: (1) to ascertain the selection forces responsible for tine variation pattern, and (2) to assemble many geographic variants of the species for use in future hybridization and selection studies. These objectives could be realized in whole or in part within the 2-year duration of the study. The phase dealing with selection forces will be described in a later paper.

The present study is part of a long-range program for which there are two additional objectives. These are: (3) to determine the correlation between juvenile and mature performance, and (4) to determine the way in which different genotypes of ponderosa pine react in different environments. For this reason the collection of 60 origins was outplanted in permanent test plantings in the spring of 1962. Four test plantings were established in southern Michigan, one at Lincoln, Nebraska, and one at Moscow Idaho.

The Michigan work will also benefit from a comprehensive study of variation in ponderosa pine being conducted by the Institute of Forest Genetics at Placerville, California. That study includes detailed analyses of cones, foliage, bark, and seeds of collections from 130 different areas. It also includes controlled environment tests of germination and early seedling development. Later comparisons of the Michigan and California data will result in greater understanding of phenotype-genotype and parental-offspring correlations.

Taxonomy

Ponderosa pine is a member of subgenus *Diploxylon*, group Australes. According to MIROV (1961) the other pines of this group are: longleaf pine (P. palustris MILL.), slash pine (P. elliottii ENGELM.), loblolly pine (P. taeda L.), shortleaf pine (P. echinata MILL.) and spruce pine (P. glabra WALTER) of the southeastern United States; Caribbean pine (P. caribaea MORELET), and P. occidentalis SWARTZ, of the northern and western Caribbean area; and Washoe pine (P. washoensis MASON and STOCKWELL) of Nevada and California. Also included are a number of Mexican pines: P. michoacana MARTINEZ, P. *pseudostrobus* LINDL. and P. rudis ENDL. which all occur in southern Mexico. Between this area and the ponderosa complex in northern Mexico and the southwestern United States occur three other pines of the group Australes. These are P. durangensis MARTINEZ, P. eooperi BLANCO, and Apache pine (P. engelmannii CARR). Ponderosa pine is also closely related to Jeffrey pine (P. *jeffreyii* GREV. and BALFOUR), which MIROV places in the group Macrocarpae on the basis of the composition of its turpentine.

Crossability studies conducted by the Institute of Forest Genetics at Placerville, California indicate that ponderosa pine is more closely relatod to Apache pine and the Mexican members of the group Australes than it is to the other pines of the group.

Several workers have considered Jeffrey pine a variety of ponderosa pine (ENGELMANN, 1880; SARGENT, 1897; SHAW, 1914). MIROV (1929, 1961) assigned both of them specific status on the basis of the composition of their turpentines. HALLER (1957) made a comprehensive morphological study which provided strong evidence that Jeffrey pine is entitled to specific status.

Jeffrey pine is associated with the typical variety of ponderosa pine in southeastern Oregon, northeastern California, and along the entire west slope of the Sierra Nevada where the upper elevational limits of ponderosa pine meet the lower elevational limits of Jeffrey pine. Natural hybrids occur between the two but they are relatively rare and both species are distinct in this area. Hybrids have been obtained by controlled pollinations between Jeffrey pine and ponderosa pine (RIGHTER and DUFFIELD, 1951). The cross is quite difficult to malre, however, more so than would be expected if the two were merely varieties of a single species.

In 1938 Pinus washoensis was discovered on Mount Rose in western Nevada (MASON and STOCKWELL, 1945). In 1961 HALLER reported its occurrence in greater abundance in northeastern California. HALLER investigated the relationship between Washoe, ponderosa, and Jeffrey pines and found evidence that Washoe pine had arisen through hy-

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bridization between Jeffrey pine and the Rocky Mountain variety of ponderosa pine (HALLER, 1957). He also described an area in northeastern California where introgressive hybridization of Washoe pine into ponderosa pine was taking place. MIROV's analysis of the turpentine of Washoe, Jeffrey, and ponderosa pines, however, indicated that Washoe pine originated by selection from ponderosa pine or as a result of hybridization between two varieties of ponderosa pine, one of which is now extinct.

HALLER (1957), on the basis of morphological characters, and MIROV (1961), by analysis of the turpentine, both hypothesize an ancient relationship between Coulter pine (*P. coulteri* DON.) and ponderosa pine. Crossability studies have also indicated that these two species are similar to the extent that they will both cross with Jeffrey pine although they have not been successfully crossed with each other (RIGHTER and DUFFIELD, 1951).

Within the species itself there is a great deal of variation. Two wide-ranging and well-defined forms occur in the United States. *Pinus ponderosa* var. *ponderosa* grows west of the crest of the northern Rocky Mountains, throughout the Pacific Northwest, and in California. *Pinus ponderosa* var. *scopulorum* grows east of the crest of the northern Rocky Mountains, throughout the central and southern Rocky Mountains, and in the Black Hills of South Dakota. According to SARGENT (1897) and SUDWORTH (1908) the two forms intergrade to some extent in the northern Rocky Mountains. BAKER and KORSTIAN (1931), however, considered the two varieties distinct in this area. Two progenies from western and central Montana in the present study and in WEIDMAN's (1939) study were also quite distinct from each other. If there is a zone of intergradation, it is probably confined to the valley between the Bitterroot range and the Lewis range of the northern Rocky Mountains. Farther south the two varieties are widely separated by the arid Great Basin and are distinct.

The third variety is Arizona pine (*Pinus ponderosa* var. *arizonica* [ENGELM.] SHAW). It is primarily a Mexican tree. Its distribution in the United States is limited to a few scattered stands in southern New Mexico and Arizona (LITTLE, 1950). In Mexico, it extends south into Durango (SUDWORTH, 1917; MIROV, 1961). According to MARTINEZ (1949), who regards Arizona pine as a distinct species, a variant occurs in the northeastern Mexican state of Nuevo Leon. He describes this as *Pinus arizona* var. *stormiae* MARTINEZ.

In the southwestern United States and in the Mexican border region the taxonomic relationships between ponderosa pine and the other hard pines of the area are poorly understood. *Pinus ponderosa* var. *scopulorum, Pinus ponderosa* var. *arizonica,* and *Pinus engelmannii* all occur in this general area.

North of southern New Mexico and Arizona the Rocky Mountain variety of ponderosa pine is associated with none of the pine species with which it is closely related. This is also true of the typical variety north of southern Oregon. This is of significance in the determination of the causes of variability within the species because it eliminates the possibility of interspecific hybridization in many areas. Variability in these regions must be the result of the combined effects of selection pressures and population structure.

MIROV (1961) has found that the turpentine of ponderosa pine varies widely in its physical characters and chemical composition. He found that Δ^3 carene is the characeristic terpene of the species. This terpene is present in the turpentine of ponderosa pine, in varying amounts, throughout its range. MIROV has established that the physical characters and chemical composition of ponderosa pine turpentine are under genetic control by comparing the turpentine of trees of known origin growing in the arboretum at Placerville with the turpentine of trees growing in different part of the natural range.

The taxonomic division between the typical variety of the Pacific coast and the Rocky Mountain variety is justified by MIROV's work. The Pacific Coast variety contains cadinene and lacks longifolene. The Rocky Mountain variety contains cadinene and longifolene, and sometimes only longifolene. The distribution of the minor constituents of the turpentine affords additional evidence of the existence of discrete entities within the species. Limonene, which is the only monocyclic terpene in many widespread areas, is accompanied by another monocyclic terpene, terpinolene, in southwest Idaho, southeast Wyoming, and central Montana. In central Colorado and the Black Hills limonene is completely replaced by terpinolene. Myrecene was found in all parts of the range except central Colorado and the Black Hills.

Previous Work on the Genetics of Ponderosa Pine

A major portion of our understanding of the genetics of ponderosa pine has been a result of work carried out by the Institute of Forest Genetics at Placerville, California. Emphasis has been placed on species crossability and variation within the ponderosa pine population on the western slope of the Sierra Nevada Mountains. Minor projects have included the production of polyploids and attempts at vegetative propagation. This work was started in the 1920's and continues today. Other work on ponderosa pine consisted of the establishment of a series of rangewide provenance tests that have been evaluated by WEIDMAN (1939), MUNGER (1947), and SQUILLACE and SILEN (1962).

Species Crossability

At Placerville, attempts have been made to cross the typical variety of ponderosa pine with the other two varieties and with most of the other pines of the group *Australes*. In spite of repeated attempts the typical variety has not been crossed successfully with the pines from the southeastern United States and the Carribbean area, but hybrids have been obtained with Jeffrey pine, Apache pine, Washoe pine, Montezuma pine, and the Rocky Mountain and Mexican varieties of ponderosa pine. The intravarietal hybrids and those with Apache pine and Montezuma pine are being tested on a fairly large scale for reforestation purposes (Pacific Southwest Forest and Range Expt. Sta., 1955).

Geographic Variation

Provenance tests were started in the early 1900's by the U. S. Forest Service. These tests were under the direction of RAPHAEL ZON who patterned them after the provenance experiments than being established in Europe by the International Union of Forest Experiment Stations.

A small, 3-origin test was established near Pikes Peak, Colorado, in 1910 (HAYES, 1913). Seed from southern Idaho, the Coconino National Forest in Arizona, and the Pike National Forest in Colorado were represented. The seed from the Pike National Forest germinated best and produced the hardiest seedlings. There was considerable second-year germination in the Arizona seed. In 1916 HAYES established a larger, unreplicated, 10-origin test which

Table 1. — Results of ponderosa pine seed source studies at Fort Valley, Arizona (From PEARSON, 1950).

Characters	Performance of progenies from		
	Black Hills	Colorado Utah	Arizona
Needle length	Short	Intermediate in all characters but more like Black Hills	Long
Seed size	Small		Large
Foliage color	Yellowish green		Bluish green
Crown form	Compact		Loose
Year of terminal bud formation	Third		Several years later
Overall size	Small		Large

sampled the region from the Black Hills of South Dakota to southern Colorado. The detailed results of this test have not been reported but in 1927 BATES examined the plantation and found that deer has browsed heavily on the plot of Black Hills provenance and had left the other sources untouched. He hypothesized that differences in chemical composition associated with provenance were present in ponderosa pine.

PEARSON (1950) briefly summarized the results of growing ponderosa pine from the Black Hills, Colorado, Utah, and Arizona in a nursery at Fort Valley, Arizona *(table 1)*. These impressions were the result of observations over an extended period of time rather than formal studies.

