GENETIC VARIATION AND HYBRIDIZATION OF PONDEROSA PINE

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ABSTRACT

Ponderosa pine's (*Pinus ponderosa* Laws.) geographic range is centered in the montane western United States, where it is the most widely adapted and ubiquitous conifer. A western variety, *P. ponderosa* var. *ponderosa*, extends from the mountains of southern California, northward, on the western and eastern sides of the Sierra Nevada-Cascade crest to Canada. It comes into contact with an eastern variety, *P. ponderosa* var. *scopulorum* Engelm., near the Continental Divide in west-central Montana. The eastern variety extends southward throughout mountains, plains, and basins to scattered stands in the Sierra Madre Occidental and Sierra Madre Oriental of northern Mexico. A 5-needled pine (*P. arizonica* Engelm.) of Mexico, with scattered populations in southern Arizona and New Mexico, was commonly represented as a variety of *P. ponderosa*, but recent field studies support species status for the taxon.

Morphological observations, biochemical analyses, and growth responses of provenances in nursery and plantation trials indicate that ponderosa's varieties consist of well differentiated geographic races (Southern California, Pacific, and North Plateau races in the west, Rocky Mountain and Southwestern races in the east).

Native ponderosa pines encounter and hybridize with other western yellow pines (*P. jeffreyi* Grev. & Balf., *P. washoensis* Mason & Stockwell, *P. arizonica*, and *P. engelmannii* Carr.) and one of the California big-cone pines (*P. coulteri* D. Don). Controlled crosses verify that Pacific race ponderosa pines will hybridize, but have strong barriers to crossing with *P. jeffreyi*; Pacific race pines are moderately compatible with the Rocky Mountain race, a rare and closely related species in California (*P. washoensis*), and five species in subsection *Ponderosae* in Mexico.

The failure of ponderosa pine to cross with two Mexican species (*P. teocote* Schiede & Deppe and *P. lawsonii* Roezl) that were previously included in subsect. *Ponderosae* is evidence that those two species were misclassified. Since *P. teocote* crosses with *P. patula* (Schiede & Deppe), both *P. teocote* and *P. lawsonii* appear more closely aligned with the closed-cone pines in subsect. *Oocarpae* than with the pines of subsect. *Ponderosae*.

Patterns of genetic variation among races and cross compatibility with Mexican pines suggest ponderosa's center of origin was Mexico. Ponderosa and its relatives appear to have been poorly adapted to the cool moist climates during full-glacial episodes of the Pleistocene; they are largely missing from the North American fossil record. Over the last 3,000 to 8,000 years, as western environments became warm and arid, ponderosa's drought and fire tolerances permitted it to become the most wide-spread and prevalent conifer of western United States.

INTRODUCTION

Owing to its extensive geographical range and distinctive appearance in open-grown, old-growth stands, ponderosa may be the trees most people picture in their mind's eye as typical forests of the American West. By virtue of their superior drought tolerance, fire resistance, and aggressive regeneration, they are the major large trees bordering the western plains, basins, and valleys. They grow in pure and mixed species stands throughout mid-elevations and approach alpine forest conditions at their upper-elevational limits of growth. The oldest and largest trees reproduce regularly and prolifically in nature. Ponderosa pine seedlings are easy to grow in nurseries, transplants are hardy, and plantations are vigorous. Both natural and planted stands of young-growth ponderosa pine provide superior recreational, ecological, and timber values, and this species constitutes the greater part of forest management in the interior mountains of western United States.

Common distinguishing features make it easy to recognize ponderosa pines anywhere they grow. But on close examination, the trees have regional differences in morphological traits (e.g. numbers of needles per fascicle) and biochemical traits (xylem monoterpenes and enzyme genes). Provenances can also be grouped on the basis of similar growth in greenhouse, nursery, and field trials to provide further evidence of inherited differences between regions (Wang 1977).

Local variation in numerous traits has been reported elsewhere: California, Sierra Nevada growth patterns related to elevation of seed source (Callaham *et al.* 1961, Conkle 1973, Conkle and Westfall 1984, Echols and Conkle

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1971, Mirov *et al.* 1952, Namkoong and Conkle 1976); Oregon (Ager and Stettler 1983, Silen and Rowe 1970, Smith 1981, Sturgeon 1979); Washington, Idaho, and Montana (Graham *et al.* 1985, Madsen and Blake 1977, Rehfeldt 1980, 1984, 1986a, 1986b); summary of reports about provenance performances in particular plantations in the Great Plains (pp.3, Read 1983) and summarizing that variation is beyond the scope of this report.

Variation between species is important because hybridization can introduce new genes into ponderosa pine, and the hypothetical limit of ponderosa's gene pool is all of its range-wide variation plus new variation in all the species that can be linked to ponderosa through controlled crosses.

LIFE-HISTORY CHARACTERISTICS

Ponderosa pines possess superior adaptation to drought by virtue of having rapid growing seedling tap roots and deep, extensive root systems as mature trees. Those characteristics serve the pine well in the summer-dry climates of California and in the summer-rainfall but low precipitation regions in the North Plateau, Rocky Mountains, and Southwestern Basin and Ranges. The species often thrives on south-facing sites and porous soils where most others fail. Drought tolerance and fire resistance are some of the adaptations that allow ponderosa pines to dominate sites as a climax species throughout the montane west.

Seed cones are widely distributed over a ponderosa's crown and the lower crown conelets on some trees probably receive frequent dustings of self pollen. But trees differ in their capacity to produce self-pollinated seeds; values range between 4 and 76 percent (mean 37) of outcross production in control pollinations (Sorensen 1970).

The production of selfed seed is kept at low-levels within stands by the deluge of out-cross pollen on seed conelets and by seed development processes that select against the selfed progeny without reducing sound seed set. Examinations of wind-pollinated seed from well stocked stands indicate that more than 95 percent of the embryos are from outcross pollinations (Mitton *et al.* 1977).

Natural selection against inbred individuals continues during the establishment and growth of stands. Selfed-seedling survival is about 5 percent less than that of comparable outcross seedlings, and growth rates are only 70 percent of outcrossed-seedling rates (Sorensen 1982). Many small seedlings that fail to meet minimum size grades in nurseries are probably inbred progenies. Growth depression of selfs continues after establishment and during stand development; their stem elongation rates during the first 10 years are only about 65 percent of rates for out-crossed progeny (Sorensen 1982). That depression places them at a severe disadvantage when competing for dominant positions in stands.

Ponderosa pines produce abundant seed crops every 2 to 5 years (Krugman and Jenkinson 1974). Pollen production begins at younger ages than seed cone production during the life cycle of individual trees (Linhart and Mitton 1985). A modest proportion of the trees in stands (as low as 20 percent) produce most (>65 percent) of the seed cones (Linhart and Mitton 1985). Seed production is concentrated on the trees with the largest diameters, and the same individuals tend to produce cones year after year. Pollen production is less predictable and is independent of seed cone production. Thus, the production, mixing, and migration of pollen from a variety of trees in stands is a major way ponderosa pine distributes genetic variation in populations.

The distance of seed migration is probably less than the distance of pollen migration, but wind carries ponderosa seeds substantial distances. Ponderosa pine seeds are the lightest among the western United States yellow and bigcone pines (Krugman and Jenkinson 1974). Seeds of Jeffrey pine are 3 times heavier, Coulter's are 9 times, and Digger and Torrey pines, more than 20 times heavier than those of ponderosa pine. Ponderosa seeds have long, wide wings and aerodynamic properties that result in free-fall rates that are slightly faster than those of Douglas-fir and slightly slower than white fir seeds (Siggins 1933). The wind-disseminated seeds of ponderosa pines have potentially greater flight distances than the heavier seeds of Jeffrey and Coulter pines, while Digger and Torrey seeds have only rudimentary wings that are ineffective for wind dissemination.

Wind-dispersed ponderosa seeds can provide a substantial mix of seed-parents and dense seed-fall for areas near mature stands. For example, the 4-year total seed-fall from ponderosa pines adjacent to 10-acre clearcuts in the Sierra Nevada averaged about 5,500 sound seeds per acre near the seed trees and about 2,500 near the centers of clearcuts (McDonald 1980). When wind-blown ponderosa pine seeds arrive on open, disturbed sites, their rapid germination and deep root growth often result in prolific seedling establishment.

