GEOGRAPHIC VARIATION AND EVOLUTIONARY TRENDS OF PONDEROSA PINE, LIMBER-BORDER PINE AND DOUGLAS-FIR, BASED ON NURSERY PERFORMANCE IN SOUTHERN MICHIGAN

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ABSTRACT

GEOGRAPHIC VARIATION AND EVOLUTIONARY TRENDS OF PONDEROSA PINE, LIMBER-BORDER PINE AND DOUGLAS-FIR BASED ON NURSERY PERFORMANCE IN SOUTHERN MICHIGAN

By

Fan Hao Kung

Ponderosa pine (Pinus ponderosa Laws), limber-border pine (Pinus flexilis James and Pinus strobiformis Engelmann, respectively) and Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) are three of the most widely distributed species in the western United States. They also have approximately the same range of distribution. The purpose of this study was to examine geographic variation in the three species, find similar and dissimilar evolutionary trends in them, and determine the factors responsible for evolution.

Seed had previously been collected over the entire natural range of each species and seedlings had been grown in the nursery at Michigan State University, East Lansing, Michigan. Modified randomized complete block design were used. Permanent test plantations were established between 1962 and 1965 in southwestern Michigan. Growth data collected in the nursery and some plantations were used in conjunction with previously collected data to show geographic variation patterns. Analysis of variance and the summation of differences technique were the principal statistical tools used.

Coastal and interior seedlings of Douglas-fir can be distinguished by degree of winter injury, height, needle length and date at which buds set or start growth. Coastal and interior seedlings of ponderosa pine can be distinguished by the same traits and foliage color.

Coastal seedlings were usually more susceptible to winter injury, faster growing, greener, and formed buds and started growth later. Within the interior region comparisons among all three species are possible, seedlings from northern Utah and northern Colorado were slow growing and winter hardy, had short and light green needles, set buds early and started growth early. In other regions where comparisons were possible, trends differed among species. Because of differences in range coverage, some clearly visible trends in one species could not be studied in the others.

Each species is composed of more or less distinct ecotypes although the degree of distinctness varies among species and among regions. Especially in the Rocky Mountain region where strong selection pressures and isolation induced much differentiation. The limber-border pine complex can be separated into two populations so distinct as to have been recognized as separate species -- limber pine from Alberta to Colorado may be regarded as _P. flexilis_ and border pine from Arizona and New Mexico as _P. strobiformis_. In ponderosa pine northern interior, central Rocky Mountain, and southern Rocky Mountain ecotypes were recognized. In Douglas-fir, there are seven interior ecotypes: 1) northern interior, 2) northern Continental Divide, 3) Bitteroot Range, 4) Okanogan Highland, 5) northern Utah-Colorado, 6) southern Utah-Colorado, and northern Arizona-New Mexico, and 7) southern Arizona-New Mexico. Within the coastal region, ponderosa pine could be separated on the present data into California and Columbia Plateau ecotypes, Douglas-fir into western Oregon-Washington, and eastern Cascades ecotypes.

Boundaries among ecotypes usually agree with treeless areas, dividing lines between climatic zones or boundaries between distinct elevational zones. The treeless areas along the eastern slopes of the Cascade and Sierra Nevada Mountains, along the Snake River valley in Idaho and the grassland in the Wyoming Basin, and along the Little Colorado River in Arizona and U. S. Route 66 in New Mexico, are very effective isolation barriers to gene exchange. The first two are common boundaries for both ponderosa pine and Douglas-fir, and the last one is a common boundary for three species. The summits of the Cascade Mountain and the Continental Divide in Montana separate eastern and western slopes into different moisture regimes and may serve as boundaries between ecotypes in ponderosa pine and Douglas-fir.

Differences among seedlots within ecotypes usually exist. However, in some cases no differences were found among neighboring seedlots. The formation of these homogeneous groups of provenances may be due to the combined effects of isolation, selection pressure and duration of isolation.

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As a geneticist, I believed this study was made possible through inherited intelligence and acquired knowledge.

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TABLE OF CONTENTS

Page

1. Introduction 1
2. Description of the species -- ponderosa pine, limber-border pine, Douglas-fir. 3
3. Past works on genetic variation in Rocky Mountain species -- provanance research, Douglas-fir, ponderosa pine, limber-border pine. 11
4. Material and methods -- seed procurement, nursery procedure, outplanting procedure, measurement method, analysis. 16
5. Winter injury -- ponderosa pine, limber-border pine, Douglas fir, comparison between species. 23
6. Height -- ponderosa pine, limber-border pine, Douglas-fir, contrasts between species. 36
7. Length of secondary leaves -- ponderosa pine, limber-border pine, Douglas-fir comparison between species 49
8. Foliage color -- ponderosa pine, limber-border pine, Douglas-fir, comparison between species. 55
9. Dormancy of buds -- ponderosa pine, limber-border pine, Douglas-fir, comparison between species. 61
10. Separation of ecotypes by seedling characteristics -- key to ponderosa pine, key to limber-border pine, key to Douglas fir. 67
11. Geographic distribution of ecotypes -- ponderosa pine, Douglas-fir, limber-border pine, comparison between boundaries of species. 80
12. Problem of finding a representative seedlot. 89

Page

13. Homogeneous groups of provenances. 92

14. Summary. 95

15. Literature cited 98

16. Vita 102

LIST OF TABLES

Page

1. Rank correlation of winter injury among 2-year nursery, 4-year Russ plantation and 6-year Kellogg plantation data. . . 25
2. Characters for limber-border pine. 28
3. Height of ponderosa pine in the nursery and plantations. . . . 37
4. Intra-ecotype height correlations for three different sites or ages(a) for ponderosa pine 38
5. Relative heights of ponderosa pine ecotypes grown in southern Michigan (7 years), Oregon and Washington (30 years) and northern Idaho (45 years). 40
6. Correlation between average spring temperature at place of origin and height of ponderosa pine progeny. 41
7. Characters of Douglas-fir in a 3-year nursery study. 44
8. Needle length of ponderosa pine in present 2-year southern Michigan and 26-year northern Idaho studies. 50
9. Foliage color of ponderosa pine seedlings in southern Michigan. (Data from Wells, 1964a) 56
10. Bud dormancy in ponderosa pine. (Data from Wells, 1964a). . . 60
11. Beginning and end of bud dormancy in Douglas-fir seedlings in southern Michigan. 64
12. Variance component for characters of ponderosa pine. 68
13. Variance components for characters of limber-border pine . . . 69
14. Variance components for characters of Douglas-fir. 70
15. Degree of similarity between progenies from the Pacific Coast variety (<u>Pinus ponderosa</u> var. <u>ponderosa</u>) of ponderosa pine. (Table from Wells, 1964a). 71

Page

16. Degree of similarity between progenies from the Interior variety (*Pinus ponderosa* var. *scopulorum*) of ponderosa pine. (Table from Wells, 1964a). 72

17. Degree of similarity between stand-progenies from limber pine (*Pinus flexilis*). (Table from Steinhoff, 1964) 73

18. Degree of similarity between stand-progenies from border pine (*Pinus strobiformis*) and two limber pine (*Pinus flexilis*) stand-progenies. (Table from Steinhoff 1964). 74

19. Degree of similarity between stand-progenies from the coast variety (*Pseudotsuga menziesii* var. *menziesii*) of Douglas-fir. 75

20. Degree of similarity between atand-progenies from the interior variety (*Pseudotsuga menziesii* var. *glauca*) of Douglas-fir . . 76

21. Seedlot number of the collection showing high similarity to the largest number of other seedlots from each area of three species. 90

22. Seedlot number of the collection showing the most common characteristics from each area of three species. 91

LIST OF FIGURES

Page

1. Distribution of the Pacific Coast variety (Pinus ponderosa var. ponderosa) and the interior variety (Pinus ponderosa var. scopulorum) of ponderosa pine in the United States and British Columbia, showing the location of the stand collections used in this study. (Range map prepared by O. O. Wells, 1964a, from data supplied by E. L. Little Jr. of the U. S. Forest Service) 5
2. Distribution of limber pine (Pinus flexilis) and border pine (Pinus strobiformis) in North America. (Range map prepared by R. J. Steinhoff, 1964, from data supplied by E. L. Little, Jr. of the U. S. Forest Service). 7
3. Distribution of Douglas-fir in the western United States. (Range map by E. L. Little, Jr., U. S. Forest Service). 10
4. Ecotypic division of 60 stand-progenies of ponderosa pine grown for 2 years in East Lansing, Michigan. A=California, B=North Plateau, C=Southern Interior, D=Central Interior, E=Northern Interior. The dashed lines within the Central Interior ecotype indicate divisions that are less well-defined than the primary ecotypic division. Two seedlots MSFG 2091 and 2071 may be considered as Willamette Valley ecotype but they show close resemblance to some California seedlots. (Map by Wells, 1964a) . 81
5. Ecotypic division of 62 stand-progenies of limber-border pine grown for 2 years in East Lansing, Michigan. (Map by Steinhoff, 1964) 82

Page

6. Ecotypic division of 128 stand-progenies of Douglas-fir grown for 2 years in East Lansing, Michigan. A=Coastal Pacific Northwest, B=E. Cascade, C=Okanogan Highland, D=Bitteroot Range, E=N. Continental Divide, F=Northern Interior G=N. Colorado-Utah, H=S. Colorado-Utah & N. Arizona- New Mexico, I=S. Arizona-New Mexico. Seedlot numbers from 001 through 150 on this map represent MSFG number 1501 through 1650 respectively. Seedlot numbers from 221 through 273 represent PA number 21 through 73 respectively. 83

INTRODUCTION

Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), ponderosa pine (Pinus ponderosa Dougl. ex Loud.) and the limber-border pine complex (Pinus flexilis James and P. strobiformis Engelm.) are three of the most widely distributed trees of western United States. Many environmental adaptive trends undoubtedly are similar in all three species. For instance, the changing of day length from north to south; the decrease of temperature from lower to higher altitudes; and differences in amount and seasonality of precipitation over the range probably cause similar selection pressures to act similarly upon all three species. Then the interesting question is, "What forms of convergent evolution can be seen among them?"

On the other hand, although they all require space, sunlight, water, inorganic nutrients and air, each species has its unique ecological "niche" which accommodates it to the presence of the other species in its area. With a minor alteration of its niche, how would a subpopulation equip itself to fully exploit the niche? Or, what is the adaptive radiation within the species?

Sewall Wright (1931) defined evolution "as a process of cumulative change that depends on a proper balance of the conditions, which at each level of organization--gene, chromosome, cell, individual, local race--make for genetic heterogeneity or genetic homogeneity of the species." If we concentrate on the level of local race, what type and rate of evolution can we expect to see in these three species? What degree of genetic homogeneity or genetic heterogeneity can be seen in each species? What are the major causes of the genetic homogeneity and genetic heterogeneity observed?

Selection and isolation together may spell speciation. Widespread species are more likely to be differentiated into ecotypes than are ones with a limited range. Thus, for a wide-ranging taxon to occupy a range with variable environments and variable arrays of other species requires various directions of adaptive adjustment. Presumably the taxon's basic niche or strategy for coping with its physical and biological environment remain similar though the precise tactics may shift drastically from place to place. Genetic variation is related to habitat differences and to barriers which prevent free gene interchange. Are the isolation mechanisms the same and do they result in the same number of recognizable ecotypes in these three species?

This study was made to obtain insight into these problems. Materials used were a series of experiments on geographic variation on forest trees carried out at Michigan State University. Studies of the ponderosa and limber pine experiments were previously made by Osborn Wells (1964a, 1964b) and Raphael Steinhoff (1964) respectively. Their data, as well as my own, will be used to make comparison with the Douglas-fir study. Unless specified, the common name of ponderosa pine includes both varieties of *Pinus ponderosa* (var. *ponderosa* and *scopulorum*); limber pine includes *Pinus flexilis* and *Pinus strobiformis*; and Douglas-fir includes *Pseudotsuga menziesii*. var. *menziesii* and var. *glauca*.

DESCRIPTION OF THE SPECIES

The following information is abstracted from Silvics of Forest Trees of the United States (U. S. Forest Service 1966), Woody Plant Seed Manual (U. S. Forest Service 1948), and Rocky Mountain Trees (Preston 1947) to give a general description of the species.

Ponderosa Pine

It was so named because of its huge size. Mature trees grow 150 to 230 feet tall with massive stems 5 to 8 feet in diameter. The bark is dark brown to nearly black and deeply furrowed on young trees, yellow brown to bright cinnamon-red and scaly on old trunks. Leaves are in 3's or 2's and 3's, dark yellow-green, 5 to 11 inches long. Male flowers are yellow, female dark red. Cones are elliptical, borne at right angles to the twig, sessile, and 3 to 6 inches long. Seeds are ovoid, acute, ½ inch long with 1 inch wing.

Ponderosa pine is found generally in subhumid regions with a range in precipitation from 10 to 21 inches. The summers are usually dry. Average annual temperatures in its distribution area are between 42^{0} and 50^{0} F. Annual extremes are from -40^{0} to 110^{0} F. This tree has a wide range of edaphic tolerance. It grows on soils ranging from gravel to clay loam and with a pH from 4.9 to 9.1. The best sites are probably well-drained deep sandy loams.

The species bear cones as early as 16 years. Most seed falls within 125 feet of the parent tree.

Seedlings of ponderosa pine can utilize dew at night to withstand prolonged drought. Fast growing taproots enable young seedlings to survive and become dominant on the most exposed sites.

Of the three species, ponderosa pine is most successful in resisting high surface soil temperatures, but is least resistant to fire.

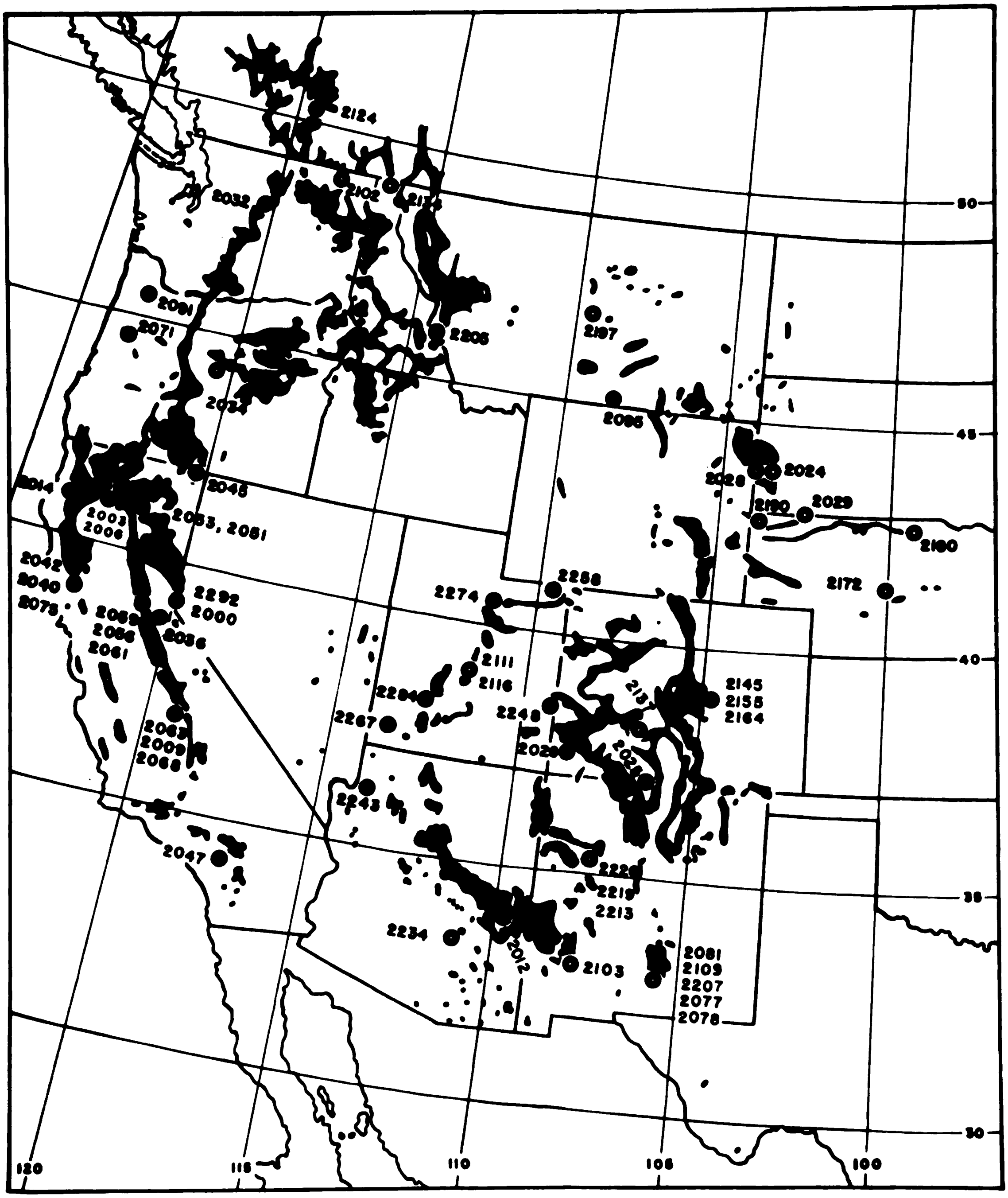
Figure 1 shows the range of ponderosa pine in the western United States. Actually, the southern limit extends to Durango, Mexico. Within the vast area, pure stands are found in the Black Hills of South Dakota, the Blue Mountains of Oregon, the Columbia Plateau; Northeastern Sierra Nevada Mountains, and in northern Arizona and New Mexico. Mixtures also occur with western Larch (*Larix occidentalis* Nutt), and Douglas-fir on the eastern slope of the Cascade Range. After cutting or an increase in soil moisture in these stands, ponderosa pine is usually succeeded by Douglas-fir. A similar succession is found in the Rocky mountains. On the western slope of the Sierra Nevadas of California ponderosa pine occurs in mixture with Douglas-fir, sugar pine (*Pinus lambertiana* Dougl.) White fir (*Abies concolor* Lind. and Gord.), Jeffrey pine (*Pinus jeffreyi* Grey. and Balf.) and incense-cedar (*Libocedrus decurrens* Torr.)

