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Parallel and Divergent Evolution in Rocky Mountain Trees

By FAN HAO KUNG and JONATHAN W. WRIGHT[1])

The Rocky Mountains of western United States are the home of several tree species which grow well in the north central states. Some are planted commonly as ornamentals, Christmas trees or for timber production. Because there is an active demand for provenance information, a series of provenance tests was undertaken in Michigan as part of the NC-51 regional tree improvement project.

The tests were designed to yield practical information, but theory and practice can not be divorced in such work. Equal emphasis was placed on the study of the factors involved in the evolution of genetic differences. The tests covered four tree species inhabiting somewhat the same geographic ranges. Each species has been the subject of a separate detailed report. It is the purpose of the present paper to place the evolutionary data from all four species in one common focus.

The provenance tests on which the present paper is based have been described in greater detail in a series of previous papers each dealing with one species: ponderosa pine *(23, 24, 28),* Douglas-fir *(8, 26),* white fir *(5,* 9, *29),* limber and southwestern white pines *(21, 27).*

Biological Subdivisions of the Four Species

PONDEROSA PINE, Pinus ponderosa LAWS. — Three taxonomic varieties have been recognized:

Var. ponderosa of the Pacific Coast states, Idaho and Montana.

Var. scopulorum ENGELM. from the southern Rocky Mountains to central Montana and the Black Hills of South Dakota

Var. *arizonica* (ENGELM.) SHAW from SW New Mexico, SE Arizona and N Mexico; not included in the present experiments.

A related species, P. washoensis MASON and STOCKWELL, occurs on the east side of Mt. Rose, western Nevada.

HALLER (1957, cited in *23, 24)* on the basis of field study, recognized races from California, the Pacific Northwest south to the Shasta Valley of N California, S Arizona-New Mexico, the high plateau of N Arizona-New Mexico and S Utah-Colorado and the northeastern quarter of the range.

Five extensive-range provenance studies which have been conducted in other regions have been summarized in papers by SQUILLACE and SILEN *(20),* WELLS *(23, 24)* and WANG *(22).* These studies were a 20-origin 1-site experiment in Idaho, a 10-origin 6-site experiment in the Pacific Northwest, a 13-origin 1-site experiment in New Zealand, a small nursery experiment in Arizona and a 126-origin nursery experiment in California. From these studies the following races were recognized as reasonably distinct: California, North Plateau (= Pacific Northwest), Arizona-New Mexico (= southern Rockies), central and northern Rockies-Black Hills.

CALLAHAM and LIDDICOET *(3)* described an elevational cline in California from an elevational transect study.

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From the Michigan provenance tests *(23, 24, 28)* following races or ecotypes were recognized:

Var. *ponderosa* — S California, N California, W Oregon, Nevada (= *P. washoensis*), North Plateau (E Oregon, E Washington, Idaho, W Montana, British Columbia)
Var. *scopulorum* — Arizona-S New Mexico, S Utah-S Colorado-N New Mexico, N Utah, central Colorado and Northern Interior (E Montana, South Dakota, Nebraska)

The racial difference recognized by Wells and by Wright *et al.* but not by previous authors were generally much smaller than those recognized by all authors, or were due to differences in intensity of sampling. Therefore it is fair to conclude that there is general agreement on the major geographic subdivisions of the species. However, Callaham and Liddicoet's elevation clines were not observed in the Rocky Mountain populations tested in Michigan.

DOUGLAS-FIR, *Pseudotsuga menziesii* (Mirb.) Franco. — Little *(13)* recognized West Coast var. *menziesii* (confined to the coast ranges and west slopes of the Cascade-Sierra Nevada Mountains) and var. *glauca* (Beissn.) Franco from the inland portions of the range. Several other authors have also recognized var. *caesia* (Schwerin) Franco from central British Columbia as intermediate between the West Coast and inter varieties.

Flous *(7)* of Toulouse subdivided interior Douglas-fir into several species. Rol *et al.* *(17)* are among the few who have used Mlle. Flous names in their report on trees growing in the Arboretum des Barres, France. They did not mention *Pseudotsuga macrolepis* Flous or *P. globulosa* Flous but recognized

Pseudotsuga glauca Mayr (= *P. menziesii* var. *glauca*), Rocky Mountains,
P. flahaulti Flous, S Rocky Mountains,
P. guinieri Flous, S Arizona and N Mexico,
P. Merrilli Flous, Utah, Idaho and Montana,
P. rehderi Flous, central Rocky Mountains south into Mexico.

Douglas-fir is the most important timber species on the West Coast. The West Coast variety has received attention from many tree breeders. Among the provenance tests dealing only with var. *menziesii* are those reported by Munger and Morris *(15, 16)* Morris *et al.* *(14)*, and Ching and Bever *(4)*.

Provenance tests of interior origins have been more limited. Baldwin and Murphy *(1)* grew one coastal and three interior origins in New Hampshire. Byrnes *et al.* *(2)* grew many coastal and interior origins in Pennsylvania. Schober *(18)* and Schober and Meyer *(19)* grew many origins, most of them from the West Coast in Germany. Heit *(10)* grew a large number of interior origins in his New York nursery over a period of years. In all these experiments the standard procedure was to plant a few seedlots on one site or at one time, a few other seedlots on another site or at another time, etc. With such procedures it is difficult to make exact comparisons.

The NC-51 experiment started in Michigan was also planted in Nebraska and Pennsylvania *(8, 26)*. From this experiment the following races were recognized:

COAST (= var. *menziesii*), C WASH (central Washington), INEMP (Inland Empire, NE Washington, N Idaho, NW Montana), NOROC (Northern Rockies, W Montana, north-central Idaho), C MON (central Montana, N. Wyoming, probably also south-central Idaho), ALB (Alberta), NOCOL (N Colorado, N Utah, S Wyoming), SOCOL (S Colorado, adjacent parts of Utah, Arizona, New Mexico) ARINEM (most of Arizona-New Mexico).

