GEOGRAPHIC VARIATION IN PONDEROSA PINE
(*PINUS PONDEROSA* DOUGL. EX LAWS.)

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(*PINUS PONDEROSA* DOUGL. EX LAWS.)

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ABSTRACT

GEOGRAPHIC VARIATION IN PONDEROSA PINE

(*PINUS PONDEROSA* DOUGL. EX LAWS.)

by Osborn O. Wells

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. The latter analyses were made between seedling characters and 10 climatic factors at the place of origin, and among seedling characters. Most of the statistical work was done on an electronic computer.

Between-provenance differences significant at the 1 percent level were demonstrated for 19 seedling characters.

General observation in the nursery, the variation pattern of individual characters, multicharacter 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 correlation analyses indicated that many of the seedling characters were significantly associated with factors of the climate. This indicates that selection pressure has been the primary differentiating force responsible for the present characteristics of the ecotypes. Minimum winter temperature, especially, was significantly correlated with factors of the climate.

The isolation barriers which allowed the ecotypes to differentiate genetically in response to different selection pressures were geographic for the most part. The crest of the Sierra Nevada separates the California and Pacific Northwest ecotypes in northeastern California. The Cascade Mountains isolates the Willamette Valley populations from the more extensive inland populations of the Pacific Northwest. The extensive treeless area between the Mogollon Plateau in southern New Mexico and Arizona, and the Colorado Plateaus to the north, separates the Southern Interior and Central Interior ecotypes. The combined effects of selection pressure due to minimum winter temperature and geographic isolation was postulated to be responsible for genetic differentiation among the Utah progenies. The combined effects of selection pressure, population density, and reproductive isolation appear to be responsible for differences among progenies from near Colorado Springs, Colorado.

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The differences in seedling characters within a variety were often associated with factors of the climate. However, the larger differences between progenies from the typical variety and the progenies from the Rocky Mountain variety were not. This indicates that the two varieties arose earlier in geological time than the ecotypes. The selection forces and other factors responsible for their evolution are not reflected in modern weather records.

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 the permanent outplanting 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.

GEOGRAPHIC VARIATION IN PONDEROSA PINE
(*PINUS PONDEROSA* DOUGL. EX LAWS.)

by

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I. INTRODUCTION

Ponderosa pine (Pinus ponderosa Dougl. ex Laws.) is one of the most important timber species in the world. It is the mainstay of the economy of large areas in the western United States where it is often the only timber tree found. Its tall, straight trunks and its soft, easily worked wood are highly valued by lumbermen. Tourists, campers, and sportsmen greatly appreciate its open stands in which one can walk as easily as in a city park. Its great variability and the ease with which it crosses with related species have long made it a subject of experimentation by foresters.

In the words of Charles Sprague Sargent, "Possessed of a constitution which enables it to endure great variations of climate and to flourish on the well-watered slopes of the California Mountains, on torrid lava beds, in the dry interior valleys of the north and the sun baked mesas of the south, and to push out over the plains boldly, where no other tree can exist, the advance guard of the Pacific forest, ponderosa pine is the most widely distributed tree of western North America. Exceeded in size by the sugar pine of the Sierra Nevada, it surpasses all its race in the majesty of its port and the splendor of its vitality; and an emblem of strength, it appears as enduring as the rocks, above which it raises its noble shafts and stately crowns."

Ponderosa pine was well named. Both its common and scientific names mean ponderous or huge. Trees over 200 feet in height and over 8 feet in diameter have been found in California and Oregon. It attains its best development in the central Sierra Nevada of California but in almost every part of its range it attains heights of 150 feet and diameters of 3 feet. These large trees are old and have been naturally pruned. Hence, they commonly produce long, clean boles and large quantities of clear lumber.

The natural range of ponderosa pine covers most of the western United States. It is not surprising, then, that the species has received a great deal of attention from forest geneticists. Most of the work has been done at the Institute of Forest Genetics, Placerville, California. The Institute focused its attention on species hybridization but also conducted studies on local and geographic variation and explored other phases of the species' genetic behavior. Elsewhere in the West there has been long but sporadic interest in the establishment of medium-sized provenance tests. Tree breeders outside the natural range have shown interest in the tree but have done little work with it. It has been used extensively in afforestation in New Zealand and Australia with little accompanying genetic experimentation. In eastern United States and Europe work has been limited to small trials of Placerville-produced species hybrids, one small provenance test, and trials of stock of unknown origin in arboreta and small forest plantings.

Some of the Placerville hybrids have shown much promise, both inside and outside the natural range. Some of the exotic plantings have also shown promise. These results have caused a heightening of interest in the species' genetics. The Placerville program continues on an expanded basis and there are comprehensive new projects at Corvallis, Oregon; Moscow, Idaho; and Lincoln, Nebraska. The present 60-origin provenance test is related to work at those places and is the most extensive genetic project on the species outside the natural range. It has as its ultimate objectives the delimitation of the genetic variation pattern in ponderosa pine and the location of the best seed collection areas for planting in Michigan.

II. TAXONOMY

Ponderosa pine is a member of subgenus Diploxylon *Koehne*, group *Australes* Koehne. 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*) 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. all occur in southern Mexico. Between these pines 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. cooperi* 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.[1]

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[1] Mirov's work with the gum turpentines of pines has contributed much to our knowledge of the taxonomic affinities of ponderosa pine. His results have been obtained by subjecting the oleoresinous exudate of the pines to steam distillation. This separates the exudate into a non-volatile residue (rosin) and a volatile portion (gum turpentine). The latter generally consists of cyclic hydrocarbons or terpenes. He has used the presence or absence of specific terpenes in different pine species and varieties as a character in their taxonomic classification.

Crossability studies conducted by the Institute of Forest Genetics at Placerville, California indicate that ponderosa pine is more closely related 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, 1917). 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 form 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 make, 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 hybridization between Jeffrey pine and the Rocky Mountain variety of ponderosa pine (Haller, 1957). He also described an area in northeastern California where introgression 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 postulate 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* (Engelm.) Shaw 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, were able to distinguish the two varieties in this area. "In Montana the gap between the two forms is narrow and cannot be located definitely as outlying sporadic occurrences of both forms are frequent. . . ." The progeny from western and central Montana in the present study are quite distinct from each other and the corresponding progeny in Weidman's (1939) study, which were separated by only 100 miles, were also quite distinct. 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 quite 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 Neuvo Leon. He describes this as *Pinus arizonica* 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 form of ponderosa pine is associated with none of the pine species with which it is closely related. This is also true of the typical form 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 population structure and selection pressures exerted by different environments.

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 characteristic 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 parts 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 only cadinene. 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.

The synonymy of ponderosa pine is as follows (from Rehder, 1949 and Little, 1953).

Pinus ponderosa var. _ponderosa_

Pinus ponderosa Dougl. ex Laws. Agricultural Manual 354. 1836.

Pinus ponderosa Dougl. ex Loud., Hort. Brit. 387. 1830: _nomen nudem_.

Pinus Benthamiana Hartweg, Jour. Hort. Soc. London 2: 189. 1847.

Pinus brachyptera Engelm. in Wisliz., Memoir Tour Northern Mexico 89. 1848.

Pinus Beardsleyi A. Murray, Edinburgh New Philos. Jour. n. ser., 1:286 t. 6. 1855.

Pinus Craigiana A. Murray l.c. 288, 6. 7. 1855.

Pinus Parryana Gordon, Pinetum 202, 1858.

Pinus ponderosa var. Benthamiana (Hartw.) Vasey, Report U.S. Dept. Agriculture 1875: 178 (Catalogue Forest Trees U.S. 30) 1876.

Pinus ponderosa var. scopulorum Engelm. in S. Wats., Botany of California 2: 126. 1879.

Pinus scopulorum (Engelm.) Lemm., Garden and Forest 10: 183. 1897.

Pinus ponderosa var. arizonica (Engelm.) Shaw, Pines of Mexico 24. pl. 4, pl. 17, fig. 4. 1909.

Pinus arizonica Engelm. in Rothr., Wheeler Rpt. U.S. Geographic Survey West 100th Meridian 6: 260. 1878.

III. DISTRIBUTION

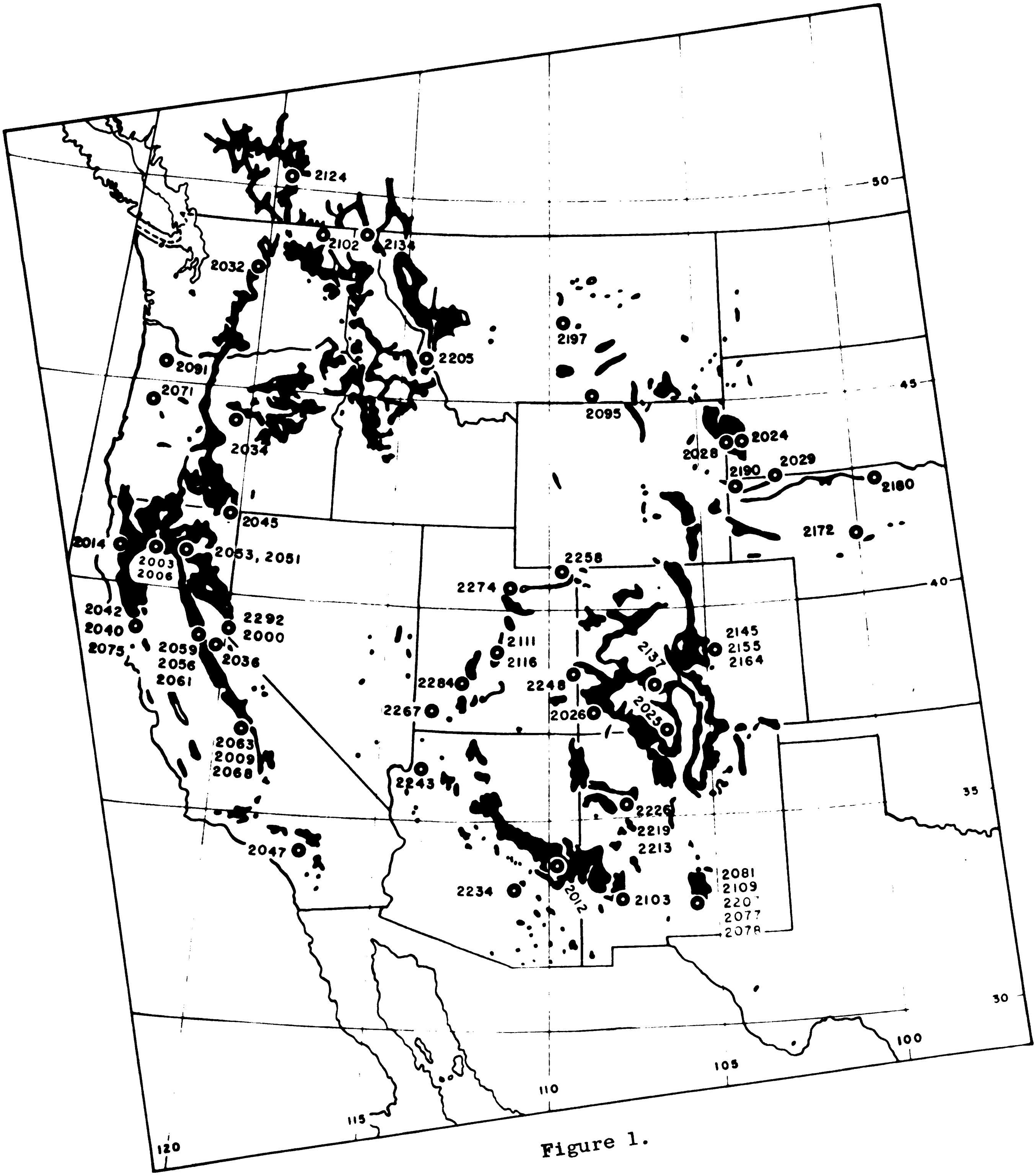
Natural Distribution

Figure 1 shows the range of the typical variety of ponderosa pine 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.

In British Columbia it grows along the valleys of the dry interior regions at elevations between 1500 and 2000 feet where the annual precipitation is about 15 inches. Its form is poor in this northern extremity of its range.

In northwestern United States extensive stands of ponderosa pine occur on the eastern slopes of the Cascade Mountains, in the Blue Mountains of northeastern Oregon, and in the northern Rocky Mountains of eastern Washington, Idaho and western Montana. In the Cascade Mountains it ranges up to 5000 or 6000 feet elevation. In the interior most of the stands occur between 1500 and 3500 feet elevation where the annual precipitation is between 15 and 30 inches. In general terms, the climate is cold and dry with little summer rainfall. Ponderosa pine is more drought resistant than the other forest trees of the area; thus it has the lowest altitudinal limits of any tree species in the region. It thrives on coarse, well-drained soils in this area although it will grow satisfactorily on a wide variety of soils. On the poorer sites there is little understory and the stands have a characteristic park-like appearance with a low number of trees per acre. The stands are usually uneven-aged with the different age classes occurring as small even-aged groups.

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 (distribution map by E. L. Little, Jr., U. S. Forest Service).


2124
2102
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2205
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2172
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2053, 2051
2258
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2009
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2213
2047
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2109
2207
2077
2078
2234
2012
2103
50
45
40
35
30
120
115
110
105
100

Figure 1.

Ponderosa pine also occurs in small scattered stands in the Willamette Valley from central Oregon north to Puget Sound. Here the climate is cool and moist and the tree grows on sandy and gravelly river benches.

In California it grows throughout the northern part of the state and extends south the full length of the western slope of the Sierra Nevada. In the mountains of southern California it is common on the higher coastal-facing slopes as far south as Cuyamaca Lake in San Diego County (Haller, 1959). Isolated stands also occur in the coast ranges of southern and central California. Martinez (1949) reported its occurrence in some abundance in Baja California but other workers consider the pine of that area to be Jeffrey pine (Wiggins, 1940; Duffield and Cumming, 1949). In going from north to south along the Sierra Nevada the average elevation of ponderosa pine increases although its range of altitudinal distribution decreases. In the north it grows from about 1000 to 5000 feet elevation and in the south from 5000 feet to 7000 feet elevation (Haller, 1959).