Ponderosa seeds dispersed long distances can colonize new sites resulting in groups of trees that may differ genetically from one another. They may differ owing to the chance migration of different and limited genetic samples from the parental gene pool (Linhart *et al.* 1981) and by different selection pressures acting across significant environmental gradients at the new sites (Mitton *et al.* 1977, 1980; Beckman and Mitton 1984). But the significant proportion of total genetic variation in an area, more than 95 percent, is between individual trees within any one stand (Linhart *et al.* 1981, Woods *et al.* 1983).

GEOGRAPHIC DISTRIBUTION

Ponderosa pines grow from the mountains of southern California, near the border with Baja California, north throughout the Sierra Nevada. They span a remarkable elevational gradient in the Sierra Nevada, where scattered trees approach sea level adjacent to the Central Valley. They dominate a zone up to mid-elevation mixed-conifer

stands, are a major component of the mixed-conifer forests, and reach to the true fir forests at elevations between 7,000-8,000 feet. There, ponderosa pine is replaced by its high elevation near relative, Jeffrey pine. Ponderosa occupies coast range sites in central California where it often grows in special conditions like those of deep-stranded dune sands near Monterey Bay. It can not compete with Douglas-fir and redwood for fertile sites near the coast; it occurs on dryer sites inland, often on decomposed granitic or infertile, ultramafic soils throughout the Klamath and Siskiyou Mountains of northwestern California and southern Oregon. Ponderosa pine in the Willamette Valley of western Oregon probably represents the northern extension of the Pacific region populations.

Volcanic peaks of the Cascade Mountains form a continuous range from Mount Lassen in northeastern California, north and northeast through central Oregon and Washington, and into southern British Columbia. They are a physiographic boundary between the Pacific and North Plateau populations of ponderosa pine. Ponderosa pines grow east of the Sierra Nevada-Cascade crest on droughty slopes, in basins, and on mountain ranges of northeastern California, central and eastern Oregon and Washington, and north into the Okanogan Highlands of southern British Columbia. These North Plateau populations are contiguous with stands in the Bitterroot Range of Idaho and the northern Rocky Mountains of western Montana.

Populations become sparse and scattered in Montana at a geographic bottleneck associated with the Continental Divide. Ponderosa pines east of the Divide are the dominant conifers on the discontinuous geological formations of the high plains in Montana, Wyoming, North and South Dakota, and Nebraska. Dense, pure ponderosa stands blanket the Little Belt Mountains of central Montana and the Black Hills, Pine Ridge, and Sand Hills of South Dakota, Nebraska, and Wyoming.

The species extends southward throughout the central and southern Rocky Mountains, and scattered stands dot the minor ridges of the eastern Great Basin in Nevada and Utah. It occupies a broad belt that includes much of the plateau country of north-central Arizona and New Mexico.

Scattered populations grow on disjunct mountains in southern Arizona where a chain of island populations continues into the Sierra Madre Occidental of western Mexico. A more widely scattered but similar chain of populations extends through south-central New Mexico and western Texas into the Sierra Madre Oriental of eastern Mexico.

GEOGRAPHIC VARIATION

Three kinds of evidence have been used to gain information about broad geographic patterns of genetic variation in ponderosa pine: 1) identifying morphological traits that differ among regions, 2) using biochemical methods to identify the frequencies of gene products that vary in native stands from region to region, and 3) testing range-wide provenance samples in common garden trials to identify growth response differences between seed sources from different regions.

Morphological Differentiation

The compact, brushlike, bushy-tuft (scopulate) appearance of ponderosa foliage in the Rocky Mountains differed from the open, plumelike foliage in western areas, and var. *scopulorum* was coined in recognition of that characteristic (Engelmann 1880). Another foliage characteristic used to distinguish between the typical variety (*P. ponderosa* var. *ponderosa*) with three needles and var. *scopulorum* is the latter variety's moderate to high proportion of 2-needle fascicles (Figure 1). The proportions of 2 vs. 3-needle fascicles are influenced by tree age, and climatic and site factors; higher proportions of 2-needle fascicles are produced on young trees than on older trees and in response to harsh climates and sites than to more favorable growth conditions (Haller 1965). Var. *scopulorum* referred originally to Rocky Mountain ponderosa pine but through common usage has been extended to include ponderosa in Southwestern areas, those of southern Utah, and north-central

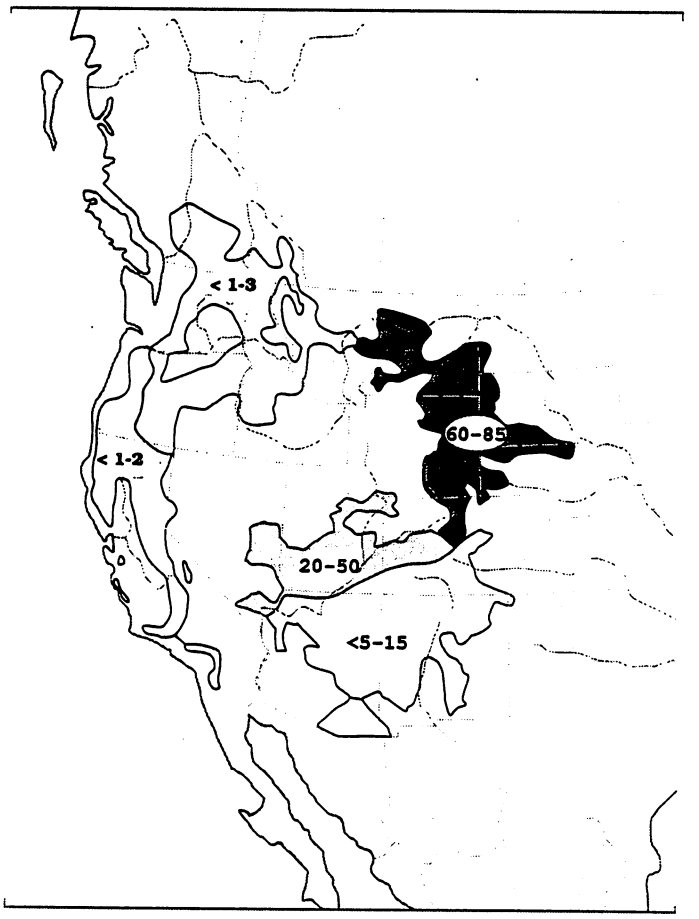

Figure 1.—Average frequencies of 2-needle fascicles on (mature/young) native ponderosa pines (Haller 1965). Similar results were reported by Weidman (1939) and Read (1980) for native and plantation grown pines.

Arizona and New Mexico. The extension is unfortunate because the pines of the Southwestern region have open foliage and lack 2-needle fascicles.

Generalized distinctions between trees in four regions (Pacific and North Plateau regions within western parts of the distribution and Rocky Mountain and Southwestern regions within eastern) have been identified (Table 1). In addition to the high proportion of 2-needle fascicles on trees in the Rocky Mountains, needles there are shorter than elsewhere. Pines in eastern parts of the distribution have stiff needles with sunken stomata when compared with flexible needles with surface stomata in the western parts. Cones and seeds are larger in western ponderosas than in eastern. Lastly, all ponderosas have rapid early growth, but eastern region trees reach their maximum heights at earlier ages than western region trees; in comparison, the western ponderosas become massive by continuing height growth through significantly older ages (Pfister *et al.* 1977).

Studies of regional differences in gene products provide additional information about geographic differentiation in ponderosa pine. Two included here are Smith's (1977) range-wide characterization of monoterpene compositions and newly developed information about isozyme allele frequency variation.

Xylem Monoterpene Variation

Smith's (1977) monumental study involved collecting xylem resin samples from about 75 individual trees at each of nearly 70 selected locations in the western United States. He used gas-liquid chromatography to determine the percentage of each of five major component monoterpenes that made up the volatile fraction of each tree's whole resin sample. Then each of the locations was characterized by averaging the appropriate component tree values.

The average monoterpene composition of the various locations revealed five broad regional groups with similar values for different sample locations within groups, and significant and readily observable differences between groups (Figure 2).