It is difficult to make meaningful comparisons between the results of NC-51 and previous experiments. The western experiments obviously provide the most meaningful data on variation within var. *menziesii* — all coastal origins were equally unsuccessful in eastern United States.

In the NC-51 experiment, 3-year data from Pennsylvania and Michigan were correlated very strongly. The Pennsylvania trees had been grown in Michigan 1 year, so such a result is not definite proof that performance will remain the same in the two states.

Data from 8-year-old trees planted in Nebraska and Michigan were also strongly correlated as regards relative performance of the ARINEM, SOCOL and NOCOL races and the distinctness of the northern and southern groups of races. However, in Nebraska all northern races were regarded as near-failures whereas there was a great deal of differentiation among the C WASH, INEMP, NOROC, C MON and ALB races according to the Michigan data.

All provenance experiments which include coastal and interior seedlots confirm the wisdom of regarding var. *menziesii* as different from the remainder of the species.

Data from the NC-51 experiment and from Heit's nursery tests in New York show that Douglas-fir from inland regions is extremely variable geographically. There is considerable merit in Mlle Flous' proposal that several species be recognized. It is likely that her *P. merrillii* is an approximate equivalent of the C MON race, that her *P. rehderi* is an approximate equivalent of the NOCOL and/or SOCOL races, and that her *P. guinieri* is an approximate equivalent of the ARINEM race. It is also likely that *P. menziesii* var. *caesia* deserves recognition.

WHITE FIR, *Abies concolor* (Gord. and Glend.) Lindl. — Little *(13)* recognized a single species, without varieties. Several European writers have separated the white firs of Oregon-northern California *(A. lowiana* [Gord.] A. Murr. = *A. concolor* var. *lowiana* [Gord.] Lemm.) from the Rocky Mountain-southern California white firs *(A. concolor* var. *concolor)*.

The Michigan provenance test *(29)* includes origins from the southern Rocky Mountain portion of the range as well as a few Oregon-California origins. The California provenance test *(5, 9)* includes origins from the Oregon-California portion of the range and a few origins from Nevada, Utah and Arizona.

The California and Michigan experiments agree in showing very large differences in foliage color and arrangement among the Oregon, northern California and southern California-Rocky Mountain portions of the range. Hamrick showed clearly that introgression from *Abies grandis* (Dougl.) Lindl. has affected white fir as far south as central California and that *A. concolor* var. *lowiana* is a recognizable taxon.

Only two Rocky Mountain origins are common between the Michigan and California experiments. In both experiments Utah trees grew much more slowly and had shorter needles than Arizona trees.

LIMBER PINE *(Pinus flexilis* James) and SOUTHWESTERN WHITE PINE *(P. strobiformis* Engelm. = *P. flexilis* var. *reflexa* Engelm.) — Andresen and Steinhoff *(21)* cleared up the nomenclatural confusion surrounding these taxa, showing that limber pine grows from Utah and Colorado northward, with a slight range extension westward to extreme eastern California, and that southwestern white pine grows in Arizona, New Mexico, western Texas and probably northern Mexico. The two taxa were treated as varieties in Little *(13)* and as species in Critchfield and Little *(6)*. There is still confusion regarding *P. strobiformis* and *P. ayacahuite* Ehrenb. of Mexico and central America.

The NSF-NC-51 provenance test with plantations in Michigan and Nebraska *(21, 27)* is the only large one in either species. Provenance results from the two states agree and indicate no overlap between *P. flexilis* and *P. strobiformis* in growth characters.

Materials and Methods

The four series of provenance tests were conducted in Michigan as part of the NC-51 regional tree improvement

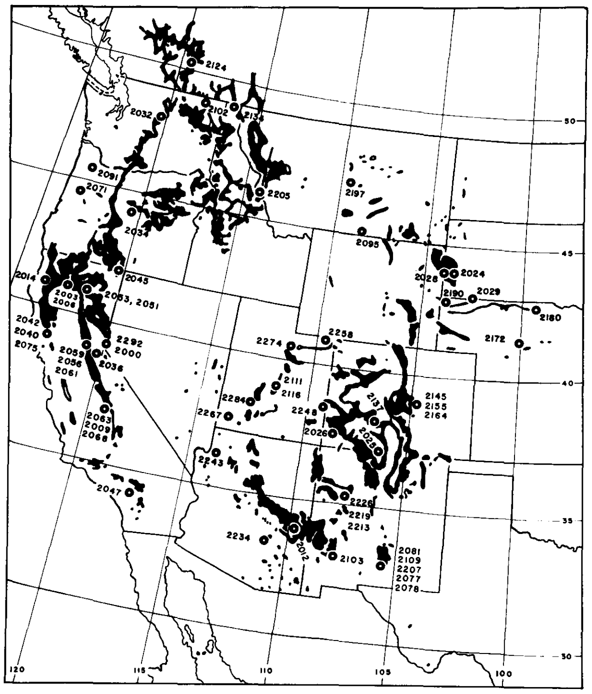

Figure 1. — Natural range (black) of ponderosa pine and locations of stands from which progeny were grown (numbered circles). After Wells *(23)*.