The altitudinal distribution of ponderosa pine is also great. It occurs from near sea level in the Willamette Valley of Oregon to 6,000 feet elevation in the Cascade Range; from 1,000 to 5,000 feet in the north and from 5,000 to 7,000 feet in the southern Sierra Nevada Mountains; from 5,000 to 9,000 feet in central and southern Rocky Mountains.

Limber Pine

The flexible branches of limber pine give this tree its scientific and common names. Mature trees are usually 20 to 50 feet tall and 2 to 4 feet in diameter. Bark is thin, creamy white to greenish gray in young trees, with rectangular dark brown scaly plates in old trees. Leaves are in 5's, 1½ to 3 inches long dark green. Female flowers are scarlet. Cones are oval, horizontal, sessile, dark purple, 3 to 7

Figure 1. - Distribution of the Pacific Coast variety (*Pinus ponderosa* var. *ponderosa*) and the interior variety (*Pinus ponderosa* var. *scopulorum*) of ponderosa pine in the United States and British Columbia, showing the location of the stand collections used in this study. (Range map prepared by O. O. Wells, 1964a, from data supplied by E. L. Little Jr. of the U. S. Forest Service.)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inches long. Seeds are oval, ½ inch long, wingless, sweet and edible.

Limber pine is found generally in subhumid to semiarid regions. It can survive in very adverse environments. It thrives on dry shallow rocky soils as well as on heavy clays. Limber pine even grows on the lava found in Craters of the Moon National Monument, Idaho. Its ability to withstand cold and wind enable it to grow at higher elevations than other pines.

Seed is produced abundantly at 3 or 4 year intervals. Small amounts are borne every year. Much of it is eaten by rodents. In former years Indians collected it.

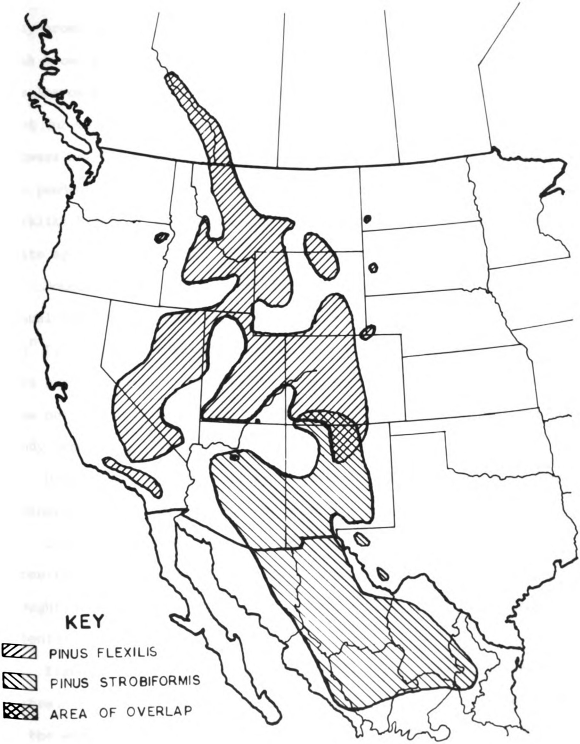
Figure 2 shows the range of limber pine in the western United States. It is found mainly in the Rocky Mountain and nearby ranges with a few isolated occurrences in North and South Dakota, southwestern California, and the Wallowa Mountains in Oregon.

Limber pine grows at much higher elevations than ponderosa pine. The altitudinal distribution is 4,000 to 10,000 feet elevation in the northern Rocky Mountains, 6,000 to 11,000 feet in Colorado, and 8,000 to 12,000 feet in the southern Rocky and Sierra Nevada Mountains.

Douglas-fir

The common name of Douglas-fir commemorates the Scotch botanist, David Douglas, who studied the tree in 1825. Its scientific name was derived from "pseudo" meaning false in Latin and "tsuga" meaning hemlock in Japanese. However, this species is only remotely related to the true hemlocks. Douglas-fir is the largest tree in the Pacific Northwest and second only to the giant sequoias in the United States. Trees in the virgin forest of the Pacific Northwest average 200 feet

Figure 2. - Distribution of limber pine (<u>Pinus</u> <u>flexilis</u>) and border pine (<u>Pinus</u> <u>strobiformis</u>) in North America. (Range map prepared by R. J. Steinhoff, 1964, from data supplied by E. L. Little, Jr. of the U. S. Forest Service.)


KEY
▨ PINUS FLEXILIS
▧ PINUS STROBIFORMIS
▩ AREA OF OVERLAP

high and 4 feet in diameter. In the drier interior it grows to 100 feet in height and 3 feet in diameter. The bark is smooth, thin, dark gray-brown on young trees, 6 to 12 inches thick and divided into reddish brown ridges separated by deep irregular fissures on old trees. Its leaves are 1 inch long dark yellow-green to bluish green, persistent for more than 8 years. Male flowers are orange red. Female flowers have slender elongated bracts deeply tinged with red. Cones are pendant, 3 to 5 inches long, ovoid-cylindric with exserted, 3-lobed forklike bracts. Seeds are light reddish brown with large irregular white spots, ½ inch long.

Douglas-fir is found generally in mild humid regions with average annual temperatures ranging from 45^{o} to 55^{o} F, with extremes of -30^{o} to 110^{o} F. Annual precipitation varies from 20 to 100 inches but the summers are usually dry. Douglas-fir grows on a variety of soil types, but does not thrive on poorly drained soils. It grows best on well drained sandy loams at pH 5 to 5.5.

Douglas-fir produces seed as early as 10 years. Seed can be disseminated by wind to a distance of about one-half mile.

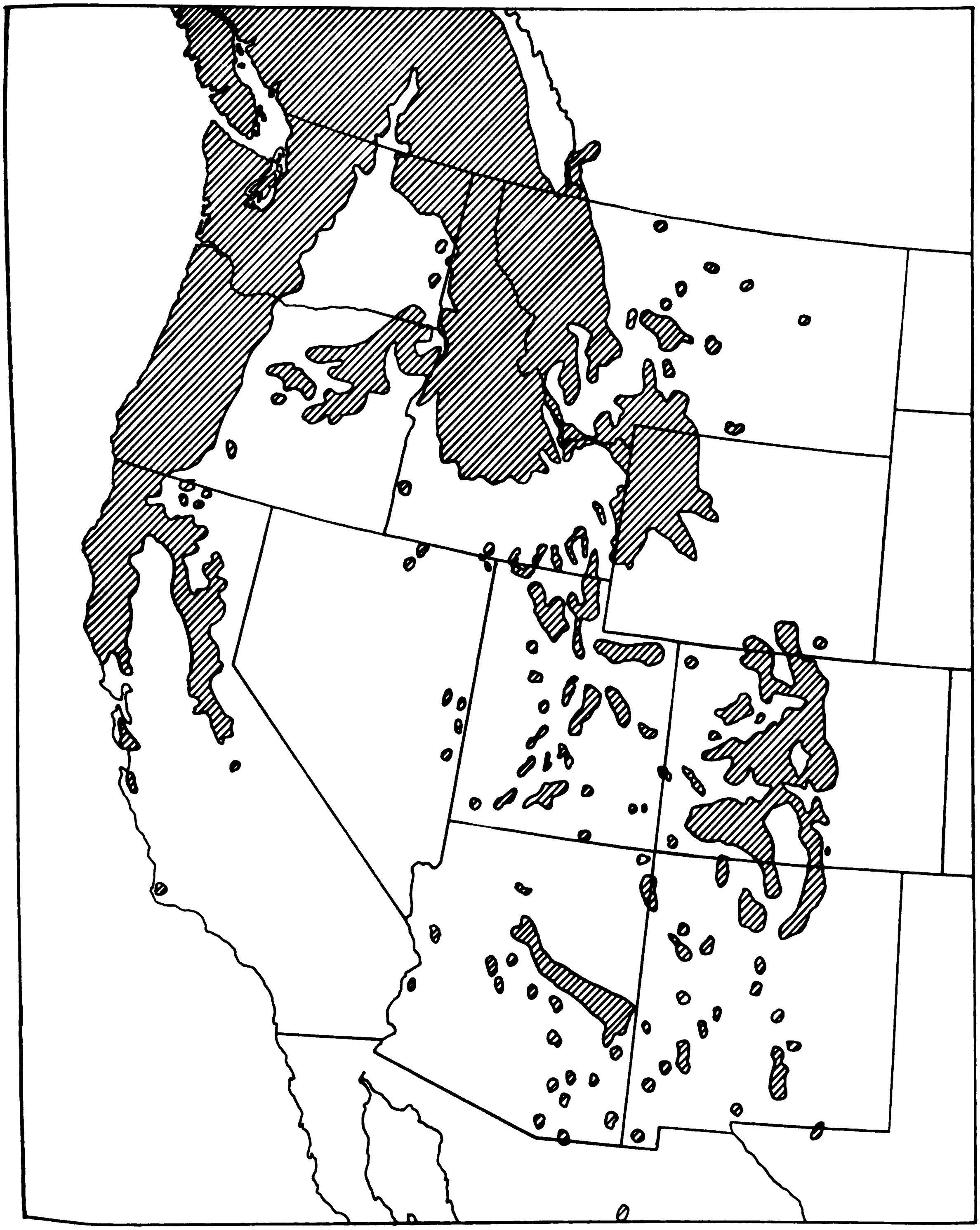
Seedling mortality is often high in the first two years. About three-fourths of the seedlings usually die of heat injury to stem, drought, competition, frost, insects, root rot and damping off, and rodents.

Figure 3 shows the range of Douglas-fir in the western United States. Pure stands of Douglas-fir are found in the Coastal Range and on the western slope of the Cascade Mountains. Mixed stands of Douglas-fir, sugar pine, ponderosa pine, incense cedar and white fir are found in the Sierra Nevada Mountains. Douglas-fir is mixed with lodgepole pine (Pinus contorta Loud.) in moist parts of the montana area of the northern and central Rocky Mountains. Fires are an important factor in the distribution of Douglas-fir in relationship with its associated species,--lodgepole pine usually monopolizes burns to the exclusion of Douglas-fir. On the other hand, fires usually help the regeneration of Douglas-fir at lower altitudes toward the northerly coastal limits of its range. Without fires to prepare seedbed, Douglas-fir would hardly regenerate naturally and would likely be succeeded by its more tolerant close competitors, namely the western hemlock (Tsuga herophylla (Rafn.) Sarg.), western red cedar (Thuja plicata D. Don.), and Sitka spruce. (Picea sitchensis (Bong.) Carr.) (Munger, 1940.)

From north to south Douglas-fir occupies progressively higher elevations as shown in the following tabulation:

Locality	Elevation, feet
Coastal Range	0-6,000
Cascade Mountain	0-6,000
Sierra Nevada	3,000-6,000
Idaho, Montana, Nevada, Northern Wyoming	2,400-9,000
Southern Wyoming, Colorado, Utah, Nevada	6,000-9,000
Arizona, New Mexico	7,000-11,000

Figure 3. - Distribution of Douglas-fir in the western United States. (Range map by E. L. Little, Jr., U. S. Forest Service.)



PAST WORK ON GENETIC VARIATION IN ROCKY MOUNTAIN SPECIES

Provenance research. -- Provenance in forestry refers to the particular place where trees are growing naturally or the place of origin of seeds or trees. Thus, provenance has a biological meaning roughly equivalent to a local population. Forest geneticists, in concentrating on provenance work, have studied ecological and genetic variability.

With the blossoming field of tree improvement and the increasing number of forest geneticists, provenance studies have undergone much change during the past half century. The philosophy has changed from mere seed source trials to experimental taxonomy. The number of traits observed has increased from survival and growth to as many as 60. Recently, chemical and physiological analysis promise new insight into the morphological and growth traits which have been studied so long. Some early provenance studies included only 2 or 3 seed sources whereas many modern tests sample 50 to 100 different areas. Along with such changes there have been very great improvements in design.

The experiances of the pioneer tree breeders certainly paved the way for the present study.

Douglas-fir provenance research started in 1912 when the United States Forest Service started an experiment in northwestern Oregon and western Washington. Seeds were collected from 120 trees in 13 localities (Munger and Morris, 1936, 1942.) The parents were selected to typify various conditions as to age, site, and disease resistance. In 1913-14 the seeds were sown and two years later the seedlings were outplanted, using the same arrangement at each planting site. The progeny of each parent formed a single row. It is worthwhile recounting the principal findings.

In this early Douglas-fir study, trees from two localities (Granite Falls and Darrington, Washington) were superior in growth at all test sites. Date of bud bursting, which was measured only at the Wind River and Mount Hood test sites, was also found to be genetically controlled. Trees from localities with warm spring nights and days started growth earlier than trees from localities with warm days but cool nights in the springtime (Morris et al., 1957).

In a nursery study covering somewhat the same range of materials as covered by Munger and Morris, there was a moderate correlation (r=.59) between latitude of origin and resistance to frost damage (Ching and Bever, 1960). The correlation (r=.38) between latitude of origin and growth rate was relatively low although there was some tendency for the northern origins to grow fastest.

Baldwin and Murphy (1956) tested the adaptability of Rocky Mountain Douglas-fir in New Hampshire. Douglas-fir from a high elevation (9000 feet) in New Mexico showed the best survival and height growth after 9 years from seed; it was followed by lots from Idaho, Montana, and Washington.

Douglas-fir varietal tests for Christmas tree plantation in Pennsylvania were reported by Byrnes et al. (1958). Seedlings from the central and southern Rocky Mountains were winter hardy but subject to late spring frost. On the other hand, seedlings from coastal and western interior sources were not damaged by late spring frosts but were susceptible to winter injury.

Differences in response to photoperiod in Douglas-fir were investigated by Irgens-Moller (1957-1958). Plants collected from seven localities in Oregon along an east-west transect from Snow Creek (elevation

4,000 feet) to tidewater were grown in Corvallis under various daylengths. High-altitude sources from Snow Creek were the latest to start growth under natural daylength and were affected most by long-day treatments. Long days hastened bud burst.

Irgens-Moller also studied variation in the time of growth cessation in Douglas-fir seedlings from Oregon, Washington and British Columbia. Trees native to the coast stopped height growth one to four weeks later than those from interior British Columbia and high elevations. The longer growth period resulted in greater growth of the coastal trees. Seedlings from interior British Columbia showed the greatest sensitivity to variations in photoperiod.

Nursery performance of 14 provenances of Douglas-fir in the Pacific Northwest region were reported by Ching and Bever (1960). Seedlings from the southern part of Vancouver Island, British Columbia, and the Shelton area of Washington grew taller and had longer needles. There was some correlation between needle length and total height growth of these 14 groups of Douglas-fir. Seedlings from southern Vancouver Island set buds earlier and also had lower frost damage than other provenances. But correlation between earliness of bud set and frost damage was not significant.

Provenance study of Douglas-fir in other countries was started first in the spring of 1910 when Rafael Zon of the U. S. Forest Service collected Douglas-fir seeds from northern Washington to central New Mexico and sent them to Professor Münch in Germany, who planted a single plot of each origin with a 6x6 foot spacing in 1914. The plantation was under observation for more than 40 years (Rohmeder 1956). There was a strong juvenile-adult correlation. The order of growth rate of the ten provenances did not change in 44 years. A provenance from Snoqualmie, Washington was the best volume producer. Second best was from Pecos, New Mexico.

Another series of provenance studies was reported by Schober and Meyer (1954-1955). In 1929, seed from 17 different areas in the Fraser river valley of British Columbia, western Washington and Oregon, and the Rocky Mountains of Colorado were sent to Germany. Outplantings were made in Germany, Denmark and Hungary. At all test sites progenies from Colorado were failures. They grew only 40 percent as fast as the others and were injured severely by frost and needle blight, caused by *Rhabdocline pseudostugae*. Trees from Washington and British Columbia were best in growth rate and disease resistance. Interestingly, progenies from the hilly country of Washington grew best in the hills and lowlands of northwestern Germany, progenies from the western Cascade Mountains in Washington grew best in continental eastern Germany and the Black Forest. Oregon Douglas-fir grew 10 percent less than average in height and volume growth.

Thirty provenances of Douglas-fir from west of the Cascade Range and Sierra Nevada Mountains were planted in Roturua, New Zealand (Sweet 1965). The tallest progeny was from Santa Cruz, California. Possibly Douglas-fir in this isolated area had developed superior growth as a result of warmer and longer growing season. The shortest progeny was from Klamath Mountains, California where the forest-free period is only 30 days. The consistent differences in bud set among provenances suggests strong genetic control which is adapted according to the date of early frost and the severity of winter.

Geographic variation of ponderosa pine and limber-border pine was summarized by Wells (1964a) and Steinhoff (1964) respectfully.

MATERIAL AND METHODS

Seed Procurement

Ponderosa pine: -- Dr. R. Z. Callaham of the Institute of Forest Genetics in Placerville, California, originally designed and supervised the procedure of seed collection. On each odd-numbered parallel, he located field plots at elevation intervals of 1500 feet from sea level to 10,500 feet in the southern part of the natural range. Seed collectors were asked to be accurate within five miles horizontally and within 200 feet vertically to the predesignated point of collection. In the autumn of 1959, the Institute of Forest Genetics sent part of their seed collections to Michigan State University. This gift from Placerville consisted of 30 or 80 seeds from each of 298 individual trees in 60 stands from the entire natural range.

Limber pine: -- In June 1959, Dr. J. W. Andresen of Michigan State University sent requests for seed collection to U. S. Forest Service personnel, asked them to collect cones and a foliage specimen from each of ten trees in a native stand, and to keep the collection separated by each tree. A total of 325 individual trees in 61 stands were included in this study.

Douglas-fir: -- In the autumn of 1961, Dr. J W. Wright and Professor Ira Bull of Michigan State University sent letters to U. S. Forest Service district rangers, people whom Dr. J. W Andresen had contacted previously, and people in the MSU alumni list. Cooperators were asked to collect 10 to 20 cones from each of about 10 trees in a native stand at least ten acres in size. Cones collected within a five-mile radius could be lumped together. Seeds were received from a total of 141 stands.