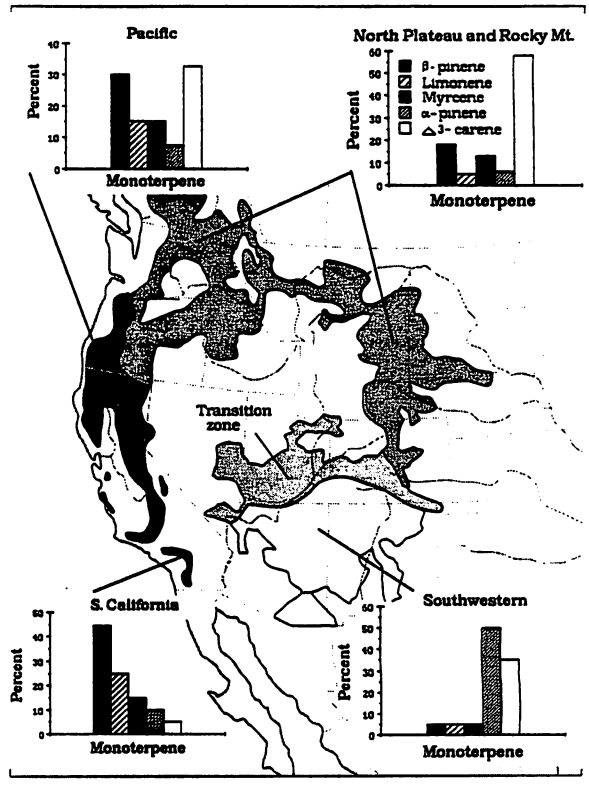

Figure 2.—Average amounts of the major monoterpene components in xylem resin of native ponderosa pines (Smith 1977).

Samples from southern California had a high proportion (45 percent) of ß-pinene and nearly lacked Δ^3-carene. There was an abrupt transition zone in the Transverse Ranges. Locations in the Pacific region west of the Sierra-Cascade crest had nearly equal proportions (about 30 percent) of two major components, ß-pinene and Δ^3-carene. East of the Sierra-Cascade crest, throughout the North Plateau and continuing through Montana into the central Rocky Mountains of Colorado, monoterpenes were about 60 percent Δ^3-

Table 1.—Characteristics of native ponderosa pines from four regions [(+) = present or true for the trait; (-) = lacking or not true].

	Western areas		Eastern areas		
Trait	Pacific	N. Plateau	Rocky Mt.	Southwestern	Reference[1]
2-needled fascicles	-	-	+	-	a,d
Short needles	-	-	+	-	d
Stiff needles	-	-	+	+	d
Stomata sunken	-	-	+	+	d
Large seeds	+	+	-	-	c
Rapid growth rates, massive adult sizes	+	+	-	-	b

[1] a Haller 1965;
b Pfister *et al.* 1977.
c Read 1980;
d Weidman 1939.

carene. Smith characterized an extensive area from eastern Nevada, across Utah, southern Colorado, and into northern New Mexico as a transition zone between the North Plateau-Rocky Mountain types and a distinct Southwestern type centered in Arizona and New Mexico. The Southwestern type was distinguished by a high proportion (50 percent) of α-pinene. The presence of Mexican yellow pines in southern Arizona and New Mexico complicates the resin story; Smith's samples from there consisted of close to 100 percent α-pinene.

There are noteworthy geographic trends in component compositions corresponding to the potential gene flow pattern that exists between contiguous regions. The trends extend in a clock-wise pattern making a nearly complete circle beginning at the monoterpene race in southern California, and continuing through the Pacific and the North Plateau-Rocky Mountain to the Southwestern race. The major component in Southern California ponderosa, ß-pinene, diminishes steadily reaching its lowest levels in the Southwestern area; the trend in limonene is similar. A major component in Pacific, North Plateau-Rocky Mountain, and Southwestern races, Δ^3-carene, is absent or in only minor amounts in southern California and in extreme southern Arizona-New Mexico. α-pinene is below 10 percent in all but the Southwestern race, where it is the major component.

Knowledge of these patterns leads to several conclusions about ponderosa pine. First, the monoterpene races are distinct; transitions are sharp between: 1) Southern California and Pacific, 2) Pacific and North Plateau-Rocky Mountain, and 3) the Southern California-Pacific and Rocky Mountain-Southwestern races. These three transition zones correspond to physiographic barriers that are respectively: 1) Transverse Ranges at the narrow southern tip of the Sierra Nevada, 2) the crest of the Sierra Nevada and Cascade ranges, and 3) the low elevation Mohave-Sonoran desert region south of the Great Basin. There are several explanations for sharp transitions. In the southern region, the Great Basin and Mohave-Sonoran Desert areas effectively isolate the Southern California-Pacific races from the Southwestern-Rocky Mountain racaes). Some races may have come together only recently and have had little time for gene exchange (Critchfield 1984). Biological differences between races such as in the timing of flowering, resistance to pests (Pacific and North Plateau races, Sturgeon 1979; Peterson 1984), or the maladaption of hybrid offspring, could severely restrict gene flow. Or, less likely in our judgement, selection for particular monoterpene types may be intense in different regions.

Second, an extensive transition zone between the Rocky Mountain and Southwestern monoterpene races suggests either substantial blending of genes from two differentiated races or intermediate selection pressures. Lastly, ponderosas of the North Plateau and Rocky Mountains surprisingly posses identical monoterpene compositions. There is no differentiation between the northern populations within *P. ponderosa* var. *ponderosa* and *P. ponderosa* var. *scopulorum*, and correspondingly, there is no east-west differentiation associated with the population bottleneck that coincides with the Continental Divide in west-central Montana.

Monoterpene patterns give clues about the evolutionary history of ponderosa pine. The proliferation of related western yellow pine species in Mexico is reason to hypothesize that pines of subsect. *Ponderosae*, including ponderosa, evolved from southern progenitors (Axelrod 1986). Since the ponderosa pines in the southern regions, those from Southern California and the Southwest, differ significantly in monoterpene compositions, they may have evolved along different lines from distant Mexican populations. The Southern California monoterpene type prompts a hypothesis that its progenitors had high proportions of ß-pinene and limonene.

Recent divergence from, or introgression with other related California species is unlikely. Jeffery, the other major western yellow pine and Coulter, Digger, and Torrey pines, the three California big-cone pines that might have had a common progenitor or have been a source of genes through processes of hybridization and introgression, all contain only trace amounts (< 2 percent) of ß-pinene (Smith 1967b, Zavarin 1967). Jeffrey pine resins are 95 percent heptane with only trace amounts (<1 percent) of ß-pinene and limonene, ponderosa pines lack heptane.

Arizona pine (*P. arizonica* Engelm.), the five needled pine that many considered to be a variety of ponderosa pine, may be a close relative of Southwestern ponderosa, but it is again recognized as a distinct species (Peloquin 1984). Peloquin found numerous differences between Arizona and 3-needled Southwestern ponderosa pines; he reported that Arizona pine lacked Δ^3-carene, and its monoterpenes were close to 100 percent α-pinene. Since 72 of 74 trees Smith sampled in two stands on the Coronado National Forest of southern Arizona lacked Δ^3-carene (Smith 1977), it is possible that the majority of those samples were Arizona pine.

Apache pine (*P. engelmannii* Carr.), the third western yellow pine in southern Arizona-New Mexico, also lacks Δ^3-carene, and like Arizona pine has monoterpenes consisting of close to 100 percent α-pinene (Peloquin 1984). The relatively high proportion of α-pinene in Southwestern ponderosa distinguishes it from Southern California, Pacific, and North Plateau-Rocky Mountain monoterpene types with low proportions. Since resins of both Apache and Arizona pines consist of α-pinene, there are reasons to hypothesize either close phylogenetic relationships or introgression to account for the relatively high proportions of α-pinene in Southwestern ponderosa.

A final postscript to the evolutionary considerations raised by monoterpene data is to question whether Δ^3-carene, the prevalent monoterpene in the northern populations, might trace to a progenitor that migrated northward from the Sierra Madre Oriental of eastern Mexico along a route that

included the Sacramento Mountains of central New Mexico to reach and spread northward through the Rocky Mountains.

Allozyme Variation

We know of no published reports about range-wide variation in ponderosa pine isozymes—the allelic variants of enzyme genes that are detected using electrophoresis. But a Forest Service study provides data that are being prepared for publication (Niebling and Conkle, in prep.). That study focused on Washoe pine, but it included ponderosa pine samples bulked from different geographic areas to represent the Pacific, North Plateau, and Rocky Mountain regions. Sample sizes used to compute allele frequencies were equivalent to about 100 diploid genotypes for each of the three regions. Allele frequencies were evaluated for 36 genes.

Average heterozygosities for samples from the Pacific, North Plateau, and Rocky Mountain regions (0.14, 0.18, and 0.16 respectively) were similar to previous reports for ponderosa pine (Allendorf *et al.* 1982, O'Malley *et al.*1979) and were near the mean of values (range from 0.0 to about 0.34) reported for other conifer species (Ledig 1986).