During the period 1911—1917, 20 seed sources of ponderosa pine were established by the U. S. Forest Service at the Priest River Experimental Forest in the Kaniksu National Forest in northern Idaho. This planting was briefly described by KEMPFF in 1928 and intensively studied by WEIDMAN in 1939. Forty-year results were recently reported by SQUILLACE and SILEN (1962).

WEIDMAN found striking differences among progenies in foliage characteristics and growth rate. In order to determine whether or not these differences were genetic in nature, WEIDMAN compared the progenies with trees growing in the parent localities. The foliage characters he measured were number of needles per fascicle, needle length, needle persistence, internal needle structure, needle thickness, needle stiffness, and foliage color. He found that all of these characters except "persistence" were similar in both the progeny plots and the parent localities. The design of the experiment and the lack of replication precluded precise determination of the degree to which these characters were inherited, however.

WEIDMAN investigated the inheritance of height growth by comparing progeny height with site-index curves applicable to the parent localities. Again, a statistical comparison was not possible but by graphing the data for the progenies and the site-index curves for the parent localities. WEIDMAN was able to demonstrate that the progenies from western Montana and Idaho reflected the relatively rapid growth of trees in the parent localities and that the progenies from eastern Montana, the Black Hills, Arizona and New Mexico reflected the relatively slow growth of trees in their parent localities. This relationship did not hold for one progeny from southwestern Oregon, where the climate is considerably milder than that of the test locality.

Tabulating all data on height and foliage characteristics, WEIDMAN divided the species into the following races, the boundaries of which coincide closely with major topographic features and precipitation zones of the western United States.

1. A race occurring near the coast north of California.
2. A race occurring in western Montana, Idaho, and the inland portions of Washington and Oregon.
3. A race occurring in Arizona, New Mexico, southern Utah, and southeastern Colorado.
4. A race occurring east of the Continental Divide as far south as southern Colorado and west of the Continental Divide in northwestern Colorado and northern Utah.

In this Priest River study, provenances from western Montana, Idaho, and the inland portions of Washington and Oregon appeared to have the most value for planting in northern Idaho. The trees from the Kaniksu National Forest, where the test plantation was located, were third best. They were surpassed in growth rate and hardiness by two origins from 90 miles and 160 miles southeast of the test site.

In 1928 the U. S. Forest Service established a series of plantings designed to test several seed sources of ponderosa pine on several sites. Ten widely separated provenances, representing the entire range of the species, were planted on six contrasting sites in the Pacific Northwest. The 20-year heights and mortality data were reported by MUNGER in 1947 and 30-year measurements by SQUILLACE and SILEN in 1962. Although the individual plantings were not replicated it is possible to subject the data to analysis of variance by using provenance X planting-site interaction as the error term (SQUILLACE and SILEN, 1962). This analysis does not provide an estimate of the environmental variance within a single location but it is precise enough to show conclusively the presence of genetic differences among seed sources. The Oregon sources were generally tallest and the South Dakota, Arizona, and New Mexico sources were generally shortest in all plantations. The "local" seed origin was usually not the tallest in a planting.

STARKER'S (1940) more intensive analysis of one of these plantations revealed differences attributable to seed source in height growth, lateral bud length, branch characteristics, needle length, foliage color, needle angle and crown form.

In 1927 a seed source study was started on the Kaingaroa Forest near Rotorua, New Zealand with seed from 13 origins. Ten of these were from California and British Columbia, two were from New Mexico, and one was from Colorado. The results were reported in 1944 by MOORE and the planting was measured again in 1952 (New Zealand Forest Service, unpublished). The planting was not replicated and plot size varied from 75 to 5,000 trees.

There were pronounced differences in total height among the different seed sources in the New Zealand test. In both 1944 and 1952 the central Sierra sources were the tallest, the New Mexico and British Columbia sources were similar to each other and intermediate in height, and the Colorado source was the shortest. MOORE considered the central Sierra type as well adapted to the area. Of particular significance are the strong correlations between MOORE's 2-year nursery heights and the heights at 17 and 25 years of age. They indicate that the 2-year nursery results would have been of considerable value in predicting 17- and 25-year performance.

In 1929, the Eddy Tree Breeding Station (now the Institute of Forest Genetics) at Placerville, California, initiated a comprehensive, rangewide seed source study. AUSTIN (1932) briefly described the study and the preliminary results. Seed was collected from 765 trees in 126 stands in 12 western states and British Columbia. The seedlings were grown for two years in a 4-replicated test in the nursery at Placerville. A few California origins were outplanted. The provenances from the central and northern Rocky Mountains were less vigorous than those from the Pacific Coast, Arizona, and New Mexico. When all Pacific Coast sources were considered, there was no significant relationship between growth rate and place of origin although trees grown from seed collected near Placerville were the tallest. AUSTIN was particularly impressed with the fact that among the "west-side" Sierra Nevada seed sources, as elevation increased, vigor decreased.

During the period 1934–1936 AUSTIN started new tests at Placerville to get more precise data on the relationship between elevation of seed source and growth rate. He directed the collection of seed from 627 trees located along an east-west transect in the Sierra Nevada Mountains near the 39th parallel. Seed from each of these parent trees was sown in a replicated nursery test at Placerville in 1937. After measurements had been made for two years, 81 progenies were outplanted in a replicated test at Placerville.

In 1938 seed from 89 parent trees of the 1934–1936 collections were sown in three nurseries located at high, medium, and low elevations on the western slope of the Sierra Nevada Mountains. The same progenies were represented in all nurseries. Permanent, well-replicated field plantings were established near each nursery and in the northern Coast range of California. The following workers have published accounts of these tests: MIROV *et al.* (1952), CALLAHAM and METCALF (1959), CALLAHAM and LIDDICOET (1961), CALLAHAM and HASEL (1961). Their most significant findings are as follows.

1. There are elevational races within the ponderosa pine population on the west slope of the Sierra Nevada. With respect to height and diameter growth, there is an elevational zone of optimum development between 1000 feet and 2000 feet. Growth superiority of progenies from this zone is expressed in plantings at high, medium, and low elevations at age 12 and in plantings at medium and low elevations at age 20. Progenies from high elevations grow slowly at all elevations.
2. Variation in 15-year height is significantly associated with 2-year height growth.
3. Within 500-foot elevational zones the average heritability of height growth in half-sib families is 0.392.

Materials and Methods

Seed Procurement

Seed for this experiment was collected in 1955 and 1956 by district rangers of the United States Forest Service, acting on a request from Dr. R. Z. CALLAHAM of the Pacific Southwest Forest and Range Experiment Station. The collections were made from natural stands throughout the species range (*figure 1*).

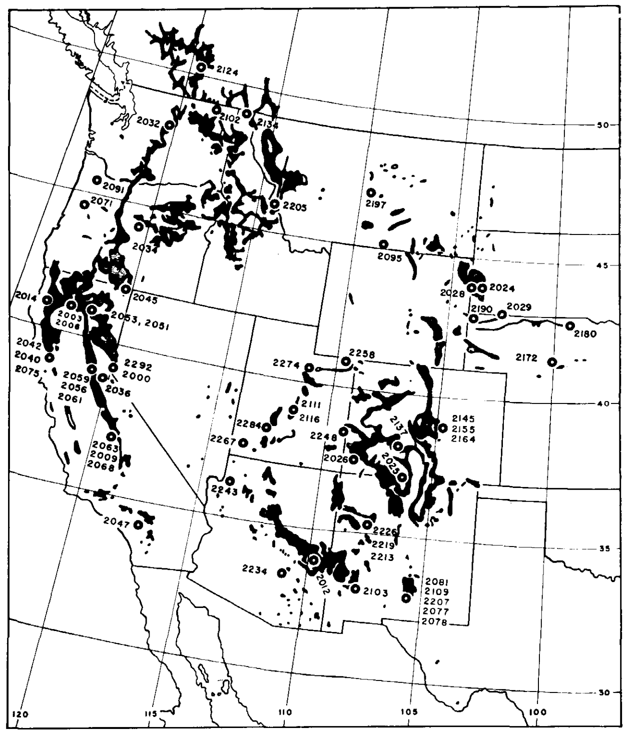

Figure 1. — Distribution of the Pacific Coast variety (*Pinus ponderosa* var. *ponderosa* and the interior variety (*Pinus ponderosa* var. *scopulorum*) of ponderosa pine in the United States and British Columbia, showing the location of the stand collections used in this study (Range map by E. L. LITTLE, JR., U. S. Forest Service).

The cones were collected from one to ten trees from a native stand in the collectors' vicinity. In any one stand the selected parents were located within five miles horizontal distance and within 200 feet vertical distance of the point designated in the origin data. Thrifty, immature trees of average phenotypes were selected. The cones from each tree were kept separate. Foliage, bark specimens, information about the parental stands, and information about the locality of origin were sent with each seedlot.

The cones and herbarium specimens were sent to the Institute of Forest Genetics, Placerville, California. There the seed was extracted, sorted, cleaned, and subjected to detailed biometrical study. Some of the seed was germinated for controlled environment studies. The rest was stored under cool, dry conditions. In the autumn of 1959 the Institute of Forest Genetics sent Michigan State University seeds from 298 individual trees in 60 stands from all parts of the natural range.

Pertinent origin data are shown in *tables 2 and 4*.

Seed Handling and Nursery Treatment

Soon after receipt in East Lansing the full seeds were weighed. The weight of a single seed was determined by weighing all the seeds from a parent tree and dividing by the number of seeds. There were generally either 30 or 80 seeds from each parent tree. The seed was then stored dry in a refrigerator until two weeks prior to sowing. At that time each seedlot was covered with water and replaced in a refrigerator kept at 40° F., following the "cold water stratification" treatment recommended by RUDOLF (1950). The stratification lasted two weeks, until immediately before sowing.

The seeds were sown in Michigan State University's Bogue Tree Research Nursery May 6 and 7, 1960. The seeds were sown in 40-inch rows which were six inches apart. Within a row the seeds were placed two inches apart. The location of the rows and the individual seed spots were made accurate to within 1/4-inch by means of steel tapes and templates. Immediately following sowing the seeds were covered 1/4-inch deep with coarse sand. Then each seedbed was covered with a lath shade which remained in place until germination was complete. The entire sowing required 25 man-hours for approximately 1200 plots.

The seedlings were given routine care during their stay in the nursery. This care included the application of mineral spirits to control weeds, water as needed to keep the soil moist below a 1/2-inch depth, and application of 1/2-inch of sawdust mulch the first winter to prevent frost heaving.