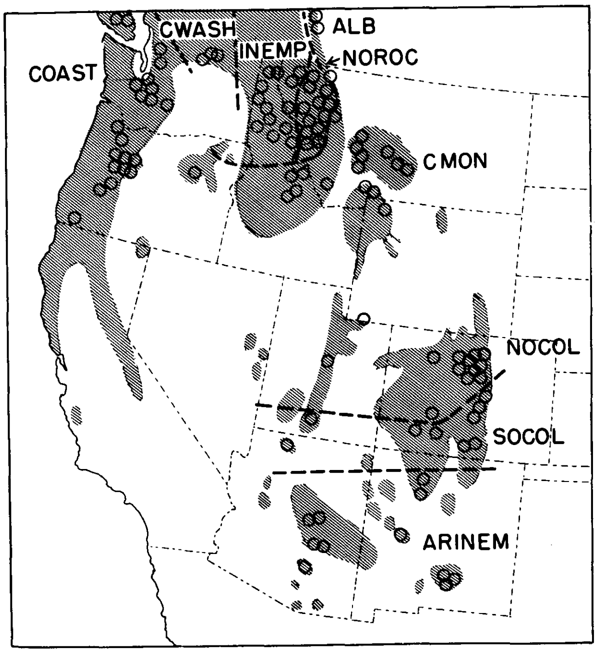

Figure 2. — Natural range (shaded) of Douglas-fir and location of stands from which progeny were grown (circles). The racial designations are: ALB = Alberta, NOROC = Northern Rockies, C MON = central Montana, INEMP = Inland Empire, C WASH = central Washington, NOCOL = northern Colorado and Utah, SOCOL = southern Colorado and Utah, ARINEM = Arizona and New Mexico, COAST = West Coast.

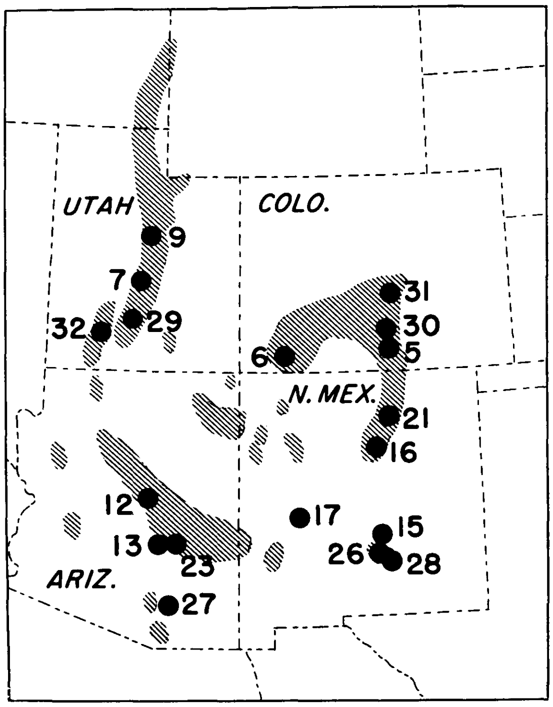

Figure 3. — Natural range (shaded) of white fir in the Rocky Mountains and location of stands from which progeny were grown (numbered dots).

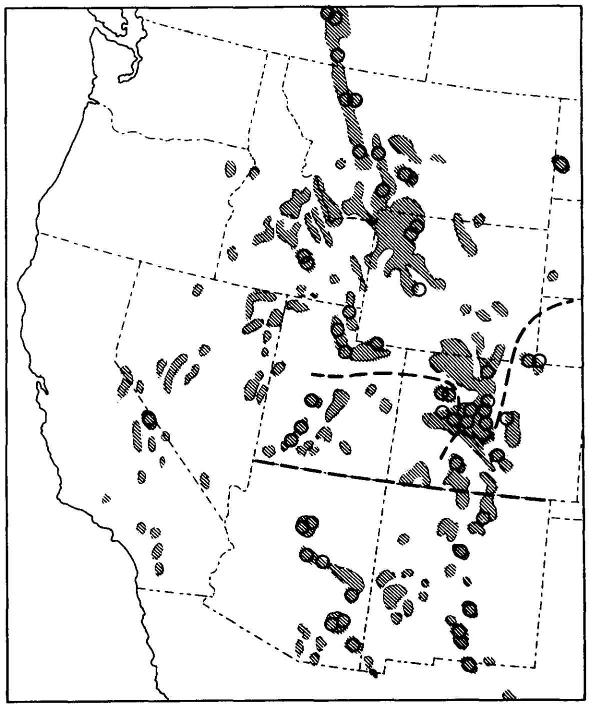

Figure 4. — Natural range (shaded) of limber pine (Utah-Colorado and northward) and southwestern white pine (Arizona—New Mexico) and location of stands from which progeny were grown (circles).

project. The Douglas-fir and white fir experiments were organized by the Michigan Agricultural Experiment Station; later the white fir experiment became cooperative with a similar experiment conducted by the University of California and U. S. Forest Service in California. The ponderosa pine experiment was organized by R. Z. Callaham while he was working for the U. S. Forest Service in California; seed supplied by Callaham was used by O. O. Wells in his Michigan work. The early phases of the limber-southwestern white pine experiments were financed by a grant from the National Science Foundation.

Between 1955 and 1961 seeds were collected from native stands in western United States *(figures 1 to 4)*. The numbers of stands from which progenies were grown are as follows:

Ponderosa pine — 60 stands,
Douglas-fir — 128 stands,
White fir — 18 stands in the Rocky Mountains, with limited data from 15 stands in the Sierra Nevadas and Cascades,
Limber-southwestern white pine — 51 stands.

Most stands were represented by seed from several average trees. In the pine experiments, seedlings were kept separate by female parent in the nursery but were bulked by stand in the field plantations because of a low amount of within-stand variability. In the Douglas-fir and white fir experiments, seeds were bulked by stand before sowing.