Nursery Procedure

A modified randomized block design was used for each of the three species in the nursery. A plot consisted of a single 4-foot row in which 20 (ponderosa pine and Douglas-fir) or 25 (limber pine) seeds were sown. The rows were spaced 1 foot apart. Germination was nearly complete in the ponderosa pine and in most seedlots of Douglas-fir. It was low in the majority of limber pine seedlots, with the result that many plots contained only 1 to 5 seedlings.

The ponderosa pine seed was sown in Michigan State University's research nursery on May 6-7, 1960, after being given a 2-week coldwater stratification to induce prompt germination. They were sown in a randomized complete block design with 4 replications. Seeds from each parent were kept separated. Each stand progeny was represented by 5 to 10 rows which were 6 inches apart. Germination was excellent so that each row contained the desired number of seedlings spaced equally.

Before sowing, the seedbeds had been treated with the commercial soil disinfectant "Mylone". This was effective so that a slight amount of hand weeding was sufficient to keep the nursery beds weed free. The seedlings were watered as necessary. A sawdust mulch applied at the end of the first growing season effectively reduced frost heaving. The soil, which was a sandy loam, had been kept at a high fertility level for several years prior to the experiment, so that growth was greater than obtained with ordinary commercial stock of the same species.

A similar practice was followed with the limber pine, which was sown May 20, 1961. In this case the several plots representing a single stand were scattered through a replicate. This influenced the amount of measurement time but not the results. Unfortunately, germination was much lower than in the ponderosa pine, with the result that some rows were blank and many others contained only one or two seedlings. This reduced the statistical adequacy of the experiment and also increased appreciably the variation in growth due to spacing. Trees in the very sparse rows did not grow as well as those in the fully stocked rows.

There was every intention of following the same procedure with Douglas-fir. The seeds were sown May 15, 1962, one stand progeny per 4-foot row. The seed was sown in excess, to permit later thinning. Variations in germination resulted in actual seedbed densities of 10 to 40 seedlings per row for most seedlots. As in the ponderosa pine, four replications were used.

In the spring of 1963, construction operation made it necessary to abandon the nursery. The 1-0 Douglas-fir were moved 60 miles to the Southern Michigan State Nursery near Brighton. At that nursery they were replanted in two replicates, the seedlots being systematically arranged in both. The transplanting, hurriedly done, varied from good to bad. Mortality was high in the very slow growing origins, presumably because some of the roots were left exposed. Mortality was also high in the fast-growing coastal origins, presumably because of cold damage suffered during the previous winter. The transplanting resulted in an obvious check to the growth of the seedlings during the following year but growth was normal in 1964. As an end result, the first-year Douglas-fir data were reliable and comparable to the first-year data from the other two species. The second and third year data must be interpreted with more caution.

Outplanting Procedure

Ponderosa pine seedlings from 60 different stands were planted by

Wells and others in the spring of 1962. The plantation follows a randomized complete block design. There are 7 replicates and 6 trees per plot. Spacing between trees was 8 feet. Data on winter injury and on height growth were collected from outplantings at the W. K. Kellogg Forest and Fred Russ Forest.

The test plantation of limber-border pine at the W. K. Kellogg Forest was planted by Steinhoff and others in the spring of 1964. There are 20 replications of 1-tree plot in a randomized complete block design. Data on winter injury were taken for this study.

Several outplantings of Douglas-fir were made but no data were included in this study.

Measurement Methods

Before making a set of measurement, an entire plantation was inspected once to determine whether measurement was necessary. First, there should be a noticeable difference between plots. That is, the range of difference between plots should be greater than difference within plot. Second, there should be some degree of consistency among progenies in all replicates. An objective test for consistancy was by probability analysis. (Wright 1962, p.314).

Metric traits such as total height and needle length were measured to an accuracy of 5 percent of the range between extremes. Units of millimeter, centimeter, inch, and 1/10 feet were used for convenience. Normally, the tallest trees per quarter-plot were measured.

Other quantitive traits such as the proportion of trees having lammas shoots and winter injury were recorded in percentage or in designated grade. In this case the whole plot was considered. Color scoring was done by comparing the average performance of the plot with a certain color grade in the observer's mind. A series of color grade was best constructed if it resulted in normally distributed data and additive differences between grades.

Analysis

Analysis of variance was used for each single character in order to detect differences among seedlots. Plot means were used as observations. Data on ponderosa pine and on limber-border pine were previously treated by Wells and Steinhoff, respectively.

A typical analysis of variance table for the ponderosa pine nursery study was as follows:

Sources	Degree of Freedom	Parameters Estimated
Individual tree provenance	124	$\sigma_e^2 + 4\,\sigma_t^2$
Replicate	3	
Error	372	σ_e^2
Total	499	

The standard error of a stand progeny mean applicable to ponderosa pine was

$$S = \sqrt{\frac{\text{mean square for error}}{rn}}$$

n= harmonic mean of number of parents per stand

r= number of replicates

A typical analysis of variance table for the limber pine nursery study was as follows:

Sources	Degree of Freedom	Parameters Estimated
Stands (s)	60	$\sigma_e^2 + 4\sigma_t^2 + 4.16\sigma_s^2$
Tree within stand (t)	217	$\sigma_e^2 + 4\sigma_t^2$
Error (e)	834	$\sigma_e^2 +$
Total	1111	

The standard error of a stand-progeny mean applicable to limber pine was calculated in the same manner as for ponderosa pine.

In the Douglas-fir nursery study and in all the permanent outplantings, all offspring from a stand were treated similarly. That is, a plot contained offspring of several trees within a stand. The ponderosa pine plantation at W. K. Kellogg Forest contained trees from 60 different stands and 7 replicates. Therefore, in a typical analysis of variance for that plantation there were 59, 6, and 354 degrees of freedom for stand, replicate, and error respectively. Similar types of analysis were used whenever stand progenies were treated as units.

In order to learn which stand-progenies differed from each other, the approximate L.S.D. (Least Significant Difference) applicable to stand-progenies means was computed for each trait. For the ponderosa and limber pine nursery data, Wells and Steinhoff used Duncan's multiple range test as a basis for the L.S.D. calculations, using multipliers equal to a rank difference of 15. For the rest of the data, I used Tukey's method for multiple comparisons. The Tukey confidence intervals are slightly greater than those obtained when using Duncan's method. But the conclusions were essentially similar.

In order to examine the pattern of geographic variation on the basis of a group of traits, the "Summations of Differences" method by Wright and Bull (1962) was used. The formula is as Follows:

$$\text{Summation of Difference} = \frac{\sum(Xi-Xi')-LSD.05}{LSD.05} \times 4$$

in which Xi-Xi' is the difference between two means in one trait and 4 is a multiplier to eliminate the use of decimals.

The traits used by Wells in the summation analysis in ponderosa pine are as follows:

Germination date, yellow trees, foliage color in August, secondary needle length, winter injury, date of growth started, percent of trees having Lammas growth, and height at age 2.

Eleven characters were used by Steinhoff for limber-border pine: date of bud set, length of growing period, cotyledon number, cotyledon length, diameter of hypocotyl, 1-year foliage color, length of secondary leaves, degree of leaf serrulation, 1-year height, 2-year height, and amount of height growth increment.

Eight characters in Douglas-fir were considered by the present author: percent of dead trees after transplantation, percent of 2-year trees killed by winter cold, percent of winter-killed foliage, percent of early frost damaged leaves, 2-year height, date of bud set, leaf length and leaf color.

After ecotypes have been delineated, one would like to obtain objective estimates of the degree of variation associated with varieties and ecotypes. It is also desirable to know which character is a satisfactory criterion for these separations. Analysis of variance for a nested design was used to partition variance components. An example of the analysis of variance for data from bud set in Douglas-fir is as follows:

Source of variation	Degree of Freedom	Expected mean squares
Between varieties	1	$\sigma e^2+16.65\sigma eco^2+33.75\sigma var^2$
Within varieties	126	
Among ecotypes	7	$\sigma e^2+13.34\sigma eco^2$
Within ecotypes	119	σe^2
Total	127	

WINTER INJURY

Ponderosa Pine

Winter injury in ponderosa pine was shown by the presence of yellow to red coloration of leaves. Tips of the current-year leaves were most susceptible, old leaves being winter hardy. This type of leaf damage was much more severe in the nursery than in plantations. Cambial damage was less common than leaf damage and was shown by dieback of the previous year's shoot. As a result of such dieback, one year of height growth was lost and a side branch became dominant. Rarely did cambial damage extend to all the tree above snow line in the plantation. Winter injury to roots usually was not shown until after transplanting. Progenies susceptible to winter injury also had a lower survival rate in the first year after outplanting.

The geographic variation pattern is as follows:

Origin of Trees	Winter Injury Pattern
California and Willamette Valley	Severe browning of upper needles of all year-old seedlings; stem dieback on a few trees; up to 25 percent of current year's needles killed each year in plantation.
Southern Rockies (Arizona and Southern New Mexico)	Moderate browning of needle-tips of some year-old seedlings; less than 1 percent of current year's needles killed each year in plantation.

Columbia Plateau (Eastern Oregon and Washington British Columbia, Idaho Western Montana)	Light browning of needle-tips of some year-old seedlings; less than 1 percent of current year's needles killed each year in plantation.
Northern Interior and Central Rockies (Eastern Montana, Nebraska, South Dakota, Utah, Colorado, Northern New Mexico)	Browning of needle-tips of a few year-old seedling. No current year's needles killed in plantation.

The repeatibility of winter injury was high in ponderosa pine. Although the amount of damage varied by year, the rank of different groups of origins remained practically the same. A rank correlation coefficient of r=.75*(1) was found between nursery and 4-year Russ plantation data and of r=90** between nursery and 6-year Kellogg plantation data (Table 1). Repeatibility of winter injury pattern among origins within a group ranged from low to high. Within the most variable California group, rank correlation was high (r=.59**) between nursery and Kellogg but low (r=.18) between nursery and Russ.

(1) As used here and later in the text, * and ** denote statistical significance at the 5 and 1 percent levels, respectively.

Table 1. Rank correlation of winter injury among 2-year nursery, 4-year Russ plantation and 6-year Kellogg plantation data.

	Correlation applied to		
	Nursery-Russ	Nursery-Kellogg	Russ-Kellogg
		Among groups	
Entire species	.750*	.902**	.712*
		Among provenances within groups	
California	.176	.592**	.528*
Columbia Plateau	.782*	.536	.913**
Southern Rockies	.420	.680**	.519*
Central Rockies	.893***	.660**	.576*
Northern Interior	1.000***	.657	.750*

*,**,***, denote statistical significance at the 5, 1, and .1 percent level respectively.

These results agreed with the frost injury pattern on five 30-year-old plantations in Oregon-Washington reported by Squillace and Silen (1962). The comparison was as follows:

Origin of Seedling	Damage Pattern	
	Squillace and Silen Study	Present Study
California and Oregon	Severe damage in one origin, complete mortality in others.	All year-old seedlings injured.
Southern Rockies	Needle damage but little permanent injury.	Up to 5 percent of all leaves injured.
Columbia Plateau	Little or no damage.	Less than 1 percent of leaves injured.
Northern Interior	Little or no damage	No damage.

Coastal origins were more susceptible to winter injury than interior origins. Of the total variance in winter injury in the nursery, 63 percent was due to differences between region, 34 percent to differences between groups within region. The contrast between coastal and interior origins was reduced somewhat in later years as seedlings became better established. Seedlings from the Columbia plateau seemed to have acquired cold acclimatization and became as hardy as interior seedlings. The between-region variance component was reduced to 26 percent while among groups variance was increased to 44 percent in the 6-year-old Kellogg plantation.

One suspects that the greater cold resistance in later years was a result of initial natural selection to low temperature. It was found from the nursery test that amount of winter injury was associated with the average January temperature at the place of origin. (r=.53** for coastal regions and r=.73*** for interior region). However, judging from observations in the Kellogg plantation, minimum temperature may have been a more important limiting factor than average temperature in January. There was an unusually warm January in 1964; the average temperature was 28.2° F. and a minimum temperature was -10° F. But progenies MSFG 2012, 2243 from Arizona and MSFG 2213, 2219, 2226 from New Mexico showed winter injury on '63-'64 needles. They were all from areas with lower average temperature but with higher minimum temperature than experienced in the plantation.

Limber Pine

The seedlings of this species seemed to be winter hardy in the nursery. However, they were well protected under snow cover during much of the most severe freezing periods and not subject to dehydration by low temperature and dry wind. In the winter of 1965-66, the average temperature at Kellogg Forest was 16.7° F. in January and the maximum snow cover was 6 inches deep. During that winter the fast growing progenies in the Kellogg plantation showed browning on the tips of 5 to 20 percent of the current year's needles. The length of browning was only half inch and in no case were entire needles damaged. On the other hand, most of the slow growing (4 to 9 inches tall) progenies from Idaho, Utah, and Colorado were protected from exposure to cold wind and showed little winter damage. From general observation of the plantation I infer that

Table 2. Characters for limber-border pine.

Area of origin	Characters						
	Height	Needle length seedling	Needle length parents	Foliage color[(a)]		Date of bud set	Winter injury
	age 2	age 2		age 1	age 2	age 1	age 4
	--------mm---------			--grade--		day of year	percent of trees
			PINUS FLEXILIS				
SW. Alberta, Montana, W. North Dakota, & NW. Wyoming	46	27	51	1.9	3.3	244	10
SW. Wyoming, SE. Idaho, NE. Utah	53	31	51	1.7	3.3	245	2
SW. Nebraska & SE. Wyoming	60	41	61	2.6	4.2	268	7
E. Cent. Calif.	43	25	56	1.9	3.4	236	0
N. & Cent. Colorado	45	29	50	1.7	3.4	245	14
S. Utah-Colorado & N. New Mexico	68	36	55	2.6	3.9	250	9
Average	52	36	52	2.0	3.4	246	9
			PINUS STROBIFORMIS				
N. Arizona-New Mexico	119	55	69	3.7	4.6	266	29
Cent. & SE. Arizona	125	71	81	4.4	4.9	281	74
S. New Mexico, & NW. Texas	134	63	76	4.5	5.0	278	57
Average	126	65	79	4.2	4.8	276	55
Standard deviation of mean for an area of origin	5.1	2.0	2.4	.22	.13	4.0	--
L.S.D. 5 percent level	21.9	9.0	10.5	.90	.59	18.1	--
L.S.D. 1 percent level	-	10.8	12.6	-	-	21.6	--

(a) Grade 1= Yellow-green, 5= Blue-green.

differences in winter injury were due to differences in external protection rather than differences in internal cold resistance. The geographic variation pattern of winter injury on 371 seedlings in 7 replications of limber pine in the Kellogg plantation was shown in Table 2. It appeared that the southern population of limber pine in Arizona and New Mexico was different from the northern population in winter injury (X^2=86.77**). Within the southern population of limber pine, seedlings from northern New Mexico and northern Arizona had lower percentages of damaged trees, while seedlings from central and southeastern Arizona had a significantly higher (5 percent level) percentage of damaged trees than the average of the southern population level. The northern population of lumber pine was more uniform than the southern but slight differences were evident. Seedlings from southwestern Wyoming, southeastern Idaho, and northeastern Utah were a little more hardy and seedlings from north and central Idaho were a little less hardy than average; the small differences were significant at 10 percent level.

Douglas-fir

The seedlings of Douglas-fir were susceptible to frost damage and winter injury. Early frost in late September 1962 wilted the tops of nearly all coastal seedlots but did no harm to any Rocky Mountain seedlings in the nursery. On the other hand, a late frost in May 1963 did no damage to coastal seedlings but severely damaged many Idaho and Colorado seedlings and some Montana seedlings. Fresh leaves with a length less than 5 millimeters long suffered most; fully expanded leaves suffered little.

Winter injury in Douglas-fir was shown by deep purple coloration on leaves, and by dehydration of the stem. The geographic variation pattern is as follows:

Locality of origin	Damage from transplanting and winter weather
A.&B. Pacific Northwest (British Columbia, Western Washington and Oregon)	All leaves on all trees turned deep purple; the majority of trees died of dehydration of stem in the nursery.
C. Okanogan Highland	Leaves on 50 percent of trees turned yellow to purple, 20 percent of trees died from transplanting, 3 percent of the total foliage was damaged in the plantation.
D. Bitteroot Range	Leaves on 78 percent of trees turned purple, 11 percent of trees died from transplanting, 4 percent of the total foliage was damaged in the plantation.
E. Continental Divide in Western Montana	Leaves on 74 percent of trees turned purple. 25 percent of trees died from transplanting. 3 percent of the total foliage was damaged in the outplanting.

F. Northern Interior (Alberta, South central Montana, Central Idaho, Northwestern Wyoming, Eastern Oregon-Washington)	Leaves on 76 percent of the trees turned purple. Stem damage was slight; 36 percent of the trees died after transplanting.
G. Northern Colorado and Utah	Leaves on 8 percent of the trees turned yellow in the nursery; 12 percent of the trees died from transplanting; 3 percent of the total foliage was damaged in the plantation.
H. Southern Colorado and Utah Northern Arizona and New Mexico	Leaves on 62 percent of the trees turned yellow to purple in the nursery; 10 percent of the trees died from transplanting; 3 percent of the total foliage was damaged in the plantation.
I. Southern Arizona and New Mexico	Leaves on 63 percent of the trees turned yellow to purple in the nursery; 11 percent of the trees died from transplanting; 3 percent of the total foliage was damaged in the plantation.

The pattern of low temperature damage in Michigan was similar to that found in Pennsylvania, where seedlings from the central and southern Rocky Mountains were winter hardy but damaged by late spring frost; seedlings from coastal sources were not so damaged but were susceptible to winter injury (Byrnes, <u>et</u>. <u>al</u>. 1958).

There is slight reason for the introduction of coastal Douglas-firs into Michigan because of their limited genetic variation in cold resistance but progenies MSFG 1626, 1627, and 1628 from the Puget Sound lowland near Olympia, Washington may offer an opportunity to tree breeders who might wish to improve cold resistance. These seemed less susceptible to winter injury than other coastal seedlots in our nursery. Seedlot MSFG 1627 was also found to be the best in survival, the best in height growth and to suffer least winter injury among all coastal origins in Pennsylvania (Gerhold, 1966).

