

CROSSABILITY AND RELATIONSHIPS OF WASHOE PINE

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ABSTRACT

Washoe pine, related to ponderosa pine but occurring at higher elevations along the western edge of the Great Basin, crosses freely with the Rocky Mountain race of ponderosa despite evidence of long-term separation. Washoe is morphologically distinct from the parapatric Pacific race of ponderosa pine, and the two taxa are kept separate partly by genetic barriers that reduce seed yield by about two-thirds. Washoe pine most closely resembles North Plateau ponderosa pine, and may be a late-Pleistocene offshoot of this race, which occupies the Pacific Northwest interior.

Washoe pine (*Pinus washoensis* Mason and Stockwell) is the most recently described and one of the most puzzling of California's remarkable assortment of pines. It is a western yellow pine in subsection *Ponderosae* (subgenus *Pinus*, section *Pinus*: Critchfield and Little 1966), and there is general agreement that it is allied to two other members of *Ponderosae*: ponderosa and Jeffrey pines (*P. ponderosa* Dougl. ex Laws., *P. jeffreyi* Grev. & Balf.). Widely divergent views have been expressed concerning its origin and taxonomic status, however. J. R. Haller, one of the first students of Washoe pine, has questioned its species status (1965a), and has proposed that it originated either from hybridization between ponderosa and Jeffrey pines (1959) or from hybridization between races of ponderosa pine in the Pacific and Rocky Mountain regions (1965a). Mirov (1961) dismissed Jeffrey pine as a possible ancestor on chemical and morphological grounds, and suggested that Washoe pine is "a variety or mutant" of ponderosa pine. Smith (1967b, 1971) concluded from resin composition that Washoe pine may be most closely related to Rocky Mountain ponderosa pine, from which it is separated by much of the Great Basin.

Washoe pine was discovered in 1938 on the east slopes of Mt. Rose, Nevada, the highest peak in the mountains north and east of Lake Tahoe. In their description, Mason and Stockwell (1945) likened it to a small-coned version of Jeffrey pine, with which it is associated on Mt. Rose, and asked the question: "Whence came this pine?" We now know much more about Washoe pine—its distribution (Haller 1961, Critchfield and Allenbaugh 1965), ecology (Talley 1977), adult morphology (Haller 1957), seedling morphology

and physiology (Wells 1964, Jenkinson 1980), resin composition (Mirov 1961; Smith 1967b, 1971), seed proteins (Prager et al. 1976), and ability to cross with other pines (Critchfield 1966). This paper reviews our knowledge of the species and presents a fuller account of its crossing behavior. Summarized are all crosses involving Washoe pine and all crosses between ponderosa pine races carried out by the Institute of Forest Genetics (IFG), near Placerville, California. Despite contradictions between different kinds of evidence, these data provide a tentative answer to the question posed by Mason and Stockwell: Washoe pine is probably not of hybrid origin, but most likely originated as a Pleistocene derivative of the North Plateau race of ponderosa pine, which now occupies the interior Pacific Northwest.

THE WESTERN YELLOW PINES OF THE U.S.

Subsection *Ponderosae*, a large and predominantly Mexican group, includes only three taxa with distributions centered in the western U.S.: Jeffrey, ponderosa, and Washoe pines. Jeffrey pine is widely distributed in California, mostly at upper elevations, and extends into Oregon, Nevada, and Baja California (Fig. 1). The distributions of ponderosa and Washoe pines are sharply contrasting: they are respectively the most widespread and most narrowly restricted taxa in *Ponderosae* (Critchfield and Little 1966).

The distribution of ponderosa pine encompasses much of the montane West (Fig. 1). The western (var. *ponderosa*) and eastern (var. *scopulorum* Engelm.) parts of this broad distribution are widely separated from each other except in central Montana, where they meet and intergrade.

Each variety is made up of two or three discrete geographic races. These races are delimited by differences in adult morphology and growth in natural stands and in a common environment (Weidman 1939), seed and seedling characters (Wells 1964, Read 1980), and monoterpenes of xylem resin (Smith et al. 1969, Smith 1977). Included in var. *ponderosa* are the North Plateau, Pacific, and southern California races. The Rocky Mountain and Southwestern (South Plateau) races comprise var. *scopulorum*.

All three northern races—North Plateau, Pacific, and Rocky Mountain—have been implicated in the ancestry of Washoe pine. The Continental Divide has traditionally been accepted as the eastern limit of the North Plateau race (and that of var. *ponderosa*); but in Read's (1980) transect across Montana, the most abrupt change was near the 110th meridian, about 200 km east of the Divide. In northeastern California the North Plateau race is replaced by the Pacific race through a zone extending from the Cascades to the western edge of the Great Basin. This zone is best defined by shifts