Ponderosa pine attains its finest development on the deep clay-loam soils of the west-side Sierra Nevada Mountains where the annual precipitation is between 40 and 60 inches and the temperature is mild. There is little or no summer rainfall. There it is associated with Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) and white fir (Abies concolor Gord. and Glend.) Lindl.). Near the upper limits of its range it grows with Jeffrey pine and near the lower limits with Digger pine (Pinus sabiniana Dougl.). It forms pure stands on the drier sites but this tendency is less than in the Pacific Northwest. On the east slope of the Sierra Nevana the climate is much drier and colder.

Ponderosa pine is common in northeastern California where it is associated with Jeffrey pine. Its range extends south along the east slope but south of Lake Tahoe it is rare (Haller, 1957).

In the central Rocky Mountains ponderosa pine occurs between 5000 and 9000 feet elevation where the annual precipitation averages between 15 and 20 inches. About one-half of this occurs during the growing season. The climate is dry and cold. The soils are mostly granitic and coarse grained and the generally pure stands of pine are dissected by grassland and brushy areas. The western extensions of variety scopulorum which occur in Utah and eastern Nevada occur on porous, slope soils or near streams where soil moisture conditions are exceptionally good (Baker and Korstian, 1931).

Extensive stands of ponderosa pine occur in the Black Hills of South Dakota and Wyoming and the Bear Lodge Mountains of Wyoming where the climate is more humid and cooler than on the surrounding grassy plains. The precipitation averages from 15 to 25 inches annually in this area and a substantial portion of it occurs during the summer. Ponderosa pine is the dominant forest tree. It occurs in pure stands which are generally even-aged or two-storied. Soils are generally shallow, coarse, and well-drained.

The largest continuous, virgin forest of ponderosa pine occurs on the Mogollon Plateau in central Arizona and western New Mexico (Little, 1950). The elevational range of the species in this area is between 6500 feet and 8500 feet where the precipitation averages from 18 to 22 inches with an appreciable amount occurring during the summer. The climate is cold and dry. Frost may occur in any month. The species grows on a wide variety of soils. It occurs on soils derived from igneous formations such as basalt, granite, or cinders, as well as on soils of sedimentary origin. (Pearson, 1950). It reproduces beston sandy or gravelly soils but growth on the heavier clay soils is good once the seedling stage is passed. Near the upper limits of its range ponderosa pine is associated with Douglas-fir. At the lower elevational zones it grows in extensive, pure, park-like stands which are uneven-aged. The different age classes occur in small groups. According to Pearson (1950), both temperature and moisture are limiting factors in its distribution. "There is much evidence that in most of its interior range the tree grows in climate too cold or with a growing season too short for optimum development. . . .It is only by ascending to the higher slopes and tablelands that sufficient moisture is obtained but this ascent is also accompanied by a drop in temperature and as moisture approaches the optimum, the heat deficit becomes prohibitive. . . .Ponderosa pine makes extraordinary growth when planted and watered in the warm valleys below its natural range."

South of the Mogollon Plateau the Rocky Mountain variety occurs only as scattered stands. In northern New Mexico it is replaced by the 5-needled variety, Arizona pine.

Planted Distribution

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. Occasionally it has been brought to lower elevations and watered. In such instances it has made rapid growth.

It was introduced into England in 1827 when David Douglas sent seed to the London Horticultural Society. It was also introduced into continental Europe at an early date. The performance of different seed sources in Germany was reported by Von Sievers in 1898 and Schwappach in 1901. Trees from California grew well for a few years and then died for unknown reasons.

Ponderosa pine has been used for forest planting on a large scale in New Zealand. Weston (1957) summarized its use in that country. It was planted extensively as early as the 1870's and 1880's. Planting increased rapidly in the early 1900's and reached a peak during the period 1920-1940. In 1957 there were more than 90,000 acres planted to ponderosa pine. This placed it second only to Monterey pine (*P. radiata* D. Don.). Most of these plantings are at high elevations on cold sites and poor soils unsuited to other species. Unfortunately, the extent of the genetic diversity within the species was not recognized until many of the plantings had been established. Several different seed sources were used. They were generally mixed indiscriminately with the result that there is a great deal of genetic variation among and within plantations.

From the results of a provenance test and from planting experience with different seed sources it seems that the most promising source of seed for New Zealand is the west side of the central Sierra Nevada Mountains in California. Plantations grown from seed collected in that general area have yielded 10,000 cu. ft. per acre at 50 years of age and have attained heights of 105-110 feet (Moore, 1944; Weston, 1957).

In spite of the good performance of the central Sierra sources, future planting of ponderosa pine in New Zealand will be only experimental in nature. Current feeling is that other species are more suitable. At the lower elevations it cannot compete with Monterey pine on the basis of growth rate, wood quality, and resistance to injury by animals. At the higher elevations European black pine (*P. nigra* Arn.) is preferred for the same reasons.

Ponderosa pine has been planted with some success in southern and southeastern Australia. It does best in the cooler, more elevated areas that have good rainfall, particularly in Victoria and New South Wales. In these districts it grows well on fairly poor soils (Anderson, 1956). Its future use will probably be restricted to poorer sites where Monterey pine will not grow. European black pine is also planted on these sites.

In Great Britain ponderosa pine is well known to horticulturists. According to McDonald *et al*. (1957), specimen trees dating from the nineteenth century are common. Its use in forestry, however, has been limited and there are only a few recent plantations. Balfour (1932) states that it grows well in southern England but does not thrive in Scotland. Headfort (1932) lists individual trees that are growing well in Ireland. Very little is known about the effect of provenance in Great Britain. In 1930 two small seed source studies were established but the range of collections was limited to a restricted area in British Columbia and little information was gained. Its growth rate compares favorably with Scotch pine (*P. sylvestris* L.) but not with Douglas-fir or Sitka spruce (*Picea sitchensis* (Bong.) Carr., which are preferred on the better sites. Its range of possible use on the drier, colder sites corresponds to that of European black pine which is preferred (McDonald *et al*., (1957).

A few experimental plantings were established in the Union of South Africa in the 1920's and 1930's. The species was tried at different elevations and on different soils, but no attention was given to seed source. All stands were failures (Poynton, 1957).

Johnsson (1956) reported 14-year-old experimental plantings of ponderosa pine in southern Sweden. A British Columbian provenance grew fastest. It grew slightly slower than Scotch pine, jack pine (*P. banksiana* Lamb.), or lodgepole pine (*P. contorta* Dougl.) but grew faster than eastern white pine (*P. strobus* L.). Its potential for forest planting in Sweden, however, is nil.

In the United States 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. Individual trees are found in most major northeastern arboreta. In nearly all cases the plantings are of unknown provenance.

Lorenz (1949) reported the 5-year performance of 10 seed sources growing in 6 plantings in Illinois. Growth was poor in all cases and differences in survival and height growth were not marked. Examination of the plantings in 1962 showed that all were heavily infected with a needle spot disease [*Scirrhia acicola* (Learn.) Siggers] and had to be considered failures (J. J. Jokela, personal communication).

In Iowa, Hansen and McComb (1958) reported the performance of several hardwood and conifer species. The 18-year-old ponderosa pine was the slowest growing of the six pines represented. Seed source was not indicated. In northern Minnesota, Schantz-Hansen (1932) reported that 10-year-old ponderosa pine of probable Black Hills origin was unsuited to the area and suffered heavy rabbit damage.

In Nebraska, ponderosa pine is native only on residual soils. It is found in most abundance along the Niobrara River and its canyons along the northern border of the state and the nearby Pine Ridge of southwestern South Dakota. It also occurs along the Platte River in southwestern Nebraska and small patches are found in the canyons of the Loup River and on sandstone outcrops near the center of Nebraska. However, considerable ponderosa pine has been planted on the previously unforested sand hills in the region between the Niobrara and Platte Rivers. The sand hills occupy an area of about 24,000 square miles in northwestern and central Nebraska. Planting started in 1902. Seed from New Mexico, Colorado, Nebraska, and the Black HIlls of South Dakota was used. The Nebraska and South Dakota stock gave the best results (Higgins, 1927). New Mexico seed sources were very susceptible to tip moth (Rhyacionia frustrana var. bushnelli Busck (Bates, 1927).

Several ponderosa pine plantings appear promising in New York. According to Littlefield (1944, 1955), a 45-year-old plantation in Clinton county is "maintaining height growth and reproducing in an open field . . .and within the stand itself." There is only slight damage by the sweetfern blister rust (Cronartium comptoniae Arth.) in spite of an abundance of the alternate host, sweetfern (Comptonia asplenifolia (L.) Fern.). Littlefield also mentioned promising plantings in Oswego, Erie, and some southwestern counties of New York.

Ponderosa pine is considered one of the best trees for shelter belt planting on the northern Great Plains (George, 1953). This is very largely due to its drought resistance and frost hardiness. No seed source recommendations were given.

In southern Michigan ponderosa pine is a promising species for forest planting. There are numerous individual trees and small stands growing in the East Lansing area. Most of them are vigorous and thrifty (figures 2 and 3). There are small forest plantings in Cass and

Kalamazoo counties in southern Michigan. The provenance of these trees is not known. Their growth rate is similar to that of red pine (*P. resinosa* Ait.).

A 50-year-old windbreak planting near Lansing, Michigan, is particularly interesting. It is on the grounds of Rose Lake Wildlife Experiment Station of the Michigan Conservation Department. The original trees were planted 2 to 3 feet apart in a narrow strip about 200 feet long. They are thrifty but not impressive as forest trees. Interest lies in the abundant natural reproduction in a field west of the windbreak (figure 4). Some of this reproduction is interspersed with planted red pine. Growth rate and form of the two species are about equal. The ponderosa pine showed the least attack and the best recovery from European pine shoot moth (Rhyacionia buoliana Schiff. (W. E. Miller, personal communication).

The probable superiority of ponderosa pine to red pine with regard to shoot moth resistance was confirmed in other Michigan localities according to a recent study by Miller and Heikkenen (1959). These authors ranked red pine as very susceptible and ponderosa pine, European black pine, and Scotch pine as moderately susceptible.

In the University of Michigan's Stinchfield Woods near Ann Arbor is a small ponderosa pine forest planting. The planting was little damaged by mice and rabbits which took a heavy toll in nearby Scotch pine and Japanese red pine (P. densiflora Sieb. and Zucc.) plantings (Young, 1929). Later growth has been satisfactory.

A small forest planting on the Michigan State University campus in East Lansing was established on a dry, sandy knoll in 1913. When reported by Herbert in 1921, ponderosa pine was the most promising of several species tested. The stand has recently been removed to make room for a building.

Prior to 1920 there was considerable interest in ponderosa pine in Michigan for the fixation of sand dunes along the eastern shore of Lake

Figure 2. Natural seedling of ponderosa pine at Rose Lake Wildlife Experiment Station, Lansing, Michigan.

Figure 3. Planted ponderosa pine in East Lansing, Michigan, south edge of Baker Woodlot. Diameter 4.5 feet from ground = 13.5 inches. Height = 50 feet. Age, about 50 years.

Figure 4. Natural reproduction of ponderosa pine at Rose Lake Wildlife Experiment Station, Lansing, Michigan. Parent trees are in the background.

Figure 2.

Figure 3.

Figure 4.

Michigan. It grew very well but was heavily attacked by sweetfern blister rust (Karl Dressel, personal communication). This rust has also caused heavy mortality among planted ponderosa pine in northern Michigan and in the Higgins Lake State Nursery (Kauffman and Moins, 1915; Boyce, 1938).

In summary, ponderosa pine has performed well in southern Michigan, Nebraska, and New York; and poorly in Iowa, Illinois, Minnesota, and northern Michigan. Most of these plantings are of unknown seed source, however, and as there is a great deal of genetic variability within the species, it should not be written off in areas where a planting from a single unknown seed source has failed.

IV. PREVIOUS IMPROVEMENT WORK WITH PONDEROSA PINE

A major portion of the improvement work with ponderosa pine has been 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 methods of vegetative propagation. This work was started in the 1920's and continues today. Other work with ponderosa pine consisted of the establishment of a series of range-wide provenance tests in the Pacific Northwest during the period 1911-1928. Thorough analysis of the results had been undertaken on only one of these tests (Weidman, 1939) until recently when Squillace and Silen (1962) evaluated the entire series of seven plantings.

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 it has not been crossed successfully with the pines from the southeastern United States and the Caribbean 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 intervarietal 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 Experiment Station, 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 then 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 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 had 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 impresssions were the results 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. The test plantation was located in an area where

Table 1. Results of pondersoa pine seed source studies at Fort Valley, Arizona. (from Pearson, 1950)

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

ponderosa pine occurs naturally. The climate at the planting site is characterized by a mean annual precipitation of 29 inches, a lack of summer rainfall, a moderately deep accumulation of snow, and a mean annual temperature of 43°F. Frost may occur in any month. The soil was a well-drained sandy loam and soil pits indicated no obvious discontinuities. The site was level and pH and soil moisture determinations indicated negligible variation in these factors. A single plot of each seed source, containing either 50 or 100 trees, was represented.

There were striking difference among progenies with respect to 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.

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 progenies originating 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 6 contrasting sites in the Pacific Northwest. The 20-year heights and mortality data were given by Munger in 1947 (table 2). Although the individual plantings were not replicated it is possible to subject the data to analysis of variance by using provenance

Table 2. 20-year heights of ponderosa pine at 7 planting sites. (From Munger, 1947 and Weidman, 1939)

Seed origin	Planting site						
	Central Oregon	N.E. Oregon	N.W. Oregon	S.W. Wash.	N.W. Wash.	East. Wash.	North. Idaho
	- - - - - - percent of plantation mean - - - - - - -						
West. Oregon	150	140	143*	121*	92	--	--
S.W. Oregon	131	121	135	125	121	112	108
Central Oregon	136*	128*	130	123	128	105*	86
West. Montana	145	131	126	108	126	--	122*
N. Central Calif.	100	107	171	97	107	--	Died
North Calif.	100	116	59	88	100	98	--
N.W. Wash.	78	80	148	87	74*	--	--
Central Ariz.	69	56	65	90	93	99	82
North New Mexico	54	63	70	86	81	76	69
Black Hills, S.D.	36	59	67	80	73	114	101
	- - - - - - - - - - - - - feet - - - - - - - - - - - - -						
Plantation mean	2.2	8.1	16.7	11.1	12.2	20.8	11.0

* = the provenance nearest the planting site.

<u>Analysis of variance</u>

Source	d.f.	F
Between provenances	9	4.99[1]
Between plantings	4[2]	
Provenances X plantings	36	
Total	49	

[1] significant at the 1 percent level

[2] plantings in east. Wash. and north Idaho not included in analysis.