Percent of the total foliage suffering winter injury in the nursery was the most distinctive character between coastal and interior Douglas-fir. Of the total variance in this trait, 91 percent was accounted for by the difference between coastal and interior regions; only 1 percent by differences among ecotypes within regions.

Percent of the trees suffering winter injury in the nursery may be used to separate ecotypes. Differences among ecotypes within the region were significant at the 5 percent level and contributed 10 percent of the total variance in this trait. The Southern Rocky Mountain ecotype was less variable than those from the central or northern Rocky Mountains; coefficients of variability were 25, 67, 58 percent respectively for those three populations. Consistency of damage to the same provenances was high. The correlation between damage in the nursery and the

Russ plantation was r=.53*. Cold resistance ranking of the Rocky Mountain ecotypes remained unchanged through the years; the central ecotype remained most winter hardy, and the southern ecotype the least. The same pattern was reported in Pennsylvania (Gerhold 1966).

The trend of cold resistance in Douglas-fir probably was governed by natural selection and migration. The mild climate of the Pacific Northwest imposed little selection pressure for hardiness. Seedlings from the coastal region therefore are not hardy enough for Michigan. The higher-than-expected percentage of winter injury to Idaho seedlings suggests a genetic affinity between the northern Rocky and coastal populations. Because this "inland empire" region shows other phytogeographic evidences of coastal influence, the route of migration in Douglas-fir possible is from the Pacific Northwest, through British Columbia to the northern Rocky Mountains and selection pressure can explain the differences between the central and southern groups of origins.

Comparisons Between Species

Of the three species, limber pine was the most winter hardy and Douglas-fir was the least. Ponderosa pine has a lower altitudinal distribution than Douglas-fir. This may explain its greater hardiness. Also, ponderosa pine has the ability to send down a vigorous taproot quickly, which could be a selective advantage when the surface soil is frozen. Because of this, ponderosa pine needles would be less susceptible to dehydration by cold dry winds. The lesser damage in plantations than in the nursery in both species may also be explained by better establishment of root systems.

Both coastal ponderosa pine and Douglas-fir seedlings were more susceptible to winter injury than seedlings from interior sites because the coastal climate is mild in the winter. Selection pressure for cold resistance would not be strong and seedlings could not become adapted with protective tissue to counteract the long and severe Michigan winters.

The hardiest seedlings of ponderosa pine were from eastern Montana and Wyoming, the Black Hills of South Dakota, and Pine Ridge of Nebraska. The hardiest seedlings of limber pine were from southwestern Wyoming, southeastern Idaho and northeastern Utah. The hardiest seedlings of Douglas-fir were from northern Colorado and northern Utah. Incomplete sampling prevented comparison among species in all these areas. Within the areas in which comparisons were possible, northern Utah was a source of the most cold-resistant seedlings in all three species.

Seedlings from southeastern Arizona were the least winter hardy of all interior seedlings. The most susceptible progenies MSFG 2234 of ponderosa pine, MSFG 3729 of limber pine and MSFG 1545 of Douglas-fir were all from that area. Limber pine seedlings from southern New Mexico were hardier than those from southern Arizona but a similar difference was not evident in the other two species.

Limber pine seedlings from northern Arizona-New Mexico seemed to be hardier than those from southern Arizona-New Mexico. The contrast between origins from those regions was less strong in ponderosa pine and very weak in Douglas-fir. The difference between Colorado-New Mexico and Utah-Arizona seedlings was very strong in limber pine, strong in ponderosa pine, and weak in Douglas-fir.

In contrast, Douglas-fir from southern Utah-Colorado, northern Utah-Colorado, and areas to the north of these states were noticeable different in hardiness, the trees from northern Utah-Colorado being the most hardy. In limber pine, the boundary between hardy and non-hardy types seemed to be farther north, the hardiest being from southern Idaho, northwestern Wyoming, and northeastern Utah. In ponderosa pine, there were no evident differences in hardiness from Colorado northward.

To summarize, all three species had different patters of geographic variation but they were similar in both extremes; the most cold-resistant seedlings were from northeastern Utah and the most cold-susceptible seedlings were from southeastern Arizona.

HEIGHT

Ponderosa Pine

The tallest seedlings of ponderosa pine at age 1 were from California and New Mexico. Lacking cold resistance, the tall California seedlings suffered severe winter injury. Many were killed back to the snow line because of cambial damage. Growth in later years was greatly retarded. Seedlings from New Mexico showed light to intermediate leaf damage in the nursery, but growth rate did not seem to be affected. Seedlings from the Columbia plateau and the northern interior had a slow start but grew vigorously later. Geographic variation of height growth in ponderosa pine is presented in Table 3. The ranking of ecotypes was consistent between two plantations, but not between nursery and plantations at the 5 percent level.

The tallest progenies at age 7 in Kellogg plantation were MSFG 2124 from British Columbia, MSFG 2180 from eastern Pine Ridge in Nebraska, MSFG 2109 and 2103 in southern New Mexico. The slowest growing progenies were MSFG 2063 from near King Canyon National Park in California and MSFG 2274 from northeastern Utah. The difference between the tallest and the shortest progenies was 76 percent of the plantation means.

Origins which grew taller in the nursery at age 2 had a tendency to grow taller at both Russ and Kellogg Forests. This trend was more evident in the Columbia Plateau ecotype and Central Rocky Mountain ecotypes than in others. (Table 4)

Height differences among ecotypes were most obvious in later years. Of the total variance in height among progenies, 37 percent was accounted for by differences of ecotype in the nursery; 40 percent and 64 percent in the Russ and Kellogg plantations, respectively. The coastal

Table 3. Height of ponderosa pine in the nursery and plantations.

Ecotypes	Height-rank at				Height at			
	Nursery		Russ	Kellogg	Nursery		Russ	Kellogg
	age 1	age 2	age 4	age 7	age 1	age 2	age 4	age 7
	rank (1=tallest)				centimeters			
Columbia Plateau	3	2	1	1	4.6	16	42	132
Southern Rockies	2	1	2	3	5.1	21	41	121
Northern Interior	5	3	3	2	3.8	14	37	124
Central Rockies	6	7	4	4	3.7	10	35	99
Nevada	7	5	7	5	3.5	13	30	97
Oregon	4	6	5	6	4.4	11	33	94
California	1	4	6	7	5.5	13	32	90
Average of species					4.6	15	37	107
Standard error of an ecotype mean					.24	.8	1.5	3.4
L.S.D. .05 between ecotype means					.97	3.3	5.9	13.7

Table 4. Intra-ecotype height correlations for three different sites or ages(a) for ponderosa pine.

Correlations involve progrnies (and number of progenies) within this ecotype	Simple correlation when comparison is between		
	Nursery and Russ	Nursery and Kellogg	Russ and Kellogg
Columbia Plateau (7)	.67*	.85*	.82*
Southern Rockies (12)	.49	.10	.51
Northern Interior (5)	.55	.78	.33
Central Rockies (12)	.78**	.60*	.58*
California (16)	.39	.11	.18
Entire Species (56)	.43**	.26*	.68***

*, **, *** = Significant at 5, 1, and .1 percent levels respectively.

(a) Ages of ponderosa pine were 2, 4, and 7 years for nursery, Russ Forest and Kellogg Forest respectively.

variety (California and Columbia plateau ecotypes) was significantly taller than the interior variety at the end of the first growing season but not in later years. At age 1 the difference between varieties accounted for 9 percent of the total variance among progenies. Suffering from winter injury, California seedlings later were as slow growing as Central Rocky Mountain seedlings and the difference between varieties became insignificant. Squillace and Silen (1962) also found significant difference in total height between seed sources in a 30-year Oregon-Washington study and a 45-year northern Idaho study but no difference between Pacific and interior varieties (Table 5).

The height superiority of the Columbia plateau ecotype was also evident in northern Idaho (Hanover, 1963). In most western studies coastal trees seemed best, in contrast to the Michigan results (Squillace and Silen, 1962; Schreiner, 1937; Moore 1944). The southern Rocky Mountain ecotype was better than average in Michigan as in Hanover's but not in Squillace and Silen's study. Trees from the Central Rockies have been slow growing in all tests.

Spring temperature seemed to be an important climatic factor governing height growth. For the nursery data, the relationship was evident only if all interior origins were considered. For the Kellogg plantation, the relationship was also evident within some ecotypes as shown in Table 6 .

Squillace and Silen (1962) reported a similar relation. Ponderosa pine has a 35 to 52-day height-growth period beginning in early April or May (Hanover 1963). Therefore, warm average spring temperatures offer greatest opportunity for growth and development. Thus, difference in height growth probably arose as the outcome of adaptations to spring

Table 5. Relative heights of ponderosa pine ecotypes grown in southern Michigan (7 years), Oregon and Washington (30 years) and northern Idaho (45 years).

	Relative Height		
Ecotype	Idaho (a)	Oregon-Washington (a)	Michigan
California	Failed	114	80
Western Oregon	126	124	85
Columbia Plateau	117	121	117
Northern Interior	81	69	110
Central Rockies	85	-	87
Southern Rockies	79	86	107

(a) Data from Squillace and Silen (1962).

Table 6. Correlation between average spring temperature at place of origin and height of ponderosa pine progeny.

Ecotype	Number of progenies	Coefficient at Nursery	Coefficient at Kellogg
A. Calif., Oregon, Nevada	20	-.24	-20
B. Columbia Plateau	6	-.26	.47
C. Southern Rockies	12	.67*	.85***
D. Central Rockies	11	.42	.92***
E. Northern Interior	6	.49	.92**
C+D+E	29	.60***	-
B+C+D+E	35	-	.91***

temperature.

Because the growth rate of California seedlings was greatly retarded by winter injury, the trend within this ecotype must be interpretated with caution.

Limber Pine

The limber pine complex was separated into two distinct species by Steinhoff (1964). The northern species (*P. flexilis*), from Alberta, Montana, Idaho, North Dakota, Wyoming, Utah, Colorado, Nebraska, and northern New Mexico, grew significantly less than the southern species (*P. strobiformis*) from Arizona and New Mexico (Table 2). Of the total variance in 2-year height among progenies, 92 percent was accounted for by the difference between species. Four percent of the total variance was accounted for by differences among groups of origin within species.

At high latitudes, limber pine usually grows at lower elevations. Thus, differences in temperature and annual precipitation due to changing latitude are possibly compensated by differences in elevation. However, in areas where latitude and elevation of progenies are unrelated, (SW. Alberta, Montana, W. North Dakota, NW. Wyoming) growth rates were significantly (1 percent level) higher in the south than in the north. Other environmental factors (e. g. day length, soil type) vary throughout the area and are not compensated. Lack of response to them may have involved an intricate physiological buffering mechanism. Possibly individual trees are plastic enough to adapt to different environments without genetic change.

Douglas-fir

Douglas-fir seedlings from west of the Cascade Range were the tallest in the nursery at age 1 (Table 7). Because of winter injury, their subsequent growth was greatly retarded. The blue Arizona-New Mexico origins were also fast growing. Growth rates of sources from northern Idaho and northwestern Montana, were greatly superior to the remainder of the seedlots from these states. Seedlings from southern Colorado-Utah were significantly taller than those from northern Colorado-Utah.

The rapid growth of coastal and Arizona-New Mexico seedlings may be due to a longer growing season. Most of these seedlings set their buds in early October, in contrast to mid-August for seedlings from northern Colorado-Utah. The northern Idaho and northwestern Montana sources set buds one week later than other slower growing seedlots from these states. The other possible reason for rapid growth of northern Idaho and northwestern Montana seedlings may be the more abundant rainfall and milder climate in these areas than in some other parts of the states. In areas with a long growing season and a favorable climate, natural selection may favor fast growing seedlings for their competitive ability. On the other hand, in areas with severe winter, natural selection may favor trees with a shorter growing season and consequently less height growth.

The difference in growth rate between coastal and interior seedlings was most obvious at age 1 at which time the difference contributed 72 percent of the total variance among progeny means. Because of severe winter injury to coastal seedlings, their growth rates were greatly retarded. Later, the difference between coastal and interior varieties accounted for 60 and 33 percent of the total variance at ages 2 and 3 respectively. In Pennsylvania where Douglas-fir survived better than in Michigan, coastal sources were tallest (Gerhold 1966). Thus, coastal

Table 7. Characters of Douglas-fir in a 3-year nursery study.

Ecotype	Height				Needle length	Foliage color
	Rank at age		Height at age		age	Oct.
	1	3	1	3	2	1963
	-rank[a]		-cm-		-mm-	-grade[b]-
COASTAL VARIETY						
A. British Columbia, W. Washington-Oregon	1	3	8.8	28	18	5.7
B. Eastern Cascade	2	4	8.1	26	17	6.5
Average			8.7	28	18	5.8
INTERIOR VARIETY						
C. Okanogan Highland	5	5	6.0	23	17	6.3
D. Bitteroot Range	4	6	6.5	22	18	5.7
E. N. Continental Divide	8	8	5.0	15	15	5.1
F. Northern Interior	9	9	3.9	11	13	4.4
G. N. Colorado-Utah	7	7	5.1	17	15	6.3
H. S. Colorado-Utah, N. Arizona-New Mexico	6	2	5.9	29	18	9.7
I. S. Arizona-New Mexico	3	1	7.0	37	20	9.8
Average			5.4	20	16	6.3
Standard error of an ecotype mean			.22	2.1	.6	.36
L.S.D. .05 between ecotype means			1.0	9.4	2.5	1.53

(a) Rank 1= tallest, 9= shortest.

(b) Key to grade 1= yellowish-green, 5= green, 10= blue-green.

Douglas-fir is the fastest growing variety but only if there is no winter injury.

Differences among ecotypes within regions were highly significant. The variance component of ecotypes within regions increased from 18 percent at age 1 to 45 percent of the total variance at age 3. Within the interior region, the southern Arizona-New Mexico seedlings (especially Sacramento Mountain) were the tallest, which agreed with Gerhold's (1966) finding. The present data also agree with his, that sources from northern Idaho and the northwestern corner of Montana were superior in growth rate. Within the coastal region, seedlings from the Shelton area in western Washington were the best in survival, winter injury, and height at age 3. However, Shelton seedlings were still inferior to many Arizona-New Mexico seedlings in Michigan.

Contrasts between Species

On the basis of height growth, the strongest contrast between coastal and interior progenies was manifest at age 1 in both ponderosa pine and Douglas-fir. Coastal seedlings were taller than interior seedlings before the first winter but soon became inferior to interior seedlings because of winter injury. Separation of coastal and interior varieties were better defined in Douglas-fir than in ponderosa pine as shown by the between-region variance components in the following tabulation.

Age	Between-variety variance components in	
	Ponderosa pine	Douglas-fir
-- year --	-- percent --	
1	9	72
2	0	60
3	0	33
7	0	--

The greater of between-variety difference in Douglas-fir may have arisen from the following reason: 1) Differentiating forces on height growth is stronger between varieties of Douglas-fir than of ponderosa pine. 2) Geographic separation between varieties in more complete in Douglas-fir than in ponderosa pine. 3) Common ancestry of the varieties is more remote in Douglas-fir than in ponderosa pine.

Within the interior region, limber pine can be separated into two distinct non-overlapping species whereas ponderosa pine and Douglas-fir can be separated into 3 and 6 overlapping ecotypes respectively, according to the 2-year height data. Seedlings from southern Arizona and southern New Mexico were tallest, and seedlings from northern Utah and northern Colorado were shortest in all three species. Seedlings from southern Utah-Colorado and northern Arizona-New Mexico were better than average. Northwestern Montana and northern Idaho were the best seed source in the Northern Rockies in Douglas-fir, but a limited sampling of limber pine and ponderosa pine in these areas prevents further generalization.

A close look at progenies from New Mexico revealed a striking example of how selection pressure caused similar trends in the three species. Progenies MSFG 2213, 2219, and 2226 of ponderosa pine, MSFG 2612 of limber pine and MSFG 1546 of Douglas-fir, from the Cibola National Forest near Albuquerque, New Mexico, grew much less than progenies from the surrounding neighborhood. That area has a low January mean temperature and short growing season. In the nursery, the Cibola progenies were winter hardy and early to set buds. Presumably natural selection in the Cibola acted by favoring trees with a short growing season and consequently less height growth.

The Colorado Front Range is an isolation barrier permitting differentiation in height growth in all three species. MSFG 2145 of ponderosa pine is from a small stand in the relatively level area northeast of Colorado Springs and is isolated from the continuous forest to the west by about 4 miles. Another progeny MSFG 2155 is from 7200 feet elevation about 3 miles northwest of Colorado Springs, although one would not expect much difference between two stands within such a short distance. The former was significantly taller than the latter in the nursery and plantations. This is possibly related to the 18-day longer growing season at the place of origin of MSFG 2145. In limber pine, MSFG 902 from a stand 20 miles north of Colorado Springs grew faster than MSFG 2523 and 909 from which it was isolated by 40 miles. In Douglas-fir, MSFG 1609 from 18 miles north of Colorado Springs was much taller than MSFG 1537 and 1635, from which it was separated by about 70 miles.

LENGTH OF SECONDARY LEAVES

Ponderosa Pine

Secondary leaves were formed on more than half of the interior seedlings but on less than 1 percent of coastal seedlings the first year. At the end of the second growing season, pines from the interior had much longer needles than those from the coast (Wells, 1964a). The significant (1 percent level) difference between varieties accounted for 66 percent of the total variance among progeny means. The longer length of secondary leaves of interior seedlings may be due to their earlier growth start. The present results did not agree with those from Weidman's (1939) northern Idaho study in which coastal progenies and parents had longer needles. The discrepancy may be due to winter injury on coastal seedlings in Michigan. (Table 8)

Differences in needle length among ecotypes were greatest in the interior varieties. Weidman's and Well's studies showed that Arizona and New Mexico sources had the longest needles of all interior seedlots. Of the total variance among progeny means, only 7 percent were accounted for by difference among ecotypes within region.