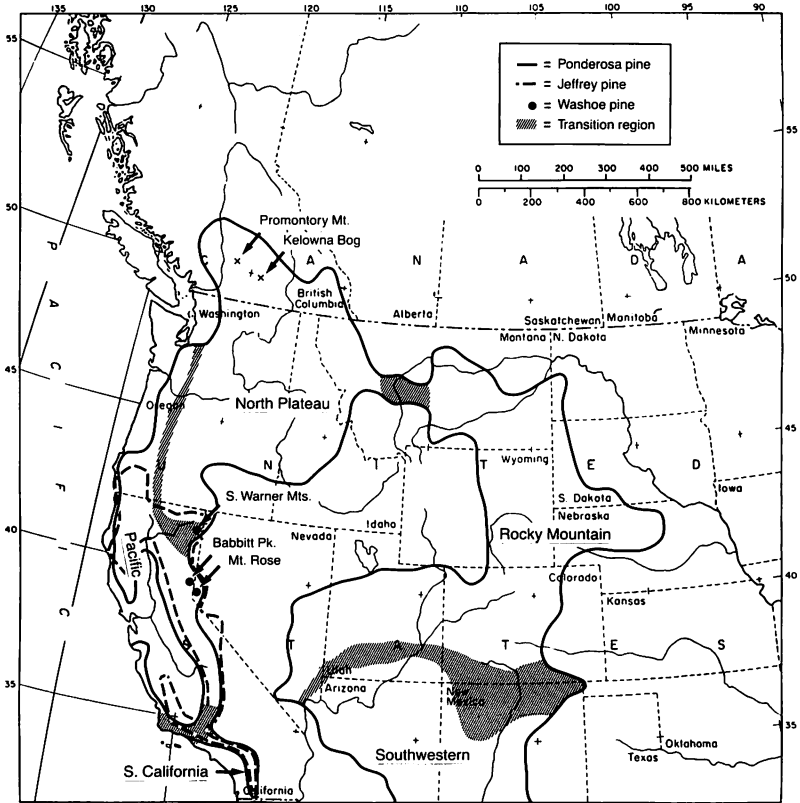


Fig. 1. Distribution of western yellow pines in the U.S. and Canada. Geographic races of ponderosa pine are underlined.

in two well-studied characters: resin composition (Smith 1977, Sturgeon 1979) and color of immature seed cones (Smith 1981). The Pacific race is distributed throughout most of California and extends north to include most or all of the stands west of the Cascades in Oregon and Washington (Sturgeon 1979, Wells 1964). Populations in the southern California mountains are here considered a separate race, primarily because of their distinctive resin composition (Smith 1977).

The Rocky Mountain race, to which the varietal name *scopulorum* was originally restricted (Engelmann 1880), reaches its western limits in Nevada, where scattered stands in isolated mountain ranges of the eastern and southern Great Basin are separated from the nearest Washoe pines by about 400 km of sagebrush steppe (Fig. 1). Engelmann described the needles of var. *scopulorum* as "often in pairs,"

and this useful character distinguishes most populations of the Rocky Mountain race from all other ponderosa races, which have most or all of their needles in fascicles of three (Haller 1965b). The Rocky Mountain and Southwestern races intergrade in southern Utah, southern Colorado, and northern New Mexico. The replacement of the Southwestern race near the Mexican border by a complex of poorly defined, predominantly Mexican taxa is beyond the scope of this paper.

The three well-known populations of Washoe pine are located at the eastern edge of the coniferous forests that cover the mountains of the Pacific Slope, and are all within sight of the Great Basin sagebrush steppe (Fig. 1). In addition to the type locality on Mt. Rose, Washoe pine stands have been found at two California localities: the Babbitt Pk. area, about 30 km northwest of Mt. Rose (Critchfield and Allenbaugh 1965), and the southern Warner Mts., in the northeastern corner of California about 200 km north of Mt. Rose (Haller 1961). Elsewhere in northeastern California, Washoe characteristics are sometimes present in variable stands of ponderosa pine (Haller 1961, Griffin and Critchfield 1976). Trees resembling Washoe pine occur at scattered localities in eastern Oregon (Haller 1965a), and another stand of Washoe pine has been found in southern British Columbia (J. R. Haller, pers. comm., Oct. 1981).

Washoe pine grows at higher elevations than ponderosa pine, which reaches its upper limits at about 2000 m in this region. On Mt. Rose, mixed stands of Washoe and Jeffrey pines extend above 2500 m to the subalpine forest zone. Washoe pine reaches its lower limits at about 2100 m on Mt. Rose, but pure stands of Jeffrey pine extend down to 1600 m, where they are replaced by sagebrush. The distribution of ponderosa pine is sporadic in the Tahoe-Mt. Rose region; one stand at 1950 m is less than 2 km east of the nearest Washoe pines (Haller 1957). A more extensive ponderosa stand is at Incline, 13 km to the southwest on the north shore of Lake Tahoe. At Babbitt Pk., Washoe pine grows in nearly pure stands at 2400 to 2600 m; at lower elevations (down to 2300 m) it is associated with other conifers (Talley 1977). Jeffrey pine is not common in this area, but below 2450 m it is sometimes a minor component. Ponderosa pine stands have not been observed in the immediate vicinity of Washoe pine in the Babbitt Pk. area, but they are present within a few km (Griffin and Critchfield 1976).

In the Warner Mts., Washoe pine occurs at lower elevations (about 1950 to 2400 m) than at the two southern localities. Jeffrey pine is mostly restricted to a narrow zone below Washoe pine (Haller 1961). Ponderosa pine is common at lower elevations in this region, which is in the transition zone between the Pacific and North Plateau races.

The Babbitt Pk. and Warner Mts. stands have not been heavily logged, but the Mt. Rose stand is mostly second-growth. The forests

on the east slopes of Mt. Rose were the nearest major source of timber to the mining center of Virginia City, Nevada, and were clear-cut during the exploitation of the Comstock Lode in the 1860s and 1870s. Washoe pines that predate logging are not rare, however. The oldest tree I have found in the Mt. Rose area, on the northeast slope of Slide Mountain, had an estimated age exceeding 300 years in 1962. In the same stand as the tree from which we believe the type specimen was collected, several trees had estimated ages of 100 to 250 years.

Mason and Stockwell (1945), in what was intended to be the first in a series of reports on Washoe pine, provided a fairly complete description of the species but gave little indication of how it differed from ponderosa or Jeffrey pines. They noted that it had short, stout needles; short, red-purple pollen cones; small seed cones with many cone scales; and seeds with short wings.

Haller (1957) contrasted Mt. Rose Washoe pine with ponderosa and Jeffrey pines in several quantitative characteristics. He sampled ponderosa and Jeffrey pines on Mt. Rose and ponderosa in eastern Nevada and central Montana. Washoe pine resembled the Rocky Mountain trees—and differed from local ponderosa and Jeffrey pines—in its short, stout needles and small cones. It differed from all ponderosa (but not Jeffrey) in its dense cones, and had relatively shorter seed wings than the other pines. Haller concluded that Washoe pine was most like the Rocky Mountain race of ponderosa, differing from it in the direction of Jeffrey pine.