X planting-site interaction as the error term. 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 the tallest and the South Dakota, Arizona, and New Mexico sources were generally the shortest in all plantations. Trees from seed of "local origin" were not usually 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, nedle 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 1 was from Colorado. The results were reported in 1944 by Moore and the planting was remeasured in 1952 (Moore, 1944; J. W. Duffield, personal communication). The planting was not replicated. Plot size varied from 75 to 5000 trees.

The climate of the planting site is cool and moist. Average annual rainfall is about 51 inches and well-distributed. The maximum summer temperature is 82° F. and the minimum winter temperature is 23° F. Frosts occur at any time between February and December. Snowfall, generally in June and July, is light. The soil is a siliceous, sandy loam over pumice. The site is exposed to rather strong winds which have resulted in a considerable amount of malformation in the fastest growing provenances.

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 high correlations between Moore's 2-year nursery heights and the heights at 17 and 25 years of age. The correlation coefficients are: $r_{2\text{-}17 \text{ years}} = 0.857$ and $r_{2\text{-}25 \text{ years}} = 0.807$. This indicates 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, range-wide, 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 2 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, vigor decreased as elevation increased.

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 2 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 3 nurseries located at high, medium, and low elevations on the western slope of the Sierra Nevada. 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 populations on the west slope of the Sierra Nevada Mountains. 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 zones the average heritability of height growth in 1/2-sib families is 0.392.

3. Polyploidy

Colchicine[2/] induced polyploids of ponderosa pine have been produced by Mirov and Stockwell (1939) and Hyun (1954). In all cases they were dwarfed and misshapen. Some of the polyploids produced by Hyun are still surviving under cultivation at the Institute of Forest Genetics at Placerville. Naturally occurring polyploids of ponderosa pine are unknown in the field. The arboretum of the Institute of Forest Genetics contains one polyploid ponderosa pine that was discovered in the nursery. Its chromosome number was determined by S. K. Hyun (Institute of Forest Genetics, unpublished data). This tree has grown to a height of 3 feet in 30 years and is barely surviving. It has the unusual characteristics of producing only primary foliage. In the field it is likely that occasional polyploids occur but are immediately eliminated by natural competition. The phenomenon is of no foreseeable importance in improvement of the species.

[2/] Colchicine is an alkaloid ($C_{22}H_{25}NO_6$) that is obtained from the liliaceous genus Colchicum. It acts on cells at mitosis by preventing the formation of spindle fibers. In the absence of these fibers the chromosomes fail to move into an equatorial plate. They remain scattered throughout the cytoplasm. The chromosomes divide, separate, and go through regular telophasic transformation. A new membrane finally forms around the nucleus which now has a doubled chromosome number.

V. OBJECTIVES

The objectives of this study were: (1) to determine the pattern of genetic variation in seedlings of ponderosa pine, (2) to ascertain the selection forces responsible for the pattern of genetic variation, (3) to assemble many geographic variants of the species for use in future hybridization and selection studies, and (4) to determine the best seed sources for planting in Michigan. These objectives could be realized in whole or in part within the 2-year duration of the study.

The present study is part of a long-range program for which there are two additional objectives. These are: (5) to determine the correlation between juvenile and mature performance, and (6) to determine the way in which different genotypes of ponderosa pine react in different environments. For this reason the 60 origins were 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. Some of the 60 collections had previously been shipped to the Northern Institute of Forest Genetics, Rhinelander, Wisconsin for controlled environment studies.

The Michigan work will also benefit from a comprehensive study of variation in ponderosa pine being conducted by the Western 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.

VI. MATERIALS AND METHODS

1. 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 one to ten trees from native stands in the collectors' vicinity. In any one stand the selected parents were located within 5 miles horizontal distance and within 200 feet vertical distance of the point designated in the origin data. Thrifty immature trees of average phenotype 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. The herbarium specimens, including a few scales from a cone of each collection, are on permanent file there. At Placerville the seed was extracted, sorted, cleaned, and subjected to detailed biometrical study. Some of the seed was germinated for short term phytotron 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. Upon receipt in East Lansing the seed lots were assigned MSFG (Michigan State Forest Genetics) numbers and entered in the accession record. The corresponding California seedlot numbers are given in Appendix I.

Pertinent origin data are shown in tables 3, 4, and 5.

2. 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 2 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 2 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 6 inches apart. Within a row the seeds were placed 2 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 1005 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 nursery soil had been kept at a high fertility level for several years previous to the experiment. No additional fertilizer was added for the present study.

Table 3. Climatic factors at place of origin for 60 seed sources of ponderosa pine (*P. ponderosa*). (Compiled by R. Z. Callaham, Pacific Southwest Forest and Range Experiment Station)

Origin	Progeny number M573-	TEMPERATURE Average April-June	 July mean	 January mean	 July minus January	GROWING SEASON Period 1/	 Date start	 Day length at start	PRECIPITATION Sept.-June	 Annual	 Sept.-June / Annual
		degrees F.	degrees F.	degrees F.	degrees F.	days	date	hours	inches	inches	percent
Calif.	2047	52.2	68.0	34.0	34.0	224	Apr. 8	12.83	43.60	44.20	.986
Calif.	2068	59.6	75.5	39.5	36.0	312	Feb. 2	10.50	33.40	33.50	.997
Calif.	2063	56.1	71.6	39.3	32.3	288	Feb. 26	11.25	30.39	30.58	.994
Calif.	2009	49.8	62.5	37.4	30.1	197	Apr. 24	13.50	33.70	34.00	.991
Calif.	2042	59.5	71.2	37.5	33.7	290	Feb. 27	11.25	31.85	32.00	.995
Calif.	2075	59.7	68.4	37.0	31.5	262	Mar. 11	11.75	57.21	57.28	.999
Calif.	2040	54.5	67.0	33.0	34.0	228	Apr. 4	12.75	46.75	47.00	.995
Calif.	2059	63.7	77.4	45.2	32.2	360	—	—	33.69	33.72	.999
Calif.	2056	59.2	75.2	40.4	34.8	330	Feb. 1	10.25	52.49	52.53	.999
Calif.	2061	52.1	66.6	36.8	29.8	252	Mar. 20	12.17	58.80	58.92	.998
Calif.	2036	52.8	68.8	31.9	36.9	218	Mar. 30	12.58	19.42	20.06	.968
Calif.	2014	61.2	71.8	37.7	34.1	285	Feb. 19	10.83	65.50	65.80	.995
Calif.	2003	57.9	71.2	36.9	34.3	281	Feb. 17	10.75	67.57	67.97	.994
Calif.	2006	54.0	65.9	30.4	35.5	199	Feb. 30	11.25	53.20	53.80	.989
Calif.	2053	57.6	70.5	34.2	36.3	252	Mar. 4	11.42	17.18	17.49	.982
Calif.	2051	52.0	65.2	27.0	38.2	201	Apr. 3	12.75	22.80	23.00	.991
Nev.	2000	50.3	64.7	30.6	34.1	205	Apr. 9	13.00	17.96	18.39	.977
Nev.	2292	43.2	55.5	16.2	39.3	129	May 9	13.50	23.50	25.00	.940
Ore.	2071	56.0	66.1	39.2	26.9	317	Feb, 13	10.33	38.92	39.62	.982
Ore.	2091	57.7	68.6	39.4	28.2	304	Feb. 9	10.17	41.07	42.26	.972
Calif.	2045	43.5	64.5	22.8	41.7	173	Apr. 21	13.58	22.50	23.20	.970
Ore.	2034	46.0	58.2	19.5	38.7	167	Apr. 29	14.08	21.50	23.50	.914
Mont.	2205	51.5	65.4	24.4	41.0	196	Apr. 4	12.92	14.30	15.99	.897
Wash.	2032	52.5	68.0	22.2	45.8	209	Mar. 28	12.58	13.50	14.00	.964
Wash.	2102	56.1	69.0	23.5	45.5	213	Mar. 25	12.42	16.76	18.43	.909
Ida.	2134	50.3	66.1	23.2	42.9	200	Apr. 4	13.08	17.71	19.52	.907
B.C.	2124	54.0	67.0	21.0	46.0	203	Apr. 1	12.92	12.58	14.88	.844
Ariz.	2243	44.5	60.0	16.5	43.5	158	May 3	13.92	12.00	16.00	.750
N. Mex.	2081	60.2	68.0	37.8	30.2	258	Mar. 7	11.67	9.40	18.40	.511
N. Mex.	2109	59.5	68.3	35.9	32.4	253	Mar. 6	11.67	11.58	17.99	.644
N. Mex.	2207	53.2	61.3	33.8	27.5	222	Mar. 16	12.00	14.10	23.50	.600
N. Mex.	2077	52.4	61.5	32.0	29.3	214	Apr. 1	12.50	16.80	26.80	.627
N. Mex.	2078	50.8	59.8	30.4	29.4	201	Apr. 9	12.83	15.29	25.01	.611
N. Mex.	2103	55.6	66.4	30.8	35.6	225	Mar. 23	12.25	10.41	17.79	.585
Ariz.	2234	55.8	64.0	30.0	24.0	202	Apr. 3	12.50	27.75	33.00	.841
Ariz.	2012	47.5	58.0	22.0	36.0	162	May 5	13.67	25.70	32.20	.798
N. Mex.	2213	56.0	67.5	27.0	40.5	195	Apr. 10	12.92	7.26	11.67	.622
N. Mex.	2219	53.0	62.5	23.0	39.5	163	Apr. 30	13.58	13.50	17.50	.771
N. Mex.	2226	47.0	58.0	17.0	41.0	125	May 25	14.25	17.00	22.75	.747
Colo.	2025	43.1	60.8	19.3	41.5	158	May 7	13.92	10.63	14.54	.731
Colo.	2026	49.6	63.0	22.4	40.6	187	Apr. 16	13.08	14.40	18.75	.768
Utah	2267	54.8	70.0	26.3	43.7	208	Apr, 5	12.75	14.53	19.02	.764
Utah	2284	43.5	62.5	20.2	42.3	170	Apr. 25	13.58	17.28	21.15	.817
Utah	2248	46.5	60.5	18.0	41.5	157	May 5	14.00	17.50	21.50	.814
Colo.	2145	50.5	64.0	27.0	37.0	193	Mar. 30	12.58	12.50	16.75	.746
Utah	2111	44.5	60.0	16.5	43.5	158	May 3	13.92	23.80	27.60	.862
Utah	2116	44.5	60.0	16.5	43.5	158	May 3	13.92	23.80	27.60	.862
Utah	2274	49.9	67.1	20.8	46.3	182	Apr. 20	13.50	17.67	20.22	.874
Utah	2258	44.2	60.3	15.2	45.1	154	May 6	14.17	13.90	16.80	.827
Colo.	2137	42.9	57.0	13.0	44.0	146	May 10	14.00	9.94	12.33	.766
Colo.	2155	50.7	66.2	27.2	39.0	192	Apr. 17	13.33	13.44	19.11	.703
Colo.	2164	47.0	59.0	22.0	37.0	156	May 6	13.83	17.00	21.70	.783
Nebr.	2172	58.7	75.2	24.0	51.2	214	Mar. 30	12.58	15.07	19.81	.760
Nebr.	2180	58.1	74.3	21.0	53.3	209	Apr. 3	12.75	16.82	22.65	.742
Nebr.	2190	52.3	71.0	21.2	49.8	194	Apr. 13	13.33	15.31	18.77	.815
S. Dak.	2029	55.8	74.2	22.9	51.3	212	Mar. 31	12.67	12.71	16.89	.752
S. Dak.	2024	47.6	63.9	21.7	42.2	174	Apr. 23	13.83	13.23	18.15	.729
S. Dak.	2028	49.5	66.0	16.2	39.8	155	May 6	14.42	13.77	18.15	.758
Mont.	2095	52.1	68.5	23.2	45.3	189	Apr. 11	13.33	11.35	13.85	.819
Mont.	2197	50.0	65.6	20.6	45.0	188	Apr. 15	14.75	14.45	17.99	.803

1/ Number of days per year over 42° F.

Table 4. 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	Germination Percent in second year	Yellow trees	Foliage color in			Stem color	Trees forming secondary needles in first year	Secondary Needles Length	Secondary Needles Needles in clusters of 2	Secondary Needles Needles in clusters of 4
							in June 1960		July 1960	Aug. 1960	Oct. 1960	Oct. 1961	June 1961				
	character designation →					(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	
		° '	° '	feet	No.	mg.	date	percent	percent	---- grade	-----		grade	percent	mm.	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	ns	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

Table 5. 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	115
Calif.	2045	41 54	120 19	0	6	16	1	182	9	12	1	0	48	145
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				ns	.7	4.6	.3	17.8	.8	4.8	--	ns	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	--

Table 6. 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 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	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.	2051	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	ns	ns	1.01	.85	.91	1.19	7.64	5.78	--	--
L.S.D. 5 percent level							3.18			3.47	3.12	3.11	3.19	26.12	19.76		
L.S.D. 1 percent level							4.11			4.48	3.98	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

Table 7. Characters 12 through 22 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.	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	ns	19.76	1.24	ns	--	5.72	3.70	8.99
L.S.D. 5 percent level				2.67	1.96	22.23		67.58	4.22			19.56	12.65	30.74
L.S.D. 1 percent level				3.45	2.53	28.73		87.34	5.46			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	--

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. In total there were about 8600 seedlings in the test.

3. 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. The actual layout of the experiment in the nursery was identical to a conventional split-plot design if the stand progenies were regarded as one type of treatment and the individual-tree progenies as another. There was no biological interaction between the stand-progenies and the individual-tree progenies, however, since they are merely different tabulations of data from the same seedlings and thus the design was not a split plot.

Because there were 298 individual-tree progeny to be tested, the modified randomized block 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 correctly anticipated 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 had been scattered throughout a replicate they would have been 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.

4. Measurement Methods

In all cases the basic unit of observation (plot) was the individual-tree progeny in a single row.

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 5 tallest out of 60 in each of 3 replicates is $60(5/60)^3 = .0347$ = less than 5 percent. Accordingly, if a single stand-progeny proved to be among the 5 tallest in each of 3 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 but some may have predictive value if they prove to be correlated with mature characters of economic importance. However, all of 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 seedlings and later converted to a percentage basis. Characters such as color were described 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 recognizeable 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 needles 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, it would be reflected in a significant "F" value by 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 in all cases bore out the validity of the color differences discernible by observation.