The seedlings were grown undisturbed for two years in the nursery. In April of the third year (1962) they were lifted for placement in permanent outplantings.

Experimental Design

A modification of a randomized block design was used in the nursery. The modification consisted of keeping the individual-tree progeny from any one stand in adjacent rows in any one replicate. Because there were 298 individual-tree progeny to be tested, this design had several advantages over conventional, complete blocks. First, it gave maximum precision for the detection of differences among single-tree progenies within the same stand. It was anticipated (and found to be true) that these differences would be small in comparison with the differences between stand progenies. Each complete replicate was 150 feet long and contained obvious soil differences. If the single-tree progenies from a single stand were scattered throughout a replicate they would be tested less precisely than if grouped together in a compact unit.

The second advantage of this design was the relative ease with which the data could be recorded and tabulated. For non-metric characters the stand progenies could be graded as a unit if no within-stand differences were visible. In effect this reduced the number of progenies to be considered from 298 to 60. Of course, if inspection revealed the probable presence of within-stand genetic variation all 298 progenies had to be considered.

Both advantages proved to be very real. The amount of within-stand variation was so small in most cases that it would not have been detected if complete randomization within replicates had been practiced. The summarization and statistical work was reduced about 50 percent as compared with a similar-sized experiment established according to a complete randomized block design.

This design possessed one disadvantage in that it caused an overestimation of within-stand variance as compared with between-stand variance. The grouping of the individual-tree progenies by stands caused an increase in the precision of their testing.

Measurement Methods

Characters were chosen for measurement in two ways. First, there had to be sufficient differences among some adjacent plots to indicate the probable presence of between-progeny genetic differences in the trait. Second, a few selected progenies were scored or measured and a rapid probability analysis was calculated. For example, the probability of a single stand progeny being among the five tallest out of 60 in each of three replicates is $60(5/60)^3 = .0347$ = less than five percent. Accordingly, if a single stand progeny proved to be among the five tallest in each of three replicates, significant height differences could be assumed as of that date.

The characteristics chosen for measurement were all visible to the naked eye. Not all of them are of obvious economic importance at the present time. Some may become so if they prove to be correlated with mature characters of economic importance. However, all the characters are of value in describing the geographic variation pattern.

Metric traits were measured to an accuracy of about 1/20 of the range between extremes. Presence-absence traits were measured as the number per 20 trees and later converted to a percentage basis. Characters such as color were measured according to a system of numbered grades. The grade series were defined anew for each trait at each measurement time according to the amount of recognizable variation visible at the time. The grade-units were so defined as to result in normally distributed data and equal differences between adjacent grades. The standard grade-units were always defined in terms of living trees in the experiment. Particularly for color, this resulted in considerably greater statistical precision than if an attempt had been made to match neeedles against color cards. The reliability of this method is indicated by the results of the analysis of variance. If the observer assigned the same grade to a progeny in all of the replications a statistically significant number of times, this would be reflected by a significant "F" value in the analysis of variance. If the observer did not consistently assign a single progeny to the same grade in the different replications the "F" value would be non-significant. In practice the color scoring system worked well. The statistical analysis bore out the existence of the color differences discernible by observation in all cases.

Height was measured by recording the mean of the tallest and shortest tree in each plot. Theoretically, this method is valid if the heights are normally distributed. The reliability of this method was checked by recording the mean of all trees in 100 plots and computing the correlation between the true mean and the tallest-shortest mean. The correlations were $r = .953$ for 1-year height and $r = .937$ for 2-year height. These were considered high enough to warrant the use of the short-cut method.

Observer bias was eliminated by doing the measurement or scoring rapidly and in such a manner that a plot's identity was not learned until after the measurement had been recorded.

In all the measurement work only the plot means were recorded. Not that there was no within-plot variability. There was, but there was no way in which that variability could be assigned either genetic or environmental causes.

General Description of the Experiment

Germination averaged better than 90 percent for the experiment as a whole. This, together with the precise spacing within and between rows, kept competition fairly uniform for the first year. During the second year there was considerable within-row competition. This did not affect the results, however, since only row (plot) means were recorded. No "border effect" was observed either within rows or over the seedbeds as a whole.

The experimental design reduced the effects of competition between rows because progenies of similar growth rates were in adjacent rows.

The few weeds which escaped chemical control were removed by hand. Thus, weed competition was not a factor. The sawdust mulch was completely effective in controlling frost-heaving.

No damping-off was observed and there was little post-germination mortality from other causes. The small amount that did occur was confined to the California sources. It corresponded to the "yellow trees" (character 4) in *table 4.*

In general, all of the Interior and North Plateau sources grew very well under Michigan conditions. Conditions were not optimum for the development of the California and Willamette Valley progenies. The apparent uniformity of the California progenies in this experiment is to some extent a reflection of this fact. With a few exceptions the California sources were healthy and vigorous for the first growing season but without exception they suffered severe injury during the first winter. The snow cover during the first winter was light and more protection was afforded the shorter progenies. Some of the shorter progenies that were not damaged by cold during the first winter could have been damaged in the complete absence of snow. The tall California progenies were killed back to the snow line but practically none of them were completely killed. During the second growing season they assumed a bushy appearance and grew quite vigorously. The entire experiment was covered by deep snow during the second winter and no damage was sustained by any of the progenies.

Statistical Analyses

The data for each measured character (except seed weight, number of growth periods, and number of needles per fascicle) were subjected to analysis of variance. Plot means were used as items. For a typical analysis of the data from the 175 individual-tree progenies that were replicated three times, the degrees of freedom were as follows: provenance — 174, replicate — 2, error — 348, total — 524. For a typical analysis of variance of the 125 individual-tree progenies that were replicated four times, degrees of freedom were as follows: provenance — 124, replicate — 3, error — 372, and total — 499.

The variance analyses gave information applicable to individual-tree progenies. In order to determine whether or not there were significant differences among the means of the stand progenies, the approximate LSD (= Least Significant Difference) applicable to stand-progenies was computed for each trait. To do this the harmonic mean of the number of individual-tree progenies per stand was first computed by the formula: N/harmonic mean $= 1/n_1 + 1/n_2 + 1/n_3 \ldots$, in which N = number of stands and n_1, n_2, n_3, etc. = number of parent trees in stands 1, 2, 3, etc., respectively. Then the standard deviation of an individual-tree progeny mean was reduced to a standard deviation of a stand-progeny mean by the formula:

$$\sigma_{\text{stand progeny mean}} = \frac{\sigma_{\text{individual-tree progeny mean}}}{\sqrt{\text{harmonic mean of number of parents per stand}}}$$

This stand-progeny mean standard deviation was then converted to an LSD at the 5 or 1 percent level by multiplication with an appropriate multiplier from DUNCAN'S (1955) tables, using a rank difference of 15. The use of LSD's calculated in this manner tends to over-estimate the statistical significance of differences between stands represented by 2 or 3 progenies and to underestimate the statistical significance of stands represented by 9 or 10 progenies. In actual practice, however, these LSD's gave a realistic picture of the genetic variation among stand-progenies. There were very few instances in which the difference was of just such a size as to be judged significant by one calculation method and not by another.

In order to have an objective means of evaluating the variation pattern on the basis of several characters "Summations of Differences" were calculated, following the methods outlined by CLARK (1952) and WRIGHT and BULL (1962). Eight physiologically independent characters were chosen for the analyses. The summations were calculated separately for the Pacific Coast and Interior groups of progenies. For each character a difference-value between every pair of stand-progeny means was calculated according to the scheme shown in the following tabulation.

The difference-value between stand-progeny means was	If the difference between stand-progeny means was
units	*LSD.* 05 *units*
0	0 to 0.99
1	1.00 to 1.25
2	1.26 to 1.50
3	1.51 to 1.75
4	1.76 to 2.00
4 (n—1.00)	n—.24 to n

By using difference-value there was no need to use decimals and the calculation was made much less laborious. After the difference-values were calculated for each of the eight characters they were summed for every progeny-progeny comparison.

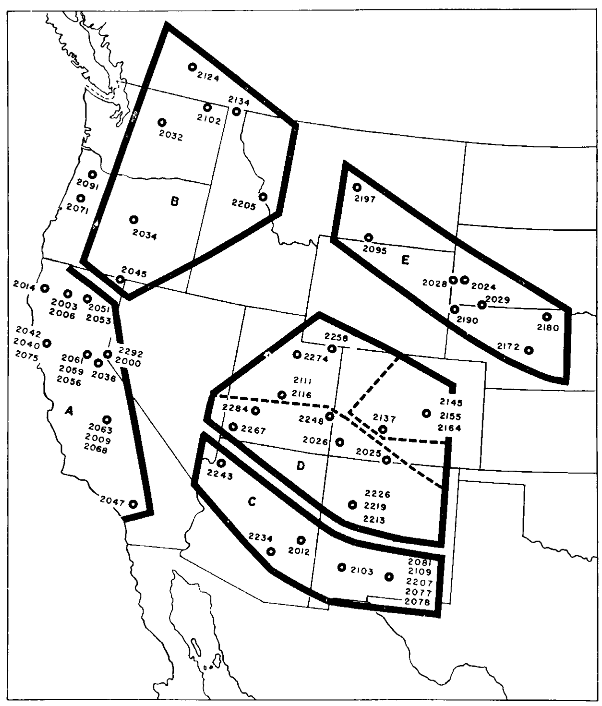

Figure 2. — Ecotypic division of 60 stand-progenies of ponderosa pine grown for 2 years in East Lansing, Michigan. A = California, B = North Plateau, C = Southern Interior, D = Central Interior, E = Northern Interior. The dashed lines within the Central Interior ecotype indicate divisions that are less well-defined than the primary ecotypic division.

Table 2. — Characters 1 through 11 for the Pacific Coast variety (*Pinus ponderosa* var. *ponderosa*) of ponderosa pine grown for 2 years at East Lansing. The provenances are arranged geographically and by degree of similarity.