The dissimilarity of Washoe pine and Pacific ponderosa pine was also underscored in Wells's (1964) rangewide provenance test of ponderosa pine, which included Washoe pine from Mt. Rose. This study was based on 1- and 2-year-old seedlings grown in Michigan. Washoe seedlings differed from nearly all ponderosa provenances in their lesser height, shorter secondary needles, and greener foliage at 2 years. They suffered much less winter injury than most western provenances, and differed from eastern provenances in the delayed production of secondary needles and in having fewer lateral buds at 2 years. In a multi-character analysis (Summation of Differences = SD) restricted to western provenances (var. *ponderosa*), Washoe pine was more like the North Plateau race (SD 23–42) than the Pacific race (SD 50–69), differing from the nearby Incline stand by SD 50.

Washoe pine also differs from Pacific ponderosa pine in the ability of its dormant seedlings to produce new roots after one growing season in the IFG nursery (Jenkinson 1980). Ponderosa seedlings from central and northern California, lifted and tested at intervals throughout the winter, had a single peak or plateau in root production. Mt. Rose Washoe pine resembled most Jeffrey provenances in its two-peaked pattern of root production, with one peak in late fall

or early winter and the other in late winter. Most ponderosa seedlings of other provenances (including south-central Oregon and eastern Nevada) also had a single peak or plateau in root production; the two-peaked pattern was restricted to one Rocky Mountain provenance (Wyoming) and all four provenances of the southern California race.

Seedlings of Washoe pine allocate a larger fraction of growth to the root system than Pacific ponderosa or Jeffrey pine seedlings (S. H. Strauss, pers. comm., Jan 1983). Seedlings grown from Mt. Rose seed had a mean shoot-root ratio of 0.60 at 5 months, compared with ratios of 1.03 and 0.98 for ponderosa and Jeffrey seedlings from the west slope of the Sierra Nevada.

Washoe pine is completely different from Jeffrey pine in the composition of the turpentine (low-boiling-point) fraction of its wood resin, but within the range of variation of ponderosa pine. Jeffrey pine turpentine consists mostly (89–99%) of heptane (Smith 1967b). Washoe pine lacks this hydrocarbon, and ponderosa resin only occasionally has trace amounts (Smith 1977). Five monoterpenes—alpha-pinene, beta-pinene, 3-carene, myrcene, and limonene—are the major constituents of ponderosa and Washoe turpentine, and all are highly variable within and between ponderosa races (Smith 1977).

Washoe pine turpentine is characteristically high in 3-carene (more than 55%) and low in limonene (less than 2.4%). Of 24 trees sampled on Mt. Rose, 20 were of this type (Smith 1967b). This combination is rare in Pacific ponderosa pine, which typically has moderate amounts of all five monoterpenes (Smith 1977). Among 951 trees of this race sampled by Smith (1964, 1977, and unpubl. data), fewer than 1% had both low limonene and high 3-carene. A transect of 47 trees on the west slope of the central Sierra Nevada included no low-limonene trees and only one with high 3-carene (Smith 1964). In a smaller sample near Incline on Lake Tahoe, 11 of 12 trees were like the west-slope trees, but one resembled Washoe pine in its low limonene and high 3-carene.

The contrast between Washoe and ponderosa pines is less marked in the Warner Mts. region, where ponderosa is transitional between Pacific and North Plateau races. Trees with low limonene and high 3-carene—rare in the Pacific region—are common throughout the North Plateau region, and ponderosa of the south Warner Mts. is intermediate. Below 1830 m, 57% of 74 trees were low in limonene and 26% were high in 3-carene (Smith 1971). Above 1950 m, in the Washoe zone, 93% of 63 trees were low in limonene and 83% were high in 3-carene.

Throughout the broad distribution of ponderosa pine, only the North Plateau and Rocky Mountain races have frequencies of low-

limonene, high-carene trees approaching that of Washoe pine. This combination was most common in 627 North Plateau trees sampled by Smith (1977, and unpubl. data): 47% overall, ranging from a high of 56% (near Bend, Oregon) to a low of 34% (Bitterroot Mountains, Idaho). The Rocky Mountain race is more variable. Overall frequency of low-limonene, high-carene trees was 29% (of 1165 trees), decreasing from a high of 73% in the east (Wyoming) to a low of 13% in the eastern Great Basin (389 trees).

PREVIOUS REPORTS OF HYBRIDIZATION

In the lower part of its distribution on Mt. Rose, Washoe pine appears to have been influenced by ponderosa pine (Haller 1957, 1959), and in the Warner Mts. the two taxa form what Haller (1965a) described as a morphological continuum. The elevational change from ponderosa to Washoe pines in the Warner Mts. is best documented for resin composition (described above) and immature cone color (Smith 1981). The deeply pigmented, dark red-purple to purple-black cones of Washoe pine contrast with the green cones of Pacific ponderosa pine, and the stands of this region form a gradient from predominantly green cones at low elevations to predominantly dark purple cones at high elevations.

Washoe pine also hybridizes with Jeffrey pine, but natural hybrids are uncommon. Of 124 trees sampled as Washoe pine on Mt. Rose, two trees about 0.5 km apart had turpentine consisting of 80–85% heptane, with 3-carene as the next most abundant constituent (5–6%) (R. H. Smith, pers. comm., Feb 1981). This level of heptane is more than twice that of F_1 hybrids between Jeffrey and either Washoe or ponderosa pines (Smith 1967a), and these trees were probably backcrosses of Washoe-Jeffrey hybrids to Jeffrey pine.

Verified F_1 hybrids of Washoe and California ponderosa pines from controlled crosses in both directions were first reported by Righter and Duffield (1951), Jeffrey $\times$ Washoe hybrids by Liddicoet and Righter (1960), and Washoe $\times$ Rocky Mountain ponderosa hybrids by Keng and Little (1961). Needle characteristics of these combinations were described by Keng and Little (1961), and other morphological and growth attributes by Little and Righter (1965). Smith (1967a) described the turpentine composition of a Jeffrey $\times$ Washoe F_1 (32% heptane, 45% 3-carene, 1% limonene) and a California ponderosa $\times$ Washoe F_1 (much like the female parent). Critchfield (1966) reported that crossability was high in crosses of Washoe with ponderosa and low in crosses with Jeffrey pine or Apache pine (*P. engelmannii* Carr.), the latter a member of *Ponderosae* native to northern Mexico and southern Arizona. No hybrids were obtained from crosses of Washoe pine with Coulter pine (*P. coulteri* D. Don), a California species in subsection *Macrocarpae*.