Within the coastal variety needle length was not associated with geography or climate, possibly because of differential winter injury. Two isolated California progenies, MSFG 2040 and 2075, were separated by 25 miles and 1300 feet in elevation. Their nursery and outplanting performance were similar in all characters but needle length. MSFG 2075 had significantly longer (by 3.4 cm) needles than MSFG 2040.

Within the interior variety long secondary leaves were associated with a narrow annual temperature range, high average January temperature, and a long growing season. Thus, long needles may have a selective

Table 8. Needle length of ponderosa pine in present 2-year southern Michigan and 26-year northern Idaho studies.

	So. Michigan Well's study		No. Idaho Weidman (1939) study		
Ecotype	Progenies	Needle length	Progenies	Needle length Progenies	Needle length Parent
	-number-	-mm-	-number-	-mm-	
COASTAL VARIETY					
A. California	16	118	0	--	--
B. Nevada	2	107	8	--	--
C. Oregon	2	109	1	150	163
D. Columbia Plateau	7	120	10	145	148
Average		117		146	116
INTERIOR VARIETY					
A. S. Rockies	12	165	2	120	147
B. Cent. Rockies	13	148	3	104	114
C. N. Interior	8	138	3	102	141
Average		152		107	132
Standard deviation of mean of an ecotype		4.8		--	--
L.S.D. 5 percent level		19.4		--	--
L.S.D. 1 percent level		24.7		--	--

advantage in mild and warm areas but become disadvantageous in cold regions. Winter injury was found mostly on the tips of longer needles. The correlation between needle length and winter injury was r=.70**.

Limber Pine

Based on the length of secondary needles, the limber pine complex was separated into two species (Steinhoff 1964). Southern *P. strobiformis* had longer needles than northern *P. flexilis*. Of the total variance among provenance means, 95 percent and 91 percent were accounted for by difference between species in the seedling and in the parental generations, respectively. Of the total variance among provenance means, less than 3 percent was accounted for by differences among areas of origin within species.

Secondary needles on 2-year old seedlings were shorter than on their parents. However, strong rank correlation between parent and offspring (r=.94**) was found among areas of origins. When provenance means were used, the parent-offspring correlation in the northern species was significant at the 1 percent level but in the southern species was non-significant at the 5 percent level.

In both species, seedlings from areas with a long growing season have the longest secondary needles. Other effects were less consistent.

Douglas-fir

Measurement of needle length was made in the nursery at age 2. Coastal Douglas-fir had needles averaging 18 millimeters long, with a range from 13 to 22 millimeters. Interior Douglas-fir had needles averaging 16 millimeters long with a range from 13 to 22 millimeters. The difference between coastal and interior varieties accounted for only 2 percent of the total variance.

Within the coastal variety, seedlings with the longest needles were from the Puget Sound area in Washington and those with the shortest needles were from near Vancouver, British Columbia. Needle length of Douglas-fir seedlings in Michigan was 6 millimeters shorter than on comparable trees in Oregon, where the longest (25 mm.) needles were from southeastern Vancouver Island and Shelton, Washington, and the shortest (21 mm.) needles were from the northern tip of Vancouver Island. The average of 14 coastal progenies was 24 mm. (Ching and Bever 1960). The shorter growing season in Michigan may decrease growth of needles.

Within the interior region, seedlings from southern Arizona-New Mexico, and northern Idaho-northwestern Montana had significantly longer needles than those from the rest of Montana-Idaho, and northern Utah-Colorado (Table 7). It was an amazing coincidence that when needle length was measured in units of 1/8 inch, the length of the needle indicated from which of Rehder's (1940) plant hardiness zones the seedling came. For example, seedlings with the shortest needle length of 4/8 inch came from zone 4 (January minimum temperature of -30° to -20° F.), and seedlings with a needle length of 7/8 inch came from zone 7 (0° to 10° F.).

There was some association between needle length and height in Douglas-fir seedlings in Oregon (Ching and Bever 1960). Possibly, some common genes control both height growth and needle development. In my study, the correlation between 2-year height and length of secondary needles was .78** if ecotype means were used as items. The environmental factors responsible for differentiation in needle length appear to be minimum temperature and length of growing season. Long needles are advantageous under most conditions but are susceptible to winter injury, so must be confined to areas with a long growing season or with less severe winters.

Comparison between Species

Based on needle length at age 2, both Douglas-fir and ponderosa pine showed a difference between coastal and interior varieties significant at the .1 percent level. Interior ponderosa pine had longer needles than coastal, but interior Douglas-fir had shorter needles than coastal. The separation of coastal and interior varieties was better defined in ponderosa pine than in Douglas-fir. Of the total variance among progeny means, 66 percent was accounted for by differences between varieties in ponderosa pine, 2 percent in Douglas-fir.

The interior variety was more variable than the coastal in both species as measured by the range, standard error, and coefficient of variation. Possibly, this is due to a greater diversity of environment-- particularly in elevation, latitude, rainfall, and temperature.

Although differences among ecotypes were not significant in the coastal varieties, they were (5 or 1 percent level) in the interior populations of all three species. Douglas-fir seedlings from northwestern Montana and northern Idaho had longer needles than those from the rest of these states. Insufficient sampling hindered such comparisons in the other two species. Seedlings of all three species from southern Utah-Colorado and northern Arizona-New Mexico seemed to have longer needles than those from northern Utah-Colorado. The contrast was strong in Douglas-fir; moderate in ponderosa pine; and weak in limber pine. Southern Arizona-New Mexico seedlings of three species also seemed to have longer needles than northern Arizona-New Mexico seedlings. The contrast was most distinct in limber pine.

Length of secondary leaves in the three species seemed to be related to height growth. Length of the growing season and winter temperature may act as the selection force for the needle length.

FOLIAGE COLOR

Ponderosa pine

Seedlings of ponderosa pine showed a strong difference in foliage color between coastal and interior varieties. First-year foliage color in August 1960 was yellow-green to green in coastal seedlings and green to blue-green in seedlings from the interior. These observations agree with Weidman's (1939). The difference between varieties in my study was significant at the .1 percent level and accounted for 84 percent of the total variance among progeny means. No significant differences were found among ecotypes within a variety. Differences among progenies were significant at the 1 percent level within Californis, Columbia Plateau, Central Rockies, and Southern Rocky Mountain ecotypes. Of the total variance, 14 percent was accounted for by differences within ecotype.

Fall coloration was found in the first year when all interior seedlings turned purple. One northern Idaho progeny with several coastal traits developed purple color. All coastal seedlings remained green. This between-variety difference, significant at the 0.1 percent level, accounted for 75 percent of the total variance in fall coloration. Within the interior region, the Central and the Southern Rocky Mountain ecotypes had a deeper purple color than the Northern Interior one (Table 9). The variance component for ecotypes within varieties was 5 percent. The other 20 percent was accounted for by differences among progenies within ecotypes. Fall coloration of ponderosa pine failed to repeat itself in later years.

The second-year foliage color in October 1961 was gray for interior seedlings, and dark green, light green or gray in coastal seedlings. The difference between varieties was significant at the 0.1 percent

Table 9. Foliage color of ponderosa pine seedlings in southern Michigan. (Data from Wells, 1964a).

Ecotypes	Foliage color Aug. 1960	 Oct. 1960	 Oct. 1961
	------------	grade	------------
COASTAL VARIETY			
California	3.6	.1	15.1
Nevada	4.0	.7	11.0
Oregon	4.0	.0	15.5
Columbia Plateau	3.6	1.0	8.6
Average	3.7	.4	13.2
INTERIOR VARIETY			
S. Rockies	8.5	5.7	16.0
Cent. Rockies	8.7	5.9	15.5
N. Interior	10.5	3.1	15.9
Average	9.1	5.1	15.8
Standard deviation of an ecotype mean	.5	.5	.5
L.S.D. 5 percent level	2.0	2.2	2.1
L.S.D. 1 percent level	2.4	2.7	2.6

Date	August 1960	October 1960	October 1961
Grade 0	Yellow-green	Green	--
Grade 4	Intermediate	Light purple	--
Grade 8	Green	Intermediate	Dark green
Grade 12	Blue-green	Dark purple	Light green
Grade 16	Blue	--	Gray

level and accounted for 20 percent of the total variance. The interior seedlings were extremely uniform. One may suspect that the gray color is possibly a threshold trait, failing to develop beyond a certain point. The Columbia Plateau ecotype was separated from the rest of the interior population by having dark green to light green color. Half of the total variance was accounted for by differences among progenies. No climatic variable was found associated with variation among progenies except within the Columbia Plateau ecotype, where seedlings with dark green foliage seemed to be from areas with a long growing season and high annual precipitation. If the dark green foliage should have a higher efficiency in photosynthesis than light green or gray foliage, then dark green foliage may be a result of adaptation to higher temperature and precipitation. On the other hand, gray foliage may have higher reflection qualities and be important in reducing needle heating and moisture loss, therefore, seedlings from hot and dry interior regions have gray foliage.

Limber and border pine

This complex could be separated into two species by foliage color at the seedling stage. Seedlings of *P. flexilis* from areas in the north were light green the first year and green the second year. On the other hand, seedlings of *P. strobiformis* from Arizona-New Mexico, were dark green the frist year and blue-green the next year. Differences between species accounted for 89 and 86 percent of the total variance among provenance means at ages 1 and 2.

No differences among areas of origins within species were observed the first year but significant differences were found in *P. flexilis* the second year, possibly because the foliage was greenest the second year and color trait was expressed better (Table 2). A seedlot from the Uinta Mountains of Utah had exceptionally light green foliage. It was found that less than 6 percent of total variance was accounted for by differences among areas of origins within species.

Greener seedlings usually were taller and had longer needles. Foliage color may be associated with growth traits and therefore may be subjected to similar selection forces.

Douglas-fir

Seedlings from coastal Pacific Northwest had a uniform dark green color. Interior Douglas-fir seedlings from western Montana, Idaho, eastern Washingron, and northern Utah-Colorado were about the same color as coastal origins. Seedlings from central Montana were yellowish green, and those from southern Utah-Colorado, Arizona, New Mexico were blue. Difference between coastal and interior varieties was not significant but differences among ecotypes within regions were highly signif icant and accounted for 69 percent of the total variance among progeny means (Table 7).

The geographic variation pattern of foliage color in Douglas-fir seems to agree with the pattern for the average number of clear days per year. Seedlings with blue foliage were from areas with more than 160 clear days. Longer clear periods in the southern Rocky Mountains may favor blue foliage because it can preserve auxin by reflecting harmful blue light. One action of blue light which is of highest intensity at low latitudes and high elevations, is photo-destruction of auxin (Galston and Baker, 1949). On the other hand, blue light is necessary in photosynthesis and its beneficial effects on photosynthesis may overcome auxin photo-destruction in areas where light intensity and number of clear days are low. Thus, coastal and northern interior Douglas-fir may have become adapted to the action spectrum for photosynthesis and absorb mostly red and blue light in its yellow-green foliage.

Comparison between Species

A contrast between coastal and interior varieties was manifested in ponderosa pine. Coastal seedlings had yellow-green to green first-year summer color, dark green to gray second-year fall color, whereas, interior seedlings were green to blue-green at first and gray later. Interior ponderosa pine seedlings also developed purple coloration the first fall. No significant difference was found between coastal and interior Douglas-fir.

Within the coastal variety, ecotypic differences in foliage color were found in ponderosa pine but not in Douglas-fir. Ponderosa pine seedlings from Columbia Plateau had dark green foliage, whereas, those from California were gray in the second fall.

Within the interior region, all three species varied among ecotypes. First-year seedlings of ponderosa pine from Utah, Colorado, Arizona and New Mexico had a dark purple color. Foliage of limber pine was the bluest for seedlings from Arizona-New Mexico. In Douglas-fir, the bluest seedlings were from southern Utah-Colorado, Arizona and New Mexico.

Variation among provenances within ecotype was great for Douglas-fir, intermediate for ponderosa pine, and small for limber pine. Foliage color seemed to be associated with height growth. Tall origins uaually had a blue-green or dark green color, and shorter seedlings usually were yellow-green or light green.

Table 10. Bud dormancy in ponderosa pine. (Data from Wells, 1964a).

Ecotypes	Trees with bud set at age 1(a)	Date of grow start second year(b)
	-percent-	-day in May-
COASTAL VARIETY		
California	1	16
Nevada	3	14
Oregon	4	16
Columbia	29	7
Average	9	14
INTERIOR VARIETY		
S. Rockies	4	12
Cent. Rockies	12	8
N. Interior	38	3
Average	15	8
Standard deviation of mean of an ecotype	2.9	.8
L.S.D. 5 percent level	12.8	3.4
L.S.D. 1 percent level	14.5	4.2

(a) Between-variety and between-ecotype-within-variety differences were not significant and significant at the 0.1% level and accounted for 0 and 70 percent of the total variance, respectively.

(b) Between-variety and between-ecotype-within-variety differences were significant at the .1% level and accounted for 36 and 43 percent of the total variance, respectively.

DORMANCY OF BUDS

Ponderosa Pine

In the percent of 1-year seedlings forming terminal buds in the fall of 1960, Well's found no significant difference between coastal and interior varieties. In each variety the most northern ecotype set buds earliest (Wells 1964a).

Within the coastal variety, early bud set was associated with low annual precipitation, low January temperature and wide temperature range at the place of origin. Northern seedlings with early bud set were hardiest in Michigan. Late bud set may be favored in places with milder winters and more abundant moisture.

Within the interior variety, early bud set was associated with high average July temperature and low summer precipitation, indicating that water economy may be a major factor. Date of growth initiation was recorded in May 1961.

The interior variety started growth earlier than the coastal variety, which difference accounted for 36 percent of the total variance. In each variety northern trees started growth earliest (Table 10).

Thirty and 21 percent of the total variance was accounted for by variation within ecotype in date of bud set and start of growth, respectively. The California and the Southern Rocky Mountain ecotype was variable. This may indicate the central Rockies as the center of distribution, following the "center of distribution-center of variation" hypothesis. In a boundary area with extreme environmental factors, individuals have to be specifically adapted to a niche which they occupy, whereas, near the more favorable center of distribution individuals can be more variable and survive.

Seedlings from areas with late killing frost started growth early in Michigan and those from areas with early killing frost started late. This indicates that timperature rather than day-length is responsible for time of growth initiation.

Limber border pine

Terminal bud formation was observed on the 1-year old seedlings in the nursery by Steinhoff (1964). The average date ranged from mid-August to mid-September among limber pine seedlots and from mid-September to mid-October among border pine seedlots. The difference between the two species accounted for 81 percent of the total variance.

Differences among areas of origin within species were not significant except for one isolated stand in SE. Wyoming and SW. Nebraska with especially late bud set (Table 2). The average January temperature in this stand was 25° F., as compared to 10°-20° F. in the main distribution of limber pine in the northern and central Rocky Mountains. Thus, selection and isolation may have caused this stand to differentiate from the main body in time of the bud set.

Of the total variance, 15 percent was accounted for by difference among seedlots within an area of origin. Seedlings from Montana, Wyoming and Utah, which were accustomed to early bud set, went into dormancy early in Michigan, even under favorable growing conditions. Date of bud set in Michigan was about two weeks ahead of the average date for the first killing frost at the place of origin. It may be argued that bud set in these species is triggered by day-length prior to the onset of cold, this might reduce the probability of damage from killing frosts in the native habitat. It seems unlikely that bud set was triggered by the temperature regime in southern Michigan where mid-August is normally far from the date of the first killing frost. Vaartaja (1959) postulated that buds induced by short photoperiods have a greater safety margin against frost damage than those induced by low temperatures.

Douglas-fir

Date of bud set was recorded in the fall of 1962 on 1-year old seedlings. Coastal Douglas-fir set buds from early September to mid-October, interior trees from mid-August to mid-October.

The interior variety was significantly more variable (.1% level) than the coastal. Differences among ecotypes were significant but accounted for only 5 percent of the total variance. Two seedlots from Deschutes National Forest in eastern Oregon set buds one month earlier than seedlots from the western Cascades. Within the interior region, seedlings from southern Colorado-Utah set buds three weeks earlier than those from north. Arizona-New Mexico trees went into dormancy three weeks earlier than those of southern Colorado-Utah (Table II).

Less than 0.3 percent of the total variance was accounted for by variation within ecotype.

In nursery studies in New Zealand, date of bud set in Douglas-fir may be associated with the average date of the first killing frost at the place of origin (Sweet 1965). In my study, seedlings from Montana, Idaho, and Wyoming set buds a month before the first autumn frost at the place of origin. This was reduced to two weeks for the rest of progenies. Cold winters in the northern interior region may require more time for cold acclimatization.

Interior progenies burst buds earlier in April 1963 than coastal ones. Difference between varieties and among ecotypes within varieties

Table 11. Beginning and end of bud dormancy in Douglas-fir seedlings in southern Michigan.

Ecotypes	Date of bud set	Proportion of buds burst April 26, 1962
	-day of year-	-percent-
INTERIOR VARIETY		
S. Cent. Montana, Cent. Idaho & NW. Wyoming	222	45
W. Montana	224	55
NW. Montana, N. Idaho	230	50
E. Washington	233	50
N. Colorado-Utah	234	50
S. Colorado-Utah	254	20
N. Arizona-New Mexico, S Arizona-New Mexico.	278	3
Average	236	40
COASTAL VARIETY		
British Columbia W. Washington-Oregon	281	
E. Oregon	252	
Average	278	5
Standard error of an ecotype mean	1.3	3
L.S.D. 5 percent level	5.5	10
L.S.D. 1 percent level	6.5	15

accounted for 56 and 26 percent of the total variance respectively, both types of variation being significant. The trends were similar to those for time of bud set (Table 11).

Variation within ecotype accounted for 18 percent of the total variance. The significant differences among progenies within ecotype occurred from Colorado south. Other workers found variation in this trait but could not find strong correlation between bud burst and climate or geography of the seed source (Sweet 1964, Ching and Bever 1960, Morris, Silen and Irgens-Moller 1957). Early growth start may not be essential in Douglas-fir. For example, Irgens-Moller (1957) noted in 1955 that bud bursting of young Douglas-fir seedlings in western Oregon occurred in late April; whereas, at 4000 feet elevation of the Cascade Range, it did not occur until the middle of June. Up to three weeks delay in bud burst was found in older trees. The average date of the last killing frost in the above seed sources was at least one month ahead of the date of bud burst.