Origin	Progeny number MSFG --	North Lat.	West Long.	Elev.	Parent trees	Seed weight	Germination: Date in June 1960	Germination: Percent in second year	Yellow trees July 1960	Foliage color in Aug. 1960	Foliage color in Oct. 1960	Foliage color in Oct. 1961	Stem color June 1961	Secondary Needles: Trees forming secondary needles in first year	Secondary Needles: Length	Secondary Needles: Needles in clusters of 2	Secondary Needles: Needles in clusters of 4
character designation →						(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	
		° '	° '	feet	No.	mg.	date	percent	percent	grade	grade	grade	grade	percent	mm.	percent	percent
Calif.	2047	34 14	117 14	6000	4	62	7	0.0	1	4	0	16	7	0	116	7	18
Calif.	2068	37 04	119 15	3200	3	67	12	0.0	2	7	0	16	6	2	114	3	6
Calif.	2063	37 05	119 17	4500	4	38	7	0.2	0	4	0	14	0	0	116	5	28
Calif.	2009	37 02	119 07	6100	3	59	11	1.7	2	3	0	16	8	4	119	3	7
Calif.	2042	39 07	122 45	2800	3	42	12	2.1	2	5	0	16	0	0	110	3	3
Calif.	2075	38 50	122 42	3100	2	58	13	0.0	0	3	0	16	3	0	138	0	0
Calif.	2040	39 09	122 47	4400	2	42	13	8.1	0	4	0	16	6	0	104	0	0
Calif.	2059	38 56	121 00	1500	2	59	8	0.6	0	2	0	13	7	0	110	0	5
Calif.	2056	39 01	120 49	3200	3	64	6	1.2	12	4	0	16	1	0	125	10	3
Calif.	2061	39 05	120 45	4500	2	32	8	1.9	22	1	0	16	6	0	115	0	0
Calif.	2036	38 48	120 09	6000	4	52	8	1.6	4	1	0	16	6	0	110	—	--
Calif.	2014	40 58	123 41	1700	8	48	9	1.8	0	5	0	16	4	0	113	0	3
Calif.	2003	40 59	122 26	1600	3	54	11	0.0	2	4	0	13	5	1	127	0	0
Calif.	2006	40 59	122 32	4400	3	58	13	2.5	1	6	0	13	5	1	119	0	10
Calif.	2053	40 59	121 35	3100	3	66	8	0.4	1	2	0	16	11	6	132	0	0
Calif.	2051	41 04	120 49	4600	2	56	9	1.0	6	2	1	13	7	0	127	0	5
Nev.	2000	39 14	119 56	6500	3	52	12	2.9	1	4	1	16	8	0	108	20	10
Nev.	2292	39 21	119 54	8300	9	52	12	0.0	1	4	2	6	7	0	105	1	0
Ore.	2071	44 27	123 18	300	2	40	6	3.0	26	5	0	15	8	0	100	0	2
Ore.	2091	45 29	122 52	200	4	42	18	2.5	2	3	0	16	0	0	117	0	3
Calif.	2045	41 54	120 19	6000	2	50	9	0.0	0	4	0	7	5	0	130	0	10
Ore.	2034	44 16	120 26	5000	2	63	12	1.9	1	5	1	9	4	0	128	0	0
Mont.	2205	46 05	114 11	4200	2	59	15	1.2	1	4	1	4	5	0	110	0	0
Wash.	2032	47 58	120 18	2200	2	60	11	1.2	2	2	0	13	7	0	114	0	0
Wash.	2102	48 46	118 07	1400	1	53	11	0.0	2	4	1	10	9	6	125	0	0
Ida.	2134	48 56	116 25	1800	3	56	18	2.1	1	2	3	9	4	0	112	0	0
B.C.	2124	50 12	119 32	1700	10	57	12	0.3	0	4	1	8	5	0	122	1	3
Standard deviation of mean						--	1.0	0.88	2.6	0.8	0.6	0.7	0.7	—	5.2	--	--
L.S.D. 5 percent level							3.4	3.20	8.5	2.6	2.0	2.5	2.5		17.4		
L.S.D. 1 percent level							4.5	4.10	11.0	3.3	2.6	3.2	3.2		22.4		

KEY TO COLOR GRADES

Character	(5)	(6)	(7)	(8)
Grade 0	Yellow-green	Green	--	Green
Grade 4	Intermediate	Light purple	--	Intermediate
Grade 8	Green	Intermediate	Dark green	Intermediate
Grade 12	Blue-green	Dark purple	Light green	Light green
Grade 16	Blue	--	Gray	Intermediate
Grade 20	--	--	--	Gray

Simple correlations were calculated between seed weight, several characteristics of the parental habitat, and several characteristics of the progenies.

"MISTIC", Michigan State University's electronic computer, was used for the variance and correlation calculations.

The Geographic Variation Pattern

Ponderosa pine was divisible into two major groups or varieties and five sub-groups or ecotypes on the basis of the 2-year nursery results. These subdivisions are as follows:

Pacific Coast variety, *Pinus ponderosa* var. *ponderosa*
- California ecotype
- North plateau ecotype

Interior variety, *Pinus ponderosa* var. *scopulorum*
- Southern Interior ecotype
- Central Interior ecotype
- Northern Interior ecotype

The progenies included in each subdivision are shown in *figure 2*. The 2-year performance data for the stand progenies and ecotypes are summarized in *tables 2, 3, 4, and 5.*

Three lines of evidence indicate that it is better to consider the major variation as ecotypic or discontinuous rather than clinal or continuous. First is the variation pattern for individual traits. There are many instances in which there is no overlapping between the progenies belonging to adjacent ecotypes. Second is the variation pattern when eight traits were considered simultaneously by means of the "summation-of-difference" analysis (*tables 8 and 9*). Third are the results of the many character-character and character-environment correlation analyses. Correlations which were evident when all the Pacific Coast or Interior sources were considered were not evident or were even reversed in direction when progenies from a smaller portion of the range were considered.

The distinctions between the two varieties were greatest. During both the first and second years it was possible to say with certainty that a given progeny belonged to one or the other on the basis of several traits. The distinctions between adjacent ecotypes were more subtle. It was possible to recognize progenies belonging to the southern

Table 3. — Characters 12 through 22 for the Pacific Coast variety *(Pinus ponderosa* var. *ponderosa)* grown for 2 years at East Lansing. The provenances are arranged geographically and by degree of similarity.

Origin	Progeny number MSFG -	North Lat.	West Long.	Basal needle mortality	Winter injury	Terminal Buds: Trees forming terminal buds at age 1	Terminal Buds: Scale type	Lateral Buds per 100 trees	Growth started	Trees having lammas growth	Number of growth periods	Amount of lean	Height: Age 1	Height: Age 2
				Oct. 1961			Nov. 1961	Nov. 1961	May 1961	1961	1961	Oct. 1961	1960	1961
character designation →				(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)	(20)	(21)	(22)
		° '	° '	grade	grade	percent	grade	number	date	percent	number	grade	mm.	mm.
Calif.	2047	34 14	117 14	0	19	0	0	240	16	19	1	0	65	168
Calif.	2068	37 04	119 15	0	20	2	0	102	16	14	1	0	66	163
Calif.	2063	37 05	119 17	0	20	1	0	--	16	30	1	0	65	143
Calif.	2009	37 02	119 07	0	20	0	0	105	16	12	1	0	70	158
Calif.	2042	39 07	122 45	0	15	0	0	--	16	14	1	0	42	113
Calif.	2075	38 50	122 42	0	16	0	0	152	16	20	1	0	50	162
Calif.	2040	39 09	122 47	0	16	0	0	--	16	29	1	0	50	89
Calif.	2059	38 56	121 00	0	20	0	0	--	16	14	1	0	62	81
Calif.	2056	39 01	120 49	0	20	0	0	--	16	21	1	0	56	118
Calif.	2061	39 05	120 45	0	15	0	0	135	16	5	1	0	41	128
Calif.	2036	38 48	120 09	0	19	1	0	86	16	15	1	0	46	236
Calif.	2014	40 58	123 41	0	20	0	0	--	16	16	1	0	57	145
Calif.	2003	40 59	122 26	0	20	0	0	195	16	26	1	0	60	231
Calif.	2006	40 59	122 32	0	16	0	0	--	16	22	1	0	48	139
Calif.	2053	40 59	121 35	0	16	8	0	123	13	34	1	0	59	164
Calif.	2051	41 04	120 49	0	16	2	0	--	15	8	1	0	43	129
Nev.	2000	39 14	119 56	0	13	3	0	100	14	18	1	0	44	180
Nev.	2292	39 21	119 54	0	1	3	6	120	15	8	1	0	27	79
Ore.	2071	44 27	123 18	0	19	8	0	250	16	14	1	0	50	96
Ore.	2091	45 29	122 52	0	17	0	0	45	16	5	1	0	37	116
Calif.	2045	41 54	120 19	0	6	16	1	182	9	12	1	0	48	146
Ore.	2034	44 16	120 26	0	2	51	7	180	12	0	1	0	48	163
Mont.	2205	46 05	114 11	0	0	30	5	130	3	10	1,2	0	40	140
Wash.	2032	47 58	120 18	0	4	31	2	75	9	23	1	0	32	121
Wash.	2102	48 46	118 07	0	3	40	4	165	6	5	1	0	56	192
Ida.	2134	48 56	116 25	0	4	5	5	100	9	9	1	0	52	140
B.C.	2124	50 12	119 32	0	4	35	6	130	5	5	1	0	46	162
Standard deviation of mean				--	.7	4.6	.3	17.8	.8	4.8	--	--	3.6	9.7
L.S.D. 5 percent level					2.5	15.4	1.0	59.2	2.7	15.8			11.9	32.2
L.S.D. 1 percent level					3.2	20.0	1.3	76.4	3.5	20.4			15.4	41.6

KEY TO AMOUNT OF LEAN

Grade 0	None
Grade 40	Intermediate
Grade 80	Pronounced

KEY TO OTHER CHARACTERS

Character	(12) Basal needle mortality	(13) Winter injury	(15) Terminal bud scale type
Grade 0	None	None	Appressed
Grade 4	Light	Light	Intermediate
Grade 8	Intermediate	Intermediate	Exserted
Grade 12	Pronounced	Intermediate	--
Grade 16	--	Severe	--
Grade 20	--	Very severe	--

Interior ecotype (Arizona and southern New Mexico) with certainty from casual observation in the nursery but detailed measurements were necessary to draw a line between the Central Interior and Northern Interior ecotypes.

The geographic ecotypes were genetically variable but the variability within any one of them followed a different pattern from that prevailing in the species as a whole. For example, the progenies from the warmest part of the range (California) suffered the most damage from winter cold but this did not mean that the progenies from the southern half of California suffered more winter damage than those from northern California. In fact, within most of the geographic ecotypes the variation pattern seemed to be random.