METHODS

Parent trees. All crosses involving Washoe pine were made between 1941 and 1967 on female parents in natural stands (Table 1). Exploratory crosses between 1941 and 1948 were made with Washoe parents on Mt. Rose, the only population known then. The identity of Washoe pine was still uncertain when the first crosses were made, and the parent trees were initially labeled Jeffrey pine. The "type" tree, from which the type specimen probably came, was used as a parent in 1941 and most subsequent breeding seasons. These early crosses did not include within-species control crosses. Most crosses were made with freshly collected pollen, and within-species pollinations were often difficult or impossible to execute during short pollinating seasons.

A second series of crosses between 1962 and 1967 included within-species controls. Female parents were the type tree and three others in the same stand. From 1961 on, pollen was routinely collected and deep-frozen a year before pollinations were made, and control crosses were no longer a problem. Pollen parents of 1962 controls were other Washoe pines in the same stand as the female parents. In a 1965 set of crosses between Washoe populations, pollen parents were four trees in a Mt. Rose stand 1 km from the female parents, two trees 1 km apart near Babbitt Pk., and five trees in two stands 5 km apart in the Warner Mts. Most of the crop from these crosses was lost to Clark's nutcrackers and seed insects during the following season, and the crosses were not repeated. Pollen parents of 1967 control crosses were in the same Mt. Rose stand as the 1965 pollen parents.

Crosses between geographic races of ponderosa pine were made between 1941 and 1967 on native ponderosa pines growing near the IFG in the central Sierra Nevada. Mature trees of other races are well represented in the IFG arboretum, and have been used as pollen parents in interracial crosses (Table 1). Attempts to use them as female parents have not been successful, however. Many trees of Rocky Mountain and North Plateau origins produce few or no cones in California, and when cones are produced the seed yield is abnormally low. A total of 27 Rocky Mountain $\times$ California crosses, made in five seasons, produced an average of fewer than 7 sound (filled) seeds and 14 total seeds per cone, with maxima of 21 sound and 30 total seeds per cone. Mean seed yields in natural stands of the Rocky Mountain region are much higher: 30 germinable seeds and 42 total seeds per cone in central Colorado (Roeser 1941), 20 sound seeds per cone in northern Colorado (unpubl. data, IFG), and 32 to 55 sound seeds per cone in the Black Hills (Van Deusen and Beagle 1970). The large reduction in both sound and hollow seed yield from female parents of Rocky Mountain origin might be at-

TABLE 1. PARENT TREES OF CROSSES SUMMARIZED IN TABLES 2 AND 3 AND IN TEXT. () = number of localities; + = some crosses made with mixes of pollen from unspecified number of male parents.

Species or race	Number of parents		Location or geographic origin
	Female	Male	
<i>Natural stands:</i>			
Washoe	6	8+	Mt. Rose (2)
		2	Babbitt Pk. (2)
		5	Warner Mts. (2)
Pacific ponderosa	12	9	Central Sierra Nevada (11)
		7+	Lake, Modoc, Santa Cruz, Siskiyou Cos., California, s.w. Oregon (2)
Jeffrey	1	3	Central Sierra Nevada (2)
Lodgepole	2	2+	Central Sierra Nevada (2)
<i>Arboretum trees:</i>			
Rocky Mt. ponderosa		7	Colorado (3)
		7	Nebraska (3)
		4	Wyoming
		1	South Dakota
		1	e. Montana
		1	e. Nevada
North Plateau ponderosa		2+	British Columbia
		2+	Bitterroot Mts.
		1	Washington
		1	w. Montana
Apache		2	Arizona
Coulter		3	Unknown

tributed to an unusual sequence of reproductive barriers in these interracial crosses, except that five control crosses between Rocky Mountain trees produced slightly fewer seeds than accompanying interracial crosses (8 sound and 15 total seeds per cone, compared with 9 sound and 18 total). Two crosses of North Plateau females (Bitterroot Mts. origin) with California pollen parents were even less successful, producing fewer than 3 sound and 5 total seeds per cone. In a natural stand in the North Plateau region (central Oregon), ponderosa pine averaged 75 sound and 100 total seeds per cone (Sorensen 1970).

Techniques and terminology. Breeding and seed-processing techniques have been described elsewhere (Critchfield 1966). Except as noted, the data summaries (Tables 2 and 3) include all cone-producing crosses for which the following information was available: numbers of female strobili pollinated, cones harvested, and sound and hollow seeds.

An *attempt* is the pollination in a single season of a single female

parent with pollen from one male parent or with a mixture of pollen from two or more males. Mean number of seeds per cone is the unweighted average of all individual attempts. *Crossability* is the mean number of sound seeds per cone of all crosses (attempts) between taxa or races, expressed as a percent of the mean sound seed yield of control crosses within the maternal-parent taxon. Control crosses summarized in Tables 2 and 3 were made on the same seed parent in the same season as crosses between taxa.

Other observations. Several characteristics were studied in trees growing in the IFG arboretum and in natural stands, or in collections in the IFG herbarium:

Pollen cones—Most observations of ponderosa pine in the arboretum were made in a single season (1981). Color and length of pollen cones were recorded for 42 Rocky Mountain trees (18 provenances scattered throughout the region), 10 North Plateau trees (10 provenances), and five native trees on the IFG grounds. In other years, observations were made in natural stands of Washoe and ponderosa pines. Color was noted just before the pollen cone elongated and the pollen was shed. For arboretum trees, length was measured when the cone was fully elongated and most or all of the pollen had been shed, but most field observations were made after the elongated cone had dried up. For all trees, the longest pollen cone of a 5- to 8-cone sample is reported.