The seeds were sown in 4-replicated nursery experiments in East Lansing, Michigan in 1960 (ponderosa pine) or 1961 (other species). The seedlings were grown 2 to 5 years in the nursery and transferred to permanent plantations. In southern Michigan there are two permanent plantations for limber-southwestern white pine and three for each of the other species. Surplus stock was sent to cooperators in other states; 8-year data are available for the Douglas-fir and limber-southwestern white pines planted in Nebraska and 3-year data for the Douglas-fir planted in Pennsylvania.

The plantations were replicated, usually from 5 to 10 times with 4-tree plots. Spacing was 2.5 × 2.5 meters and the weeds were controlled by chemicals for 2 to 4 years after planting. Initial mortality varied from 10 to 50 percent and averaged about 20 percent. Most was attributed to transplanting shock and inadequacy of weed control. From 1 to 5 percent of the trees have died since the first year after planting.

Each experiment was measured several times while in the nursery and two or more times in the permanent plantations. The traits which varied enough to warrant measurement were different among species. Chi-square, variance and correlation analyses were performed on the data from individual species. Because of differences in intensity of sampling, statistically rigorous comparison between species were usually not possible.

The last measurements were made in 1969. At that time, the ages and maximum sizes of the trees were approximately as follow:

Species	Age, years	Maximum height, meters
Ponderosa pine	10	4
Douglas-fir	8	1.8
White fir	8	1.8
Limber pine	9	1
Southwestern white pine	9	2

Geographic Variation Patterns

West Coast vs. Interior

Some western origins were included although the experiments were designed specifically to study Rocky Mountain populations. In three of the four species there were major differences — enough to warrant recognition of separate varieties — between trees from the western and interior portions of the species' range.

Ponderosa pine. — Western var. *ponderosa* is confined partly to the west slope of the Sierra Nevada Mountains (California) and partly to the inland portions of the Pacific Northwest (North Plateau race of E Oregon, E Washington, Idaho, W Montana, British Columbia). In Michigan plantations this variety was characterized by more loosely appressed bud scales, browner buds, greener foliage, and higher contents of foliar N, K, P, Ca and B than var. *scopulorum* of the Rocky Mountains.

Such a variety division does not adequately describe variation in growth traits. The North Plateau race has been hardy in Michigan whereas the California and W Oregon races of the same variety have not. Because of lack of hardiness, the California races changed from tallest at age 1 to shortest at age 10. Most California trees survived, however. The interior variety is also far from uniform in growth traits.

Douglas-fir. — Western var. *menziesii* ranges along the coast ranges and west slopes of the Cascade Mountains from southern Oregon to British Columbia (and probably also in the Sierra Nevadas of California). The NC-51 provenance test included 19 origins. They were characterized by rapid first-year growth, reddish-orange twigs, susceptibility to a late-September first-year frost, light green foliage, and extreme susceptibility to winter cold in Michigan, Nebraska and Pennsylvania. Each tree died back completely to the snow line after each of the first two winters. None of the trees were field planted.

Trees from any part of the interior (i. e., east of the crest of the Cascade or Sierra Nevada Mountains) were very different. They were moderately hardy to hardy, had green or occasionally reddish-purple twigs, and had dark green to blue-green foliage.

White fir. — This has a more southerly distribution than either of the first two species, growing from N Mexico to Oregon in the Pacific states and from N Mexico to S Idaho in the interior.

In taxonomic traits there are as great differences within the Pacific States population as within the species as a whole *(5, 9, 29)*. In both California and Michigan, trees from Oregon closely resembled grand fir and trees from the northern half of California showed evidence of introgression from that species. Thus, along any eastwest line north of central California, the contrast between western and interior white firs was great.

The western-interior contrast was less in the southern part of the range. Southern California and Arizona-New Mexico trees were similar in foliage color, needle arrangement and length and twig characteristics. In Michigan, however, there was a pronounced difference in hardiness, southern California trees suffering severe leaf injury and cambial dieback after each winter.

Limber pine. — A single high-elevation source from the California-Nevada border was similar to Utah sources in Michigan plantations.

All species. — If comparisons are confined to northern California and western Oregon versus the interior (defined as east of the crest of the Sierra Nevada Mountains), there were clearcut distinctions in all species, and the trends were more or less similar — the western trees were faster growing during the first year, greener, and considerably less hardy under Michigan test conditions.

Beyond that, it is difficult to generalize. There are western and eastern varieties of ponderosa pine, Douglas-fir and white fir, but their boundaries are very different.

Arizona-New Mexico versus Utah-Colorado

Trees from most of Arizona and New Mexico were distinctive in all species. They set buds later, grew faster, had longer needles, and had different foliage color than trees from farther north. There was a twig-color difference in Douglas-fir; twigs were green or reddish-purple on trees from Arizona-New Mexico, only green on trees from farther north. Cones were larger in Arizona-New Mexico southwestern white pines than in limber pines from farther north.

The differences in relative growth rate are shown in the following tabulation, which is based on data from the Michigan nursery and test plantations.

Species	Relative height of trees from S Utah-S Colorado, expressed as percent of the height of Arizona-New Mexico trees	
	Age 2	Age 8 to 10
Ponderosa pine	72	97
Douglas-fir	67	67
White fir	90	69
Limber and southwestern white pines	41	39

The Arizona-New Mexico trees of white fir, Douglas-fir and southwestern white pine have suffered relatively little from winter cold in Michigan and the relative growth rates have remained constant with increasing age. Some foliage dieback has been evident on the Arizona-New Mexico ponderosa pines after severe winters and the initial growth advantage of these origins has nearly disappeared.