In order to statistically demonstrate that the Pacific Coast variety was different from the Interior variety analyses of variance were performed on stand-progeny means from each region for 19 of the 22 characters listed in *tables 2, 3, 4, and 5.* The degrees of freedom were as follows: total — 59, between regions — 1, error — 58. F values significant at the 5 percent level were obtained in each case.

California ecotype. — The California ecotype included all the stand-progenies from California with the exception of MSFG-2045 from the extreme northeastern part of the state. This ecotype extends to the crest of the Sierra Nevada-Cascade Mountains in northeastern California. The progeny from extreme northeastern California (MSFG-2045) was very different from other California progenies and quite similar to the North Plateau progenies.

The two stand-progenies from the Willamette Valley more closely resembled California progenies than they did progenies from west of the Cascades. These two sources, MSFG-2071 and MSFG-2091, suffered severe winter injury and had many yellow seedlings during the first year. Also their seeds were among the lightest in the experiment.

Table 4. — Characters 1 through 11 for the interior variety (*Pinus ponderosa* var. *scopulorum*) of ponderosa pine grown for 2 years at East Lansing. The provenances are arranged geographically and by degree of similarity.*)

Origin	Progeny number MSFG --	North Lat.	West Long.	Elev.	Parent trees	Seed weight	Germination Date in June 1960	Germination Percent in second year	Yellow trees July 1960	Foliage color in Aug. 1960	Foliage color in Oct. 1960	Foliage color in Oct. 1961	Stem color June 1961	Trees forming secondary needles in first year	Secondary Needles Length	Secondary Needles in clusters of 2	Secondary Needles in clusters of 4
character designation →						(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	
		° '	° '	feet	No.	mg.	date	percent	percent	---- grade		-----	grade	percent	mm.	percent	
Ariz.	2243	36 07	113 48	6100	5	49	6	0.0	0	9	4	16	14	62	164	4	6
N. Mex.	2081	32 54	105 29	6000	9	51	7	0.0	0	10	3	16	17	92	111	0	5
N. Mex.	2109	32 58	105 50	7200	2	53	8	0.0	0	10	8	16	17	88	174	0	5
N. Mex	2207	32 56	105 35	7500	6	48	6	0.0	0	10	4	16	14	82	157	3	13
N. Mex.	2077	33 00	105 47	8000	1	40	6	0.0	0	6	5	16	17	100	182	0	0
N. Mex.	2078	33 00	105 42	9000	2	43	6	0.0	0	6	5	16	15	55	176	2	0
N. Mex.	2103	33 10	107 45	7300	6	44	6	0.0	0	10	3	16	17	89	194	2	0
Ariz.	2234	33 18	110 50	7400	9	41	8	0.0	1	9	8	16	17	55	128	0	4
Ariz.	2012	33 58	109 48	9000	2	35	9	0.0	1	8	6	16	17	84	187	0	25
N. Mex.	2213	35 13	107 43	7500	6	25	7	0.0	1	6	9	16	14	43	181	0	3
N. Mex.	2219	35 16	107 38	9000	7	33	7	0.0	0	10	5	16	12	68	168	0	4
N. Mex.	2226	35 15	107 34	10300	8	26	7	0.0	0	8	8	16	12	64	157	1	1
Colo.	2025	37 04	106 15	8600	1	27	8	0.0	0	8	9	16	12	38	164	0	0
Colo.	2026	37 31	108 29	7500	1	34	6	0.0	0	10	8	16	13	80	185	0	0
Utah	2267	37 23	113 30	6800	7	38	8	0.0	0	11	4	16	14	50	152	3	0
Utah	2284	38 15	112 28	7500	8	35	6	0.0	0	7	7	16	9	50	157	1	1
Utah	2248	38 25	109 08	8900	10	33	6	0.4	0	7	7	16	12	41	160	8	1
Colo.	2145	39 00	104 46	7100	10	36	7	0.0	0	9	6	16	10	43	154	1	0
Utah	2111	38 59	111 22	8200	5	30	8	0.0	3	9	3	16	11	15	135	4	0
Utah	2116	39 00	111 19	8200	6	34	8	0.0	0	11	6	16	10	39	143	3	2
Utah	2274	40 38	111 10	7500	10	39	6	0.0	0	7	5	16	10	42	140	4	1
Utah	2258	40 53	109 38	7600	9	36	7	0.0	0	8	9	16	9	42	142	1	0
Colo.	2137	38 15	106 42	9000	8	34	8	0.0	0	8	5	12	10	55	137	18	0
Colo.	2155	38 54	104 57	7200	9	35	7	0.0	0	9	4	16	11	45	127	17	0
Colo.	2164	39 00	105 00	9100	8	33	7	0.0	0	10	3	13	12	42	129	21	0
Nebr.	2172	41 28	100 01	2800	6	49	7	0.0	0	12	5	16	10	36	129	9	0
Nebr.	2180	42 45	99 32	2100	9	53	8	0.0	0	12	2	16	13	51	151	6	0
Nebr.	2190	42 44	103 48	4500	7	54	8	0.0	0	11	1	15	9	55	142	10	0
S. Dak.	2029	43 04	102 38	3000	1	40	6	0.0	0	10	1	16	11	76	150	50	0
S. Dak.	2024	43 57	103 36	5400	1	30	6	0.0	0	9	3	16	10	50	129	10	--
S. Dak.	2028	43 53	109 02	6200	1	36	8	0.0	0	9	8	16	9	18	127	0	0
Mont.	2095	45 15	108 28	4500	4	41	7	0.0	0	11	4	16	11	66	137	9	0
Mont.	2197	46 59	109 29	4500	8	40	8	0.0	0	10	1	16	9	30	135	11	0
Standard deviation of mean						--	.93	--	--	1.01	1.30	.91	1.19	7.64	5.78	--	--
L.S.D. 5 percent level							3.18			3.47	4.75	3.11	3.19	26.12	19.76		
L.S.D. 1 percent level							4.11			4.48	6.04	4.02	5.06	33.76	25.54		

KEY TO COLOR GRADES

Character	(5)	(6)	(7)	(8)
Grade 0	Yellow-green	Green	--	Green
Grade 4	Intermediate	Light purple	--	Intermediate
Grade 8	Green	Intermediate	Dark green	Intermediate
Grade 12	Blue-green	Dark purple	Light green	Light green
Grade 16	Blue	--	Gray	Intermediate
Grade 20	--	--	--	Gray

*) Late correction by author: change the longitude of progeny number 2028 to 104° 02'.

None of the progenies from north central and northwestern California sampled the North Plateau ecotype. Hence the northern boundary of the California ecotype cannot be precisely delimited in north central California from this experiment. HALLER (1957) however, on the basis of field study, designates the Shasta Valley in northern California as the northern boundary of the California race.

The crest of the Sierra Nevada in the vicinity of Lake Tahoe does not delimit this ecotype as well as it does farther north. The progeny from the vicinity of Lake Tahoe (MSFG-2000) exhibits many characteristics of the typical California ecotype. The third "east-side" Sierra Nevada progeny (MSFG-2292) is actually Washoe pine, a distinct although very closely related species. It was very different from all other progenies.

The most distinctive features of the seedlings belonging to the California ecotype were the rapid 1-year height growth, severe first-year winter injury and consequent small 2-year size, lack of secondary needles and terminal buds during the first growing season, prevalence of Lammas growth during the second year, and fibrous root systems.

North Plateau ecotype. — The North Plateau ecotype was represented by the progenies from northeastern California, and the portions of Oregon, Washington, and British Columbia west of the Cascades. It was incompletely sampled so neither its exact boundaries nor its degree of homogeneity are accurately known. As considered here the southern boundary is the crest of the Sierra Nevada-Cascades in northeastern California and the eastern boundary is the treeless Great Basin and the area between the Bitterroot range and the Lewis range of the northern Rocky Mountains.

Table 5. — Characters 12 through 22 for the interior variety (*Pinus ponderosa* var. *scopulorum*) of ponderosa pine grown for 2 years at East Lansing. The provenances arranged geographically and by degree of similarity.*)

Origin	Progeny number MSFG–	North Lat.	West Long.	Basal needle mortality	Winter injury	Terminal Buds: Trees forming terminal buds at age 1	Terminal Buds: Scale type	Lateral Buds per 100 trees	Growth started	Trees having lammas growth	Number of growth periods	Amount of lean	Height Age 1	Height Age 2
				Oct. 1961			Nov. 1961	Nov. 1961	May 1961	1961	1961	Oct. 1961	1960	1961
character designation →				(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)	(20)	(21)	(22)
				grade	grade	percent	grade	number	date	percent	number	grade	mm.	mm.
N. Mex.	2243	36 07	113 48	4	4	1	0	200	12	8	1,2	0	70	237
N. Mex.	2081	32 54	105 29	4	5	5	0	185	10	1	2	0	53	237
N. Mex.	2109	32 58	105 50	11	6	5	0	210	12	0	1,2	0	53	232
N. Mex.	2207	32 56	105 35	3	5	11	0	190	9	0	1,2	0	49	219
N. Mex.	2077	33 00	105 47	4	8	0	0	185	12	0	1	0	60	200
N. Mex.	2078	33 00	105 42	0	6	0	0	170	10	0	2	0	44	171
N. Mex.	2103	33 10	107 45	3	6	10	0	180	11	0	2	0	57	262
Ariz.	2234	33 18	110 50	2	8	0	0	200	15	0	1,2	0	52	202
Ariz.	2012	33 58	109 48	1	7	4	0	190	10	5	2	0	50	198
N. Mex.	2213	35 13	107 43	2	2	3	0	165	14	2	1	0	39	173
N. Mex.	2219	35 16	107 38	1	2	3	0	185	12	0	1	1	44	178
N. Mex.	2226	35 15	107 34	1	0	2	0	165	11	0	1	1	43	165
Colo.	2025	37 04	106 15	0	0	0	0	195	14	0	1	10	38	163
Colo.	2026	37 31	108 29	1	0	2	0	140	14	8	1	0	37	185
Utah	2267	37 23	113 30	1	0	6	0	170	12	1	1	0	40	163
Utah	2284	38 15	112 28	2	0	6	0	175	11	1	1	8	43	150
Utah	2248	38 25	109 08	2	0	0	0	190	10	0	1	0	49	165
Colo.	2145	39 00	104 46	3	0	9	0	185	7	2	1	7	41	164
Utah	2111	38 59	111 22	0	0	9	0	125	5	4	1	6	30	126
Utah	2116	39 00	111 19	1	0	15	0	130	6	4	1	3	38	142
Utah	2274	40 38	111 10	1	1	9	0	160	8	9	1	17	39	117
Utah	2258	40 53	109 38	1	0	11	1	150	2	2	1	0	42	142
Colo.	2137	38 15	106 42	5	0	35	0	140	2	0	1	37	31	136
Colo.	2155	38 54	104 57	3	0	40	0	120	2	0	1	37	32	117
Colo.	2164	39 00	105 00	5	0	10	0	130	4	1	1	65	29	106
Nebr.	2172	41 28	100 01	6	0	53	1	160	2	0	1	0	35	135
Nebr.	2180	42 45	99 32	10	0	52	0	225	2	0	1	0	46	183
Nebr.	2190	42 44	103 48	1	0	36	0	170	2	2	1	0	33	130
S. Dak.	2029	43 04	102 38	0	0	32	0	185	3	4	1	0	40	162
S. Dak.	2024	43 57	103 36	0	0	50	0	170	3	0	1	0	37	129
S. Dak.	2028	43 53	109 02	1	0	15	0	175	4	0	1	0	40	149
Mont.	2095	45 15	108 28	0	0	27	0	180	2	2	1	0	43	168
Mont.	2197	46 59	109 29	0	0	40	0	170	3	1	1	0	32	130
Standard deviation of mean				.78	.57	6.50	.49	19.76	1.24	3.70	--	5.72	3.70	8.99
L.S.D. 5 percent level				2.67	1.96	22.23	ns	67.58	4.22	ns		19.56	12.65	30.74
L.S.D. 1 percent level				3.45	2.53	28.73	ns	87.34	5.46	ns		25.58	16.35	39.73