Analyses of genetic distances between samples from the three regions showed a close genetic relationship between Pacific and North Plateau ponderosa pines (Nei's genetic distance equaled 0.01). But the genetic distances between the two western samples in comparisons with those from the Rocky Mountain region were sizable and significant: Nei's distances were 0.08 between Pacific and Rocky Mountain and 0.06 between North Plateau and Rocky Mountain samples.

Allele frequencies for several genes contributed to differentiation between the Pacific-North Plateau samples and the Rocky Mountain samples (Figure 3). The gene named alcohol dehydrogenase 2 (Adh2) (left-most positions on the graphs) shows that the Pacific and North Plateau samples had allele 1 at frequencies near 0.40 and allele 2 at frequencies near 0.60. In Rocky Mountain samples, the frequency of allele 1 increased to about 0.80 while allele 2 decreased to less than 0.05, and a third allele, not present in the western samples, was present at a frequency above 0.10. The remaining 5 genes named glutamate dehydrogenase, glutamate-oxaloacetate transaminate 3, 6-phosphogluconate dehydrogenase, isocitrate dehydrogenase, and phosphoglucomutase (Gdh, Got3, 6pgd, Idh, and Pgm) show further similarities for the allele frequencies for comparisons between Pacific and North Plateau and additional differences between the two western and the Rocky Mountain sample. The Rocky Mountain sample had allele 2 for Gdh in significant frequencies but that allele was missing from the Pacific and North Plateau samples. Idh was a gene with the reverse condition; Pacific and North Plateau samples had allele 2, and that allele was not found in the Rocky Mountain sample. Got3, 6pgd, and Pgm have major shifts in allele frequencies between Rocky Mountain and the other two samples.

These differences contrast with the resin patterns in exhibiting significant isozyme differentiation between the northern regions of ponderosa pine that are west and east of the Continental Divide. Isozyme gene flow must be minimal between western and eastern populations because some alleles, like Adh2 allele 2 and Idh allele 2 were in significant frequencies in the two western populations but had low values or were absent from the Rocky Mountains; Gdh allele 2 and 6pgd allele 3 were in significant frequencies in the Rocky Mountain, but were absent from the Pacific and North Plateau samples. Taken together, the information for these four genes supports the conclusion that there is no effective movement of region specific alleles in either direction, from west to east or from east to west.

Variation Expressed in Growth Trials

Botanical samples from nature often provide comparisons where the effects of heredity and environment are inseparable. But when seeds collected throughout the species range are grown in nurseries and transplanted to plantations, each test provides a relatively uniform environment

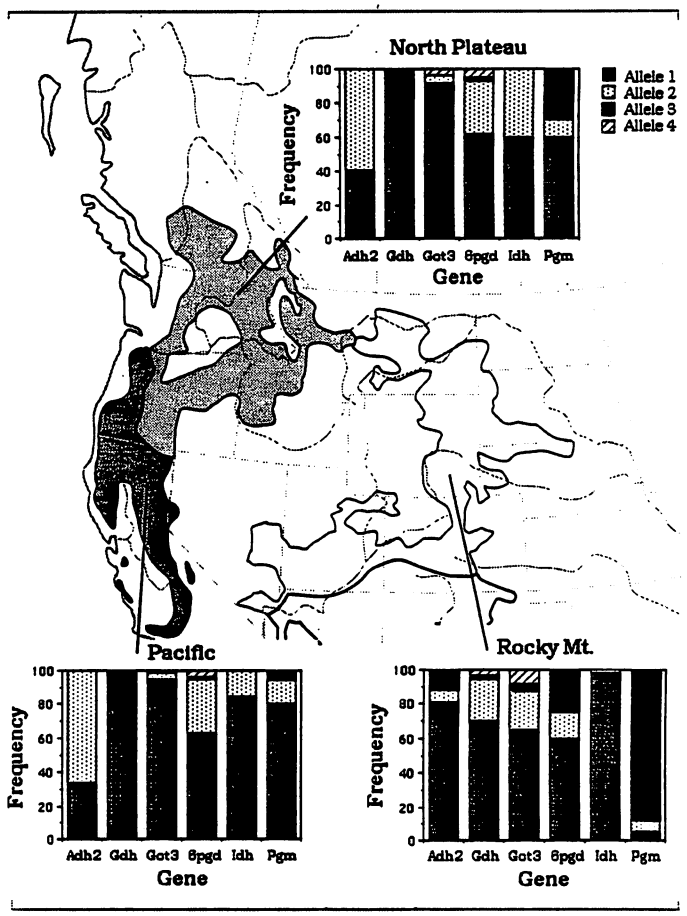

Figure 3.—Allele frequencies for 6 isozyme genes for native ponderosa pines from the northern areas of the natural distribution.

where growth differences between provenance samples are a more direct measure of genetic differences. Several range-wide provenance tests have been conducted with ponderosa pine (Weidman 1939; Squillace and Silen 1962; Wells 1964; Read 1980, 1983; Van Haverbeke 1986). In those tests, characteristics that varied from region to region were identified and geographic groups were formed consisting of provenances with similar responses.

The results from different provenance trials (Table 2) generally agree as to geographic patterns of variation, considering that the trials differed in design and implementation. Southern California samples were excluded from all the tests, but the differences in growth of other samples could be clustered into, now familiar, groups: western provenances from the Pacific and North Plateau regions, and eastern provenances from the Rocky Mountain and Southwestern regions.

Our summary of growth trial responses contains three sections. The first section (Table 2) lists characteristics that vary between western and eastern areas. Western provenances germinated at a slower rate than eastern provenances; they had seedlings with more numerous cotyledons, and they produced only primary needles on 1st season shoots.

The second section in Table 2 reports north-south differences. Provenances from the Pacific and Southwestern regions had tall 1-yr. seedlings that failed to produce winter terminal buds; northern provenances were shorter and produced buds. Northern sources were the first to produce a flush of growth in the spring.

The third section (Table 2) contains region specific growth characteristics that are listed beginning with Pacific provenances, followed by those for the North Plateau, Rocky Mountain, and Southwestern. Seedlings and trees from the Pacific region were maladapted to cold and were severely damaged or were killed during winters in most of the trials. North Plateau provenances had the best long term growth in North Plateau locations. Scopulate foliage and 2-needle fascicles were moderately heritable characteristics; Rocky Mountain provenances had appressed foliage-compact crown characteristics, short needles, and 2-needle fascicle counts that generally correspond to the trends reported in field observations by Weidman (1939) and Haller (1965). Rocky Mountain trees were the slower-growing provenances at first; their superior survival, consistent growth, and cold hardiness are reasons they become the larger trees in Great Plains trials. Trees from Southwestern provenances had tall seedlings; some produced a second flush of growth during the season, but they had inherently slow growth in subsequent seasons and were among the shorter trees in trials at ages 10 and 15 years.

SUMMARY: GENETIC STRUCTURE BELOW THE SPECIES LEVEL

Available evidence suggests that *P. ponderosa* var. *ponderosa* consists of three major geographic races (Figure 4). Provenances from Southern California are the least well known, having been omitted from most research to date. But Smith's (1977) monoterpene findings provide conclusive evidence of their strong differentiation from the Southwestern and North Plateau-Rocky Mountain types, and significant differences with nearby provenances of the Pacific race.

Pacific race pines have relatively large needles, cones, seeds, and are rapid growing, but lack the thick hypodermal cell layers in needles that contribute to stiffness and may impart cold resistance (Weidman 1939); they are the least cold-hardy trees in provenance trials outside the Pacific region.

In crown form (open plume-like foliage), 3-needle fascicles, isozyme characteristics, and poor growth in trials on the Great Plains and Michigan, the North Plateau race is closely aligned with the Pacific race. But its needles have thickened layers of hypoderm and sunken stomata; its monoterpene characteristics are indistinguishable from those of stands from throughout the Rocky Mountains.