Seed cones—Color of immature seed cones was observed on five Rocky Mountain trees in the arboretum (Nebraska, Colorado, and eastern Nevada) and in natural stands of Washoe and ponderosa pines. Observations were made during the summer of the second season of cone development, after the cones reach their full size but before they turn brown at maturity in late summer or fall.

Unpublished data on other characteristics are from a rangewide study of ponderosa pine that included a sample of Washoe pine. The study was organized by R. Z. Callaham, and the data are on file at the IFG. Characters included: number of needles per fascicle, length of needles, fascicle radius (=needle thickness), seed length, and the ratio of seed + wing length to seed length. Cone scales were counted on single cones from each tree in a few 8- to 10-tree samples from the same study.

RESULTS

Crosses of Washoe pine. Washoe pine crosses readily only with ponderosa pine. In combination with other western pines, its crossing behavior is much like that of ponderosa pine (Critchfield 1966). It has been hybridized with Jeffrey and Apache pines, but crossability is low in both combinations. Verified hybrids were produced in an early Jeffrey $\times$ Washoe cross, but no germinable seeds were obtained

TABLE 2. CROSSES BETWEEN WASHOE PINE AND OTHER SPECIES (EXCLUDING PONDEROSA PINE). ND = no data; () = range of individual attempts; ___ = verified hybrid; * = no further record of sound seed.

Parent		Minimum tree × tree combinations				Attempts	Atttempts producing sound seed	Female strobili pollinated	Strobili producing cones	Mean sound seed per cone	Mean total seed per cone
Female	Male										
1) Crosses lacking controls (1945, 1948):											
Lodgepole	Washoe	2		4		0		37	17	0	ND
Washoe	Lodgepole	2		4		0		33	2	0	41.5
Washoe	Coulter	1		2		1		28	6	0.2*	74.8
Washoe	Apache	1		2		1		15	2	1.5*	106.5
Jeffrey	Washoe	1		5		1		14	10	<u>3.4</u>	172.8
2) Crosses with controls (1962):											
Washoe	Apache	3		6		1		20	13	<u>0.1</u>	76.6 (55-105)
Washoe	Coulter	3		9		0		22	16	0	65.1 (40-83)
Washoe	Jeffrey	3		9		0		23	13	0	49.2 (16-85)
Washoe	Washoe	3		9		3		25	14	48.9 (26-78)	95.8 (68-122)

from later crosses with Washoe pine as female parent (Table 2). Sound seeds were produced twice in crosses with Apache pine. The fate of the seeds from an early cross was not recorded, but a later cross yielded a single verified hybrid.

Crosses between Washoe pine and species in other subsections were unsuccessful. A single seed from an early Washoe $\times$ Coulter cross is unaccounted for, but later crosses in the same direction produced no sound seeds (Table 2). Lodgepole pine (*P. contorta* Dougl. ex Loud.), the only representative of subsect. *Contortae* in the western U.S., has not been successfully crossed with any other western pine. The combination of lodgepole and Washoe pines, tried in both directions, produced only hollow seeds (Table 2).

Most crosses made on Washoe pine with species other than ponderosa pine produced fewer total seeds per cone than Washoe $\times$ Washoe control crosses (Table 2). Pine seed coats form at about the time of fertilization (Buchholz 1945), so the reduced number of seed coats from crosses with other species suggests that ovules pollinated with foreign pollen aborted at a higher frequency during the first year of cone development, between pollination and fertilization. The reduction is fairly consistent and sometimes large (e.g., Washoe $\times$ Jeffrey), but the data are insufficient to establish its significance.

In contrast to its low crossability with other western yellow pines, Washoe pine is fully crossable with the Rocky Mountain race of ponderosa pine (Table 3). Crossability exceeds 100%: significantly more sound seeds per cone were harvested from Washoe $\times$ Rocky Mountain crosses than from Washoe $\times$ Washoe controls (*t* test, $p = <0.05$). Interspecific crosses produced more sound seeds per cone than controls in 11 of 13 attempts and in both seasons the crosses were made, although most pollen parents and some female parents differed between years. Interspecific crosses also produced more total seeds per cone, but this smaller difference was not statistically significant.

The Pacific race of ponderosa pine, unlike the Rocky Mountain race, is partially isolated from Washoe pine by reproductive barriers (Table 3). Washoe $\times$ California ponderosa crosses showed large and highly significant reductions in sound seed yields compared to Washoe controls ($p = <0.01$). Among eight crosses with controls, estimated crossability ranged from 6 to 61%, with a mean of 30%. Mean crossability was the same in both years the crosses were made. Total number of seeds per cone was also substantially reduced: 64.1 in crosses with California ponderosa compared with 76.2 in control crosses. The size of this reduction suggests that reproductive barriers expressed before seed coat formation produced differential ovule abortion in some combinations, but overall the reduction was not statistically significant. Early Washoe $\times$ California ponderosa crosses lacking controls produced more sound seeds per cone (17.7) than

TABLE 3. INTERSPECIFIC AND INTERRACIAL CROSSES OF WASHOE AND PONDEROSA PINES. All attempts produced sound seed. ND = data incomplete or lacking; () = range of individual attempts.

Parent		Attempts	Minimum tree × tree combina- tions	Female strobili pollinated	Strobili producing cones	Mean sound seed per cone	Mean total seed per cone
Female	Male						
1) Crosses lacking controls (1941-1972):							
Washoe	ponderosa (Pacific)	10	11	366	78	17.7 (2-35) 26	46.7 (5-91) 126
Washoe	ponderosa (Rocky Mt.)	1	3	15	1		
ponderosa (Pacific)	Washoe	1	1	ND	15	18.1	73.1
ponderosa (Pacific)	ponderosa (Rocky Mt.)	9	12	808	508	32.1 (6-64)	63.1 (8-95)
2) Washoe × ponderosa crosses with controls (1962, 1967):							
Washoe	ponderosa (Pacific)	8	11	134	63	12.1 (3-35)	64.1 (26-116)
Washoe	ponderosa (Rocky Mt.)	13	18	215	113	57.5 (9-120)	81.5 (27-135)
Washoe	Washoe	6	10	92	35	41.9 (24-78)	76.2 (47-122)
3) Interracial ponderosa crosses with controls (1941-1967):							
Pacific	Rocky Mt.	20	24	557	271	17.1 (2-41)	51.3 (7-107)
Pacific	N. Plateau	7	10	162	83	23.2 (11-38)	ND
Pacific	Pacific	17	17	605	188	48.6 (6-94)	58.6 (13-103)

later crosses with controls (12.1), a difference that can perhaps be attributed to choice of parent trees.