KEY TO AMOUNT OF LEAN

Grade 0	None
Grade 40	Intermediate
Grade 80	Pronounced

KEY TO OTHER CHARACTERS

Character	(12) Basal needle mortality	(13) Winter injury	(15) Terminal bud scale type
Grade 0	None	None	Appressed
Grade 4	Light	Light	Intermediate
Grade 8	Intermediate	Intermediate	Exserted
Grade 12	Pronounced	Intermediate	--
Grade 16	--	Severe	--
Grade 20	--	Very severe	--

*) Late correction by author: change the longitude of progeny number 2028 to 104° 02'.

Seedlings from the North Plateau were characterized by dark green foliage, exserted bud scales during the second year, formation of some terminal buds during the first year, and slight winter injury. During both growing seasons growth was comparable to that of seedlings from the Central Interior or Northern Interior ecotypes. The slight amount of winter injury and the distinctive dark green color permitted easy differentiation between these and the California progenies.

Southern Interior ecotype. — This consisted of the progenies from Arizona and southern New Mexico. The natural range of this ecotype consists of a number of large, isolated forested areas, and is surrounded on all sides by wide, low-elevation, treeless zones. This was a relatively uniform ecotype and was easily distinguished from each of the other four.

Seedlings from southern New Mexico and Arizona were characterized by rapid 1-year and 2-year height growth, formation of secondary needles and terminal buds during the first growing season, little winter injury, very long and gray needles, and gray stems during June of the second year. The seeds were larger than those of the Central Interior ecotype but of the same size as those from the Northern Interior ecotype. This ecotype contained the lowest percentage of 2-needled fascicles and the highest percentage of 4-needled fascicles. During the second year many trees completed their spring height growth at the same time as the other sources, formed terminal buds, started growth again during the summer, and later formed another terminal bud. The summer flush of growth was about equal to the spring flush. When lifted at the start of the third season this ecotype was noted to have a very deep root system with few small roots in the upper six inches of the soil.

These were the tallest seedlings in the nursery and seem to offer the best possibilities for planting in southern Michigan. This expectation, based on juvenile growth, agrees with the expectation based upon a comparison of winter temperature regimes. The average minimum winter temperature in southern Michigan is more similar to that found in the parts of Arizona and New Mexico covered by ponderosa pine forest than to that found in other parts of the West.

Central Interior ecotype. — This is composed of progenies from northern New Mexico, Colorado and Utah. Within the southern part of this region the progenies were quite uniform, but there was considerably more variation among the stand-progenies from northern Utah and northern and central Colorado. This ecotype was sharply delimited from the one immediately to the south and less sharply delimited from the one to the north. The sharpness of the between-ecotype distinctions is shown by the "summation-of-differences" analyses *(table 9).*

As compared with seedlings from Arizona and southern New Mexico, this ecotype was characterized by less height growth, shorter needles, less tendency to form secondary needles during the first year, and shallower root systems. The seeds were smaller than those from any other ecotype. There was an intermediate number of 2- and 4-needled fascicles. Winter injury was practically nil.

There was some geographic stratification within the Central Interior population. The progenies from central and northeastern Utah and one progeny (MSFG-2145) from central Colorado showed certain affinities to the Black Hills and Nebraska seedlings *(table 9).* The slight break between the southern and central parts of Utah and Colorado corresponds to the break postulated by Haller (1957).

Another possibly distinct sub-population, within the Central Interior ecotype consists of three high-elevation progenies (MSFG-2137, MSFG-2155, and MSFG-2164) from central Colorado. They originated from 9000 feet elevation 100 miles southwest of Colorado Springs, 9000 feet elevation 10 miles northwest of Colorado Springs, and 7200 feet elevation three miles northwest of Colorado Springs respectively. They were the only progenies in the entire experiment which grew crookedly and non-vertically. They were also distinctive in that they started height growth earlier and grew less tall than other Central Interior progenies. A fourth stand-progeny from the Colorado Springs area (MSFG-2145) was similar to the central and northern Utah progenies.

The range of the southern Wyoming population, which was not sampled, is continuous with the population in the vicinity of Colorado Springs. Its genetic affinities are not known.

Northern Interior ecotype. — This ecotype includes the progenies from central Montana, the Black Hills of South Dakota, and Nebraska. Its western boundary is probably the valley between the Bitterroot and Lewis ranges of western Montana. This population was distinct from the others and was very uniform. To what extent this distinctness is due to incomplete sampling, however, is not known.

Progeny from the extensive population of ponderosa pine in southeastern Wyoming was not represented. This area is geographically located between the Central Interior and Northern Interior ecotypes and the possibility exists that the pine from that area is also intermediate.

The Northern Interior ecotype was characterized by early start of height growth, high percentage of 2-needled fascicles, and absence of 4-needled fascicles. As compared with the Central Interior sources these trees had shorter secondary needles, heavier seeds, the same growth rate, and a higher percentage of trees that formed terminal buds the first year.

Delimination of Ecotype Boundaries by Multi-Character Analysis

The summation of differences tables *(tables 8 and 9)* indicate the magnitude of the differences between ecotypes. They also illustrate the nature of those differences in that clinal or ecotypic variation patterns can be discerned from them. In addition, they demonstrate the magnitude of the within-ecotype variation.

The derivation of these tables was given above in the statistical analysis section. Their interpretation is best explained by considering the two hypothetical tables *(tables 6 and 7)* which illustrate idealized geographic variation patterns. They were constructed by arranging in consecutive order 10 progenies, A—J, which, we will assume, come from areas located on a north-south transect.

Assume that progeny A comes from an area located 10 miles from progeny B, 20 miles from progeny C, 30 miles from progeny D, etc., and also assume that variation in all characters is perfectly clinal. If the provenances are arranged in consecutive order the summation of differences table will appear as shown in *table 6.* If the variation pat-

Table 6. — Hypothetical summation of differences table illustrating perfect clinal variation.[1])

Progeny	A	B	C	D	E	F	G	H	I	J
A										
B	1									
C	2	1								
D	3	2	1							
E	4	3	2	1						
F	5	4	3	2	1					
G	6	5	4	3	2	1				
H	7	6	5	4	3	2	1			
I	8	7	6	5	4	3	2	1		
J	9	8	7	6	5	4	3	2	1	

[1]) Small numbers denote similarity, large numbers dissimilarity

Table 7. — Hypothetical summation of differences table illustrating a discontinuous variation pattern.

Progeny	A	B	C	D	E	F	G	H	I	J
A										
B	1									
C	2	1								
D	3	2	1							
E	4	3	2	1						
F	5	4	3	2	1					
G	10	11	10	11	13	10				
H	12	10	11	10	12	11	1			
I	10	12	13	9	11	13	2	1		
J	13	9	12	12	10	12	3	2	1	

Table 8. — Degree of similarity between progenies from the Pacific Coast variety *(Pinus ponderosa* var. *ponderosa)* of ponderosa pine.

2047																											2047 Calif.
2068	2																										2068 Calif.
2063	0	2																									2063 Calif.
2009	1	0	1																								2009 Calif.
2042	9	8	9	9																							2042 Calif.
2075	8	5	8	5	3																						2075 Calif.
2040	6	3	6	4	0	4																					2040 Calif.
2059	1	2	0	1	10	12	9																				2059 Calif.
2056	0	3	0	3	9	10	11	1																			2056 Calif.
2061	8	6	8	9	1	4	2	8	5																		2061 Calif.
2036	3	4	3	5	4	8	5	3	0	3																	2036 Calif.
2014	0	0	0	1	7	8	6	1	0	7	0																2014 Calif.
2003	2	1	1	1	10	6	8	1	3	9	3	1															2003 Calif.
2006	7	5	6	6	1	2	1	4	7	3	4	3	2														2006 Calif.
2053	2	4	1	1	5	2	5	4	1	2	4	2	2	4													2053 Calif.
2051	6	6	5	8	2	2	4	5	2	1	3	2	3	1	2												2051 Calif.
2000	12	10	12	11	0	4	0	11	12	1	7	7	10	1	6	2											2000 Nevada
2292	61	68	67	69	54	60	56	64	67	55	63	62	63	52	52	51	50										2292 Nevada
2071	2	5	2	6	6	13	8	1	2	3	0	0	4	9	8	5	9	65									2071 Oregon
2091	19	9	19	12	3	4	3	14	17	8	8	10	10	3	14	8	6	59	16								2091 Oregon
2045	39	39	29	35	25	25	28	29	31	24	31	30	28	27	21	23	25	34	38	41							2045 Calif.
2034	63	71	69	73	63	62	64	68	73	63	70	60	66	58	56	56	57	42	71	31	31						2034 Oregon
2205	91	85	88	87	73	76	73	82	100	78	95	85	80	69	62	70	66	23	85	76	30	20					2205 Mont.
2032	48	47	46	49	33	38	36	44	48	33	40	45	45	36	31	30	25	34	53	40	10	30	28				2032 Wash.
2102	61	59	58	61	53	43	53	56	63	53	59	60	56	48	37	47	46	34	62	64	15	14	12	12			2102 Wash.
2134	67	57	64	61	49	51	48	57	67	54	61	60	53	44	46	48	42	28	66	51	21	18	15	23	13		2134 Idaho
2124	75	72	72	75	63	63	64	59	73	67	70	70	67	59	54	56	58	31	73	69	20	10	7	20	5	10	2124 B.C.