Height was measured by recording the mean of the tallest and shortest tree in each plot (row). 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.

The nursery map was made on ruled paper, each plot being given a single line. The blank columns were available for measurement data, a column being given to each characteristic as the occasion arose. All plots were measured in the same sequence each time. Observer bias was reduced 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 to either genetic or environmental causes.

5. Statistical Analysis

The data for each measured character (except seed weight, number of growth periods, and number of needles per fascicle) were subjected to analyses of variance. Plot means were used as items. For a typical analysis of the data from the 175 individual-tree progenies that were replicated 3 times, the degrees of freedom were as follows: provenance - 174, replicate - 2, error - 348, total - 524. For a typical analysis of variance from the 125 individual-tree progenies that were replicated 4 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 progeny means. 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: harmonic mean = $1/N\ (1/n_1\ 1/n_2\ 1/n_3\ .\ .\ .)$, 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:

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

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 significantly 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) (tables 8 and 9). 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 standard 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-values 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.

Simple correlations were calculated between seed weight, several characteristics of the parental habitat, and several characteristics of the progenies. Stand means or stand-progeny means were used as items in all these calculations. Therefore the correlations apply specifically to stands rather than to single seedlings or to individual-tree progenies.

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

VI. GENERAL DESCRIPTION OF THE SEEDBEDS

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 except for the two rows of each stand-progeny that were adjacent to other stand-progenies, 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.[3/] 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 Pacific Northwest sources except the two from the Willamette Valley, grew very well under Michigan conditions. Conditions were not optimum for the development of the

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[3/] MYLONE (3,5-dimethyl-1,3,5.2 H-tetrahydrothiadiazine-2-thione), a fungicide-herbicide, was applied to the seedbeds in the fall before sowing (fall, 1959).

California progenies. Their apparent uniformity 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.

VIII. GENETIC VARIABILITY WITHIN STANDS

In the Interior region there were 22 stands which were represented by 5 individual-tree progenies each. This sampling was considered sufficient for the calculation of the relative amounts of within-stand and between-stand genetic variance. This was done by computing the components of the expectation mean squares, using single-tree progeny means as items. The expectation mean squares are shown in the following tabulation.

Source of variation	Degrees of freedom	Expectation Mean Square
Between stands	21	${}^2_{ws+e} + 5\,{}^2_{BS}$
Within stands	88	${}^2_{ws+e}$
Total	109	

Three-replicate means were used as items in this analysis; hence the within-stand genetic variance cannot be separated from the environmental variance attributable to replicate differences. In the above tabulation (${}^2_{ws+e}$) is the variance component attributable to within-stand genetic variance plus environmental variance.

The results of these analyses are summarized in table 8. From these results it is possible to determine which of several selection procedures might result in the most genetic improvement in certain traits. In any improvement program there is a practical limit to the number of progenies which can be tested. Suppose this limit is 500

progenies. Should a test include (1) 500 stand progenies, (2) 5 single-tree progenies from each of 100 stands, (3) 100 single-tree progenies from each of 5 stands, or (4) 500 single-tree progenies from one stand? If working with a trait such as winter hardiness (character 13 in table 8), the within-stand variance is so small as compared with the between-stand variance as to indicate little possibility of improvement by selecting within stands. Therefore, possibilities 1 or 2 offer the most chance of obtaining a strain with improved hardiness. The same would be true, but to a lesser extent, of improvement in needle length and rate of growth.

At the other extreme is a character such as foliage color, in which the within-stand variance is greater than the between-stand variance. In this trait emphasis should be placed on single-tree selection as in possibilities 3 or 4.

The magnitude of the within-stand variability in seven characters is presented in table 9. This table covers the entire species' range. A "+" indicates the presence and "-" the absence of statistically significant (at the 5 percent level) differences among the progenies of individual trees within a single stand. Each stand was represented by 5 to 10 single-tree progenies. Presumably, if more trees had been selected within each stand, there would have been more instances of genetically variable stands. Also, the sampling error for the 5- to 10-parent samples was relatively large. Therefore, the variability pattern found for a particular stand might be different if another 10 parents from the same stand were to be tested.

Table 9 leads to the same conclusions regarding the relative merits of stand and single-tree selection as does table 8. For example,

Table 8. Within-stand versus between-stand genetic variances in the Interior variety, based on 22 stands represented by 5 single-tree progenies each.

Comparison	Genetic variance in -- Foliage color October 1960 (6)	Needle length (10)	Winter injury (13)	1-year terminal buds (14)	Lammas growth (18)	1-year height (21)	2-year height (22)
	number	number	number	number	number	number	number
Within stands	.57	178.72	.02	5.64	.54	7.53	632.51
Between stands	.26	839.77	.39	12.50	.52	14.64	1795.61

Table 9. Within-stand variability for progenies of ponderosa pine (*P. ponderosa* Dougl. ex Laws) grown for 2 years at East Lansing.

			Presence (+) or absence (-) of within-stand genetic differences in --						
Ecotype	Origin	Progeny number MSFG-	Foliage color (6)	1-year terminal buds (14)	Lammas growth (18)	1-year height (21)	2-year height (22)	Winter injury (13)	Needle length (10)
Calif.	Calif.	2047	-	-	+	-	-	-	-
	Calif.	2068	-	-	+	-	-	-	-
	Calif.	2063	-	-	+	-	-	-	+
	Calif.	2009	-	-	-	+	-	-	-
	Calif.	2042	-	-	+	-	-	-	-
	Calif.	2075	-	-	+	-	-	-	-
	Calif.	2040	-	-	-	-	-	-	-
	Calif.	2059	-	-	-	-	-	-	-
	Calif.	2056	-	-	+	+	-	-	-
	Calif.	2061	-	-	-	-	-	-	-
	Calif.	2036	-	-	+	-	-	-	-
	Calif.	2014	-	-	-	-	+	-	-
	Calif.	2003	-	-	-	-	-	-	-
	Calif.	2006	-	-	+	-	-	-	-
	Calif.	2053	-	-	-	-	-	-	-
	Calif.	2051	-	-	-	-	-	-	-
	Nev.	2000	-	-	-	-	+	-	-
	Nev.	2292	-	-	+	-	-	-	+
Pacific Northwest	Ore.	2071	-	-	-	-	-	-	-
	Ore.	2091	-	-	-	-	-	-	-
	Calif.	2045	-	-	-	-	-	-	-
	Ore.	2034	-	-	-	-	-	-	-
	Mont.	2205	-	-	-	+	-	-	-
	Wash.	2032	-	+	-	-	-	-	-
	Ida.	2134	-	-	-	-	-	+	-
	B.C.	2124	-	-	-	-	+	+	+
Southern Interior	N. Mex.	2081	+	-	-	-	-	-	-
	N. Mex.	2109	-	-	-	-	-	-	-
	N. Mex.	2207	+	-	-	-	-	-	-
	N. Mex.	2078	-	-	-	-	-	-	-
	N. Mex.	2103	+	-	-	-	+	-	-
	Ariz.	2234	-	-	-	-	-	-	-
	Ariz.	2012	-	-	-	-	-	-	-
	Ariz.	2243	-	-	-	-	-	-	-
Central Interior	N. Mex.	2213	+	-	-	-	-	-	-
	N. Mex.	2219	+	-	-	-	-	-	-
	N. Mex.	2226	-	-	-	+	+	-	+
	Utah	2267	+	-	-	+	+	-	-
	Utah	2284	+	-	-	+	+	-	+
	Utah	2111	-	-	-	-	-	-	-
	Utah	2116	-	+	-	-	-	-	-
	Utah	2274	+	-	+	-	-	-	+
	Utah	2258	+	-	-	-	+	-	-
	Colo.	2137	+	-	-	-	-	+	-
	Utah	2248	+	-	-	-	+	-	-
	Colo.	2145	+	-	-	-	+	-	+
	Colo.	2164	-	-	-	-	-	-	+
	Colo.	2155	+	-	-	-	-	-	-
Northern Interior	Nebr.	2172	-	+	-	-	-	-	+
	Nebr.	2180	+	-	-	-	+	-	+
	Nebr.	2190	+	-	-	-	-	-	-
	Mont.	2095	-	-	-	-	-	-	-
	Mont.	2197	-	+	-	-	-	-	+
Percent of stands with significant within-stand differences			28.3	7.5	20.8	9.3	22.6	5.7	23.9

if one were selecting for rapid height growth within the Southern Interior ecotype, improvement could be made by selecting within stand MSFG-2103, but not by selecting within the other stands. There would be more progress by selecting stand progenies. The same is true for other characters in this ecotype. Only in the case of foliage color was there sufficient genetic variability within stands to warrant the assumption that selection within any stand would be fruitful.

Table 9 also illustrates the difficulty of obtaining an appreciable amount of genetic improvement in more than a single trait when practicing single-tree selection within a stand. Fifty-three stands and seven characters are listed in the table. There were significant differences between female parents (at the 5 percent level) in 0 characters in 17 stands, in 1 character in 21 stands, in 2 characters in 8 stands, in 3 characters in 8 stands, and in 4 characters in 1 stand. In other words, most of the stands contained differences between female parents in 0 or 1 characters.

The effort necessary for simultaneous selection for three traits can be illustrated by stand MSFG-2274 in Utah. This stand was represented by 10 single-tree progenies and was genetically variable in three traits. However, no single 1-parent progeny was superior in all three traits. To obtain such a progeny would require the progeny testing of approximately $10^3 = 1000$ parents.

The data in table 9 also indicate that estimates of heritability of a few trees from a single stand are not necessarily valid for other stands or for the population as a whole. For example, in the Southern Interior ecotype the indicated heritability of foliage color is zero for stands MSFG-2012, MSFG-2078, MSFG-2109, MSFG-2234, and MSFG-2243, but is appreciably greater than zero for stands MSFG-2081, MSFG-2103, and MSFG-2207. An estimate computed from the nursery data for any single stand would apply specifically to the progenies included in the nursery test but would be misleading if applied to the ecotype as a whole.

IX. THE GEOGRAPHIC VARIATION PATTERN

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

Pacific Coast variety, *Pinus ponderosa* var. *ponderosa*
- California ecotype
- Pacific Northwest 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 figures 1 and 5. The 2-year performance data for the stand progenies and ecotypes are summarized in tables 4, 5, 6, and 7; and figure 6.

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 traits in which there is no overlapping between the means of 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 12 and 13). 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

Figure 5. Ecotypic division of the progenies included in this study. A = California, B = Pacific Northwest, 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.

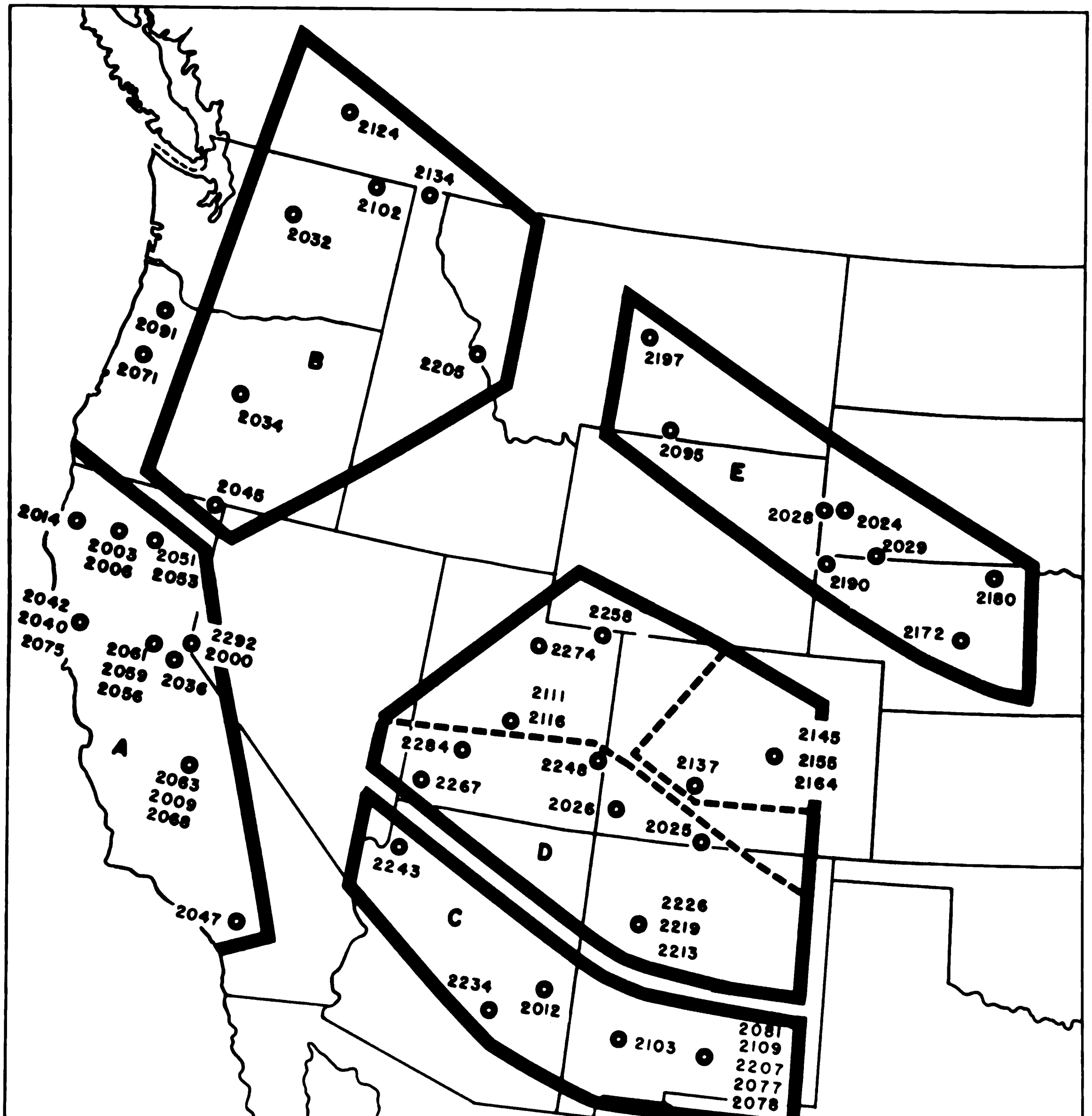
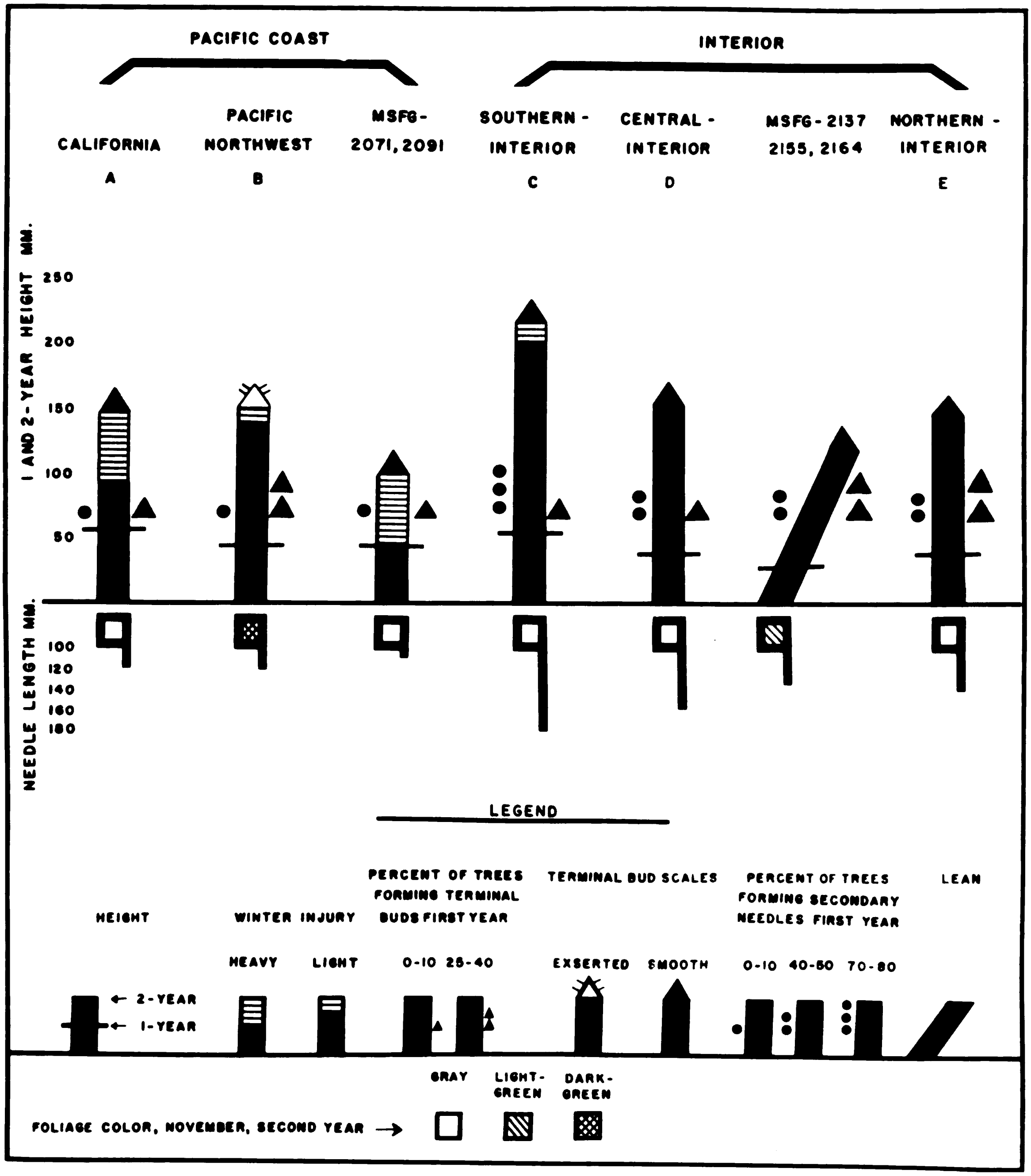