One may postulate that bud burst in Douglas-fir is less affected by environment than by physiological condition of the trees and especially by the activities which go on during the winter rest period. I found the time of bud burst was related to the time of bud set. A test of rank-correlation of Sweet's data showed that progenies with early bud set also resumed growth early.

Comparisons among Species

Differences in date of bud burst between coastal and interior varieties were evident in two species but larger in Douglas-fir than in ponderosa pine.

In the date of bud set, varietal differences were found in Douglas-fir but not in ponderosa pine. The coastal variety of Douglas-fir set buds the latest.

Within the coastal varieties of ponderosa pine and Douglas-fir, seedlings from colder regions set buds and started growth earliest.

All three species showed significant difference among interior ecotypes. Seedlings of ponderosa pine and Douglas-fir from Arizona and New Mexico were very late in the date of bud set and bud burst. In border-limber pine this was also true (data on bud set only). In ponderosa pine and Douglas-fir, but not in limber pine, seedlings from southern Utah and Colorado were later in the date of bud set and bud burst than those from farther north.

The major variance component in Douglas-fir was between coastal and interior varieties, but in ponderosa pine it was between ecotypes within varieties. In limber-border pine, represented only from the interior, the major differences were between species.

Seedlings of all species from areas with warm climates were late in time of bud set and bud burst. Bud set may be induced by photo-period and bud burst by temperature.

SEPARATION OF ECOTYPES BY SEEDLING CHARACTERISTICS

Variance component analysis indicate that differences among varieties, and differences among ecotypes within varieties account for the major portion of the total variance in all three species (Table 12-14). Two other lines of evidence suggest that ecotypes seem to be appropriate when describing the variation pattern of the three species. First, there is little or no overlapping in many traits. Second, by considering several traits simultaneously, the sums of difference between seedlots within the same ecotypes are smaller than those of adjacent ecotypes (Table 15-20). Keys to the principal ecotypes as judged by performance in southern Michigan follow:

Pinus ponderosa

A. Winter injury severe to light, secondary needle length from 10 to 14 centimeters, yellow-green to green summer foliage.
. . . . var. ponderosa (Coastal)

A_1 Dark green foliage in fall, light winter injury, early bud set and bud burst.
. . . . Columbia Plateau ecotype

A_2 Gray foliage in fall, severe winter injury, late bud set.
. . . . California ecotype

B. Winter injury light of none, secondary needle length from 13 to 19 centimeters, green to blue-green summer foliage.
. . . . var. scopulorum (Interior)

B_1 Light winter injury, late bud set and bud burst.

Table 12. Variance component for characters of ponderosa pine.

	Character												
Variance component	Winter injury at			Height at				Needle length at	Foliage color in			Bud set at	Bud burst at
	Nurs. age 2	Russ age 4	Kell. age 7	Nurs. age 1	Nurs. age 2	Russ age 4	Kell. age 7	age 2	1960 in Aug.	1960 in Oct.	1961 in Oct.	Nurs. age 1	Nurs. age 2
							----percent----						
Between varieties	62	7	34	9	0	0	0	66	84	75	20	0	36
Among ecotypes within varieties	34	21	44	39	37	40	64	8	2	5	50	70	43
Among seedlots within ecotype	4	72	23	52	63	60	36	26	14	20	30	30	21

Table 13. Variance components for characters of limber-border pine.

Variance component	Characters			
	Height	Needle length	Foliage color	Bud set
	----percent----			
Between species	92	95	89	81
Among ecotypes within variety	3	2	2	4
Among seedlots within ecotype	4	3	9	15

Table 14. Variance components for characters of Douglas-fir.

Variance component	Characters						
	Winter injury	Height		Needle length	Foliage color	Bud set	Bud burst
		age 1	age 3				
				----percent----			
Between varieties	91	72	33	2	0	95	56
Among ecotypes within variety	1	18	46	55	69	5	26
Among seedlots within ecotype	8	10	22	43	31	0	18

Table 15. Degree of similarity between progenies from the Pacific Coast variety (*Pinus ponderosa* var. *ponderosa*) of ponderosa pine. (Table from Wells, 1964a)

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

Table 16. Degree of similarity between progenies from the Interior variety (*Pinus* *ponderosa* var. *scopulorum*) of ponderosa pine. (Table from Wells, 1964a)

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 Aris.																									
2012	7	1	0	4	0	0	0	2	2012 Aris.																								
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 17. Degree of similarity between stand-progenies from limber pine (Pinus flexilis). Table from Steinhoff, 1964)

Progeny, state, or province		Total difference (in summation-units)[a] between progeny listed below and progeny on left.																																													
2992	Alta.	2992
3002	Alta.	0	3002
2825	Alta.	0	0	2825
2846	Mont.	0	0	0	2846
2856	Mont.	0	1	0	0	2856
2579	Mont.	2	3	1	2	3	2579
2697	Mont.	0	0	0	0	0	1	2697
977	Mont.	0	0	0	0	0	2	0	977
990	Mont.	0	0	0	0	0	2	0	0	990
967	N. Dak.	0	2	0	0	0	4	2	0	2	967
2929	Wyo.	0	0	0	0	0	5	1	0	1	0	2929
2971	Wyo.	0	2	0	0	0	2	0	0	0	0	0	2971
2964	Wyo.	0	0	0	0	0	5	0	0	0	0	0	0	2964
1085	Idaho	0	2	0	0	0	7	2	0	2	0	0	1	0	1085
907	Idaho	6	9	7	7	5	11	9	6	9	3	4	6	2	2	907
2590	Idaho	9	11	9	9	8	15	13	8	11	4	5	8	8	4	0	2590
2819	Idaho	0	0	0	0	0	2	0	0	0	1	0	0	0	1	7	9	2819
2909	Wyo.	2	0	2	2	3	4	1	2	1	4	2	4	2	4	12	13	1	2909
2765	Utah	0	0	0	0	1	3	0	0	0	2	0	1	0	2	7	10	0	0	2765
1059	Utah	1	1	0	0	0	5	1	0	1	0	0	0	0	2	5	5	2	3	1	1059
1030	Utah	0	3	1	1	0	6	3	0	3	0	0	1	0	0	2	3	1	5	2	0	1030
930	Utah	2	1	1	1	0	6	1	0	1	0	0	1	0	0	7	6	0	3	2	0	0	930
1006	Utah	1	5	2	2	2	7	5	0	5	2	2	2	1	0	1	1	2	7	4	1	0	1	1006
1041	Utah	0	1	0	0	0	2	0	0	0	0	0	1	0	0	7	9	0	3	1	0	1	0	3	1041
2553	Nebr.	3	5	2	3	3	8	6	1	4	0	0	2	2	0	3	3	3	7	3	5	0	5	0	3	2553
2563	Wyo.	6	12	8	9	8	11	14	8	12	4	2	6	7	3	0	1	6	14	8	6	3	7	0	8	1	2563
2724	Calif.	1	0	2	1	3	2	1	1	1	4	2	4	1	4	12	14	1	0	1	2	5	6	8	4	9	15	2724
2546	Colo.	0	2	1	1	1	6	2	1	2	0	0	3	0	0	3	5	0	4	1	0	0	0	1	1	2	3	5	2546
2919	Colo.	0	0	0	0	0	3	0	0	0	0	1	0	0	1	7	12	0	2	0	0	1	0	3	0	4	13	2	2	2919
2522	Colo.	2	0	2	2	3	3	1	2	1	4	3	4	2	5	13	14	1	0	0	4	5	3	8	3	9	13	0	5	2	2522
922	Colo.	0	0	0	0	0	4	0	0	0	1	0	1	0	1	8	9	0	1	0	0	1	0	3	0	3	9	0	0	0	1	922
909	Colo.	0	0	0	0	0	5	1	0	0	0	0	1	0	0	3	3	0	2	0	0	0	0	1	0	2	7	1	0	0	2	0	909
2523	Colo.	0	0	0	0	0	3	0	0	0	0	0	1	0	0	7	8	0	2	0	0	1	0	3	0	3	9	0	1	0	2	0	0	2523
2509	Colo.	0	0	0	0	0	4	0	0	0	1	0	1	0	1	8	9	0	1	0	0	2	0	4	0	3	8	0	1	0	1	0	0	0	2509
2601	Colo.	0	2	0	0	0	4	2	0	2	0	0	0	0	0	3	4	1	4	2	0	0	0	0	0	0	3	3	0	0	5	1	0	0	1	2601
2987	Colo.	0	0	0	0	0	5	1	0	1	1	0	0	0	1	6	6	0	1	0	0	1	0	1	0	1	5	0	0	1	2	0	0	0	0	1	2987-
916	Colo.	0	2	4	1	0	7	2	0	2	0	1	4	2	0	3	4	0	4	1	0	0	0	0	1	1	3	3	0	4	7	3	0	2	4	0	0	916
2978	Colo.	0	2	0	0	0	5	3	0	2	0	2	1	0	5	5	2	1	5	2	0	0	0	0	0	0	1	5	0	1	5	1	0	0	1	0	1	0	2978
902	Colo.	5	8	6	7	5	10	9	4	8	2	4	2	3	2	1	2	3	11	6	5	2	6	1	5	0	0	11	3	7	12	5	5	5	5	3	4	3	0	902
2900	Utah	3	5	4	4	2	9	6	2	6	1	1	4	3	0	0	1	4	8	4	2	0	5	0	3	1	0	9	0	5	9	7	3	4	1	0	2	0	0	0	2900
2652	Utah	2	6	4	5	3	7	8	2	6	0	1	2	2	0	1	2	3	8	4	3	0	3	0	2	0	0	9	1	6	12	5	2	4	4	0	2	0	0	0	0	2652
2877	Utah	5	7	4	5	6	8	9	4	7	1	0	4	2	1	1	1	4	8	6	3	1	3	0	6	3	0	12	2	8	9	4	2	5	4	2	1	1	0	0	0	0	2877
2796	Colo.	8	13	10	11	11	13	14	10	12	5	4	7	8	4	2	2	7	14	10	8	4	9	2	11	1	0	16	6	10	18	10	9	10	11	6	5	3	2	0	0	0	1	2796
2599	Colo.	10	10	9	10	10	13	14	8	12	3	5	7	8	3	0	1	8	13	9	8	2	7	1	10	1	0	16	4	12	15	8	7	10	10	4	5	3	1	0	0	0	0	0	2599
2612	N.Mex.	8	13	10	10	10	13	12	10	12	5	6	6	9	5	2	5	8	16	10	10	6	11	2	11	0	1	16	10	12	16	12	11	11	12	7	6	7	3	0	0	0	1	1	0	2612
903[b]	Ariz	31	37	34	36	34	36	37	38	38	26	34	26	34	23	16	15	26	30	32	31	27	31	19	36	16	12	30	29	34	42	36	33	34	34	26	27	25	21	12	15	13	14	10	13	15	903

a. Summation-unit = $\sum 4(\text{Actual difference} - LSD_{.05}) / LSD_{.05}$ for 11 different characters.

b. *Pinus strobiformis* stand included for comparative purposes.

Table 18. Degree of similarity between stand-progenies from border pine (Pinus strobiformis) and two limber pine (Pinus flexilis) stand-progenies. (Table from Steinhoff 1964).

Progeny, State	Total differences for seedling characteristics in summation-unit[a] between progeny listed below and progeny on the left.																
	Pinus flexilis																
2599 Colo.	2599																
2612 N. Mex.	0	2612															
			Pinus strobiformis														
903 Ariz.	13	15	903														
904 Ariz.	15	13	0	904													
2569 Ariz.	23	22	1	2	2569												
2805 Ariz.	21	17	0	0	0	2805											
1023 Ariz.	28	28	4	5	0	0	1023										
2739 Ariz.	45	38	10	15	0	3	0	2739									
2621 Ariz.	30	28	0	5	0	0	0	1	2621								
2743 Ariz.	24	20	0	0	0	0	0	0	0	2743							
2755 Ariz.	16	12	0	0	1	0	0	2	2	2	2755						
2751 Ariz.	26	26	6	6	0	0	0	1	0	0	0	2751					
2763 Ariz.	39	35	12	11	1	1	0	0	3	0	1	1	2763				
932 N. Mex.	21	15	0	0	0	0	0	4	0	0	0	0	3	932			
2649 N. Mex.	33	30	7	7	0	0	0	0	0	0	3	1	0	0	2649		
905 N. Mex.	26	23	4	1	0	0	0	0	0	0	0	0	0	0	0	905		
2939 N. Mex.	29	24	0	5	0	0	0	7	0	0	4	0	8	3	2	0	2939	
2647 Texas	33	30	6	7	0	0	0	0	0	0	0	0	0	0	0	0	0	2647

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[a] Summation-unit = 4 (actual difference - $LSD_{.05}$)/ $LSD_{.05}$ for 11 different characters.

Table 19. Degree of similarity between stand-progenies from the coastal variety (*Pseudotsuga menziesii* var. *menziesii*) of Douglas-fir.

	1633	1634	1617	1620	1623	1626	1627	1628	1629	1624	1621	1568	1569	1571	1618	1613	1622	1619	1585
BCO 1633	-																		
BCO 1634	5	-																	
WAS 1617	0	2	-																
WAS 1620	1	7	3	-															
WAS 1623	0	6	2	1	-														
WAS 1626	0	3	2	1	0	-													
WAS 1627	0	1	1	2	1	0	-												
WAS 1628	0	4	2	1	0	0	0	-											
WAS 1629	0	9	3	1	0	0	2	0	-										
ORE 1624	0	7	2	1	0	0	0	0	0	-									
ORE 1621	0	6	2	1	0	0	0	0	0	0	-								
ORE 1568	1	4	1	4	5	1	4	2	2	4	4	-							
ORE 1569	0	3	2	0	2	2	2	2	2	2	3	2	-						
ORE 1571	2	2	4	0	2	2	2	2	2	2	2	2	0	-					
ORE 1618	3	2	4	3	2	2	4	2	2	4	2	2	2	3	-				
ORE 1613	3	2	4	3	2	2	4	2	2	4	2	2	3	3	0	-			
ORE 1622	0	6	2	1	4	0	1	0	0	0	0	4	2	2	2	1	-		
ORE 1619	0	1	2	3	2	0	0	4	0	0	0	4	2	2	0	3	1	-	
ORE 1585	10	12	10	11	11	13	10	9	11	16	13	14	9	9	8	14	13	11	-
ORE 1586	10	12	13	11	13	13	13	10	10	13	12	14	10	10	11	13	13	13	0

Table 20. Degree of similarity between stand-progenies from the interior variety (*Pseudotsuga menziesii* var. *glauca*) of Douglas-fir.

	1635	1636	1637	1638	1639	1640	1641	1642	1643	1644	1538	1529	1536	1532	1535	1630	1550	1601	1537	1609	1605	1530	1531	1525	1592	1528	1604	1611	1625	1610	1608	1546	1602	1594	1614	1543	1647	1544	1545	1542
COL 1635	-																																							
COL 1636	0	-																																						
COL 1637	0	0	-																																					
COL 1638	0	0	0	-																																				
COL 1639	0	1	0	1	-																																			
COL 1640	0	0	0	0	0	-																																		
COL 1641	0	0	0	0	2	0	-																																	
COL 1642	0	0	0	0	1	0	0	-																																
COL 1643	9	8	2	9	5	8	10	9	-																															
COL 1644	0	1	0	1	0	0	1	1	2	-																														
COL 1538	4	6	2	2	3	6	6	2	12	7	-																													
COL 1529	0	0	0	3	4	4	0	2	12	5	1	-																												
COL 1536	7	10	4	8	4	6	8	8	7	2	13	12	-																											
COL 1532	2	4	0	0	1	4	4	0	7	4	0	0	9	-																										
COL 1535	5	10	4	3	6	8	2	4	4	5	6	6	10	1	-																									
COL 1630	0	7	0	0	3	2	2	0	9	2	2	0	11	0	3	-																								
UTA 1550	1	4	0	2	0	2	2	4	0	0	6	4	5	0	3	1	-																							
UTA 1601	0	0	0	0	1	0	0	0	12	1	6	5	8	4	8	4	4	-																						
COL 1537	0	0	0	0	2	0	0	0	12	1	4	2	8	2	6	0	2	0	-																					
COL 1609	8	9	4	6	5	4	4	4	5	1	14	14	9	9	15	11	4	4	7	-																				
COL 1605	2	12	8	10	9	8	8	8	15	5	18	16	14	12	18	13	8	8	10	0	-																			
COL 1530	4	0	4	4	4	0	0	4	13	0	10	8	8	8	15	6	0	0	2	0	0	-																		
COL 1531	6	4	8	8	10	4	4	8	19	5	14	12	14	12	19	10	4	4	6	0	0	0	-																	
COL 1525	0	0	0	0	2	0	0	0	10	5	12	9	9	2	9	0	0	0	0	6	6	2	6	-																
COL 1592	9	12	11	13	10	9	13	15	6	4	24	21	8	15	17	16	13	9	14	7	7	8	7	12	-															
COL 1528	0	0	0	0	2	0	0	0	11	1	6	4	8	4	10	2	0	0	0	1	4	0	4	0	11	-														
COL 1604	8	8	8	10	10	8	8	12	13	4	19	18	10	12	18	8	9	8	10	2	0	4	4	8	8	4	-													
UTA 1611	6	2	6	6	7	2	2	6	14	3	12	10	12	10	15	8	2	2	4	0	0	0	0	4	7	2	4	-												
ARI 1625	2	2	5	3	6	1	3	2	8	1	12	9	12	7	8	4	3	0	2	1	2	4	5	2	7	3	4	0	-											
NME 1610	6	6	6	8	7	6	10	13	3	16	15	12	10	19	10	8	6	2	8	0	0	0	0	2	7	0	3	0	0	-										
NME 1608	2	2	4	4	6	2	3	6	12	10	14	12	12	10	14	0	3	2	4	0	0	2	1	3	7	1	3	0	0	0	-									
NME 1546	14	18	18	21	18	18	19	22	18	12	29	28	24	22	28	25	16	17	20	4	4	11	8	3	11	14	3	8	12	4	6	-								
NME 1602	15	15	16	17	17	16	16	16	17	13	25	24	22	18	29	21	16	16	17	0	1	5	5	15	12	7	1	6	8	0	3	3	-							
NME 1594	6	8	4	7	4	8	9	8	8	4	10	10	14	5	11	9	8	8	9	4	8	8	13	13	14	5	4	15	6	6	6	8	9	-						
NME 1614	9	11	12	14	13	10	13	15	17	11	21	21	19	14	25	15	12	12	14	0	0	2	3	6	8	7	2	2	4	0	0	5	0	8	-					
ARI 1543	8	10	6	9	7	12	11	10	13	7	16	16	17	10	13	7	16	10	10	0	4	6	10	12	12	6	3	6	8	2	2	4	4	0	6	-				
ARI 1647	7	6	7	9	8	10	7	10	11	5	19	15	13	11	21	10	7	9	9	2	0	0	0	9	5	3	1	0	2	0	0	7	0	7	1	5	-			
ARI 1544	7	12	6	13	6	7	13	10	15	4	20	20	8	13	17	16	12	10	13	4	4	6	11	6	2	9	4	7	8	4	0	4	6	5	6	4	3	-		
ARI 1545	8	8	9	11	9	10	9	12	10	4	20	19	15	12	20	15	8	8	11	0	0	6	6	11	7	6	2	4	4	0	2	0	0	4	0	0	1	2	-	
ARI 1542	11	13	6	12	5	8	14	14	15	7	22	18	8	12	19	12	14	14	14	8	11	7	13	10	2	10	6	11	11	9	7	9	11	6	11	7	7	0	5	-
ARI 1593	2	4	3	4	3	12	5	6	7	2	14	11	11	6	14	6	5	4	4	0	2	0	2	2	6	1	0	0	0	0	0	2	2	2	0	0	3	0	0	6

. . . . .Southern Rocky Mountain ecotype

B_2 No winter injury, early bud set and bud burst.