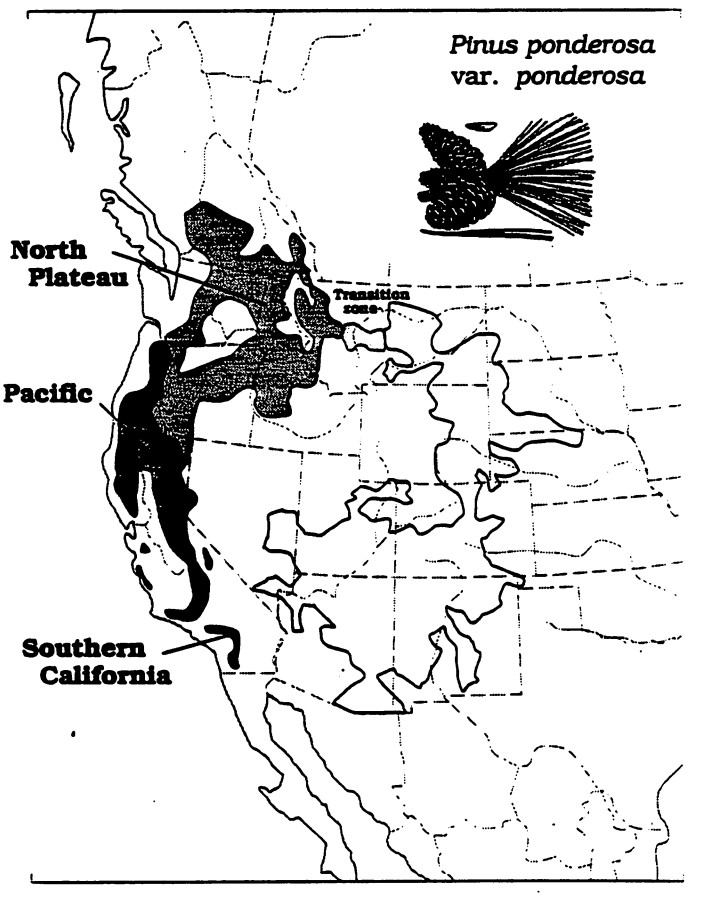

Table 2.—Growth responses in provenance trials of ponderosa pines from 4 regions [(+) = present or true for the trait; (-) = lacking or not true].

Trait	Western areas		Eastern areas		Reference[1]
	Pacific	N. Plateau	Rocky Mt.	Southwestern	
West-east differentiation					
Slow germination	+	+	-	-	a,f
Numerous cotyledons	+	+	-	-	a
1-yr. seedlings lacked mature needles	+	+	-	-	a,f
Primary needles green vs. purple on winter stems	+	+	-	-	a,f
Some seeds germinated in the 2nd season	+	+	-	-	f
Bluish green vs. grayish foliage	+	+	-	-	e,f
Seedlings produced some lammas shoots	+	+	-	-	f
Needles flexible	+	+	-	-	e
Stomata near surface vs. in deep depressions	+	+	-	-	e
Tall long-term growth in northwestern U.S.[2]	+	+	-	-	d,e
North-south differentiation					
Tall 1-yr. seedlings	+	-	-	+	a,f
Significant percent of 1-yr. seedlings set winter terminal buds	-	+	+	-	f
Growth began early in the season	-	+	+	-	a,f
Area specific differentiation					
Severe winter injury to seedlings	+	-	-	-	a,f
Needle hypoderm thin	+	-	-	-	e
Frost susceptible and cold intolerant in Idaho	+	-	-	-	e
Fascicles narrow	-	+	-	-	a,e
Shoots lacked waxy bloom	-	+	-	-	a,e,f
Good long term survival in northwestern U.S.	-	+	-	-	d
2-needle fascicles	-	-	+	-	a,e,f
Needles short	-	-	+	-	a,d,e,f
Low proportion of seedlings produced lammas shoots	-	-	+	-	a
Short 2-yr. seedlings	-	-	+[3]	-	f
Foliage compact, appressed vs. open, plumelike	-	-	+	-	e
Good long-term survival in Great Plains and Michigan	-	-	+	-	a,b,c
Tall long-term growth[2] in Great Plains and Michigan	-	-	+[4]	-	a,b,c
Fascicles broad	-	-	-	+	a,e
High proportion of seedlings had shoots with waxy bloom	-	-	-	+	a,e,f
Seedlings had 2 growth-flush periods per year	-	-	-	+	f
Tall 2-yr. seedlings	-	-	-	+	f

[1] a Read 1980, nurseries in N. Dakota (1) and Nebraska (1);
b Read 1983, plantations in Great Plains (8) and Michigan (1);
c Van Haverbeke 1986, plantations in Great Plains (6) and Michigan(1);
d Squillace and Silen 1962, plantations in Oregon (3), Washington (2), and northern Idaho (1);
e Weidman 1939, nursery and plantation in northern Idaho;
f Wells 1964, nursery in Michigan.

[2] Generally correlated with greater diameters.

[3] Particularly provenances from the central Rocky Mts.

[4] With the exception of provenances from the central Rocky Mts.

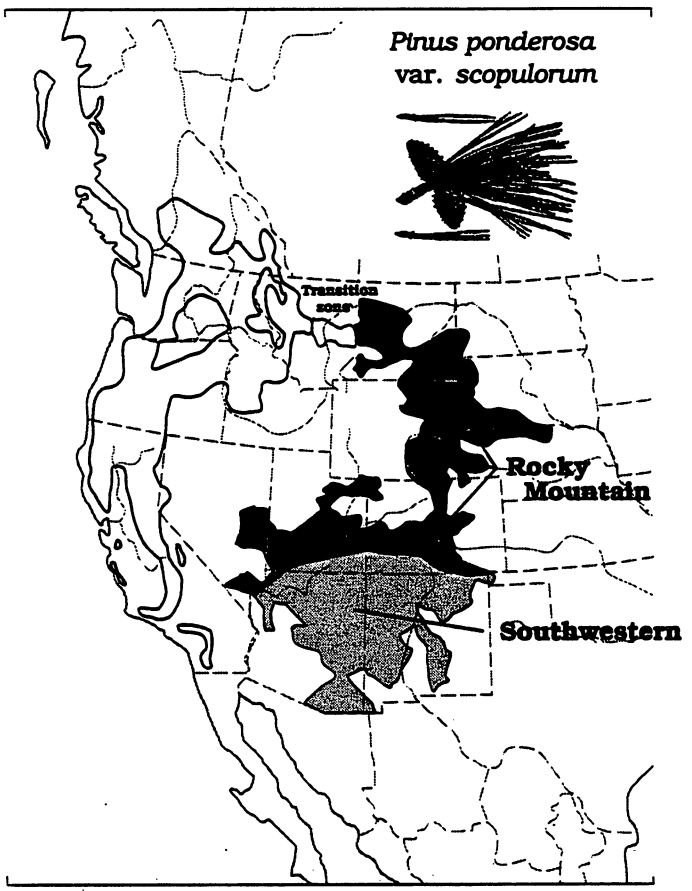

Figure 5.—Eastern geographic races of ponderosa pine, excluding poorly understood populations in central Mexico.

P. ponderosa var. *scopulorum* consists of two major races (Figure 5). The Rocky Mountain race is distinguished by compact foliage, 2-needle fascicles, isozyme alleles, and growth in trials. At its contact zone with the North Plateau race, near and perhaps just east of the Continental Divide, a few stands have intermediate characteristics. The abrupt transition zone in the north contrasts with a broad transition zone between the Rocky Mountain and Southwestern races; the southern transition zone stretches from stands in the eastern Great Basin in Nevada, across Utah and central Colorado. The latter zone has stands with reduced proportions of 2-needle fascicles and monoterpene characteristics that are intermediate between stands from the northern and central Rocky Mountains and stands of the Southwestern race.

The Southwestern race has relatively open crown foliage, low proportions of 2-needle fascicles and resins with distinctive monoterpene composition.

HYBRIDIZATION: A SOURCE OF VARIATION ABOVE THE SPECIES LEVEL

Pinus monographer G. R. Shaw (1914) placed the western yellow pines of subsection *Ponderosae* in his *Australes* group III which included most of the New World hard pines having cones that open and shed their seeds promptly at maturity. Shaw's *Australes* was divided into groups XI and XII (southern and western yellow pines, respectively) by Duffield (1952). Duffield's group XI was re-classified as subsection *Australes* and his group XII as subsections *Ponderosae* and *Sabinianae* (the California big-cone pines: *P. torreyana* Carr., *P. sabiniana* Dougl., and *P. coulteri*) by Little and Critchfield (1969).