2124
2134
2102
2032
2091
2071
B
2205
2034
2045
2014
2003
2006
2051
2053
2042
2040
2075
2061
2059
2056
2036
2292
2000
A
2063
2009
2068
2047
2197
2095
E
2028
2024
2029
2190
2180
2172
2258
2274
2111
2116
2284
2248
2267
2137
2145
2155
2164
2026
2025
2243
D
2226
2219
2213
C
2234
2012
2103
2081
2109
2207
2077
2078

Figure 6. Ecotype mean values for selected progeny traits of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.).


PACIFIC COAST
INTERIOR
CALIFORNIA
A
PACIFIC NORTHWEST
B
MSFG-2071, 2091
SOUTHERN-INTERIOR
C
CENTRAL-INTERIOR
D
MSFG-2137 2155, 2164
NORTHERN-INTERIOR
E
1 AND 2-YEAR HEIGHT MM.
250
200
150
100
50
NEEDLE LENGTH MM.
100
120
140
160
180
LEGEND
HEIGHT
2-YEAR
1-YEAR
WINTER INJURY
HEAVY
LIGHT
PERCENT OF TREES FORMING TERMINAL BUDS FIRST YEAR
0-10
25-40
TERMINAL BUD SCALES
EXSERTED
SMOOTH
PERCENT OF TREES FORMING SECONDARY NEEDLES FIRST YEAR
0-10
40-50
70-80
LEAN
FOLIAGE COLOR, NOVEMBER, SECOND YEAR
GRAY
LIGHT-GREEN
DARK-GREEN

were considered (tables 14 and 15). These lines of evidence were considered in greater detail in later sections.

The distinctions between the two taxonomic 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 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 demonstrate statistically 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 4, 5, 6, and 7. 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 Pacific Northwest progenies.

None of the progenies from north central and northwestern California sampled the Pacific Northwest ecotypes. Hence the northern boundary of the California ecotype cannot be precisely delimited in this area 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. MSFG-2000 has 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.

The progenies from California suffered severe injury during the first winter. The determination of within-stand variability in the California ecotype was confounded by this injury because the development of many second year traits were affected.

Pacific Northwest ecotype.--The Pacific Northwest ecotype consisted of the progenies from northeastern California, Oregon, Washington, and British Columbia. It was incompletely sampled so neither its exact boundaries nor its degree of homogeneity are accurately known. There were sufficient differences between the Willamette Valley and other provenances to indicate that the population from this region should more properly be considered a series of clines or ecotypes rather than a single unit. As considered here the southern boundary is the crest of the Sierra Nevada-Cascade Mountains 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.

Seedlings from the Pacific Northwest 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.

The two stand-progenies from the Willamette Valley of western Oregon differed considerably from the other Pacific Northwest seedlings. These two sources, MSFG-2071 and MSFG-2091, suffered severe winter injury and had many yellow seedlings during the first year. Also their seeds weighed only half as much as seeds from other parts of the region. The Willamette Valley populations are relatively small and isolated and occupy a more mild and moist environment than that occupied by ponderosa pine in other parts of the Pacific Northwest. The lack of hardiness probably represents a response to selection pressures occasioned by the mild winters of the parental habitat. Possibly some of the other distinctive traits of these populations came about as a result of genetic drift, which is a feature of small, isolated populations.

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 6 inches of the soil.

These were easily 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 3 miles northwest of Colorado Springs respectively. They were the only progenies in the entire experiment which grew crookedly and non-vertically (figure 7). They were also distinctive in that they started height growth earlier and grew less tall than other Central Interior progenies (tables 7 and 9). A fourth stand-progeny from the Colorado Springs area (MSFG-2145) was similar to the central and northern Utah progenies.

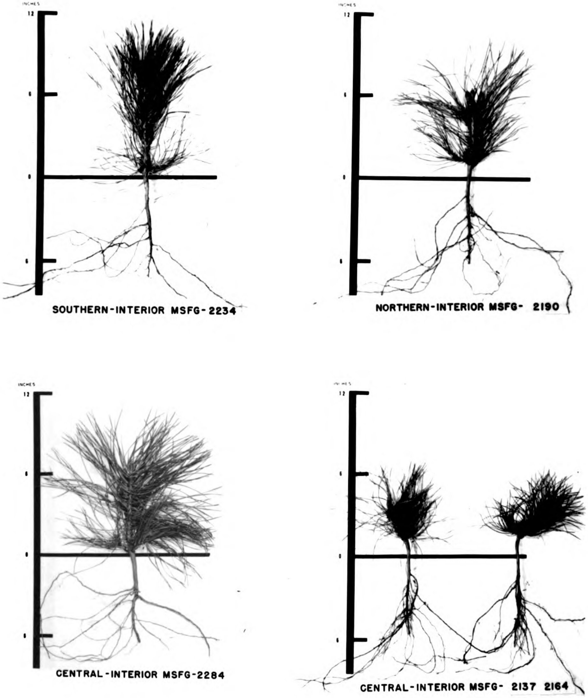
The range of the southern Wyoming population, which was not sampled, is continuous with the population in the vicinity of Colorado Springs. Its genetic affinities are not known.

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.

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.

Agreement between the present and previous data.--Of the four previous seed source studies of ponderosa pine, that by Weidman (1939) in northern Idaho, sampled the range best. It included 12 origins from the Pacific Northwest, 1 from California, and 8 from the interior region occupied by the variety scopulorum. His results agree with the present data in showing that the Pacific Northwest population is homogeneous enough to be considered a unit, which he termed the "northern plateau race." It was the most satisfactory ecotype 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

Figure 7. 2-year old seedlings of the ecotypes of the Interior variety of ponderosa pine (*Pinus ponderosa* var. *scopulorum*) grown for 2 years at East Lansing.



SOUTHERN-INTERIOR MSFG-2234

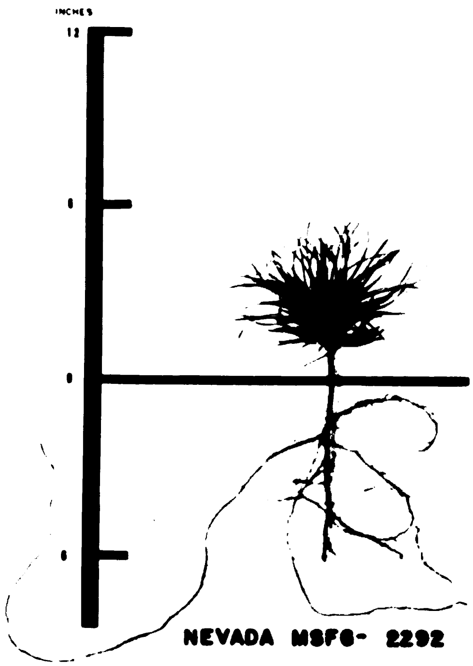
NORTHERN-INTERIOR MSFG- 2190

CENTRAL-INTERIOR MSFG-2284

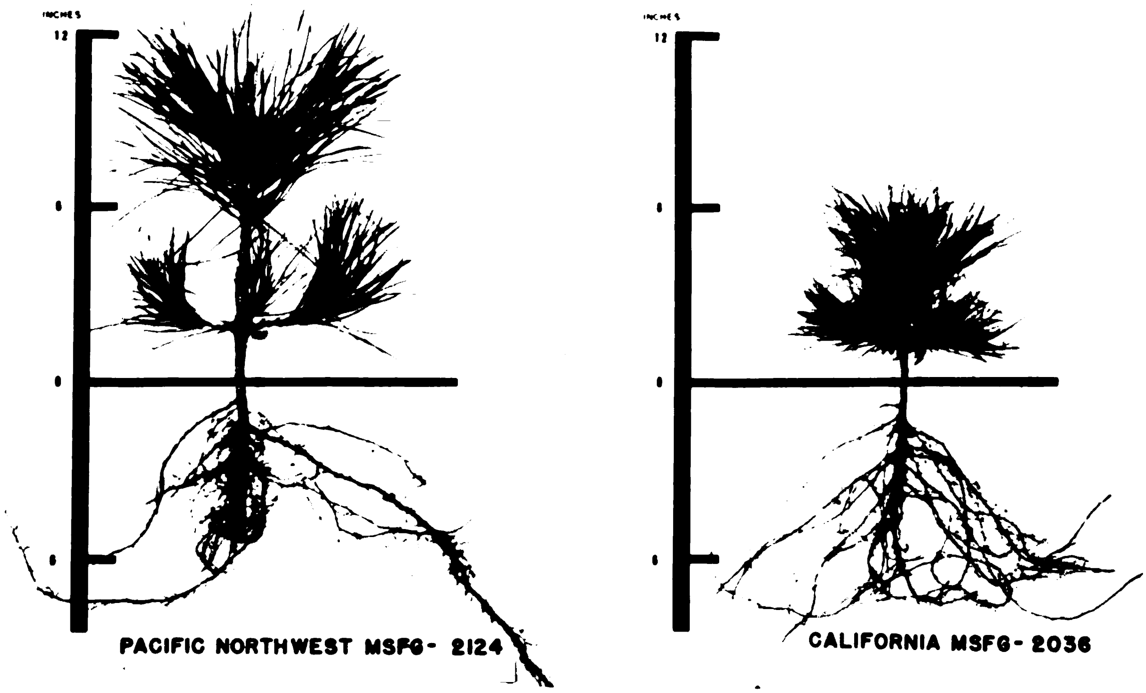
CENTRAL-INTERIOR MSFG- 2137 2164

Figure 7.

Figure 8. 2-year old seedlings of the ecotypes of the Pacific Coast variety of ponderosa pine (*Pinus ponderosa* var. *ponderosa*) grown for 2 years at East Lansing.



NEVADA MSFG- 2292



PACIFIC NORTHWEST MSFG- 2124

CALIFORNIA MSFG- 2036

Figure 8.

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 indications in the present data.

The 25-year-old New Zealand provenance test (Moore, 1944) included 13 seed sources. His data agreed with the present data in that these sources could be grouped into Pacific Northwest, 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 in New Zealand and did not suffer any winter killing under New Zealand conditions.

Data from Munger's (1947) Pacific Northwest test, which included 10 origins and 6 different planting sites, permitted separation of ponderosa pine into a fast growing Pacific Coast type and a slower growing Interior type. Survival and growth were too poor on the similar-sized Illinois test to permit estimates of the species' variation pattern (Lorenz, 1949).

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, and 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).

Geographical races of ponderosa pine have 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.

X. DELIMITATION OF ECOTYPE BOUNDARIES BY MULTI-CHARACTER ANALYSIS

The summation of differences (tables 12 and 13) 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 on page 46 of the statistical analysis section. Their interpretation is best explained by considering the two hypothetical tables (tables 10 and 11) 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 10. If the variation pattern is discontinuous, that is, two distinct populations are represented, the table would appear as in table 11. The groups of similar progeny appear as groups of small numbers near the hypoteneuse 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 12 and 13) reveal a generally discontinuous variation pattern. The most conspicuous break occurs between the California and Pacific Northwest progenies

Table 10. 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 11. 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 12. 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	5	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 13. 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	18	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.