Crosses between Washoe pine populations were made in a single season on Mt. Rose female parents using pollen from all three populations, but most of the crop was lost. Three cones on one tree survived, one cone each from crosses with pollen from Babbitt Pk., the Warner Mts., and another stand on Mt. Rose. The highest yield of sound seed was from the Babbitt Pk. cross, followed by the Warner Mts. cross. Many cones were harvested from another tree, but insect damage was heavy, and the eight crosses on the tree produced only 0–9 sound seeds per cone. Four crosses with Warner Mts. pollen produced the fewest sound seeds per cone, and three crosses with Mt. Rose pollen produced the most. These sketchy and inconsistent results show that Washoe pine populations can be intercrossed successfully, but they provide no basis for estimating crossability.

Compared with other western yellow pines, Washoe pine produces unusually large numbers of hollow seeds in intraspecific crosses. Cones harvested from controlled pollinations of Mt. Rose trees averaged a high percentage of hollow seed in all combinations: 51% with pollen parents in the same stand, 40% with parents in another Mt. Rose stand, and 54% with Warner Mts. and Babbitt Pk. trees. Overall, crosses between Mt. Rose trees averaged 45% hollow seed (Table 3), with individual combinations ranging from 30 to 62%. The proportion of hollow seed was even higher in open-pollinated cones from Mt. Rose trees (11 collections in 6 seasons). Total seed yield was low, averaging 51 seeds per cone. All collections averaged 73% hollow seed, ranging from 43 to 100%. The type tree was particularly unproductive, yielding 93 to 100% hollow seed in three different seasons. These data show that a large fraction of Washoe pine's reproductive potential is lost before the cones mature, and the significantly higher yield of sound seed from Washoe $\times$ Rocky Mountain ponderosa crosses suggests that the factors responsible for these losses are diminished or eliminated when Washoe pine is replaced as pollen parent by the Rocky Mountain race of ponderosa pine.

This large reduction in reproductive capacity is not matched by other western yellow pines. Control-pollinated cones of North Plateau ponderosa pine produced 33% hollow seed (Sorensen 1970), and California ponderosa is variously estimated to produce 17% (Table 3) and 10% hollow seed (Critchfield 1966) in controlled crosses. Digger pine (*P. sabiniana* Dougl.: subsect. *Macrocarpae*) and Jeffrey pine produced 13 and 12% hollow seed in controlled within-species crosses (Critchfield 1966). Estimates of hollow seed in open-pollinated ponderosa cones are 25% in central Oregon (Sorensen 1970), 29% in Colorado (Roeser 1941), and 27% in 20 collections from Sierra Nevada trees (unpubl. data, IFG).

Crosses between ponderosa pine races. Pacific ponderosa pine is partially isolated by reproductive barriers from the Rocky Mountain race, just as it is from Washoe pine, and crossability is similar in both combinations. The reduction in sound seed was highly significant ($p = <0.01$) in California $\times$ Rocky Mountain crosses compared with their controls (Table 3), and estimated crossability was 35%. California $\times$ Rocky Mountain crosses lacking controls, some of them carried out on a large scale in the 1970s, yielded much more sound seed per cone (Table 3), and this discrepancy too must be attributed to choice of parent trees.

The provenance of pollen parents had little effect on sound seed yield. Among 20 crosses with controls, 4 or more attempts were made with trees originating in each of three states: Colorado, Wyoming, and Nebraska. All three sets of crosses gave crossability estimates between 33 and 39%.

A few crosses between Pacific and North Plateau trees suggest that these races too are partially isolated by reproductive barriers (Table 3). These crosses, carried out in a single season on two Sierra Nevada trees in different stands, were accompanied by control crosses made with pollen from a single tree of southwestern Oregon provenance (Josephine County). Mean crossability was 50%, and individual attempts ranged from 38 to 75%. Although these data indicate the probable existence of a genetic barrier, they are too limited for a reliable estimate of its magnitude.

Reproductive phenology. The mean pollination date of Mt. Rose Washoe pine over six seasons was 28 June, with the earliest on 3 June and the latest on 9 July. In a single season (1964), all three Washoe populations (Mt. Rose, Babbitt Pk., and Warner Mts.) began to shed pollen between 24 June and 4 July.

The Mt. Rose populations of Washoe, Jeffrey, and ponderosa pines all have opportunities to intercross, although both Washoe and ponderosa are pollinated earlier than Jeffrey pine in the same stand. Jeffrey pine occupies an elevational span of nearly 1000 m on the steep eastern slopes of Mt. Rose, and in most seasons pollen must be shedding somewhere in this span through most or all of the pollination periods of ponderosa and Washoe pines. Ponderosa on Mt. Rose, below the lower limits of Washoe pine, precedes but overlaps the latter in pollen shedding. On 22 June of one year (1963), ponderosa pine at 1950 m was past its peak of pollen shedding, and a few Jeffrey pines in the same stand were just beginning to shed. In a stand 2.2 km away and 365 m higher, some Washoe pines were beginning to shed pollen and bore receptive female strobili. The pollen strobili of Jeffrey pines in this stand were estimated to be at a meiotic stage, at least two weeks before pollen shedding.