Duffield relied primarily on crossing behavior in separating the southern and western yellow pines, using results of the species hybridization program at the Institute of Forest Genetics (IFG), Placerville, California. Most species within Duffield's groups XI and XII were linked directly or indirectly by their ability to hybridize, but attempts to cross southern and western species produced only hollow seeds. A later analysis demonstrated significant levels of conelet and ovule abortion in western X southern crosses, additional indicators of the strong genetic barriers separating the two groups (Critchfield 1963).

Most crosses involving subsect. *Ponderosae* at the IFG were made on native ponderosa, Jeffrey (*P. jeffreyi*), and Washoe (*P. washoensis*) pines between 1929 and 1977. Parts of this crossing program have been described in detail elsewhere: (a) all crosses between subsections *Ponderosae* and *Sabinianae*, and all crosses of Jeffrey pine with other members of *Ponderosae* (Critchfield 1966), and (b) all crosses involving Washoe pine, and all crosses between geographic races of ponderosa pine (Critchfield 1984). This new summary includes other crosses involving ponderosa pine, as well as a few crosses in which other members of subsect. *Ponderosae* were used as female parents.

Materials and Methods

Crosses were made on 30 ponderosa pines in natural stands on the western slope of the Sierra Nevada and on IFG arboretum trees of other species (Table 3). Most taxa of subsect. *Ponderosae*, including the Rocky Mountain and Southwestern races of ponderosa pine, are native to summer-rainfall climates and do not thrive in the summer-dry environment at the IFG. Ponderosa pines of Southwestern origin rarely produce female cones in the arboretum. Rocky Mountain ponderosa pines sometimes produce cones, but they yield few sound seeds from controlled crosses (Critchfield 1984), so crosses on them have been omitted. Pines native to Mexico and Central America are additionally handicapped by the freezing weather and occasional, heavy, wet snowfalls, and the trees that survive seldom flower. Pollen representing most of the Latin American species was collected from natural stands, and voucher specimens for many of those trees are filed in the IFG herbarium. No pollen collections were available from a few species of *Ponderosae*, including *P. cooperi* Blanco and *P. michoacana* Martínez.

The taxonomy of Mexican yellow pines is poorly understood, but the identifications of trees listed in Table 3 are

Table 3.—Parent trees of crosses summarized in Table 5.

Taxon	Number of parents Female	Male	Location or geographic origin (number of localities when >1)
Natural Stands:			
Pinus arizonica Engelm. (Arizona pine)		>1	Arizona: Sta. Catalina Mts.
P. engelmannii Carr. (Apache pine)		>1	Arizona: Chiracahua Mts.
P. hartwegii Lindl.		2	México State, Veracruz
P. lawsonii Gord.		1	Veracruz
P. montezumae Lamb.		4	Hidalgo, México State (2), Michoacán
P. ponderosa	30	8	California: Sierra Nevada (16)
P. pringlei Shaw		3	Oaxaca
p. pseudostrobus Lindl. var. *pseudostrobus*		7	Guatemala; Hidalgo Michoacán (2), Nuevo León
var. *oaxacana* Martínez		2	Oaxaca
var. *tenuifolia* (Benth.) Shaw		3	Honduras (2)
P. teocote Schiede & Deppe		3	Michoacán, Puebla, Veracruz
Arboretum trees:			
P. arizonica	1	3	Arizona: Chiracahua Mts.
P. durangensis Martínez		2	Durango (2)
P. engelmannii	1	6	Arizona: Chiracahua Mts. (2)
P. montezumae	1	7	Durango, "Mexico" (2), unknown
P. patula Schiede & Deppe	5	1	Oaxaca, "Mexico" (2)
P. pseudostrobus f. *protruberans* Martínez		1	Nuevo León

fairly reliable with a few exceptions. J. P. Perry, Jr. (pers. comm. Oct. 28, 1987) checked the identity of four "*P. montezumae*" trees used in crosses and concluded that one tree could be a *P. montezumae-P. rudis* intermediate, and another tree was unidentifiable. The arboretum tree listed as *P. pseudostrobus* f. *protruberans* (Table 3), grown from seed collected in northeastern Mexico (Zobel and Cech 1957), was tentatively identified by Perry as *P. arizonica* var. *stormiae* Martínez.

Although these crosses cover a period of nearly 50 years, techniques of tree breeding and the processing of cones and seeds were standardized early in this period (Critchfield 1963). The routine use of control crosses, within-taxon crosses that accompany between-taxon crosses, did not begin until about 1960. Data on sound or germinable seed production from such paired crosses make it possible to estimate crossability for individual seed-parents. All available single-tree estimates were averaged for estimating the crossability of two taxa. Older crosses mostly lacked controls, and their crossability was estimated by expressing the average yield of sound seeds per cone for all crosses between two taxa as a percentage of the average yield for all crosses within the maternal-parent taxon (Table 4). With few exceptions, crossability estimates by these two methods have comparable values (Table 4).

Previous Reports of Hybrids

Most *Ponderosae* hybrids produced by controlled pollination at the IFG were described by Righter and Duffield (1951), Keng and Little (1961), and Little and Righter (1965). Monoturpene composition of a few hybrids was reported by Smith (1967a).

Natural hybrids are often mentioned and may be numerous in this group, but only a few have been studied. Critchfield (1966) reviewed reports of natural hybridization of Jeffrey pine (Figure 6) with ponderosa and Coulter pines.

The three yellow pines of southeastern Arizona (Figure 6)—Apache, Arizona, and Southwestern ponderosa pines (Table 2)—hybridize in nature in all combinations (Peloquin 1971). Peloquin's work also established that three-species hybrids are occasionally produced (Peloquin 1984). Southwestern ponderosa, which has 3-needled fascicles, replaces the 5-needled Arizona pine at upper elevations in the isolated mountain ranges of this region, and in one range (Pinaleno Mountains) it also replaces Arizona pine near the lower edge of the forest zone (1,500-1,900 m) (Peloquin 1971). The two taxa are elevationally parapatric and connected by zones of intergradation. Apache pine hybridizes with the other two pines, but gene exchange appears to be limited.

Martínez (1948) believed that *P. montezumae* hybridized with both *P. rudis* and *P. hartwegii*, two other Mexican pines that he grouped with *P. montezumae* in his section *Montezumae*. Another combination he mentioned was *P. montezumae* and *P. pseudostrobus*, the latter in his section *Pseudostrobus*. Mirov (1961) also believed that natural hybridization was common among the Mexican yellow pines. In

Table 4.—Estimates of crossability[1].

Male parent	All crosses		Single crosses with controls Crossability[2]		
	Number	Crossability[3]	Number	Mean	Range
P. arizonica	17	32.3			
Chiracahua Mts	15	25.3	3	13.0	4.5-26.2
Sta. Catalina Mts.	2	84.6	1	73.0	
P. durangensis	8	4.3	7	5.1	0.5-23.0
P. hartwegii	2	8.4	3	6.1	0.0-11.8
P. montezumae	18	14.4	9	24.5	0.0-75.6
P. pseudostrobus					
var. *oaxacana*	11	2.9	6	4.7	1.6-21.1
var. *pseudostrobus*	20	4.1	10	2.3	0.7-18.4
f. *protruberans*	3	20.4	3	42.0	0.0-85.2

[1] All crosses on Sierra Nevada ponderosa females.

[2] Individual crossabilities calculated from paired crosses on the same tree during the same year.

[3] Mean of sound seeds per cone from all crosses, expressed as percent of sound seeds per cone in California ponderosa pine.

addition to the combinations noted by Martínez, Mirov listed as possibilities the following: *P. oaxacana* Mirov and *P. pseudostrobus*, *P. oaxacana* and *P. montezumae*, and *P. rudis* and *P. hartwegii*. Caballero's (1967) data on seed and seedling characteristics supported the possibility of natural hybridization between *P. montezumae* and *P. pseudostrobus* at one locality in central Mexico, and between *P. montezumae* and *P. michoacana* at another locality.