Table 13. 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	18	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.

(table 12). The difference-values for the comparison between the most northern California progenies and the most southern Pacific Northwest 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 Pacific Northwest ecotype is much more variable. The difference-values within the Pacific Northwest ecotype range between 5 and 31.

The Willamette Valley sources are more similar to the California sources than to the Pacific Northwest sources. The range of difference-values for the Willamette Valley-California comparisons is from 0 to 19. The difference-values for the Willamette Valley-inland Pacific Northwest comparison range from 5 to 31. 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 13) 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 domparisons between MSFG-2243 and the other Southern Interior progenies range from 2 to 7.

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

Table 13 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, central 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.

XI. CORRELATION ANALYSES

The analysis of variance demonstrated the nature and extent of the variation in progeny characters. Correlation analyses between the progeny characters and climatic factors at the place of origin were undertaken in order to indicate the climatic forces associated for the evolution of this variation and for the purpose of predicting desirable seed collection areas by the examination of the climate in those areas (tables 14 through 16).

The objective of the analyses involving correlations among progeny traits was to determine the degree of assurance with which one can predict the performance of one character from the performance of another. Can 2-year height be predicted from 1-year height? Can the amount of winter injury that a tree will suffer in ensuing years be predicted by observing certain first year characters?

Before these questions can be answered, three limitations of correlation analysis in general and these particular data should be considered. Kempthorne (1957) stated the problem as follows: "Strictly speaking correlation analysis and the prediction of variables make no use of the causal pattern in which the variables arose, and this fact perhaps more than any other has led to the decay of the use of the correlation coefficient in statistical inference." In other words, the presence of significant correlation alone is not evidence of a cause-and-effect relationship. For example, there is no apparent physiological relationship between stem color and needle length in the Interior region in spite of a significant correlation coefficient (table 16). For this reason, a direct cause-and-effect relationship is not implied for all the relationships presented.

The second limitation is the non-normal distribution of the data for a few characters. Confidence limits are based on an assumption of normality in the bivariate population being sampled and do not apply strictly to a few of the analyses. This limitation detracts slightly from some of the correlations but does not affect the general conclusions.

The third limitation is brought about by the low number of degrees of freedom in some within-ecotype analyses. In a few cases correlations involving only one ecotype were as high as the correlations involving an entire region but were not significant due to the lower number of degrees of freedom. The correlations for which this holds true can be observed in tables 14 and 15. When the correlations vary from a significant figure within a region to zero within an ecotype, however, the loss of signivicance can not be attributed to reduced number of degrees of freedom. In this experiment when a correlation was significant within a region but not within an ecotype it was most often a consequence of the discontinuous nature of the variation.

A correlation coefficient that is true for an entire set of data is not necessarily true for segments of those data. For example the statement, "In humans, maleness is associated with greater height" is true when one considers a discontinuous population including both men and women. It is not true when one considers a continuous population of men only because men with heavy beards or deep voices (both attribute of maleness) are not necessarily taller than men with light beards or high voices. Just so with tree populations. A correlation that is true for the species as a whole may or may not be true if only a subdivision of the species is considered. For this reason each set of correlations was calculated separately for the provenances from two regions (Pacific Coast and Interior) and five ecotypes (California,[4] Pacific Northwest, Southern Interior, Central Interior, and Northern Interior). The progenies from the Pacific Coast and Interior regions were not included in a single analysis because the data showed that they should be considered as very distinct populations.

A number of hypothetical situations illustrate the manner in which correlations within sub-populations may vary from correlations within the whole population. Some of these are presented in figure 9. There can be a straight line relationship (figure 9a) so that the correlation is true for the entire population or any part of the population. There can be a grouping so that the correlations involve sub-population means rather than individual items (figure 9b). This happened frequently in this experiment and explains why so many correlations were significant if one considered all sources from a region, but not if one considered only the sources from an ecotype. If the provenances are grouped as depicted in figure 9c there will be a correlation within individual sub-populations but not within the population as a whole. This was the case with the correlations between seed weight and five of the climatic factors in the Pacific Northwest and Southern Interior ecotypes.

Prediction of the unit-increase in one character from the unit-increase in another over an entire region is not feasible if the relationship between the two characters varies discontinuously over the region. If this is the case, correlation analysis should be undertaken only within each of the populations separately.

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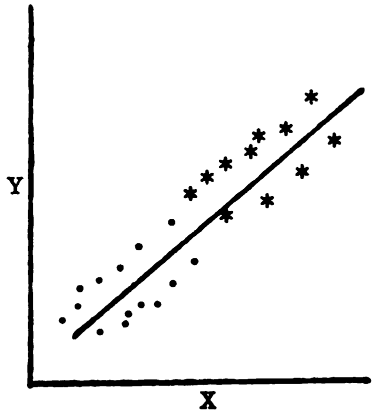
[4] MSFG-2045, from northeastern California, was considered part of the Pacific Northwest ecotype for these analyses. MSFG-2000 and MSFG-2292 were not considered part of either ecotype when they were considered separately but they were included in the analysis of the entire Pacific Coast region.

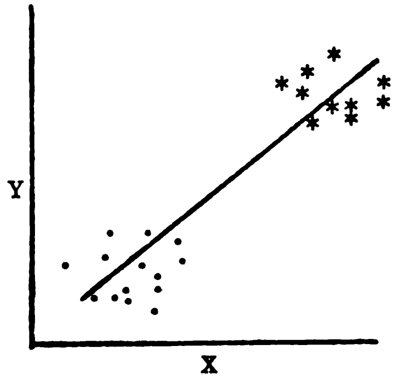
Figure 9. Scatter diagrams depicting hypothetical relationships between two variables; X and Y. Dots represent progenies from one ecotype, asterisks represent progenies from another ecotype.

A.



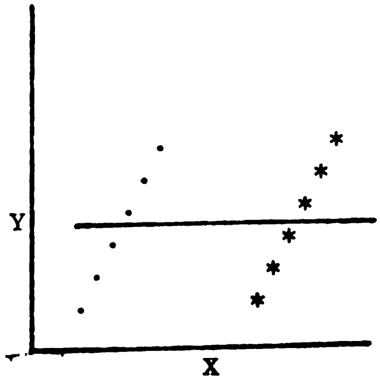
Correlation evident in sub-population and in entire population

B.



Correlation evident in entire population but not in sub-population.

C.



Correlation evident in sub-population but not in entire population

In order to test this point the significant relationships of most interest were plotted on graph paper. In this manner it was possible to tell whether or not the variation was continuous or discontinuous and whether the relationship was linear or not. The relationships which are described below are valid in this respect.

1. Correlations Between Progeny Traits and Climatic Factors at the Place of Origin

All possible simple correlations were calculated between 10 climatic factors, seed weight, and 13 progeny traits for each region and ecotype. Stand-progeny means were used as items. Thus the calculated correlation coefficients apply specifically to stand means. The relationships in which significant correlation coefficients sppear in at least one region or ecotype are presented in table 14. The three precipitation factors were each very strongly correlated with the same progeny characters. Therefore, only the correlations involving annual precipitation are presented.

Thirty-two percent of the progeny-environment correlations were significant when calculated with data from an entire region. The same correlations were evident only 3 percent of the time when calculated with data from the ecotypes separately. This illustrates that many of the correlations were among ecotype means rather than among stand means. In a few instances the within-ecotype correlation coefficients were as high as the within-region coefficients but were not significant because of the low number of degrees of freedom.

It is probable that most of the correlations involving only progenies from the Pacific Northwest were also the result of discontinuous variation. The two Willamette Valley sources (MSFG-2071 and MSFG-2091)

Table 14. Correlations between progeny traits and climatic factors at the place of origin in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.)

Correlation applies to:		Pacific Coast Region			Interior Region			
Climatic factor	Seedling character	Entire region	Pacific Northwest	California	Entire region	Southern-Interior	Central-Interior	Northern-Interior
Average spring temperature	(7) Foliage color, October, 1961	-.54**	-.60	.07	.00	.00	.00	.00
	(8) Stem color, June, 1961	-.25	.09	-.33	.52**	.09	.63**	.61
	(12) Basal needle mortality	.00	.00	.00	.49**	.67*	-.13	.75*
	(13) Winter injury	.62***	.61	.23	.42*	-.42	.00	.00
	(15) Terminal bud scale type	-.56**	-.52	.00	.00	.00	.00	.00
	(16) Number of lateral buds	--	--	--	.59***	.47	.38	.42
	(22) 2-year height	-.02	-.26	-.24	.60***	.67*	.42	.49
Average January temperature	(8) Stem color, June, 1961	-.11	-.22	-.30	.74***	-.07	.46	.36
	(10) Needle length	-.32	-.59	-.15	.54**	-.32	.27	.28
	(13) Winter injury	.53**	.94***	.52*	.73***	-.40	.35	.00
	(14) First year terminal buds	-.70***	-.72*	-.21	.08	.69*	.07	.56
	(16) Number of lateral buds	--	--	--	.43*	.15	.19	.09
	(17) Growth initiation	.71***	.73*	.30	.45**	-.02	.35	-.73*
	(21) 1-year height	.11	-.14	.50*	.50**	.09	.05	-.27
	(22) 2-year height	-.37	-.71*	-.26	.71***	.41	.20	.05
Average July temperature	(7) Foliage color, October, 1961	-.49**	-.36	.06	.00	.00	.00	.00
	(13) Winter injury	.50**	.29	.46	-.10	-.57	.00	.00
	(14) First year terminal buds	-.09	-.04	.07	.53**	.49	-.06	.33
	(15) Terminal bud scale type	-.52**	-.48	.00	.00	.00	.00	.00
	(21) 1-year height	.53**	-.18	.29	-.08	.70*	.09	-.30
Annual temperature range	(7) Foliage color, October, 1961	.69***	.63	.20	.00	.00	.00	.00
	(8) Stem color, June, 1961	.20	.34	.18	-.70***	-.20	-.31	.58
	(10) Needle length	.19	.08	.48	-.52**	.30	-.17	.74*
	(13) Winter injury	-.78***	-.88**	-.03	-.79***	-.52	.00	.00
	(14) First year terminal buds	.68***	.58	.45	.36*	-.03	.04	.53
	(15) Terminal bud scale type	.69***	.60	.00	.00	.00	.00	.00
	(17) Growth initiation	-.81***	-.84**	-.40	-.59***	-.20	-.11	-.72*
	(21) 1-year height	-.28	-.20	.08	-.54**	.62	.09	-.28
	(22) 2-year height	.20	.25	.69**	-.54**	.45	-.16	.37
Length of growing season	(7) Foliage color, October, 1961	-.59***	-.81**	.04	.00	.00	.00	.00
	(8) Stem color, June, 1961	-.32	-.09	-.40	.56***	-.14	.33	.59
	(10) Needle length	-.09	-.65	-.09	.38*	-.26	.21	.64
	(12) Basal needle mortality	.00	.00	.00	.47**	.67*	.02	.51
	(13) Winter injury	.71***	.92***	.41	.53**	-.60	.00	.00
	(15) Terminal bud scale type	-.60***	-.70*	.00	.00	.00	.00	.00
	(16) Number of lateral buds	--	--	--	.47**	.32	.06	.29
	(17) Growth initiation	.47*	.69*	.15	.21	.04	.24	.03
	(22) 2-year height	-.17	-.68*	-.29	.65***	.65	.14	.30
Date of growing season initiation	(7) Foliage color, October, 1961	.53**	.79*	-.17	.00	.00	.00	.00
	(8) Stem color, June, 1961	.35	.10	.44	-.52**	.12	-.22	-.57
	(12) Basal needle mortality	.00	.00	.00	.46**	-.67*	-.03	-.46
	(13) Winter injury	-.64***	-.87**	-.28	-.51**	.51	.00	.00
	(15) Terminal bud scale type	.56**	.69*	.00	.00	.00	.00	.00
	(16) Number of lateral buds	--	--	--	-.48**	-.31	-.12	-.27
	(22) 2-year height	.65***	.63	.08	-.63***	-.62	-.19	-.33
Day length at start of growing season	(7) Foliage color, October, 1961	.54**	.80**	-.14	.00	.00	.00	.00
	(8) Stem color, June, 1961	.35	.10	.47	-.67***	.11	-.38	-.65
	(10) Needle length	.04	.61	-.16	-.51**	.36	-.35	-.54
	(12) Basal needle mortality	.00	.00	.00	-.51**	-.67*	-.77***	-.54
	(13) Winter injury	-.65***	-.89***	-.25	-.60***	.48	.00	.00
	(15) Terminal bud scale type	.58**	.73*	.00	.00	.00	.00	.00
	(16) Number of lateral buds	--	--	--	-.46**	-.33	-.17	-.34
	(17) Growth initiation	.47*	-.62	-.02	-.36*	-.06	-.34	.66
	(22) 2-year height	.10	.64	.01	-.72***	-.62	-.32	-.46
Annual precipitation	(7) Foliage color, October, 1961	-.49**	-.71*	.02	.00	.00	.00	.00
	(13) Winter injury	.62***	.93***	.06	.46**	.78*	.00	.00
	(14) First year terminal buds	-.55**	-.62	.58*	-.26	-.52	-.11	.60
	(15) Terminal bud scale type	-.52**	-.67*	.00	.00	.00	.00	.00
	(17) Growth initiation	.63***	.89**	.49	.19	.27	-.19	-.16
Number of progenies in analysis		27	9	16	33	9	16	8
Value of r significant at 5 percent level	(= *)	.38	.67	.50	.35	.67	.50	.71
Value of r significant at 1 percent level	(= **)	.48	.80	.62	.44	.80	.62	.83
Value of r significant at 0.1 percent level	(= ***)	.59	.90	.74	.55	.90	.74	.92

were different from the other Pacific Northwest sources in several characters. If these two progenies were excluded from the analysis most of the correlations would be non-significant.

Correlations involving average April-June temperature.--When all Pacific Coast sources were considered, an increase in spring temperature at the place of origin was accompanied by an increase in the amount of winter injury among the progenies in the nursery. Also, with higher spring temperatures there were fewer trees with exserted scales on the terminal buds and the foliage was lighter green.