Foliage characteristics. Washoe pine needles are shorter and stouter than those of Pacific ponderosa pine, but they can be matched or approximated by both North Plateau and Rocky Mountain races. Needle length has been extensively studied in the ponderosa group, and comparisons between provenances planted in Idaho and corresponding natural populations have shown that it is a moderately heritable trait (Weidman 1939). Mason and Stockwell (1945) described Washoe needles as 10 to 15 cm long, and the Mt. Rose population has been variously estimated to average 15.1 cm (Haller 1957) and 14.4 cm (unpubl. data, IFG). Mt. Rose ponderosa and Jeffrey pines both have longer needles: 20.5 and 20.0 cm (Haller 1957). Other populations of Pacific ponderosa also have significantly longer needles than Washoe pine ($p = <0.05$), with means of 16.1–24.3 cm in 27 stands (unpubl. data, IFG). The North Plateau race has slightly shorter needles than the Pacific race, with means of 43 samples ranging from 13.0–20.5 cm. Populations with the shortest needles, in southern British Columbia and in eastern Oregon and adjacent Idaho, have mean lengths (13.0–15.7 cm) that do not differ significantly from that of Washoe pine. Most Rocky Mountain stands have significantly shorter needles than Washoe pine or the other races of ponderosa pine, but the range of mean lengths (8.7–17.9 cm in 31 populations) also includes that of Washoe pine. Populations equaling or exceeding Washoe pine in needle length are mostly in the eastern part of the Rocky Mountain region (unpubl. data, IFG), but include an isolated stand in eastern Nevada (Haller 1957).

The short needles of Washoe pine are wider than those of Jeffrey or ponderosa pines on Mt. Rose—8 and 20% on the average (Haller 1957). Washoe pine also has wider needles than Jeffrey pine in the Warner Mts., but the difference is not significant (Haller 1961). Washoe pine has significantly thicker needles than most populations of ponderosa pine (unpubl. data, IFG). Exceptions are five North Plateau populations—three on the east slope of the Cascades and one each in northeastern Oregon and southeastern British Columbia—and two Rocky Mountain stands in central Utah.

In number of needles per fascicle, Washoe pine differs from the Rocky Mountain race but not from the other races of ponderosa pine. This trait too is moderately heritable (Weidman 1939), although it is influenced by tree age, by branch vigor, and in some places by climatic fluctuations (Haller 1965b). Mature Washoe pines uniformly have three needles per fascicle on Mt. Rose (unpubl. data, IFG) and in the Warner Mts. (Haller 1965b). Fascicles with two needles are uncommon in the Pacific and North Plateau races, occurring at frequencies up to 1.4% (Haller 1965b; J. R. Haller, pers. comm., Oct 1981; unpubl. data, IFG). The Rocky Mountain race, in contrast, usually has moderate to high frequencies of two-needled

fascicles: 19 to 75% in the region from central Montana to central Colorado, and 17 to 39% in most populations of the eastern Great Basin (Haller 1965b). On the Colorado Plateau in western Colorado and eastern Utah, however, the frequency of two-needed fascicles drops to less than 3% in most stands (Haller 1965b; unpubl. data, IFG).

Cone and seed characteristics. Pollen cones of Washoe pine are short, stout, and deeply pigmented. Mason and Stockwell (1945) described them as red-purple and 10–20 mm long. Fully elongated pollen cones of five trees on Mt. Rose and one in the Warner Mts. were 21–27 mm long and 7–12 mm in diameter, ranging in color from red-purple to purplish-black. Pacific ponderosa pines have longer, more slender pollen cones. On three Mt. Rose trees they were 36–46 mm long and 6–8 mm in diameter. Native ponderosa pines at IFG had pollen cones 71–93 mm long, and dried cones of six trees in four other Sierra Nevada stands were 38–67 mm long. In all California trees observed, color ranges from dark red to red-purple. North Plateau trees in the IFG arboretum also have deeply pigmented cones, but in length they fall between Washoe and Pacific ponderosa pines. On 10 widely scattered North Plateau trees they were 28–69 mm long, averaging 46 mm. Rocky Mountain trees in the arboretum have pollen cones as short as those of Washoe pine, but at maturity most are unpigmented (yellow) or lightly pigmented (pink). Of 36 trees, the cones of 35 were 17–40 mm long; on one eastern Nevada tree they were 51 mm long. Only 4 of 36 trees, all of eastern origin (Nebraska, Wyoming), had red or purple pollen cones, but some Rocky Mountain populations have a higher frequency of trees with pigmented cones. In an eastern Nevada stand, R. H. Smith (pers. comm., Feb 1983) counted 15 trees with purple and 19 with yellow pollen cones.

The seed cones of Washoe pine are 5–8 cm long (Mason and Stockwell 1945). Haller (1957) estimated that their volume was 69% of Mt. Rose ponderosa cones and 19% of Jeffrey cones, but about the same as that of ponderosa cones from eastern Nevada and central Montana. In the same samples, Washoe cones were about equal in density to Jeffrey cones, and the heavy cones of both species had mean densities 32–61% greater than those of ponderosa cones. In other samples (unpubl. data, IFG), Washoe pine had shorter cones (mean length 6.4 cm) than any western population of ponderosa pine (means 7.3–12.2 cm), and the differences were significant with one exception: an eastern Oregon stand with cones 7.3 cm long. Northern and eastern Rocky Mountain stands also had small cones (means 5.2–7.9 cm), but populations nearest Washoe pine (eastern Great Basin, Colorado Plateau) had significantly longer cones than Washoe pine (means 7.8–9.3 cm).

Despite their small size, Washoe cones have more scales than most ponderosa cones. Mason and Stockwell's (1945) estimate of scale number was 160 to 190, and in a 10-tree sample from Mt. Rose I counted a mean of 173 scales per cone. In this feature, Washoe pine significantly exceeded ponderosa samples from three Rocky Mountain stands (Utah, Colorado, eastern Montana), with means of 112–141 scales, as well as samples from nearby Incline, south-eastern British Columbia, and western Montana-northern Idaho, with means of 134–137 scales per cone. It also exceeded, but not significantly, ponderosa from the Sierra Nevada west slope and from central Oregon (159 and 157 scales per cone). A single North Plateau stand, in the Okanagan region of southern British Columbia, had the same mean number of scales per cone as Washoe pine.