Leaf-length differences were almost as great (leave of Arizona-New Mexico trees longest) as the differences in growth rate. Also, except in white fir (in which the largest difference was between Arizona and New Mexico trees), there was a north-south division in foliage color, as illustrated in the following tabulation.

Species	Foliage color in trees from	
	Arizona-New Mexico	Utah-Colorado
Ponderosa pine	gray-green	green
Douglas-fir	blue-green	green and blue-green
White fir	blue-green and green	blue-green
Limber and southwestern white pines	bluest of any white pine	green to yellow-green

Elevational distribution in Arizona-New Mexico and Utah-Colorado varies in an unexpected manner in these four species groups. Normally a species grows at higher elevations south than north, but in this case each species grows at about 1,000 feet lower elevation south than north. This is indicated by the following tabulation, based upon data obtained with the seed collections used in the experiments.

Species	Elevations from which seed was collected in	
	Arizona-New Mexico	Utah-Colorado
	feet	*feet*
Ponderosa pine	6,000—10,300	6,800—9,100
Douglas-fir	5,500—9,000	7,700—10,000
White fir	6,500—9,300	8,000—10,300
Limber and southwestern white pines	7,000—9,600	8,300—11,000

In all except Douglas-fir the 37th parallel (Arizona-Utah border) is the approximate north-south boundary between races in the west. The actual boundary is probably the broad treeless area composed of the Painted Desert (NE Arizona) and the region south of Zion Canyon (S Utah). Farther east the approximate north-south boundaries are the 35th parallel through central New Mexico (white fir and ponderosa pine) or the 37th parallel (New Mexico-Colorado border) (Douglas-fir, limber-southwestern white pines).

The distinctions between Arizona-New Mexico and Utah-Colorado southwestern white and limber pines were equally great in all plantations, whether in Nebraska or Michigan. In Douglas-fir the north-south distinctions were even greater in Nebraska than in Michigan.

Multivariate analyses were performed on the nursery and/or Michigan plantation data for ponderosa pine, Douglas-fir and limber-southwestern white pines. These analyses provided methods of considering many traits simultaneously. In all three groups, the variation within Arizona-New Mexico was relatively small when compared with the differences found between the Arizona-New Mexico and the more northern races. Only in white fir foliage color (New Mexico sources greenest) was there much basis for subdividing the Arizona-New Mexico race.

Variation in the Central Rocky Mountains

In the Central Rocky Mountains area the forests are almost as discontinuous as farther south and there are large climatic differences in progressing from southern Utah to western Nebraska. However, each species behaves normally as regards elevational zonation, growing at higher elevations south than north. Thus, increasing latitude and decreasing elevation tend to compensate each other, especially with regard to temperature and length of growing season.

Each species was geographically variable within this region, but differences among races were smaller than between Arizona-New Mexico and Utah-Colorado. Also, the racial boundaries were much less distinct. Some of the "races" are probably portions of clines.

Only in Utah was the pattern consistent between species. Ponderosa pine, Douglas-fir and limber pine from southern Utah grew faster (by 15 to 100%) than the same species from northern Utah. There were no north-south differences in most other traits except in ponderosa pine, where the southern Utah sources had appreciably more Lammas growth and more bloom on the twigs.

The variation in Colorado and southern Utah did not follow exactly the same pattern in any two species. In Douglas-fir there was a north-south gradient in growth rate, the northern trees being the slowest growing. There was an east-west difference in white fir, sources from south-central Colorado being much faster growing than the sources from southern Utah. There were both north-south and east-west differences in limber pine; trees from north-central Colorado were very slow growing and trees from the east, south and west were much faster growing. In ponderosa pine a group of provenances from central Colorado were prostrate during their second year whereas all others were erect.

In white fir and ponderosa pine there were no color differences within the central Rocky Mountain populations. There were in the other two species, however. Douglas-fir origins from northern Colorado were uniformly dark green whereas both dark green and blue-green types occurred in southern Colorado. In limber pine, sources from the Wyoming-Nebraska border, eastern Colorado and southern Colorado were almost as dark green as were the *Pinus strobiformis* from states to the south. In contrast, sources of much slower growth rate or of equal growth rate but from farther west in Colorado and southern Utah were yellow green.

Differences in hardiness and leaf length were slight within the central Rocky Mountain populations.

Northern Interior vs. Central Interior

Across southeastern Oregon, southern Idaho and Wyoming is a broad zone almost devoid of forests which makes a natural division between northern and central interior forests. Climates to the north are characterized by many fewer hours of sunshine, a smaller percentage of annual precipitation in the summer, shorter growing seasons and generally cooler temperatures than in the equivalent forested zones to the south. All except white fir were represented by origins from the northern as well as the central interior.

Limber pine was the one species tested which did not vary appreciably along an 800-mile transect from southern Alberta to northern Utah and Colorado.

Douglas-fir was at the other extreme. Northern and central interior groups of races differed in two important respects. Date of first-year bud set in the Michigan nursery was August 18 or earlier for trees from Idaho and Montana, September 11 or later for trees from the central and southern Rocky Mountains. In the Nebraska plantation, mortality was 96 to 99% for northern races, 76 to 83% for southern races.

The geographic trends in growth rate were exactly opposite in northern and central-southern groups of Douglas-fir races. In the north there was a south-north trend toward increasing growth rate, culminating in the fast-growing INEMP race centered in N. Idaho. In the south there was a north-south trend toward increasing growth rate, culminating in the fast-growing ARINEM race of Arizona-New Mexico.