When all Interior sources were considered, an increase in spring temperature at place of origin was accompanied by increased basal needle mortality, number of lateral buds, and 2-year height of the progenies in the nursery. In addition, progenies from localities with low spring temperatures had bright green stems in June whereas those from warm localities had gray stems.

In general, most of the significant correlations involving spring temperature were a result of discontinuous variation. Few of the within-ecotype correlations were significant, none were strong.

Correlations involving average January temperature.--When all Pacific Coast sources were considered, an increase in January temperature at the place of origin was accompanied by an increase in amount of winter injury in Michigan and a decrease in percent of trees forming terminal buds during the first growing season. These relationships also held true for the progenies from the Pacific Northwest. The relationship between January temperature and winter injury holds true for the progenies from California.

When all Interior sources were considered, an increase in January temperature at the place of origin was accompanied by increases in needle length, amount of winter injury, number of lateral buds, 1-year height, and 2-year height. Also, seedlings from areas having low January temperatures had green stems in June and started growth early whereas those from areas having higher January temperatures have gray stems in June and started growth later in the nursery. In the Interior region January temperature accounted for much more variation in seedling characters than did July temperature.

When the ecotypes within the Interior region were considered separately, the only relationship with January temperature that held true was the one involving growth initiation.

Correlations involving average July temperature.--When all Pacific Coast sources were considered, an increase in July temperature was accompanied by increased 1-year height and winter injury. There was also a tendency for those progenies that came from localities with low July temperatures to have darker green foliage in November and to form exserted bud scales. July temperature accounted for only about 25 percent of the variation in these characters.

When all Interior sources were considered, an increase in July temperature was accompanied by an increase in percent of trees forming terminal buds the first year.

When the ecotypes were considered individually, a single strong correlation was evident. In the Southern Interior ecotype as the July temperature rose the 1-year height of the progeny increased. The coefficient of determination ($= r^2$) is .49 in this case, indicating that 49 percent of the variation in 1-year height was accounted for by variation in July temperature.

Correlations involving the difference between average July and average January temperatures.--When all Pacific Coast sources were considered, an increase in annual temperature range at the place of origin was accompanied by a decrease in winter injury and an increase in the percent of trees that formed terminal buds the first year. Progenies from localities with a small temperature range had light green foliage in November whereas those from localities with a large temperature range had dark green foliage. In addition, progenies from areas with a small temperature range had little tendency to form exserted scales on the terminal buds. These relationships were strong.

If only the Pacific Northwest sources were considered, the temperature range-seedling character correlations were significant and very strong for amount of winter injury ($r^2 = 0.78$) and date of growth initiation ($r^2 = 0.70$) but not for other seedling characters.

When all Interior sources were considered, an increase in annual temperature range was accompanied by decreases in needle length, winter injury, 1-year height, and 2-year height. In addition, progenies from localities with a small temperature range had gray stems in June and started growth late whereas those from localities with a large temperature range had bright green stems and started growth early. The relationship between annual temperature range and needle length was reversed if only the Northern Interior sources were considered.

Correlations involving length of growing season.—If all Pacific Coast sources were considered, an increase in length of growing season at the place of origin was accompanied by an increase in winter injury. There was also a tendency for those progenies from localities having short growing seasons to have dark green foliage in November and exserted scales on the terminal buds.

All of these relationships held true when the Pacific Northwest sources were considered separately. None of them held true when only the California sources were considered. The relationships were considerably stronger in the Pacific Northwest than they were over the region as a whole.

When all Interior sources were considered, an increase in length of growing season was accompanied by increases in winter injury, 2-year height, needle length, basal needle mortality, and number of lateral buds. Also, seedlings from areas that have short growing seasons had bright green stems whereas those from areas with long growing seasons had gray stems.

The relationship with basal needle mortality holds true in the Southern Interior ecotype. Other ecotypic correlations involving length of growing season were not significant.

Correlations involving date of growing season initiation.--When all Pacific Coast sources were considered, those progenies from localities where the growing season starts early tend to have light green foliage in November, teminal buds with appressed scales, and heavy winter injury. The seedlings from areas where the growing season starts early were taller at the end of the second year in spite of being killed back severely during the first winter.

All relationships except that with 2-year height were significant if only the Pacific Northwest progenies were considered. None were significant if only the California sources were considered.

When all Interior sources were considered, the progenies from areas with a long growing season tended to have gray foliage in November of the second year, more winter injury, greater 2-year heights, and more lateral buds.

Correlations involving day length at start of growing season.--When all the Pacific Coast sources were considered, short day length at start of growing season was accompanied by slight winter injury, light green foliage in November, and a slight tendency to form exserted scales on the terminal buds. All of these relationships held true if only the Pacific Northwest sources were considered but none held true if only the California sources were considered.

When all Interior sources were considered, an increase in day length at the start of growing season was accompanied by decreases in needle length, basal needle mortality, and number of lateral buds. In addition, progenies from localities with short days at the beginning of the growing season had gray stems in June whereas those from localities with long days at the beginning of the growing season had bright green stems.

The relationship with basal needle mortality held true in the Southern Interior ecotype. Other ecotype correlations involving day length at start of growing season were not significant.

Correlations involving annual precipitation.--When all Pacific Coast sources were considered, progenies from areas with high annual precipitation suffered most winter injury, started growth latest, had light green foliage, and had a high percent of trees forming terminal buds the first year.

The relationship involving first-year terminal buds was the only one which was not significant if only the Pacific Northwest sources were considered and was the only one which was significant if only the California sources were considered.

Annual precipitation was associated only with amount of winter injury within the Rocky Mountain variety.

2. Climatic Factor-Seed Weight Correlations

The seed weight-climate correlations are presented in table 15. There were higher correlations between seed weight and climate at the place of origin than between seedling characters and climate at the place of origin. Forty-one percent of all possible seed weight-climate correlations were significant at the 5 percent level whereas only 15 percent of the seedling character-climate correlations were significant. This is probably due to the fact that seed weight is a parental character and is subject to phenotypic modification by the climate at the place of origin.

In the Interior region and the Southern Interior ecotype seed weight was significantly and strongly correlated with several climatic factors. Seeds from areas with warm climates, long growing seasons, or low precipitation were largest. In the Pacific Northwest ecotype seeds from areas with low precipitation were also the largest but the relationships with growing season and temperature factors were reversed. The largest seeds came from areas with cold climates and short growing seasons. The relationship between seed weight and annual precipitation, however, is positive in both the Pacific Northwest and the Southwest. This indicates the presence of a direct cause-and-effect relationship. It lends support to the observation first reported by Toumey (1916) that conifers from low spring rainfall areas tend to have large seed. One would logically expect natural selection to have favored the development of large-seeded types in low-rainfall areas. Seeds germinating in moisture-deficient soil would benefit from large food reserves and the ability of the roots to penetrate the soil rapidly.

The seed weight-winter temperature and seed weight-length of growing season correlations were reversed between the Pacific Northwest and the Interior. This in itself is indicative that there was no direct

Table 15. Correlation between seed weight and climatic factors at places of origin for regions and ecotypes.

Correlation between seed weight and:	Region or ecotype to which correlation applies						
	Pacific Coast region			Interior region			
	Entire region	Pacific Northwest	California	Entire region	Southern Interior	Central Interior	Northern Interior
Average spring temperature	-.02	-.66	.18	.69***	.85***	-.03	.72*
Average January temperature	-.22	-.91	.02	.55	.87	.11	.26
Average July temperature	.05	-.43	.22	.62***	.75*	.32	.75*
Annual temperature range	.41*	.78*	.42	-.04	.10	.26	.80*
Length of growing season	-.16	-.86**	.07	.77	.93***	.40	.65
Date of growing season initiation	.17	.82**	-.17	.76***	-.93***	-.41	-.59
Day length at start of growing season	.17	.85**	-.15	-.66***	-.92***	-.27	-.55
Annual precipitation	-.26	-.86**	-.21	.05	-.82**	.12	.51
Number of progenies in analysis	27	9	16	33	9	16	8
Value of r significant at 5 percent level	.38	.67	.50	.35	.67	.50	.71
Value of r significant at 1 percent level	.48	.80	.62	.44	.80	.62	.83
Value of r significant at 0.1 percent level	.59	.90	.74	.55	.90	.74	.92

* Significant at 5 percent level

** Significant at 1 percent level

*** Significant at 0.1 percent level.

cause-and-effect relationship between seed weight and either climatic factor. Instead, it is more logical to assume that the relationships are indirect through precipitation. In the Pacific Northwest the high winter and spring temperatures occur near the coast where the precipitation is higher than it is inland. In the Interior region the higher temperatures occur at low elevations where the precipitation is less than it is at higher elevations.

3. Correlation Among Progeny Traits

All possible simple correlations were calculated among seed weight and the 13 progeny characters. Stand-progeny means were used as items and the analysis was repeated for each of the seven regions and ecotypes. All correlation coefficients that were significant in at least one region or ecotype are presented in table 16. A total of 98 were significant at the 5, 1, or 0.1 percent levels.

Forty-six percent of the correlations among progeny traits were significant when calculated with data from an entire region. The same correlations were evident only 18 percent of the time when calculated with data from separate ecotypes. Thus, many of the correlations were among ecotype means rather than among stand means. This indicates a discontinuous variation pattern.

Those correlations which are of value in predicting the most important economic characters (winter injury and height) are discussed below.

Within the Interior variety and within the California ecotype seed weight was correlated with 1-year height at the 10 percent level and with 2-year height at the 1 percent level of significance. There are three reasons for suspecting that these were not direct cause-and-effect

Table 16. Correlations among progeny traits (including seed weight) in ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws.).

Characters to which correlation applies		Pacific Coast Region			Interior Region			
		Entire region	Pacific Northwest	California	Entire region	Southern-Interior	Central-Interior	Northern-Interior
(1) Seed weight	(5) Foliage color Aug., 1960	.11	.19	-.15	.49**	.60	.33	.87**
	(6) Foliage color Oct., 1960	-.15	.06	-.38	-.47**	-.17	-.43	-.31
	(12) Basal needle mortality	.00	.00	.00	.55***	.68***	.68*	.65
	(13) Winter injury	-.15	-.92***	.33	.37*	-.71*	-.23	.00
	(14) First year terminal buds	.27	.36	.75***	.50**	.72*	.32	.31
	(15) Terminal bud scale type	.24	.00	.83***	.00	.00	.00	.00
	(16) Number of lateral buds	--	--	--	.47**	.37	-.14	.34
	(17) Growth initiation	-.24	-.33	-.66**	-.16	-.11	-.39	-.74*
	(22) 2-year height	.27	.54	.22	.44**	.55	-.32	.23
	(21) 1-year height	.28	-.11	.47	.30	.20	.02	.15
(5) Foliage color Aug., 1960	(6) Foliage color Oct., 1960	.09	-.24	.27	-.48**	-.11	-.49	-.22
	(17) Growth initiation	.05	.31	.11	-.40*	-.01	.13	-.88**
(6) Foliage color Oct., 1960	(10) Needle length	-.39*	-.70*	-.16	.29	-.20	.67***	-.69
	(14) First year terminal buds	.18	.15	-.33	-.48**	.02	-.44	-.42
	(17) Growth initiation	-.21	-.26	.33	.52**	.62	.48	.42
(7) Foliage color Oct., 1961	(14) First year terminal buds	.62***	.45	-.10	.00	.00	.00	.00
	(15) Terminal bud scale type	.83***	.66	.00	.00	.00	.00	.00
	(17) Growth initiation	-.76***	-.83**	.03	.00	.00	.00	.00
	(18) Lammas growth	-.45*	-.21	.05	.00	.00	.00	.00
	(13) Winter injury	-.85***	-.82**	.09	.00	.00	.00	.00
(8) Stem color June, 1961	(10) Needle length	-.06	.35	.10	.80***	.68*	.53*	.66
	(13) Winter injury	-.12	-.07	-.19	.87***	.66	.33	.00
	(16) Number of lateral buds	--	--	--		.08	.16	.86**
	(17) Growth initiation	-.17	-.57	-.31	.66***	.35	.63**	.45
	(21) 1-year height	.10	.19	.38	.59***	-.14	.02	.07
	(22) 2-year height	.15	.22	.17	.81***	.10	.47	.86**
(10) Needle length	(13) Winter injury	-.03	.42	-.14	.70***	.33	.43	.00
	(14) First year terminal buds	.22	-.33	.38	-.42*	.05	-.67**	.12
	(16) Number of lateral buds	--	--	--	.45**	-.43	.57*	.72*
	(17) Growth initiation	-.14	.33	-.46	.80***	-.15	.88***	-.38
	(21) 1-year height	.23	.50	.04	.53**	-.04	.54*	-.41
	(22) 2-year height	.42	.74	.31	.80***	.15	.92***	.63
(12) Basal needle mortality	(14) First year terminal buds	.00	.00	.00	.46**	.71*	.56*	.58
(13) Winter injury	(14) First year terminal buds	-.77***	-.20	-.70**	-.21	-.32	-.24	.00
	(15) Terminal bud scale type	-.89***	.00	-.79***	.00	.00	.00	.00
	(16) Number of lateral buds	--	--	--	.45**	-.04	.27	.00
	(17) Growth initiation	.83***	.32	.85***	.55***	.50	.39	.00
	(21) 1-year height	.57**	.78*	-.07	.67***	-.27	.22	.00
	(22) 2-year height	.07	-.71*	.29	.74***	-.49	.28	.00
(14) Trees forming terminal buds at age 1	(15) Terminal bud scale type	.75***	.00	.70**	.00	.00	.00	.00
	(16) Number of lateral buds	--	--	--	.04	.33	-.63**	.16
	(17) Growth initiation	-.79***	-.95***	-.51*	-.64***	-.18	-.76***	-.55
(15) Terminal bud scale type	(17) Growth initiation	-.71***	.00	-.60*	.00	.00	.00	.00
	(18) Lammas growth	-.56**	.00	-.52*	.00	.00	.00	.00
	(22) 2-year height	-.03	.68*	.00	.00	.00	.00	.00
(16) Number of lateral buds	(20) Amount of lean	--	--	--	-.54**	.00	-.49	.00
	(21) 1-year height	--	--	--	.47**	.36	.78***	.16
	(22) 2-year height	--	--	--	.65***	.30	.67**	.85**
(17) Date of growth initiation	(21) 1-year height	.26	.00	-.07	.54**	.35	.78***	-.23
	(22) 2-year height	-.14	-.63	-.06	.61***	.01	.64**	-.21
(20) Amount of lean	(21) 1-year height	.00	.00	.00	-.32	.00	-.71**	.00
	(22) 2-year height	.00	.00	.00	-.48**	.00	-.74***	.00
(21) 1-year height	(22) 2-year height	.32	.51	.15	.69***	.53	.65***	.06
Number of progenies in analysis		27	9	16	33	9	16	8
Value of r significant at 5 percent level	(= *)	.38	.67	.50	.35	.67	.50	.71
Value of r significant at 1 percent level	(= **)	.48	.80	.62	.44	.80	.62	.83
Value of r significant at 0.1 percent level	(= ***)	.59	.90	.74	.55	.90	.74	.92

relationships. First, both characters are correlated with a number of climatic factors of the parental habitat. Second, albino seedlings which depend for their entire growth on food reserves stored in the seed grew to only a small fraction of the size attained by green seedlings in one year. Third was the absence of significant seed weight-height correlations within the individual Interior ecotypes.