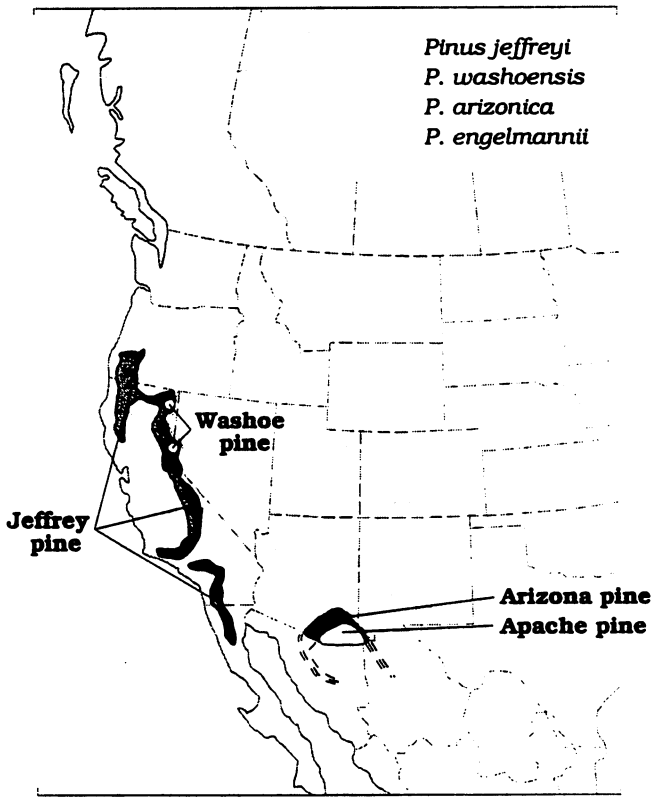

Figure 6.—Geographic distributions of the western U.S. species that are grouped with ponderosa pine in subsect. Ponderosae.

The cross between ponderosa pine and Coulter pine (*P. coulteri*) has been attempted at the IFG many times, but without success (Critchfield 1966; unpublished data, IFG). Smith (1977) identified by monoterpene composition three probable hybrids among several thousand ponderosa pines he sampled throughout the species range. The three trees were in a mixed stand near Lake Arrowhead in the southern California mountains. Their turpentine had 10-16 percent ß-phellandrene, in the range expected for a hybrid between ponderosa pine (maximum ß-phellandrene about 3 percent; Smith 1977) and Coulter pine (minimum 20 percent; Smith 1967b).

Crossing Results

With a few exceptions, the crosses (Table 5, Figure 7) validate Duffield's (1952) recognition of the western yellow pines as a distinct group. The most conspicuous exception is the failure of *P. ponderosa* to hybridize with *P. teocote* and *P. lawsonii*, a pair of Mexican pines that are morphologically similar and always classified together. These are the first crosses reported for either species. Neither one yielded any sound seed in crosses on ponderosa pine, although the same pollen collection of *P. teocote* was functional in another cross. An added indication of strong genetic barriers between *P. ponderosa* and these two Mexican pines is the reduction in numbers of hollow seeds (Table 5); this condition can probably be attributed to differential ovule abortion early in the reproductive process.

The same collections of *P. teocote* and *P. lawsonii* pollen produced putative hybrids on females of *P. patula*, a closed-cone Mexican pine of subsect. *Oocarpae* (Critchfield 1966). Analysis of monoterpene from two putative hybrids of *P. patula* X *P. teocote* and the single surviving putative hybrid of *P. patula* X *P. lawsonii* gave mixed results. The trees from the first cross were intermediate in monoterpene com-

Table 5.—Crossing results[1] at the Institute of Forest Genetics, Placerville, California, among taxa of *Pinus* in subsections *Ponderosae* and *Oocarpae*.

Male Parent	Female parent: *ponderosa* (Calif.)	*arizonica*	*engelmannii*	*montezumae*
PONDEROSAE:				
ponderosa (Calif.)	[2] 17/17 605/188 48.6/58.6	1/1 2/2 32.5/73.0	1/1 13/9 12.6/33.0	
ponderosa (Rocky Mts.)	[2] 20/20 557/692 17.1/51.3		1/1 10/3 15.7/64.3	
arizonica	17/17 1385/27 15.7/76.5		2/2 24/17 37.4/45.5	
engelmannii	18/18 1795/1115 15.3/60.6		2/2 13/11 46.8/54.3	
durangensis	8/6 109/43 2.1/46.8			
montezumae	20/19 764/368 7.0/69.3		1/1 1/1 86/87	1/1 7/3 25.3/35.3
hartwegii	3/2 81/12 4.1/56.2			1/1 6/1 1/63 [3]
pseudostrobus var. *pseudostrobus*	20/10 245/95 2.0/49.9			1/1 7/6 104.0/126.3
var. *oaxacana*	11/6 117/59 1.4/29.9			
var. *tenuifolia*	13/0 147/78 0.0/46.4			
f. *protruberans*	3/2 47/1 9.9/46.1			
OOCARPAE:				
lawsonii	1/0 40/20 0.0/23.6			
teocote	2/0 13/4 0.0/13.2			
pringlei	12/0 164/71 0.0/36.8			

[1] Key to data cells:

a/b c/d e/f	Verified hybrid Putative hybrid

a Total attempts
b Attempts producing sound seed
c Female strobili pollinated
d Cones harvested
e Sound seed per cone (mean)
f Total seed per cone (mean)

[2] Data from Critchfield 1984 (Table 3).

[3] Single seed failed to germinate.

Table 6.—Recent hybrids of western and Mexican hard pines.

Hybrid	Subsection	Pollination year	Identifying characteristics
P. montezumae (?) x *pseudostrobus*	*Ponderosae*	1963	Female parent identity in question; hybrids resemble pollen parent in fine needles and smooth twigs.
P. ponderosa x *durangensis*	*Ponderosae*	1963	Needles in fascicles of 3-5 (mean 4.6)
P. ponderosa x *hartwegii*	*Ponderosae*	1963	Long coarse needles mostly in fascicles of 3, occasionally 4.
P. ponderosa x *oaxacana*	*Ponderosae*	1965	Secondary needles on 1st-year seedlings more abundant, less stout than on *P. ponderosa* half-sibs, in fascicles of 3-4.
P. ponderosa x *pseudostrobus*	*Ponderosae*	1965	Same as *P. ponderosa* x *oaxacana*.
P. ponderosa x *"pseudostrobus f. protruberans"* [*P. arizonica* var *stormiae* (?)]	*Ponderosae*	1977	All 1st-year seedlings smaller than all *P. ponderosa* half-sibs (no surviving hybrids).
P. jeffreyi x *torreyana* x	*Ponderosae* *Sabinianae*	1967	1st-year seedlings intermediate, significantly different (p = 0.05) from both parents in germination time and height (*P. jeffreyi* half-sibs germinated faster, were shorter in height). Needles of older trees had semi-continuous or discontinuous waxy stomatal lines (*P. jeffreyi* continuous).
P. patula x *pringlei*	*Oocarpae*	1966	Monoterpenes of hybrids—much higher levels of α-pinene [abundant in *P. pringlei*, (Mirov 1961)] and lower levels of ß-phellandrene than *P. patula*.
P. patula x *teocote*	*Oocarpae* (x *Ponderosae*)	1963	Same as *P. patula* x *pringlei*.

position (Table 6), and are considered to be true hybrids. The single putative hybrid from the cross with *P. lawsonii* pollen had the same high level of ß-phellandrene as the *P. patula* parent, and is probably not a hybrid.

Apart from *P. teocote* and *P. lawsonii*, which apparently have closer affinities with subsect. *Oocarpae*, all crosses between *P. ponderosa* and other taxa of *Ponderosae* have been successful except those with pollen of *P. pseudostrobus* var. *tenuifolia*. This taxon is usually given specific status as *P. maximinoi* H. E. Moore, but its distinctness is appreciably blurred in western Mexico (Stead 1983). Its failure to cross with *P. ponderosa* could be due to inadequate pollen treatment. The data suggest alternatively that the *P. pseudostrobus* complex (*P. pseudostrobus* and its varieties *oaxacana*, and *tenuifolia*) is the least crossable element of the subsection in combinations with *P. ponderosa* (Table 5). About half of the crosses involving *P. pseudostrobus* and var. *oaxacana* produced no sound seed (Table 5), and their crossabilities with *P. ponderosa* were only 3-4 percent.

An apparent exception to the low crossability of this complex with *P. ponderosa* is *P. pseudostrobus* f. *protruberans* (Table 5), but as noted earlier the arboretum tree with this designation is most likely *P. arizonica* var. *stormiae*. Its high crossability supports this identification: on one ponderosa pine it yielded no sound seed but on two others it produced 22-23 sound seeds per cone.

The *P. montezumae* complex was generally more crossable with *P. ponderosa* than the *P. pseudostrobus* group (Tables 4, 5). *P. durangensis* and *P. hartwegii*, which Martínez

included in his section *Montezumae*, had crossabilities of 4-8 percent, and *P. montezumae* was much higher (Table 4). The individuals of *P. montezumae* used in these crosses were a heterogeneous assemblage, as noted earlier, but crosses with trees of established identity gave about the same results as the entire group.