The North Plateau race of the Pacific Northwest was very different from the northern Colorado-Utah race of ponderosa pine in several respects, the North Plateau progenies were faster growing and had greener needles, less appressed bud scales and higher foliar contents of N, K, P, Ca and B. There was almost no overlap in these traits. The amount of genetic differentiation in the eastern part of the interior was less. Nebraska, South Dakota and E Montana progenies grew 15 to 30% faster than northern Colorado-Utah progenies but did not differ from them in other respects.

Variation in the Northern Interior

In the northern interior the most favorable growth conditions for the majority of species are found in the region known as the Inland Empire — NE Washington, N Idaho, NW Montana and south-central British Columbia. Precipitation is relatively high there and any particular species grows at lower elevations than farther to the south or east. This causes a richer forest flora and faster growth rates than elsewhere in the northern interior.

Sampling of this region was most intensive in the Douglas-fir provenance test. There was considerable east-west differentiation in growth rate, less in date of first-year bud set. The INEMP race from northern Idaho grew about twice as fast in Michigan as the C MON race from central Montana and Wyoming, and grew a few days later in the summer. The transitions from INEMP to NOROC to C MON races were gradual.

The North Plateau race of ponderosa pine has been treated as a unit because all progenies were very different from those from other parts of the range. However, that "race" is variable and subsequent research may show it to consist of a number of races or clines.

From one standpoint there has been more differentiation in northern ponderosa pine than in northern Douglas-fir. There was virtually no overlap between the North Plateau (W Montana and westward) and Northern Interior (central Montana and eastward) races of ponderosa pine in date of germination, foliage color, earliness of secondary leaf formation, percentage of 2-needled clusters, bud-scale appression, date of growth initiation, or foliar content of N, P, K, Ca and B *(23, 24, 28)*. Douglas-fir from N Idaho and central Montana did not differ in so many respects and there was considerable overlap among neighboring races.

On the other hand, Douglas-fir from N Idaho grew twice as fast as Douglas-fir from central Montana. The growth-rate difference in ponderosa pine was much less.

Evolutionary Considerations

Selection for growth rate, hardiness and drought. — Most racial differences were associated with climate at the place of origin in such a manner as to suggest that natural selection has been the major factor promoting racial differentiation.

Average temperature and length of the growing season decrease in going north, in climbing a mountain, or with increasing distance from the ocean. Precipitation is normally highest near the ocean and at medium to high elevations.

Normally, the elevational zone occupied by a given species is such as to result in a more or less similar climatic regime for a species throughout its range. The opposite happens in three parts of western United States. At the same elevation the average climate is warmer along the west coast of Oregon and Washington than in the interior; it is warmer in northern Idaho than farther east in Montana; and it is warmer in Arizona-New Mexico than in the states to the north. But Douglas-fir grows at lower elevations along the west coast than in the interior and at lower elevations in northern Idaho than in Montana, and all four species-groups grow at slightly lower elevations in Arizona-New Mexico than in southern Colorado or Utah. In these three cases the climatic contrast between the more favorable and less favorable growth regions is especially marked, and so are the differences in growth rate of the tree races.

From southern Colorado and Utah to the northern parts of those states, the species do as expected. That is, they occupy lower elevational zones to the north. Changing elevation and latitude apparently do not compensate for each other from the evolutionary standpoint, however. In each of the four species-groups there were growth rate differences, the more southerly sources growing faster.

Theoretically, natural selection favors the fastest growing trees in any particular habitat, but only if those trees are fit in other respects. In Douglas-fir there was good evidence that rapid growth was achieved in part by a lengthened growing season — origins from the mild-climate West Coast and Arizona-New Mexico set buds two months later than northern interior origins during their first growing season.

In ponderosa pine and white fir, all origins had about the same length growing season but there were obvious differences in winter hardiness. California-western Oregon trees suffered in most winters, some Arizona-New Mexico trees suffered slight damage in severe winters. Apparently in these cases rapid growth is achieved at the expense of lack of preparation for winter cold.

Most growth rate differences among races from the central and northern interior were not associated with differences in length of growing season (except in Douglas-fir) or hardiness although it is possible such differences would be apparent under different test conditions. There are, however, obvious relations between these growth-rate differences and the general favorableness of growing conditions of the habitats of origin — particularly as regards moisture availability. It is probable that in dry habitats selection favored types are able to extract or utilize limited soil moisture, and that such ability is related to growth rate. The very high mortality of northern Douglas-firs in the prairie soils of Nebraska lends support to the hypothesis that selection involved drought resistance as well as growth rat and resistance to cold.

Selection in high- and low-elevation habitats. — There was a great contrast between limber pine and other species with regard to the amount of genetic differentiation between California and Rocky Mountain populations and between Colorado and more northern populations. Douglas-fir and ponderosa pine varied whereas limber pines from California, northern Utah and Alberta were nearly the same.

The most probable explanation relates to the elevational zones occupied by the species. Limber pine is a timberline species whereas the others are not. A timberline habitat is a harsh one wherever it occurs. Possibly it is equally inhospitable to trees whether in the high Sierras or in Canada.

Selection for foliage color. — In all four species-groups foliage was bluest or grayest in the southern Rocky Mountains, more specifically in Arizona and New Mexico. That area can be regarded as a center for the development of blue or gray foliage. White fir and Arizona corkbark fir *(Abies lasiocarpa* [HOOK.] NUTT. var. *arizonica* [MERRIAM] LEMM.) are the bluest of all firs, approached only by noble fir *(A. procera* REHD.) of the Pacific Northwest. Blue spruce *(Picea pungens* ENGELM.) and Engelmann spruce *(P. engelmanni* PARRY) of the Rocky Mountains are among the bluest of all spruce species, approached only by *P. montigena* MASTERS of western China. Glaucous or pubescent leaves which are bluish in appearance are common on several desert shrubs from the area.