. . . . Central Rocky Mountain ecotype

B_3 No winter injury, very early bud set and bud burst.

. . . . Northern interior ecotype

Pinus strobiformis - Pinus flexilis

A. Fast growth rate, secondary needle length 51 to 86 mm. blue-green foliage, late bud set.

. . . . P. strobiformis

A_1 Secondary needles 51 to 56 mm. long.

. . . . N. New Mexico-Arizona

A_2 Secondary needles 58 to 86 mm. long.

. . . . Cent. & SE. Arizona

A_3 Secondary needles 53 to 69 mm. long.

. . . . S. New Mexico-NW. Texas

B. Slow to medium growth rate, secondary needle length is 23 to 36 mm., yellow-green to dark green foliage, early bud set. Very little variation among seedlots. Seedlots grouped by area of origin are recognizable, but not significantly different.

. . . . P. flexilis

Pseudotsuga menziesii

A. Severe winter injury, very fast height growth in the first year only, green foliage, late to very late bud set and bud burst.

. . . . var. menziesii (Coastal)

A_1 Late bud set and bud burst.

. . . . Eastern Cascade ecotype

A_2 Very late in bud set and bud burst.

. . . . . Western Oregon and western Washington ecotypes

B. Light to no winter injury, slow to medium height growth, yellowish-green to blue foliage, late to very early bud set and bud burst.

. . . . var. <u>glauca</u> (interior)

B_1 Light winter injury, fast growth rate, very long needles, blue foliage, very late bud set and bud burst.

. . . . S. Arizona-New Mexico ecotype

B_2 Slight winter injury, medium growth rate, long needles, blue foliage, late bud set and bud burst.

. . . . S. Utah-Colorado & N. Arizona-New Mexico ecotype

B_3 No winter injury, very slow growth rate, short needles, green foliage, early bud set and bud burst.

. . . . N. Utah-Colorado ecotype

B_4 Slight winter injury, slow growth rate, short needles, green foliage, early bud set and bud burst.

. . . . .Okanogan Highland

B_5 Slight winter injury, medium growth rate, long needles, green foliage, very early bud set, early bud burst.

. . . . Bitteroot Range ecotype

B_6 Slight winter injury, slow growth rate, short needles, green foliage, very early bud set, early bud burst.

. . . . N. Continental Divide ecotype

B_7 No winter injury, very slow growth rate, short needles, yellowish-green foliage, very early bud set and bud burst.

. . . . Northern Interior

GEOGRAPHIC DISTRIBUTION OF THE ECOTYPES

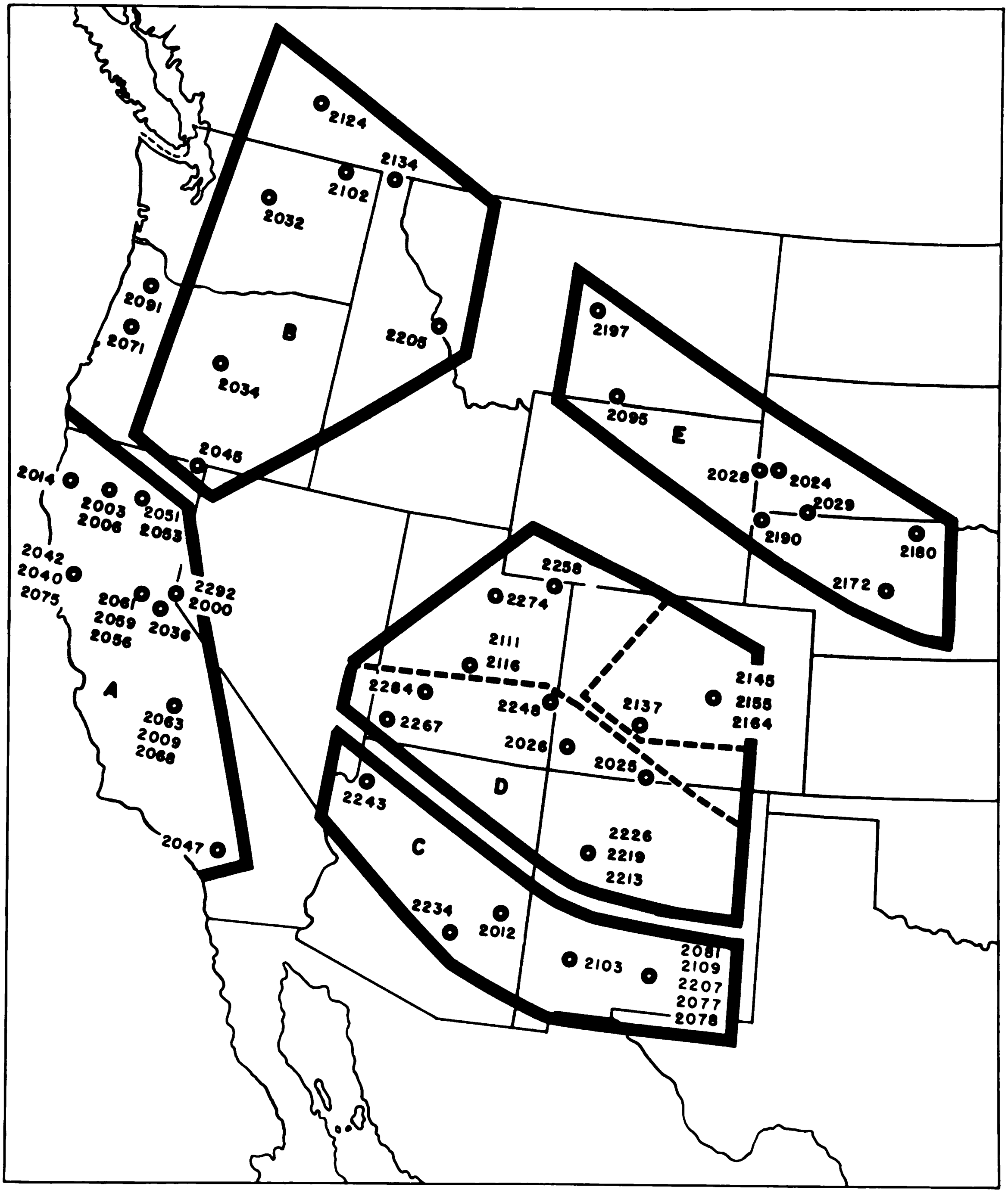
Ponderosa pine. -- The geographic boundaries among ecotypes of ponderosa pine seedlings are shown in Figure 4. The California ecotype is separated from the Rocky Mountain ecotype by the arid belt to the east of the Sierra Nevada Mountains. The boundary between the California and Columbia Plateau ecotypes possibly is the lower land area in northeastern California.

The northern Interior ecotype seems to be separated from the Columbia Plateau ecotype to the west by the Madison River of Montana; and separated from the Central Rocky Mountain ecotype to the south by the North Platte River. These two rivers describe the approximate boundaries. These rivers do not actually act as migration barriers, but the lower land areas in which they lie do. The lowland areas usually are arid, and therefore treeless. Little Colorado River in Arizona and the low valley approximately following the U. S. Route 66 in New Mexico may serve as a geographic boundary between Central Rocky Mountain ecotype and Southern Rocky Mountain ecotype. The ecological boundary here again may be due to the treeless zone in the lower land area.

These ecotype boundaries seem to be coincident with a steepening of the climatic gradients. The climatic regions in the western United States may be delimited chiefly on the basis of the seasonality of precipitation and the length of the growing season. These two climatic factors might be the major selection pressure responsible for the formation of these ecotypes.

Douglas-fir. -- Geographic boundaries among ecotypes of Douglas-fir are shown in Figure 6. The arid belt on the eastern slope of the Cascade probably serves as a boundary between the coastal Pacific Northwest

Figure 4. Ecotypic division of 60 stand-progenies of ponderosa pine grown for 2 years in East Lansing, Michigan. A=California, B=North Plateau, C=Southern Interior, D=Central Interior, E=Northern Interior. The dashed lines within the Central Interior ecotype indicate divisions that are less well-defined than the primary ecotypic division. Two seedlots MSFG 2091 and 2071 may be considered as Willamette Valley ecotype but they show close resemblance to some California seedlots. (Map by Wells, 1964a)



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
2267
2248
2137
2145
2155
2164
2026
2025
2243
D
C
2226
2219
2213
2234
2012
2103
2081
2109
2207
2077
2078

Figure 5. Ecotypic division of 62 stand-progenies of limber-border pine grown for 2 years in East Lansing, Michigan. (Map by Steinhoff, 1964)

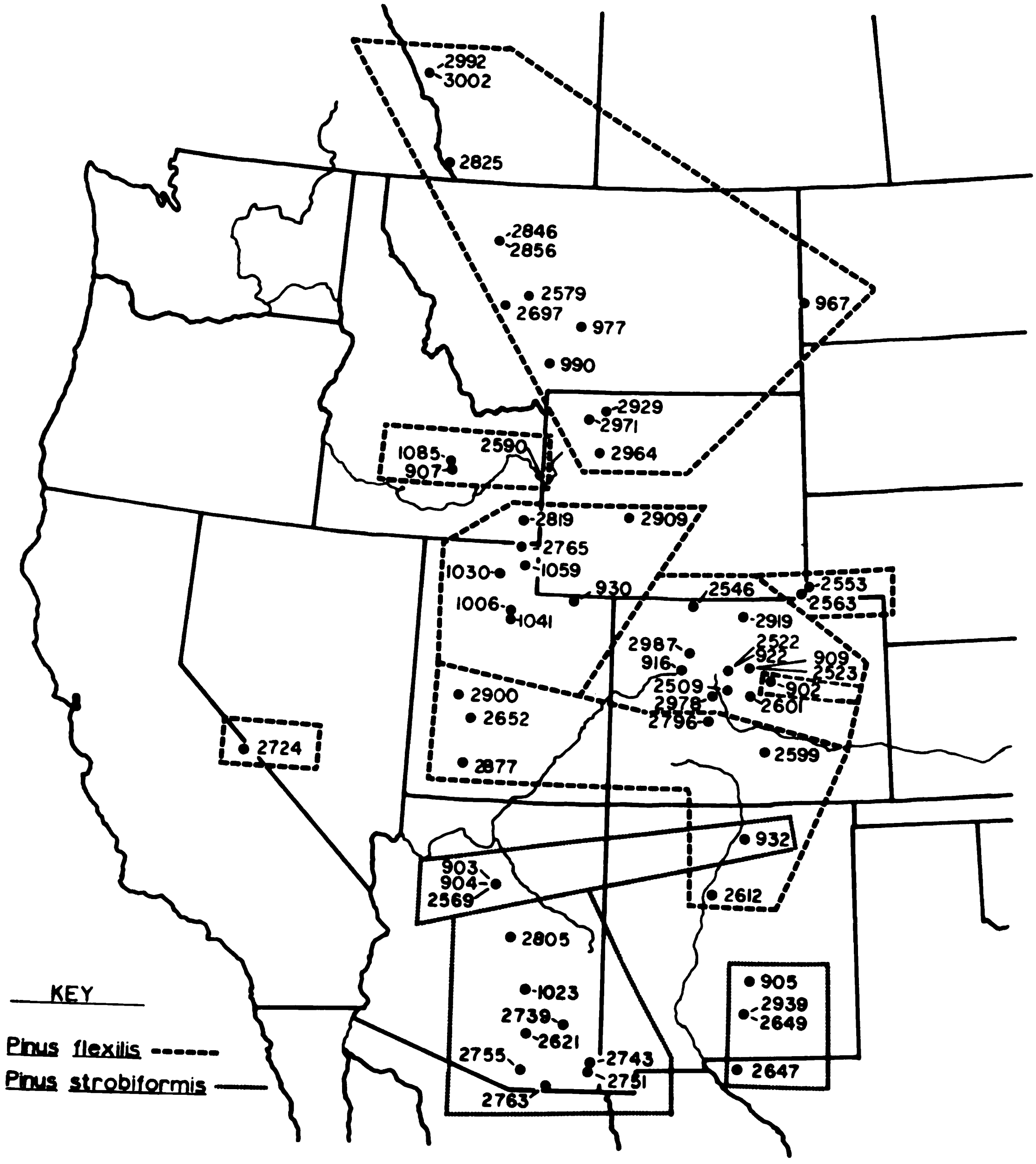
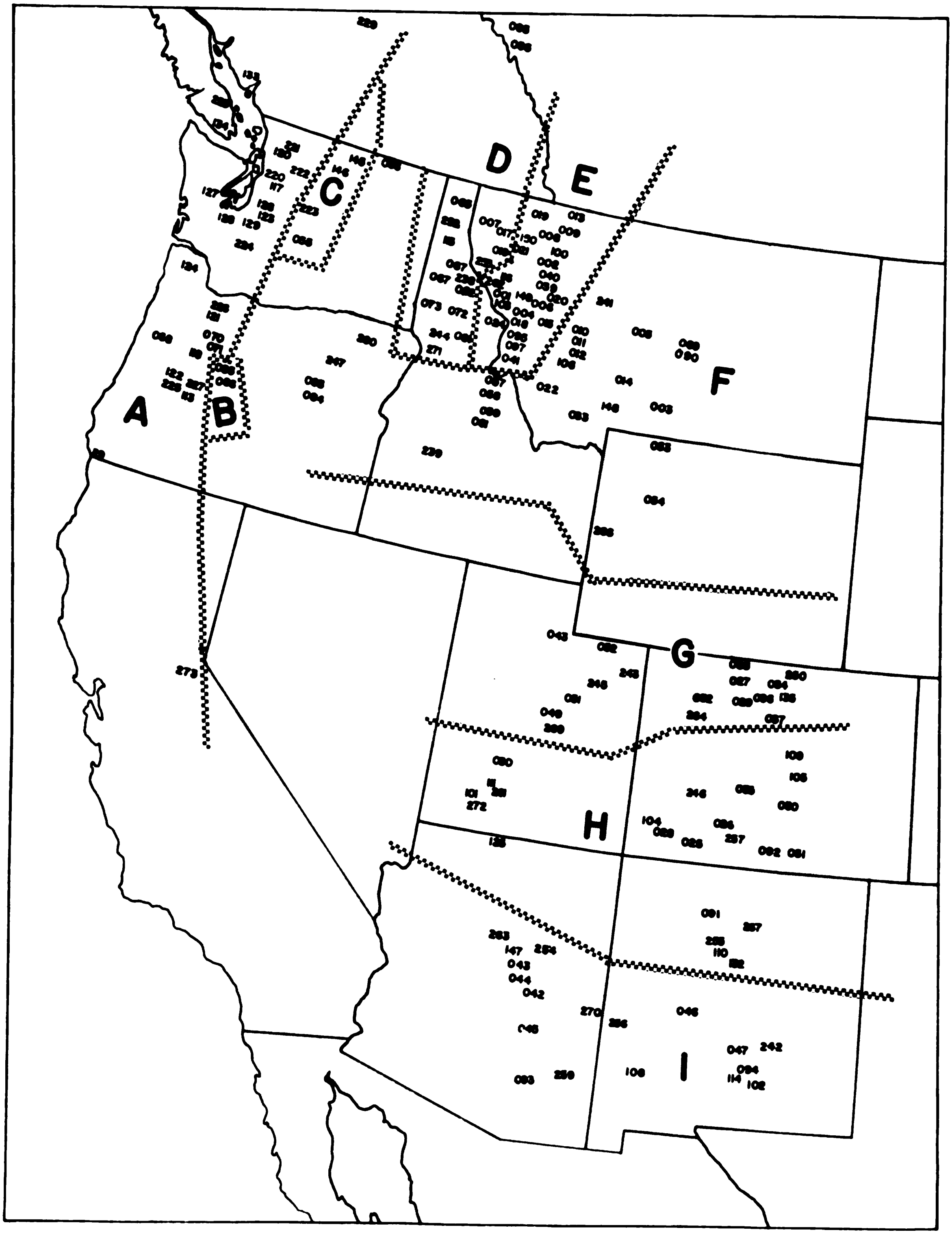

2992
3002
2825
2846
2856
2579
2697
977
990
967
2929
2971
2964
1085
907
2590
2819
2909
2765
1059
1030
930
1006
1041
2546
2553
2563
2919
2987
916
2522
922
909
2523
902
2509
2978
2601
2796
2900
2652
2599
2724
2877
932
903
904
2569
2612
2805
905
2939
2649
1023
2739
2621
2755
2743
2751
2763
2647
KEY
Pinus flexilis ------
Pinus strobiformis ——

Figure 6. Ecotypic division of 128 stand-progenies of Douglas-fir grown for 2 years in East Lansing, Michigan. A=Coastal Pacific Northwest, B=E. Cascade, C=Okanogan Highland, D=Bitteroot Range, E=N. Continental Divide, F=Northern Interior, G=N. Colorado-Utah, H=S. Colorado-Utah & N. Arizona-New Mexico, I=S. Arizona-New Mexico. Seedlot numbers from 001 through 150 on this map represent MSFG number 1501 through 1650 respectively. Seedlot numbers from 221 through 273 represent PA number 21 through 73 respectively.