Other significant character-character correlations are:

1. June stem color progressed from green to gray as winter injury, 1-year height, and 2-year height increased in the Interior variety. June stem color and 2-year height were also associated in the Northern Interior ecotype.
2. Needle length increased as 1 and 2-year height increased in the Interior variety and the Central Interior ecotype.
3. Percent of trees forming terminal buds the first year increased as winter injury decreased in the Pacific Coast variety and the California ecotype.
4. Winter injury increased as 1-year height increased in the Pacific Coast and Interior varieties and in the Pacific Northwest ecotype. Winter injury increased as 2-year height increased in the Interior variety and the Pacific Northwest ecotype.
5. One and 2-year height were significantly correlated in the Interior variety and the Central Interior ecotype. The heavy winter damage suffered by the California seedlings precluded finding such a significant correlation within the Pacific Coast population.

XII. EVOLUTION OF THE ECOTYPES

Selection pressure has been a primary differentiating force responsible for the present characteristics of the ecotypes. A number of characters are obviously adaptive and the selection mechanism responsible for their evolution can be easily postulated.

Growth rate is one of these characteristics. Similar trends were evident in both the Pacific Coast and Interior varieties. In each case the southern provenances grew faster than the northern ones. This difference in growth rate is probably in part a function of yearly duration of growth. In California and the Southwest conditions are favorable for a longer annual period of growth than farther north. In southern areas individuals which could take advantage of the long growing season would have an advantage over slower growing individuals in the competition for light and moisture. Succeeding generations would have an increasingly higher proportion of the progeny of these fast growing types. In northern areas, if fast growth rate is a function of duration of growth, the faster growing individuals would not harden off before the onset of cold weather. They would be eliminated from the population and the gene frequency for fast growth would be reduced.

Other processes which affect growth, such as rate of cell enlargement and rate of cell division, may also respond to selection pressures of the environment in a similar manner.

Resistance to cold is another character with obvious selective advantage. Again, both varieties show similar trends. The progenies from California, where winter temperatures are mild, were much more

heavily damaged than the progenies from the Pacific Northwest where lower winter temperatures prevail. Among the Rocky Mountains progenies the only evidence of winter injury was among the progenies from Arizona and New Mexico. The selection mechanism is probably quite straightforward. Cold susceptible genotypes are quickly eliminated by low minimum temperatures and cold resistant ones remain. In succeeding generations the frequency of genes for cold susceptibility would decrease rapidly.

The lack of first-year terminal buds was characteristic of the California progenies. These buds are not necessary for survival in the mild winters of California. Farther north, where lower winter temperatures prevail, seedlings that form terminal buds the first year have an advantage over those that do not. After a period of several generations a northern population would be composed mainly of cold resistant types. A similar north-south trend was evident in the Rocky Mountain progenies.

The differences in date of growth initiation are also attributable to selection pressure. A good illustration of this is afforded by the progenies from Central Colorado. At high elevations, where the growing season is short, seedlings with the ability to start growth when the spring temperatures are still low have a competitive advantage over seedlings that do not start growth until spring temperatures are higher. Over many generations the genes for growth initiation at high temperatures would be eliminated from the population. At lower elevations or at more southern latitudes, where the growing season lasts longer, selection pressure for growth initiation at low temperature is not as severe. These populations do not start growth until the temperature in the spring is higher. When grown in a uniform environment, such as the nursery at East Lansing, the high elevation and northern sources start growth when the spring temperatures are still quite low. The low elevation and southern sources start growth only when higher temperatures prevail.

A number of characters which are of equal importance in distinguishing the ecotypes are very difficult to explain on the basis of selection pressure. Foliage and stem color are in this category. The Pacific Northwest ecotype was most easily identified by the distinctive dark-green color of its foliage. The character was common to all sources from the Pacific Northwest which indicates that it is probably adaptive or linked to the genes controlling an important character that is adaptive. The physiological link between the selective factor of the climate and expression of the dark-green color in the foliage of the seedlings is not clear, however.

Number of needles per fascicle and needle length are other diagnostic characters which can not be explained easily on the basis of selection pressure. Some other factor, such as geographic or reproductive isolation, population size, population density, or genetic drift, must have had a part in the evolution of these characters.

The differences between the typical variety of the Pacific Coast and the Rocky Mountain variety is one case where factors other than selection pressure have determined evolution. When the climatic factors in the regions occupied by the two varieties are compared (table 3) the only climatic factor that shows a distinct break is the seasonal distribution of precipitation $\frac{(\text{Sept. - June})}{\text{annual}}$. This contrasts with the results of the correlation analysis which showed that many characteristics of the ecotype and varieties could be related to factors of the environment. Moreover, it does not seem reasonable to attribute the relatively large differences in morphology and growth behavior that distinguish the two varieties to the seasonal distribution of the precipitation. If there is a physiological link between this climatic factor and the development of these particular differences it is not apparent. It seems more likely that the large differences between the two varieties are of a more ancient origin than the differences between ecotypes within either one of the varieties. Whereas the smaller differences between ecotypes are reflected in climatic differences in the modern climate the larger differences between the two varieties stem from more ancient causes that are not reflected in relatively ephemeral weather records of the past 70 years.

The distinct differences among the central Colorado progenies is an example of the combined effects of selection pressure, population density, and reproductive isolation. MSFG-2137 is from 9000 feet elevation in the mountainous country about 100 miles southwest of Colorado Springs. MSFG-2164 is from 9000 feet elevation about 10 miles northwest of Colorado Springs. Progenies from these two sources are very similar when grown in the East Lansing nursery. MSFG-2155, which is from 7200 feet elevation about 3 miles northwest of Colorado Springs is similar to them in all characters even though the climatic conditions in which they grew are quite different. This is probably due to the fact that there is a lateral distance of only seven miles between MSFG-2155 and MSFG-2164 with continuous forest between. Gene flow between generations of trees growing in these two areas must have been considerable. This would have tended to negate the differentiating effects of differing selection pressures.

The third progeny from this area (MSFG-2145) is from a small stand in the relatively flat country northeast of Colorado Springs and is isolated from the continuous forest in the more precipitous country to the west by about 4 miles. A reproductive isolation barrier is indicated by the fact that the growing season starts about two and one-half weeks earlier in the parent vicinity of MSFG-2145 than it does in the parent vicinity of MSFG-2155. Presumably, these geographic and reproductive isolation barriers have allowed this population to differentiate genetically in response to the selection forces in its particular environment without being swamped by gene flow from neighboring stands.

The break in northeastern California between the California and Pacific Northwest ecotypes seems to be due to the combined effects of selection pressure and reproductive isolation. Pronounced differences between MSFG-2045 and the other California progenies indicate that the boundary between the California and Pacific Northwest ecotypes is quite pronounced. The break in seedling characters across the crest of the Sierra Nevada in northeastern California corresponds to a sharp break in January temperature. None of the other climatic factors in table 3 show such a degree of discontinuity. Apparently, low temperatures have been a strong selection force in the evolution of the two ecotypes. The available distribution data, however, indicate that the distribution of the species is continuous in this area. In order for the pronounced discontinuity between the two ecotypes to develop, an isolation barrier of some sort would have had to be present. The climatic data indicate that this barrier is reproductive in nature. The growing season starts approximately three weeks later in the vicinity of MSFG-2045 than it does in the parent vicinities of the other northern California progenies. This indicates a difference in flowering times which would effectively isolate the two ecotypes.

In the Pacific Northwest the effects of geographic isolation and selection pressure are evident in the progenies from the Willamette Valley.

These progenies differ genetically from the other Pacific Northwest progenies in a number of characters. They are located in a cool, moist environment and are isolated from the main body of the range by the Cascade Mountains. Consequently, gene migration from the inland pine is negligible and the selection pressures of the coastal environment have produced a genetically distinct race. There is some evidence that genetic drift has also had an effect on these small, isolated, Willamette Valley populations. Although the two progenies represented in this study are located close together in an area of similar environment, they differ genetically in a number of characters.

The effects of selection pressure and geographic isolation are also evident in the break between the Southern and Central Interior ecotypes and in central Utah. The selective force which caused differentiation between the Southern Interior and Central Interior ecotypes is probably minimum temperature. There are two lines of evidence to support this hypothesis. First, in the Interior region there are seven significant correlations between January temperature and progeny traits. This was more than with any other climatic factor (table 14). Second, there is a temperature break across the dividing line between the Southern Interior and Central Interior ecotypes. The average minimum temperature in the area occupied by the Southern Interior ecotype ranges from 0 to -10°F. In northern New Mexico and in Colorado the minimum temperatures are generally lower (Atlas of American Agriculture, 1936). The extensive lowland area between the Mogollon and central Colorado plateaus has apparently restricted gene flow enough to permit genetic differentiation of the two ecotypes.

In Utah, the point where the progenies begin to show some affinities to those from the Northern Interior ecotype corresponds to a break in average minimum temperature. Southeastern and central Utah have minimum temperatures from -5° F. to -10° F. Northeastern Utah has lower minimum temperatures that approach those found in the Northern Interior ecotype. Thus, the selective effect of minimum temperature is again indicated. The isolation which has allowed these populations to differentiate in response to this selection pressure is geographic. The ponderosa pine in central Utah occurs in scattered stands which are separated by areas of low elevation.

XIII. PRACTICAL APPLICATIONS

The practical applications of the present data are limited by their 2-year duration and the fact that the test was confined to one nursery. The outplantings in Michigan, Nebraska, and Idaho will give some information on genotype-environment interaction. The Idaho planting was established at Moscow in the spring of 1962 and includes 34 origins. The 50 origins sent to Lincoln, Nebraska will be transplanted for a year and established in a test plantation in 1963. The 4 Michigan plantings were established in Kalamazoo, Cass, Roscommon, and Allegan Counties. Those in Kalamazoo and Cass Counties contain all 60 seed sources and are replicated 8 times. Six-tree plots were used. Growth of older, planted ponderosa pine of unknown seed source near each of these 2 plantings indicate that they will develop well. The plantings in Roscommon and Allegan Counties contain 47 and 40 origins respectively, and are replicated 2 times. There is an abundance of sweetfern in these areas and heavy mortality from Cronartium comptoniae is expected. If there is any rust resistance associated with seed source in ponderosa pine these 2 plantings should reveal it.

Further studies will be necessary to determine more precisely the particular provenances which sould be planted on particular sites. These future tests should not be started until the present outplantings have developed further. In about 10 years it will be possible to eliminate some ecotypes from consideration and confine the work to the most promising ones. In all probability, California and central Colorado can now be eliminated from consideration as seed collection areas for stock to be planted in Michigan.

The rapid early growth rate and the low first-year winter injury of the Arizona-New Mexico provenances make them particularly interesting as potential sources of seed for planting in southern Michigan. Future collections should not be confined to this single area, however, even if 10 to 15 year results indicate they are still best. Weidman's 1939 test showed that seed from the Coconino National Forest in Arizona grew very well in the Pacific Northwest for 10 years only to fall behind at the end of 20 years.

The data comparing the within-stand and between-stand variability shows very definitely that single-tree selection for height growth should be deferred until the best stands are located. Selection of stands within the one or two most promising ecotypes can probably be undertaken in about 10 years.

For the present it would be profitable to establish small mixed plantings of ponderosa pine and other exotic and native species using seed collected from each of the three Interior ecotypes. These plantings would provide a test of the various species as well as of the Interior ecotypes. In addition, if the ponderosa pine grew satisfactorily and was well represented in the final stand it could be used as a seed production area.

The present outplantings will serve as breeding orchards. Both intraspecific and interspecific crosses will be of interest. For example, if the Arizona-New Mexico progenies are not sufficiently cold resistant for use in Michigan it will be possible to produce hybrids between the southwestern progenies and progenies from the Northern Interior ecotype that may combine the fast growth rate of one with the cold resistance of the other. Interspecific hybrids between the cold resistant ecotypes of ponderosa pine and a fast growing, cold susceptible species such as Montezuma pine might prove to be useful in the Lake States or the northeastern United States.

XIV. 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. The latter analyses were made between seedling characters and 10 climatic factors at the place of origin, and among seedling characters. Most of the statistical work was done on 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, multicharacter 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 correlation analyses indicated that many of the seedling characters were significantly associated with factors of the climate. This indicates that selection pressure has been the primary differentiating force responsible for the present characteristics of the ecotypes. Minimum winter temperature, especially, was significantly correlated with factors of the climate.

The isolation barriers which allowed the ecotypes to differentiate genetically in response to different selection pressures were geographic for the most part. The crest of the Sierra Nevada separates the California and Pacific Northwest ecotypes in northeastern California. The Cascade Mountains isolates the Willamette Valley populations from the more extensive inland populations of the Pacific Northwest. The extensive treeless area between the Mogollon Plateau in southern New Mexico and Arizona, and the Colorado

Plateaus to the north, separates the Southern Interior and Central Interior ecotypes. The combined effects of selection pressure due to minimum winter temperature and geographic isolation was postulated to be responsible for genetic differentiation among the Utah progenies. The combined effects of selection pressure, population density, and reproductive isolation appear to be responsible for differences among progenies from near Colorado Springs, Colorado.

The differences in seedling characters within a variety were often associated with factors of the climate. However, the larger differences between progenies from the typical variety and the progenies from the Rocky Mountain variety were not. This indicates that the two varieties arose earlier in geological time than the ecotypes. The selection forces and other factors responsible for their evolution are not reflected in modern weather records.

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 the 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.

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