Arizona and New Mexico have almost twice as many hours of sunshine per year as the northern Rocky Mountains. Also, those southern states are characterized by a low precipitation-evaporation ratio. The blueness of the tree leaves, usually caused by a waxy covering or by surface irregularities, has probably been of selective value in two ways. Protective coverings reduce desiccation. Also, photo-destruction of auxin is especially rapid under blue light, and reflection of blue light would be an effective auxin-control mechanism in a region of intense solar radiation.

Some color differences were not so easily explained. The western (var. *ponderosa)* variety of ponderosa pine, from a diversity of habitats from southern California to western Montana was brighter green than interior var. *scopulorum.* West Coast Douglas-fir had foliage which was lighter in color than that from either the central or northern Rocky Mountains.

Selection for ability to absorb mineral nutrients. — One of the most interesting and least understood aspects of the results was the difference between ponderosa pine varieties in foliar mineral concentration. In the southern Michigan test plantation, origins belonging to western var. *ponderosa* were consistently higher than origins belonging to eastern var. *scopulorum* in the concentration of N, P, K, Ca and B. The percentage differences were so nearly the same for all five elements as to indicate that the physiological mechanism is a general one rather than specific for each of the five elements.

It is possible that needles of the western variety have higher moisture contents (this was not tested), and that the concentrations of the five elements would be similar in the two varieties if expressed as a percent of cell sap rather than on a dry-weight basis. However, if this were done, there would be appreciable between-variety differences in Mg, Mn, Fe and Cu.

One plausible explanation relates to moisture availability. The regions inhabited by the western variety are in general more humid than those inhabited by the eastern variety. Thus western soils may be more leached and the western variety may have developed a high-uptake mechanism.

One disturbing fact is the complete absence of any such trend in four eastern American and European pine species which have been studied at Michigan State University. There was geographic variation in these other four species, but no similar east-west, north-south, or dry-moist trends for any element and there were no strong correlations among the elements.

Isolation and time. — Disjunct populations are the rule in all four species-groups. In each state it is possible to find stands separated from their nearest neighbors by 10 to 50 miles. Such isolation is sufficient to limit gene exchange to a very small fraction of one percent per generation. Presumably all range gaps shown in *figures 1 to 4* have existed during the past 1,000 years. Most have persisted much longer. Closure of almost any one of the large range discontinuities would require a climate change sufficient to cause an elevational shift in forest distribution of 1,000 feet. Closure of many of the range gaps would result only if the climate were to become as moist as in eastern United States.

Thus, when considering the small range discontinuities, we should think in terms of tens or hundreds of thousands of years. When considering the larger gaps, we should think in terms of millions of years.

Nevertheless, isolation was frequently ineffective in promoting genetic differentiation. There were numerous instances in which stand-progenies collected 100 miles apart did not differ significantly in any measured trait. There are two possible reasons for the relatively small amount of differentiation within a region such as central Montana or Arizona-New Mexico. First, selection pressures associated with a few hundred feet difference in elevation or with 100 miles north-south transfer may be too small to promote much genetic response. The very fact that many seedlots have grown well in Michigan, Nebraska and other places far from the natural range indicates a great amount of developmental plasticity on the part of individual trees; with sufficient developmental plasticity, genetic change is not necessary when a species migrates into a new habitat.

Second, the apparent amount of within-stand genetic variation was small, if judged on the basis of nursery results *(21, 23, 24)*. In the ponderosa and limber-southwestern white pine experiments, open-pollinated progenies were kept separate by female parent as well as by stand until time for field planting. In both experiments it was possible to demonstrate statistically significant amounts of within-stand variation in only one-fifth of the stands sampled, and even in these the variation was slight compared with that among stands of widely different geographic origin. With that amount of within-stand variability, and with mass selection of the type practiced in nature, appreciable genetic change would result only if selection pressures were strong and were continued for several generations.

In Douglas-fir the most effective range gap is the desert-grassland region stretching from Mexico to Canada and separating the West Coast from the interior forests. The Cascade and Sierra Nevada Mountains effectively cut off precipitation from the interior, so the inter-mountain area has probably acted as a barrier to tree migration ever since the mountains came into existence. That range gap is also effective in white fir, but apparently not in limber pine. The limber pine may have crossed it in a series of long-distance hops of one or two seeds at a time.

The Great Basin has an effective barrier between the California and southern Rocky Mountain races of ponderosa pine. Surprisingly, the Shasta Valley of northern California, even though relatively narrow, has been effective in separating the North Plateau and California races.

The Painted Desert and the treeless region south of Zion Canyon constitute the approximate boundary between the very different races occupying Arizona and Utah in all four species-groups. Along the 35th parallel in New Mexico is an equally distinct strip without forests. That strip seems to be the north-south boundary between races in ponderosa pine and white fir. In Douglas-fir and limber-southwestern white pine, the Colorado-New Mexico border seems to constitute a racial boundary even though it cuts across forested regions.

Within Utah and Colorado, the racial distinctions are not great. Even though there are noticeable range gaps common to all species (as between Colorado and Utah), these do not constitute common racial boundaries.

Variation with elevation. — There are two well-known examples of genetic differentiation along altitudinal transects in trees. LANGLET *(12)* found that seedlings of Scotch pine *(Pinus sylvestris* L.) from high elevations in Sweden had higher percent dry weight than seedlings from low elevations. CALLAHAM and LIDDICOET *(3)* reported on 20-year-old ponderosa pines grown from seed collected at elevations of 1,000 to 7,000 feet along a 70-mile transect in California, and grown at elevations of 2,700 and 5,600 feet. At the low- but not the high-elevation planting site, the low-elevation sources grew fastest.