A
B
C
D
E
F
G
H
I
220
117
127
122
222
223
146
134
070
073
072
244
271
247
007
017
130
100
002
040
020
004
041
022
014
241
239
273
043
246
248
049
101
272
104
257
081
091
110
263
147
254
044
042
270
242
047
114
102
108

ecotype and the interior ecotypes to the east. The eastern Cascade ecotype may be separated from the coastal Pacific Northwest ecotype by the summit of the Cascade Mountain. The moisture-bearing air masses off the Pacific Ocean deposit much of their moisture while being lifted up by the western slope; on the eastern slope of the Cascade Mountain they contribute much less, producing a rain shadow. Therefore, this climatic dividing line may also serve as a geographic boundary between the eastern Cascade and the western Pacific Northwest ecotypes.

The Salmon River on the south, the Flathead River on the east, and the eastern Washington desert on the west approximately outline the boundaries for the Bitteroot Range ecotype. Areas lying within these boundaries have an average elevation two thousand feet lower than areas to the east and south. Thus, while the rivers may act as boundaries, the actual limits are of an elevational nature. The Continental Divide which separates eastern and western slopes into two different precipitation zones in Montana, may serve as the boundary between the northern Continental Divide and Northern Interior ecotype.

The northern boundary of the N. Colorado-Utah ecotype is the desert area along the Snake River of southern Idaho and the treeless area in the Wyoming basin. The boundary between N. Colorado-Utah and S. Colorado-Utah ecotype may run through Rampart Range and San Juan Mountain in Colorado, then follow approximately 38° north parallel through Utah. The geological or ecological cause of this boundary, however, is not clear.

As in ponderosa pine, the treeless zone along Route U. S. 66 serves as a boundary between the S. Colorado-Utah ecotype and the Arizona-New Mexico ecotype. This treeless belt seems to separate two major continu-

ous distributions of Douglas-fir, namely those of the Gila Mountain in Arizona, and the San Juan Mountain-Sangre De Cristo Range in Colorado and New Mexico.

Limber and border pine. -- The state-line of Arizona and New Mexico at 37° N. to the west of the Rio Grande River, and the southern edge of Sangre De Cristo Range, probably is the boundary between limber pine and border pine. However, the boundary may well be the lower valley along Route U. S. 66 which seems to separate ecotypes of the other two species.

Comparison between boundaries of species. -- Both Douglas-fir and ponderosa pine were able to differentiate into coastal and interior ecotypes. The boundary of the coastal ecotype is similar in both species.

Douglas-fir is more finely differentiated in the northern Rocky Mountain region than is ponderosa pine. However, the Continental Divide in Montana separates both Douglas-fir and ponderosa pine into distinct groups. Seedlings of two species from east of the Continental Divide showed very strong interior characteristics but those from west of the Continental Divide showed affinity to coastal seedlings.

The treeless areas along the Snake River in Idaho and the desert area in the Wyoming Basin separate both Douglas-fir and ponderosa pine into northern Rocky Mountain and central Rocky Mountain ecotypes.

The northern part of Colorado-Utah seems to have a different ecological environment than the southern part of Colorado-Utah, but the expression is much stronger in Douglas-fir than in ponderosa pine.

The limber-border pine complex shows an exceedingly strong break between the central and southern Rocky Mountains. The break is also strong in Douglas-fir and ponderosa pine. The Little Colorado River in Arizona and U. S. Routee 66 in New Mexico which runs through an arid belt with precipitation less than 15 inches, seems to serve as a common boundary for three species.

Moisture is a limiting factor to the distribution of all three species at low elevations and temperature is a limiting factor at high elevations. That may generally explain the isolation mechanism in the western U. S. Three major breaks (eastern foot hills of the Cascades and Sierra Nevadas, Snake River and the Wyoming Basin, Little Colorado River and the low valley along the U. S. Route 66) are caused by treeless zones which act as barriers to gene migration. On the other hand, too much precipitation, as found on the west slope Coastal Range and western slope of the Cascade, limits the distribution of ponderosa pine. Two seedlots from the Willamette Valley in western Oregon were very different from those of California and the Columbia Plateau. The isolation barrier in this case, is the pure Douglas-fir forest which is especially adapted to the moist climate.

The absence of ponderosa pine from the Yellowstone Park area breaks the link between northern and central Rocky Mountain, and the link between northern Rocky Mountain and northern Interior populations. Possibly, the Yellowstone area is too wet and too cold for ponderosa pine. Important limiting factors in ponderosa pine are moisture-temperature index, moisture ratios, the number of hot days, and the physiological summation of temperature (Livingston & Shreve, 1921). By comparing these limiting factors with climatic data of the Yellowstone Park area, one can easily find that this area is too wet and too cold for ponderosa pine to reproduce naturally.

The dissimilarity between two ecotypes can be related to the completness of isolation. Usually, the further two ecotypes are separated, the more complete the isolation and the less the similarity. According to the distribution map of ponderosa pine (Figure 1) isolation seems to be more complete on the west side of the Northern Interior ecotype than on the south. This ecotype was shrply delimited from the Central Rocky Mountain ecotype to the south, but less sharply delimited from the Columbia Plateau ecotype to the west (Table 16). On the other hand, the continuous distribution of Douglas-fir in Washington, British Columbia and Idaho probably is the transitional zone between coastal and interior varieties (Figure 3). Seedlings of Douglas-fir from this area had a growth rate and needle length similar to those of coastal seedlings, but their pattern of bud dormancy were similar to those of interior seedlings.

However, geographic distance is not a necessary indicator of similarity between provenances. In this study seedlings from the Colorado Springs area showed strange affinities to those from southern Utah. In ponderosa pine, seedlot MSFG 2145, 30 miles west of Colorado Springs was similar to MSFG 2248, 2284 and 2267 from southern Utah. In limber pine, seedlot MSFG 902, 20 miles north of Colorado Springs was similar to MSFG 2900, 2652, and 2877 from southwestern Utah. In Douglas-fir, seedlot MSFG 1609, 18 miles north of Colorado Springs was similar to MSFG 1601, 1611 and 1550 from Dixie National Forest in southern Utah. What causes this affinity is an interesting question. Long distance dispersal by bird or wind between Colorado Springs and southern Utah seems improbable. Genetic drift to the same genotype seems to be improbable. Selection forces certainly are different between Colorado Springs and southern

Utah. One possibility might be that these provenances had a common ancient ancestry and they failed to respond to the present eco-gradients.

Surely, one should not over-estimate the importance of isolation and under-estimate the necessity of selection. As S. Wright (1931) stated that "with regard to control of evolution, it is evident that little is possible either within a small stock or a freely interbreeding large one..... A rapid and non-self-terminating advance seems to be through subdivision of the population into isolated and hence, differentiating small groups, among which natural selection may be practiced." The major force of natural selection among three species is the climates. As one looks at the complexities of the mountain climates of the west, we find a vast range from very dry desert to temperate rain forest of little seasonal difference in moisture to strong winter maxima to bimaximal areas. Temperature-wise, the range is from a growing season of less than 40 days to more than 300 days. A characteristic of the region is that the broad general climates in the region are made heterogeneous with relief effects. The eco-genetic adjustments to be expected in any species ranging over such a complex region are marked. In many places relief-induced-treeless areas sharpen eco-genetic boundaries, partly by removing areas that would have been intermediate climatically and biologically, and partly by reducing gene exchange between the two. This treeless zone tends to make some ecotypes more clearly differentiated than they might otherwise be. Thus, selection and isolation together may spell speciation.

PROBLEM OF FINDING A REPRESENTATIVE SEEDLOT

After ecotypes have been delimited, one would like to ask "from what seedlot should the most representative specimen be taken?" It can easily be seen that almost any tree within a homogeneous group can be a specimen. On the other hand, no provenance in a perfect clime should be chosen as a representative. However, the most nearly typical specimen can be identified from "Summation-of-Differences" tables. The table compares one seedlot with all other seedlots in all traits simultaneously by units of least significant difference.

Two approaches may be used. The first is to find the origin with the most zeros when compared with all other origins. If we take the Southern Rocky Mountain ponderosa pine ecotype as an example, MSFG 2234 from Arizona and MSFG 2109 from New Mexico had the maximum number of zeros, 5 of 8 (Table 16). If the specimen is taken from either stand, it differs from only three other origins within the ecotype.

Another approach is to find the origin with the smallest total summation of differences when compared with all other origins. If we consider the same ecotype as before, MSFG 2109 has a total of 5 units, MSFG 2234 has 11 units and is therefore less typical.

The first approach is less laborious than the second one. But the second approach gives a better indication because it considers how much they differ. In most cases, similar results were obtained from either approach. Results from the first and the second approaches were summarized in Tables 21 and 22 respectively.

Table 21. Seedlot number of the collection showing high similarity to the largest number of other seedlots from each area of three species.

Area	Species							
	Ponderosa pine			Limber-border pine		Douglas-fir		
COASTAL REGION								
Pacific Northwest	-	-	-	-	-	1633	-	-
California	2014	-	-	-	-	-	-	-
Columbia Plateau	-	-	-	-	-	-	-	-
INTERIOR REGION								
Northern interior	2190	-	-	-	-	-	-	-
Northern Rockies	-	-	-	977	-	1541	1517	1649
Central Rockies	2226	2284	2248	-	-	1610	-	-
Southern Rockies	2109	2234	-	2743	-	1545	-	-

Table 22. Seedlot number of the collection showing the most common characteristics from each area of three species.

Area	Species		
	Ponderosa pine	Limber-border pine	Douglas-fir
COASTAL REGION			
Pacific Northwest	--	--	1626
California	2014	--	--
Columbia Plateau	2102	--	--
INTERIOR REGION			
Northern Interior	2190	--	--
Northern Rockies	--	2929	1597
Central Rockies	2274	--	1610
Southern Rockies	2109	2743	1545

HOMOGENEOUS GROUPS OF PROVENANCES

The concept of ecotype in this study means an aggregation of neighboring provenances which are relatively uniform in comparison to provanances of other ecotypes. The uniformity is only relative, and differences exist among progenies within ecotypes. However, some groups of neighboring provenances have no significant differences among themselves, due to either of the following reasons:

1. In a homogeneous environment and under strong directional selection the provenances have reached the same adaptive peak.
2. In a heterogeneous environment, some lag between natural selection and genetic response exists among provenances with common ancestries. In other words, provenances may keep their family inheritance rather than change in response to small differences in selection pressure.

In Utah ponderosa pine, two such homogeneous groups occur, as follows: (1) High Plateau groups (MSFG 2267, 2284, and 2248). (2) Wasatch group (MSFG 2111, 2116 and 2274). In each of these groups, the seedlots were collected from isolated Utah stands with similar climates. One may postulate that ponderosa pine was once more abundant in Utah, but that changed climate forced it to retreat to refuges where moisture and temperature are within their tolerance limits. Thus, little differentiation might have been expected.

In Nebraska and South Dakota, the "Pine ridge" group (MSFG 2180, 2190 and 2029) seems to be an offshoot of the Black Hills ponderosa pine population. Possibly this group is a recent immigrant from the west. Potter and Green (1964) reported that ponderosa pine was present in western North Dakota no earlier than post-Kansan times. They found that invasion of ponderosa pine into sandy grasslands was common and that there was no evidence of retreat from the grasslands. Therefore, I suspect the Pine Ridge group may be a recent invader. If there is not enough time for natural selection, even though the "Pine Ridge" group intersects several climatic gradients (i.e. the average date of killing frost in the spring, the average annual precipitation, and the average depth of frost penetration), it may still have similar phenotypic expression.

In the limber-border pine complex, there are four such "homogeneous groups." (1) Yellowstone River group (MSFG 2964, 2971, and 2929 in Wyoming, MSFG 977 in Montana, MSFG 967 in North Dakota). These provenances are within the Yellowstone River drainage area. Seeds of limber pine may have been dispersed along the Yellowstone River sometime in the recent past. Natural selection may not have been strong enough to promote differentiation in a few generations. (2) White River Plateau group (MSFG 909, 922, 2523, 2987 from 9,900 to 10,600 feet elevation on the White River Plateau, Colorado). The environments are relatively uniform and near the upper distribution limit of limber pine in Colorado. Selection pressure has been strong in causing a "White River Plateau" type to develop but not in causing differences to develop within the area of the plateau. (3) Guadalupe Range group (MSFG 905, 2939, 2649, and 2647 from Guadalupe Range in New Mexico and Texas). This group is isolated by a treeless area from the main range of border pine in the Sangre De Cristo Mountains to the north and the Gila Mountains to the west. Probably there is no gene exchange between the Guadalupe Mountain pines and two main bodies of border pine but, possibly there is gene exchange within this 150-mile Guadalupe Range. (4) San Pedro River group

(MSFG 2743, 2621, 1023, and 2805 from southeastern Arizona). Mild winters and humid summers in this area may have caused little differential selection pressure upon the characters observed.

In Douglas-fir, several "homogeneous" groups are recognized within the main Rocky Mountain range and one in the coastal area, possibly because selection pressure was strong enough to counteract the free gene flow in a small continuous area. (1) Flathead National Forest group (MSFG 1521, 1650, 1519, and 1600 from the west of the Continental Divide in northwest Montana). (2) Lolo National Forest group (MSFG 1616, 1504, and 1506 from the eastern Bitteroot Range in western Montana). (3) Bitteroot National Forest group (MSFG 1518, 1597, 1598, and 1599 along W. Folk Creek, a narrow strip east of the Bitteroot Range and west of the Continental Divide. (4) St. Joe-Clearwater National Forest group (MSFG 1567, 1562, 1564, 1587, 1588, 1563, 1524, 1672, and 1573 west of Bitteroot Range in northern Idaho). (5) Roosevelt National Forest group (MSFG 1635 to 1642 from Rocky Mountain in northern Colorado). (6) Pike-San Isabel National Forest group (MSFG 1609, 1605, 1530, and 1531 from eastern Colorado). (7) Puget Sound-Willamette Valley group (MSFG 1623, 1626, to 1629 from Washington and MSFG 1621, 1624 from Oregon).

SUMMARY

Douglas-fir, ponderosa pine, and limber-border pine are three of the most widely distributed species in the western United States. The main objective of this study is to compare the similarity and dissimilarity of geographic variation pattern among three species, and to explore the possible selection pressure and evolutionary trends acting on them.

A modified randomized block design was used in the nursery. Data analysis concerned with analysis of variance for each single character, and "Summations of Differences" for several characters simultaneously. Measurement on winter injury, height, needle length, foliage color, and bud dormancy provided the base of comparison in geographic varation.

Winter injury was shown by yellow to red coloration of leaves. Of the three species, limber pine was the most hardy one, and Douglas-fir was the least resistant to winter injury in Michigan. Both coastal ponderosa pine and Douglas-fir seedlings were more susceptible to winter injury than interior seedlings. Within the areas in which comparisons were possible, northern Utah was a source of cold-resistant seedlings in all three species. Seedlings from southeastern Arizona were the least winter hardy among all interior seedlings. Otherwise, all three species had a different pattern of geographic variation.

Coastal seedlings of ponderosa pine and Douglas-fir were taller than interior seedlings before the first winter, but soon became inferior to interior seedlings because of winter injury. Seedlings of three species from southern Arizona and southern New Mexico were very tall and those from northern Utah and northern Colorado were very short. The role of selection pressure and geographic isolation upon height

growth was discussed.

Based on needle length at age 2, both Douglas-fir and ponderosa pine showed a significant difference between coastal and interior varieties. The interior varieties were more variable than the coastal varieties. Ecotypic differences were significant in the interior varieties, but not in the coastal varieties. Needle length was a satisfactory character for distinguishing between limber and border pines. Length of secondary leaves of three species seemed to be co-adaptive to height growth of seedlings.

Difference in foliage color between coastal and interior varieties was found significant in ponderosa pine but non-significant in Douglas-fir. Limber pine and border pine showed significant difference in foliage color. Variation among provenances within ecotype was great for Douglas-fir, intermediate for ponderosa pine, and small for limber pine. Blue foliage was common on southern Rocky Mountain seedlings. Possibility of blue foliage has selective advantage in that area was discussed.

Varietal difference and some ecotypic difference in bud dormancy were found among three species. Coastal seedlings had late bud set and bud burst. Seedlings from New Mexico and Arizona were also late. Northern interior seedlings seemed to be early in bud set and bud burst. Bud set may be induced by "biological clock" and bud burst by "biological thermostat."

Ecotypes of three species separated by phenotypic differences and by geographic boundaries were discussed. Treeless zones which act as a barrier for gene migration served well as a boundary between ecotypes. Other geographic features in the western United States, such as the skyline of the Cascades and Continental Divide which separates the eastern slope and the western slope into two distinct moisture regimes, or rivers which separate the area into different elevational zones, may also serve as boundaries among ecotypes. The dissimilarity between two ecotypes can be related to the completness of isolation. However, geographic distance was not a good indicator of similarity between provenances.

The formation of homogeneous groups of provenances may be a combined effort of isolation mechanism, selection intensity, and duration of selection. Case study had been discussed for three species.

Methods of finding the most representative seedlot from the "Summation-of-Difference" table were proposed.

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