Three crosses on a "*P. montezumae*" of uncertain status in the IFG arboretum are more difficult to interpret (Table 5), and leave the identity of this well-studied tree an open question. The pollen lots were from reliably identified individuals of *P. montezumae*, *P. pseudostrobus*, and *P. hartwegii*, all three produced authentically hybrid offspring in crosses with *P. ponderosa*. On the "*P. montezumae*" female they gave diverse and unexpected results. The cross with *P. pseudostrobus* pollen produced many more sound seeds per cone than the presumably intraspecific cross with *P. montezumae* pollen. And the cross with *P. hartwegii* pollen yielded no sound seed, although this species is believed to hybridize with *P. montezumae* in nature.

The two most crossable yellow pines, *P. arizonica* and *P. engelmannii*, are also geographically closest and most similar to *P. ponderosa*. Hybrids of both combinations were mass-produced at the IFG around 1950, and large numbers of strobili were pollinated and cones harvested (Table 5). Crossability estimates are not necessarily much more accurate, however, because nearly all crosses of both combinations were made with pollen from a few arboretum trees (Table 3). A further problem in interpreting the highly variable crossing behavior of *P. arizonica* (Table 4) is the identity of the pollen parents. Arboretum trees of this taxon have 3-5 needles per fascicle, and may have originated in a locality within the zone of intergradation between *P. ponderosa* and *P. arizonica* in the Chiracahua Mountains. Crossability was highest with pollen collected from one or more trees in the Santa Catalina Mountains (Table 4), but in this instance the identity of the parent tree(s) cannot be checked.

Conclusions from Hybridizations

The crossing data assembled here augment our understanding of the western yellow pines in two respects: (a) they provide additional evidence concerning the genetic coherence of subsect. *Ponderosae* and the ease with which genes can be moved within this extended gene pool; and (b) they further refine the limits of the group, with the proposed transfer of *P. teocote* and *P. lawsonii* to subsect. *Oocarpae*. The success of nearly all species combinations that have been attempted in *Ponderosae* supports the widely held view that natural hybridization is common within the group. Data from controlled hybridizations should be applied with caution to natural populations, however. For example, ponderosa pine is readily crossable with Arizona and Apache pines, but the Pacific race of ponderosa—not the Southwestern race—was used in all crosses; from what is known about the crossing behavior of ponderosa pine races, it is probable that the two races differ in crossability with these Southwestern pines (Critchfield 1984).

More definite conclusions can be drawn from the failure of *P. teocote* and *P. lawsonii* to hybridize with *P. ponderosa* and the successful hybridization of the former with *P. patula*. Shaw (1914) put *P. teocote* and *P. lawsonii* in his group *Australes* because their cones open and shed their seeds at maturity. When Duffield (1952) broke up *Australes*, no crossing data were available for either species, and he included them without comment in his group XII, the western yellow pines. Although this species pair is not well known, apart from their cone-opening habit they are at least as similar morphologically to the pines of subsect. *Oocarpae* as they are to the western yellow pines, with which they have long been associated mostly by default.

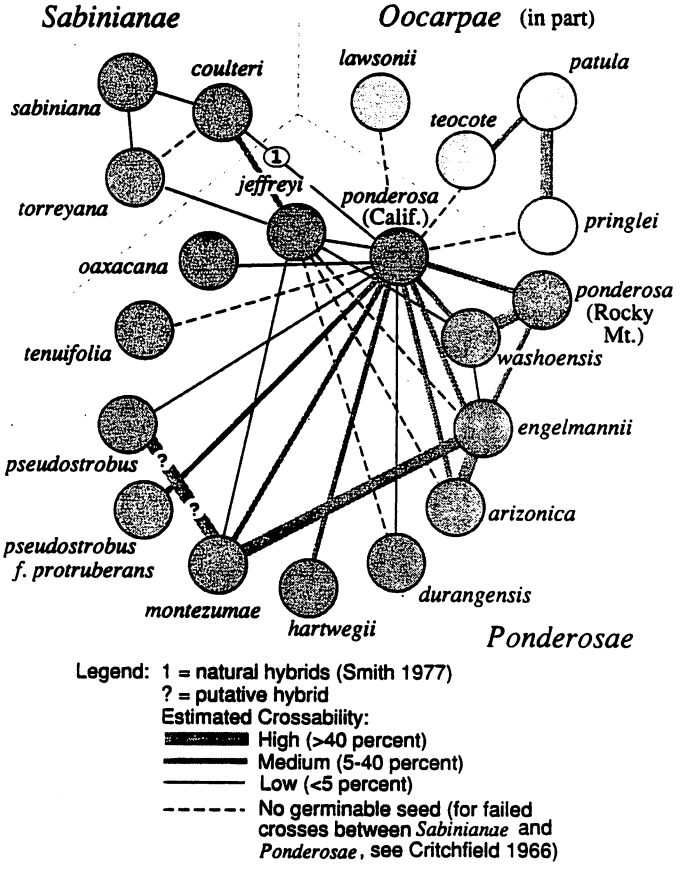

Figure 7.—Crossability of pines (Pinus) in subsections Ponderosae, Sabinianae, and Oocarpae.

In one respect, the data (Figure 7) blur rather than sharpen the limits of *Ponderosae*. The artificial hybridization of *P. jeffreyi* and *P. torreyana*, and Smith's (1977) discovery of natural hybrids between *P. ponderosa* and *P. coulteri*, establish additional bridges between subsections *Ponderosae* and *Sabinianae*, but arguments for this separation are substantial and unaltered (Critchfield 1966).

POSSIBLE EVOLUTIONARY HISTORY OF PONDEROSA PINE

Tracking the past history of ponderosa pine has been difficult because its fossils are scarce. When ponderosa-like fragments are found, the species classification is difficult because its pollen, needles, seed wings, and cone scales are similar to those of other western yellow pines. Axelrod (1986) suggests that yellow pine species were members of mixed-conifer forests in British Columbia and Colorado as early as 50 million years ago. But many fossils that he described resemble present day species that grow only in Mexico and Central America. One small cone fragment with scales resembling modern *P. ponderosa* var. *scopulorum* was recovered from the Creede, Colorado, flora dated at 26.5 million years. Wolfe (1969) only briefly mentions ponderosa pine in the Columbia Plateau-Cascade Range during the Late Miocene about 10 million years ago, but his reliance on pollen analyses may be a reason to question the species identification. Axelrod (1986) finds no macrofossil evidence of ponderosa pine in floras of Oregon, Washington, and Idaho during the Middle and Late Miocene.

The Pleistocene presented widely fluctuating environments during full- and interglacial episodes. No ponderosa pine macrofossils are known from the Pleistocene. Evidence from packrat and porcupine midden analyses, going back 40,000-50,000 years, indicates that ponderosa pine was absent from Southwestern U.S. until after the last glacial episode about 10,500 years ago (Van Devender *et al.* 1984). Ponderosa pine may possess adaptations that only permitted its extensive geographic expansion during warm interglacial times, like the present (Spaulding *et al.* 1983), while during full-glacial periods, it apparently was geographically restricted to perhaps only a few refugia.

Information to identify the lineage(s) of modern ponderosa pine is currently scant. Morphological and crossing evidence supports the conclusion that the pine's primary origins trace to the large group of western yellow pines with present distributions centered in Mexico. Biochemical evidence from monoterpenes shows strong differences between Southern California and Southwestern ponderosa pines, and isozymes indicate that the western and eastern varieties differ in alleles for several loci. The divergent monoterpene types in the south and the west-east isozyme differences in the north suggest there could have been two distant progenitor lines, perhaps one derived from west coast and another from more central montane Mexican populations. A migration route northward from Mexico along the west coast is suggested for the California big-cone and California closed-cone pines (Axelrod 1986); both groups have several species that are now largely restricted to California.

Evidence from midden research in western and Southwestern regions suggests that ponderosa pines are recent colonizers throughout much of the present species range, perhaps within the last 6,000-8,000 years. If significant climatic warming during the Xerothermic period 3,000-8,500 years ago was a primary reason for ponderosas massive range extensions, the existence of races could trace to a few, relatively restricted progenitor populations. Some transition zones between races may now represent sharp genetic gradients because recent coming together, as postulated by Critchfield (1984) of western and eastern populations in Montana has not yet permitted extensive gene flow.

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