Table 9. — Degree of similarity between progenies from the Interior variety *(Pinus ponderosa* var. *scopulorum)* of ponderosa pine.

2243																																	2243 N. Mex.
2081	2																																2081 N. Mex.
2109	3	0																															2109 N. Mex.
2207	3	1	0																														2207 N. Mex.
2077	5	3	1	5																													2077 N. Mex.
2078	6	0	0	0	3																												2078 N. Mex.
2103	5	0	1	4	1	2																											2103 N. Mex.
2234	7	0	0	0	0	0	2																										2234 Ariz.
2012	7	1	0	4	0	0	0	2																									2012 Ariz.
2213	7	4	6	5	12	5	7	10	7																								2213 N. Mex.
2219	6	3	5	9	11	5	8	9	8	0																							2219 N. Mex.
2226	10	8	9	7	17	9	14	13	14	3	1																						2226 N. Mex.
2025	11	9	11	8	16	9	15	15	12	1	1	0																					2025 Colo.
2026	13	9	11	10	17	9	12	16	11	1	1	2	1																				2026 Colo.
2267	11	9	10	7	19	10	16	13	15	4	1	0	0	3																			2267 Utah
2284	10	8	9	7	17	9	14	13	14	3	1	0	0	2	0																		2284 Utah
2248	8	7	9	7	14	9	12	14	13	2	1	0	0	2	0	0																	2248 Utah
2145	12	8	11	7	19	10	16	17	14	6	2	0	3	6	1	0	0																2145 Colo.
2111	19	17	20	11	28	15	25	26	22	12	8	5	7	12	5	4	5	0															2111 Utah
2116	14	12	15	7	22	12	20	20	16	9	5	1	5	9	1	1	0	0	0														2116 Utah
2274	10	11	11	5	19	10	16	17	15	7	2	0	3	8	0	0	1	0	0	0													2274 Utah
2258	17	17	18	10	26	17	22	23	22	14	9	5	9	14	5	5	5	1	0	0	2												2258 Utah
2137	29	26	28	18	38	26	32	34	31	21	17	13	15	21	13	11	14	5	4	3	4	3											2137 Colo.
2155	31	29	31	21	30	28	34	37	34	24	19	15	18	24	15	13	14	8	5	4	5	6	0										2155 Colo.
2164	32	30	33	23	40	28	37	38	35	24	20	16	18	25	16	14	13	9	8	9	6	11	3	4									2164 Colo.
2172	29	25	28	17	36	25	31	34	30	21	16	12	18	23	12	12	14	6	3	4	6	4	4	4	16								2172 Nebr.
2180	21	18	21	14	29	20	23	28	24	17	12	10	14	17	10	10	10	5	3	6	1	5	5	5	17	1							2180
2190	23	21	23	13	32	19	26	29	25	16	11	7	12	16	7	7	9	2	0	1	3	2	4	4	11	0	0						2190 Nebr.
2029	18	15	18	9	26	15	20	24	20	13	8	6	9	13	6	5	5	1	0	1	2	1	4	5	11	1	0	0					2029 S. Dak.
2024	26	24	27	15	34	23	30	23	28	20	15	11	16	21	11	10	11	5	3	4	5	5	4	4	14	0	1	0	1				2024 S. Dak.
2028	19	17	20	11	28	17	24	25	22	15	11	6	10	15	6	6	5	1	0	0	0	1	4	5	10	3	4	0	1	3			2028 S. Dak.
2095	19	16	19	11	28	18	23	26	23	16	11	7	11	16	7	6	6	1	0	1	3	1	4	4	11	1	1	0	0	1	0		2095 Mont.
2197	24	21	24	13	33	20	20	31	26	17	12	7	13	17	7	7	11	2	1	2	3	3	4	4	12	0	0	0	0	0	1	0	2197 Mont.

tern is discontinuous, that is, two distinct populations are represented, the table would appear as in *table 7*. The groups of similar progeny appear as groups of small numbers near the hypotenuse of the triangle. It can be seen that the variation pattern is clinal within any single group but that the overall pattern for the 10 progenies is a discontinuous one.

The actual summation of differences tables *(tables 8 and 9)* reveal a generally discontinuous variation pattern. The most conspicuous intravarietal break occurs between the California and North Plateau progenies *(table 8)*. The difference-values for the comparison between the most northern California progenies and the most southern North Plateau progenies ranged between 13 and 38. The largest difference-value within the California ecotype was 12 which shows that it is a relatively uniform population. The North Plateau ecotype is much more variable. Its difference-values range between 5 and 31.

The Williamette Valley sources are more similar to the California sources than to the North Plateau sources. The range of difference-values for the Willamette Valley-California comparisons is from 0 to 19. The difference-values for the Willamette Valley-North Plateau comparison range from 5 to 73. The two Willamette Valley sources are also quite different from each other. The difference-value between them is 16.

The summation of differences table for the Interior region *(table 9)* also indicates discontinuous variation.

The Southern Interior ecotype appears as a homogeneous group with difference-values ranging from 0 to 4 over the

Mogollon Plateau progenies. The progeny from extreme northwestern Arizona (MSFG-2243) is slightly different from the rest of the Southern Interior progenies. Difference-values for comparisons between MSFG-2243 and the other Southern Interior progenies range from 2 to 7.

The break between the Southern Interior and the Central Interior ecotype is sharp. The difference-values for within-ecotype comparisons are smaller than the difference-values for between-ecotype comparisons in almost all cases. Only MSFG-2243 represents a possible intergrade.

Table 9 indicates that the Central Interior ecotype contains moderately distinct groups of progenies as follows.

MSFG 2213 to MSFG 2248, northern New Mexico, southern Colorado, Utah. Within-group comparisons average 1.1 difference-values (range 0 to 6).

MSFG 2145 to 2258, western Colorado, central Utah. Within-group comparisons average 0.3 difference-values (range 0 to 2).

MSFG 2137 to 2164, eastern Colorado. Within-group comparisons average 2.2 difference-values (range 0 to 4).

In contrast to the low values for comparisons within these groups the between-group comparisons average 5.5, 6.0, and 18.3 difference-values for comparisons involving progenies belonging to the first and second, second and third, and first and third Central Interior groups respectively.

The Northern Interior ecotype was as uniform as the Southern Interior one. The within-ecotype comparisons for the northern population average 0.7 difference-values.

Agreement between the present and previous data. — Of the four previous seed source studies of ponderosa pine, the one established in northern Idaho sampled the range best (WEIDMAN, 1939; SQUILLACE and SILEN, 1962.) It included 12 origins from the Pacific Northwest, 1 from California, and 8 from the interior region occupied by the variety *scopulorum*. WEIDMAN's results agree with the present data in showing that the North Plateau population is homogeneous enough to be considered a unit. It was the most satisfactory race from the standpoint of hardiness and growth. The single California origin was very different and did not survive. WEIDMAN's grouping of his eight sources of the variety *scopulorum* does not correspond to the division indicated by the present data although some of the north-south trends were the same. For example, he did not consider the differences between a progeny from central Arizona and one from northern New Mexico great enough to warrant separating them into different races. Also, he included the two Colorado and two Black Hills sources in the same race, contrary to the present data.

The 40-year measurements (SQUILLACE and SILEN, 1962) substantiate the differences among progenies which WEIDMAN found.

The 25-year-old New Zealand provenance test (MOORE, 1944) included 13 seed sources. His data agreed with the present data in that it would be possible to group his sources into North Plateau, California, Southern Interior, and Central Interior ecotypes. However, the performance of the same ecotypes in New Zealand and Michigan were quite different. California sources grew much faster than the British Columbia or Rocky Mountain origins and did not suffer any winter killing under New Zealand conditions.

Data from the Oregon-Washington test, which included 10 origins and six different planting sites, permitted separation of ponderosa pine into a fast growing Pacific Coast type and a slower growing Interior type (MUNGER, 1947, SQUILLACE and SILEN, 1962).

PEARSON's (1950) observations agree generally with the Michigan study. He divided the interior form of ponderosa pine into three loosely defined groups: Arizona-New Mexico, Utah-Colorado, the Black Hills. He described the Utah and Colorado seed sources, which were grown in Fort Valley, Arizona, as intermediate but more like the Black Hills population (*table 1*).

Geographic races of ponderosa pine also been reported by HALLER (1957) on the basis of field observation. His Pacific Northwest race corresponds to that reported by WEIDMAN and the present writer. He placed the southern boundary of this race at the Shasta Valley in northern California. HALLER recognized a distinct race "in the high plateau country of northern Arizona and New Mexico and adjacent parts of Utah and Colorado," and inferred the presence of another one in southern Arizona and New Mexico. This grouping agrees with the present interpretation. He also wrote, "A reasonably well-defined geographical race or subspecies occurs west and east of the Continental Divide in Utah and Colorado, and farther north, east of the Divide to the Black Hills of South Dakota . . .". This does not agree with the present finding of consistent differences between Colorado-northern Utah, and Black Hills sources.

Summary

Two hundred and ninety-eight individual-tree progenies of ponderosa pine from 60 different stands were grown in East Lansing, Michigan, for 2 years. The collections sampled the range of *P. ponderosa* var. *ponderosa* and *P. ponderosa* var. *scopulorum* in the United States. The stock was grown in a replicated nursery test in Michigan State University's Bogue Research Nursery. In the spring of 1962 permanent outplantings of the stand progenies were established. Four of these are in Michigan, one at Lincoln, Nebraska, and one at Moscow, Idaho.

Seed weight and 22 seedling characters were scored in the nursery. The data were subjected to analyses of variance in order to determine the amount of genetic variance present, summation-of-difference analyses in order to determine the multi-character relationships between provenances, and correlation analyses. Most of the statistical work was done an electronic computer.