In both cases the elevational changes were gradual enough that distance could be an isolating factor. There was a similar case in the Douglas-fir experiment — trees from high elevations in central Montana grew more slowly than trees from lower elevations in northern Idaho.

Of greater interest in the Rocky Mountains are elevational effects in regions with abrupt topography. There are many references to such effects, but most are based on one or two sources per elevational zone or on unreplicated experiments. Of the many-source experiments with other species, two may be mentioned. WRIGHT and BULL *(25)* failed to find any consistent elevational trends in any growth trait among 31 German and Czechoslovakian origins of Scotch pine. HOLZER *(11)* grew offspring of 10 mother trees of Swiss stone pine *(Pinus cembra* L.) occurring at elevations of 1,700 to 2,100 meters in Austria. There was a moderate (significant at 5% level) negative correlation between elevation of parent and growth rate of offspring.

Conservatism. — Comparisons of the numbers of living species indicate that the gymnosperms are inherently much more conservative than the angiosperms. Some data from the provenance-test experiments also points to a inherent conservatism in the conifers.

The differences in bud and foliage characters between the western and interior varieties of ponderosa pine have already been discussed. It is difficult to explain these differences in terms of random variation or adaptation to modern environments. It is more plausible to believe that these differences arose long ago — perhaps several million years ago — and have persisted relatively unchanged. As to their manner of origin, we can only speculate. Amount of bud scale appression is not obviously adaptive and differences in this trait could conceivably have arisen as the result of genetic drift. But, N, K, P, Ca and B are all essential elements and differences in their concentrations probably had adaptive significance at some time.

Inherent conservatism is probably also the best explanation of peculiar results obtained with three Inland Empire seedlots of grand fir. These were included in the white fir experiment. The low-to-high altitudinal zonation in the Inland Empire is ponderosa pine-Douglas-fir-grand fir. If all races become equally well adapted to modern environments, and if ponderosa pine and Douglas-fir from the Inland Empire are hardy in Michigan, grand fir should also be hardy in Michigan. It was not. Grand fir suffered extensive foliage winter burn each year while in the nursery, the above-snow parts becoming almost as brown as West Coast Douglas-fir. A plausible explanation is that grand fir is a relatively recent (geologically speaking) migrant to the Inland Empire from the West Coast and has become much less adapted to interior conditions than ponderosa pine and Douglas-fir.

Hybridization. — Most features of the geographic variation pattern of white fir in Oregon and California are explained better in terms of hybridization between two previously separated species than in terms of adaptation to modern environmental conditions. As HAMRICK *(9)* showed, white fir from Oregon and northern California has botanical characteristics indicating widespread introgression between white and grand firs. And, contrary to expectations on the basis of known selection pressures, white fir from northern California was less hardy than if from southern California in a central California test *(5)*. Grand fir, despite its more northern range, is the least hardy of the two, and such a result would be expected from introgression.

There is no evidence of a similar phenomenon in the other species. Presumably the races in them are as different now as they were in times past.

Summary

Provenance tests of four western American conifers were followed for 8 to 10 years in replicated southern Michigan test plantations. In Douglas-fir, white fir and ponderosa pine there were sufficient differences in hardiness, growth rate and foliage color to justify recognition of separate West Coast and interior varieties but the size of the differences and the distribution of the varieties differed among the species.

Arizona-New Mexico sources of ponderosa pine, Douglas-fir, white fir, and limber-southwestern white pines, were from lower elevations, produced longer needles, generally had bluer foliage, and grow from 10 to 150% faster than sources of the same species from Utah-Colorado. The northern boundaries of the Arizona-New Mexico races were approximately similar in all species. There were smaller genetic differences within the central Rocky Mountain area, and the racial boundaries in that region did not coincide in any two species.

In the northern interior, races of ponderosa pine and Douglas-fir from eastern Washington, northern Idaho and northwestern Montana were faster growing than races of the same species from a few hundred miles farther south or farther east. Selection pressure, time, amount of isolation, amount of inherent variation in local poulations, amount of evolutionary conservatism, and hybridization between previously existing species influenced the development of races within the four species-groups.

Zusammenfassung

Provenienzversuche (mit Wiederholungen) mit westamerikanischen Koniferen in Süd-Michigan wurden untersucht. Bei Douglasie, *Abies concolor* und *Pinus ponderosa* fanden sich ausreichende Unterschiede in Widerstandsfähigkeit, Wachstumsrate und Nadelfarbe, um Varietäten der Westküste und solche aus dem Inland unterscheiden zu können. Sie waren aber bei den einzelnen Species verschieden ausgeprägt. — Die Herkünfte aus Arizona-Neu-Mexiko dieser Arten stammten aus tieferen Lagen und hatten längere, meist blauere Nadeln und wuchsen um 10% bis 150% schneller, als solche aus Utah-Colorado. Die Nordgrenze der Arizona-Neu-Mexiko-Rassen verlief für alle Arten ähnlich. Im Gebiet der Zentral-Rocky-Mountains wurden kleinere genetische Unterschiede gefunden, und die Rassengrenzen verliefen dort für die Arten nicht übereinstimmend. — Aus dem nördlichen Teil des Inlandes waren die Rassen der Ponderosa und der Douglasie aus Ost-Washington, Nord-Idaho und Nordwest-Montana raschwüchsiger als Rassen der gleichen Arten aus Gegenden, die nur wenig hundert Meilen südlich oder östlich lagen. — Diese Rassenentwicklung kann verschiedene Ursachen haben.

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