Between-provenance differences significant at the 1 percent level were demonstrated for date of germination, amount of second year germination, number of yellow first-year seedlings, foliage color at three dates, stem color, percent of trees forming secondary needles and terminal buds, needle length, winter injury, terminal bud scale type, number of lateral buds, amount of first-year mortality in the basal amount of Lammas growth, primary needles, amount of lean, and height growth. Large differences in number of needles per fascicle, number of growth flushes during the second year, and seed weight were also noted but not analyzed statistically.

General observation in the nursery, the variation pattern of individual characters, multi-character analyses, and correlation analyses all indicated the presence of a predominately discontinuous genetic variation pattern both between and within the two varieties of ponderosa pine in the United States. The progenies were divisible into five ecotypes which were from California; The Pacific Northwest; southern New Mexico and Arizona; northern New Mexico, Utah, and Colorado; and the Black Hills, Nebraska, and central Montana. The northern New Mexico, Utah, and

Colorado ecotype was divisible into three moderately well-defined groups.

The present results show that California and central Colorado can be eliminated as seed collection areas for stock to be grown in Michigan. On the basis of 2-year growth rate and cold resistance, the progenies from southern New Mexico and Arizona are the most promising. Future study of permanent outplantings will indicate the extent to which these 2-year results hold true. In 10 to 15 years more intensive seed collections should be made in the areas which appear most promising on the basis of the outplantings.

Résumé

Titre de l'article: *Variation géographique chez Pinus ponderosa. I. Les écotypes et leur distribution.*

298 descendances individuelles de *Pinus ponderosa* provenant de 60 peuplements différents ont été élevées à East-Lansing, Michigan, pendant deux ans. Ces collections comprenaient divers échantillons de *P. ponderosa* var. *ponderosa* et *P. ponderosa* var. *scopulorum* aux Etats-Unis. Les plants ont été élevés en pépinière avec répétitions dans la pépinière de Recherche de Bogue de l'Université de l'Etat de Michigan. Au printemps de 1962, on a planté les descendances. Quatre plantations sont dans le Michigan, une à Lincoln, Nebraska, et une à Moscow, Idaho.

Le poids des graines et 22 caractères des semis ont été enregistrés en pépinière. Les données ont été soumises à des analyses de variances afin de déterminer la quantité de variance génétique présente, à des analyses de régression multiple afin de déterminer les rapports entre les multiples caractères et à des analyses de corrélation. La majeure partie du travail statistique a été faite sur une calculatrice électronique.

Des différences entre provenances significatives au seuil de 1% ont été trouvées pour la germination, la germination au cours de la seconde année, le nombre des semis jaunes dans la première année, la couleur du feuillage à trois date différentes, la couleur de la tige, le pourcentage d'arbres formant des aiguilles secondaires et des bourgeons terminaux, le nombre de bourgeons latéraux, l'importance de la mortalité au cours de la première année, le nombre de pousses d'août, les aiguilles primaires, l'inclinaison et la croissance en hauteur. Ont également été notés sans faire l'objet d'analyse statistique, les larges différences dans les nombres d'aiguilles par fascicule, le nombre de cycles de croissance pendant la deuxième année et le poids des graines.

Les observations générales en pépinière, le schéma de variation des caractères individuels, les analyses des caractères multiples et les analyses de corrélation, tout indiquait la présence d'un schéma de variétées de *P. ponderosa* qu'à l'intérieur de celles-ci aux Etats Unis. Les descendances pouvaient être divisées en cinq écotypes provenant de Californie, du Nord-Ouest de la Côte Pacifique, du Sud du Nouveau Mexique, de l'Utah, et du Colorado, des Black Hills, du Nebraska et du centre du Montana. L'écotype du nord du Nouveau Mexique, de l'Utah et du Colorado pouvait être divisé en trois groupes assez bien définis.

Ces résultats montrent que l'on peut éliminer la Californie et le centre du Colorado en tant que zones de récolte des graines en vue des plantations dans le Michigan. Si l'on se base sur le taux de croissance au cours des deux premières années et sur la résistance au froid, les descendances du sud du Nouveau Mexique et de l'Arizona sont les plus prometteuses. Une étude ultérieure des plants indiquera dans quelle mesure les résultats de ces deux années se confirment. Pendant les 10 à 15 années à venir des récoltes de graines plus importantes devraient être faites dans les régions qui paraissent les plus prometteuses en se basant sur les repliquages.

Zusammenfassung

Titel der Arbeit: *Geographische Variation bei Pinus ponderosa. — I. Die Ökotypen und ihre Verteilung.*

298 Einzelbaumnachkommenschaften von *P. ponderosa* aus 60 verschiedenen Beständen wurden in East Lansing, Michigan, für 2 Jahre gehalten. Die Herkünfte stellten Stichproben aus dem Verbreitungsgebiet von *P. ponderosa* var. *ponderosa* und *P. ponderosa* var. *scopulorum* in den Vereinigten Staaten dar. Das Material hielt man in einem wiederholten Baumschulversuch im Bogue Research Nursery der Michigan State University. Im Frühjahr 1962 wurden mit den Bestandsnachkommenschaften längerfristige Versuche angelegt. Von diesen befinden sich vier in Michigan, einer in Lincoln, Nebraska, und einer in Moscow, Idaho.

Das Samengewicht und 22 Merkmale der Sämlinge wurden in der Baumschule erhoben. Die Daten wurden Varianzanalysen zur Bestimmung der enthaltenen genetischen Varianz, "summation-of-difference"-Analysen zur Bestimmung der Beziehungen vieler Merkmale untereinander zwischen den Provenienzen, und Korrelationsanalysen unterzogen. Der Großteil der statistischen Arbeiten wurde auf einem Elektronenrechner durchgeführt.

Bei P = 0,01 signifikante Herkunftsunterschiede wurden gefunden für Keimungsdaten, Zahl gelber Sämlinge im ersten Jahr, Nadelfarbe zu drei verschiedenen Zeitpunkten, Stämmchenfarbe, Prozentsatz der Bäume, die Sekundärnadeln und Endknospen bildeten, Nadellänge, Winterschäden, Form der Endknospenschuppen, Zahl der Seitenknospen, Mortalität in der Grundzahl des Johannistriebwachstums während des ersten Jahres, Primärnadeln, Schrägstand und Höhenwachstum. Große Unterschiede in der Zahl der Nadeln pro Kurztrieb, Zahl der Wuchsperioden während des zweiten Jahres und Samengewicht wurden ebenfalls festgestellt aber nicht statistisch analysiert.

Allgemeine Beobachtungen in der Baumschule, das Variationsmuster der einzelnen Merkmale, die "multi-character"-Analysen und Korrelationsanalysen zeigten alle das Vorliegen eines überwiegend diskontinuierlichen genetischen Variationsmusters sowohl zwischen als auch in den beiden Varietäten von *P. ponderosa* in den Vereinigten Staaten. Die Nachkommenschaften ließen sich in fünf Ökotypen unterteilen: California; Pazifischer Nordwesten: südliches New Mexico und Arizona; nördliches New Mexico, Utah und Colorado; die Schwarzen Berge, Nebraska und Zentral-Montana. Der Ökotyp aus dem nördlichen New Mexico, Utah und Colorado ließ sich in zwei mäßig gut definierbare Gruppen unterteilen.

Die vorliegenden Ergebnisse zeigen, daß California und inneres Colorado als Saatguterntebezirke für nach Michigan bestimmtes Material ausscheiden. Auf Grund ihrer Wachstumsrate in den beiden ersten Jahren und ihrer Kältewiderstandsfähigkeit sind die Nachkommenschaften aus dem südlichen New Mexico und Arizona die meistversprechenden. Weitere Untersuchungen der längerfristigen Versuche werden zeigen, in welchem Umfang sich die Ergebnisse der ersten beiden Jahre aufrechterhalten lassen. In 10 bis 15 Jahren sollten intensivere Saatgutsammlungen stattfinden in den Gebieten, die auf Grund der längerfristigen Versuche die meistversprechenden sind.

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Slash Pine, Wood and Fiber Property Heritability Study

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Recent studies have shown that several wood and fiber properties have a pronounced influence upon pulp yield and pulp quality. Because of their economic importance, genetic improvement of these properties appears highly desirable. Improvement by selection of trees with outstanding wood quality is feasible if there is sufficient natural variation in the property in question and an adequate proportion of the variation is genetically controlled.

Studies of natural variation, including recent work by Zobel, *et al.* (1960) van Buijtenen, *et al.* (1961), Goddard and Strickland (1962), and Einspahr, *et al.* (1963) have illustrated that sufficient tree-to-tree variation exists in specific gravity, fiber dimensions, fiber strength, pulp yield, extractives, and certain other wood properties to warrant tentative use of these criteria in tree selection work.

Indication of the degree of genetic control may be obtained from estimates of broad sense heritability.[2]) Comparison of the variation between clones with the variation within clones and ortet-ramet[3]) correlations furnish broad sense heritability estimates. Similar comparison and correlation using sexual progeny provide narrow sense heritability information. Specific gravity is the wood property that has been most intensively studied and heritability estimates have been obtained for slash pine (*Pinus elliottii* Engelm.) and loblolly pine (*P. taeda* L.) by Squillace, *et al.* (1962), van Buijtenen (1962), and Zobel, *et al.* (1962). Broad sense heritability estimates for specific gravity range from 0.58 to 0.84 for loblolly pine and from 0.40 to 0 62 for slash pine. Less is known about the heritability of fiber dimensions, fiber strength, pulp yield, extractives, etc., for the southern pines. Zobel *et al.* (1962) recently reported broad sense heritability for fiber length of slash pine of 0.56, and Goggans (1962), working with open pollinated loblolly pine progeny obtained heritabilities for fiber length, fiber width, cell wall thickness and several other fiber dimensions. Dadswell, *et al.* (1961) with *Pinus radiata* (D. Don.) in Australia reported gross or broad sense heritability values for basic density of 0.57 to 0.74, for per cent late wood of 0.47 to 0.54, and for average fiber length of 0.73 to 0.83.

The purpose of this study is to determine the broad sense heritability of several wood and fiber properties of slash pine. It is hoped that this information can be used to further pinpoint the wood and fiber characteristics which hold the most promise for wood quality tree improvement work.

Methods and Materials

The trees used in this study consisted of 24 grafted slash pine trees which ranged in size from 11 to 24 feet in height

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[2]) Broad sense heritability estimates obtained from clonal comparisons include nonadditive genetic variation and can be expected to give heritability predictions higher than narrow sense heritability.

[3]) Ortet is defined as the one tree from which the members of the clone are derived and a ramet is defined as an individual member of a clone.