Ponderosa pine is polymorphic in immature seed-cone color, but deeply pigmented cones like those of Washoe pine have not been observed in the Pacific race. Smith (1981) reported no ponderosa pines with purple cones in the region from the central Sierra Nevada to southern Oregon west of the Cascades. Only in and near the transition zone of northeastern California did he encounter low frequencies of trees with purple cones. The ponderosa stand on Mt. Rose is also polymorphic in cone color. Of six trees I observed, four had green cones and two had reddish-brown cones.

Trees with cones ranging in color from reddish-brown to dark purple predominate in the North Plateau region. Smith (1981) found high frequencies of trees with purple cones in southern Oregon just north of the transition zone. Sargent (1897) noted that one western Montana stand was a mixture of green- and purple-coned trees, but in another stand most trees had purple cones. Not all trees are readily classifiable: in an Idaho stand Maki (1940) counted 3 trees with green cones, 7 with deep purplish-brown cones, and 10 with varying degrees of pigmentation. In some British Columbia stands, however, all trees have dark purple cones (J. R. Haller, pers. comm., Oct 1981).

Not much information is available on seed-cone color in Rocky Mountain ponderosa pine, but purple cones have not been reported. Haller saw only green cones in central Colorado and southern Montana stands (pers. comm., Oct 1981 and Sept 1983), and five arboretum trees of Rocky Mountain provenances (eastern Nevada, Colorado, Nebraska) all had green cones.

Washoe pine has large seeds with relatively short wings. Mason and Stockwell (1945) described the seed as 8 mm long, with a wing (measured from wing tip to seed) 1.5 to 2 times as long as the seed. Mean length of Mt. Rose Washoe seed was 8.1 mm (unpubl. data, IFG), significantly longer than all 25 Rocky Mountain samples (means 5.4–7.2 mm) and 14 of 19 Pacific samples (6.5–8.1 mm), but only 2 of 10 samples from the North Plateau region (means 6.7–8.4 mm).

TABLE 4. COMPARISON OF WASHOE PINE WITH NORTHERN RACES OF PONDEROSA PINE. 1 = most similar; 3 = least similar; ND = no data. Western = eastern Great Basin, and Colorado Plateau in Utah and Colorado; eastern = central Montana to Nebraska and central Colorado; column in between represents Rocky Mt. region as a whole.

	Pacific	North Plateau	Rocky Mountain	
			Western	Eastern
Seedlings (Wells 1964)	2	1	ND	
Terpenes (Smith 1977)	3	1	2	1
Needles:				
Length	2	1		1
Thickness	3	1	2	3
Number per fascicle	1	1	2	3
Pollen cones:				
Length	3	2		1
Color	1	1		2
Seed cones:				
Volume (Haller 1957)	2	ND		1
Length	3	2	2	1
Number of scales	2	1		3
Color	2	1		2
Seeds:				
Length	2	1		3
Wing length:seed length	3	1	3	2

Seed weight differences in the same set of samples were much less striking: most western stands and two eastern Rocky Mountain stands had heavier seeds than Washoe pine (Wells 1964).

The seed of Washoe pine has shorter wings, relative to seed length, than most ponderosa pines outside the North Plateau region. The mean ratio of wing to seed length in Haller's (1957) Mt. Rose sample was 1.9, compared with means of 3.2, 3.0, and 2.3 in ponderosa from Mt. Rose, eastern Nevada, and central Montana. In other samples (unpubl. data, IFG), this ratio was 2.0 in Mt. Rose Washoe pine, 3.0–3.9 in the Pacific region, 2.1–3.4 in the Rocky Mountain region, and 1.9–2.5 in the North Plateau region. Expressed as the ratio of total (wing + seed) length to seed length, the mean ratio of Washoe pine was significantly smaller than that of all Pacific samples, all western (eastern Great Basin, Colorado Plateau) and most eastern Rocky Mountain samples, and 2 of 10 North Plateau samples.

DISCUSSION

The two kinds of data assembled in this paper—crossing, and all other—suggest different hypotheses concerning the origin of Washoe pine. In its ability to cross with other taxa, Washoe pine behaves like a fragment of the Rocky Mountain race stranded at the western

edge of the Great Basin. But most other evidence supports the hypothesis that Washoe pine is most closely linked to the North Plateau race of ponderosa pine (Table 4).

The data are in agreement, however, in narrowing the field of ancestral candidates. Mirov's (1961) conclusion that Jeffrey pine was not involved in the ancestry of Washoe pine was based primarily on the absence of heptane in Washoe wood resin, but his view is supported by morphological evidence and by the strong crossing barrier between these taxa. Among the northern races of ponderosa pine, the least likely ancestral candidate is the Pacific race. Although it is essentially parapatric with Washoe pine, in nearly all of its attributes it is less similar to Washoe pine than are the other two northern races (Table 4). The Pacific race and Washoe pine exchange genes, but the extent and consequences of hybridization appear to be limited by moderately strong reproductive barriers, by differences in pollination time, and perhaps by selection against hybrids and their derivatives in the rigorous environments to which Washoe pine is restricted.

The available crossing data provide a less than complete picture of crossability among elements of the ponderosa pine complex, including Washoe pine. The data are most complete for the Pacific race, and least so for the North Plateau race. No crosses have been made between the latter and either Washoe pine or the Rocky Mountain race, but the few Pacific $\times$ North Plateau crosses suggest that these two geographic races are partly isolated by reproductive barriers. The Pacific race is, in fact, genetically isolated to varying degrees from all other northern elements of the ponderosa complex. It is in genetic contact with both Washoe pine and the North Plateau race, and may have been in the past. In these instances the barriers could have evolved either during isolation or by selection against the products of hybridization. The latter explanation is hardly applicable to barriers of the same magnitude between Pacific and Rocky Mountain races, which are more likely to have evolved as a by-product of geographic isolation. These well-differentiated races have been separated by the western Great Basin since at least the late Pleistocene (see below), and possibly for much longer.

Genetic barriers between geographic races are not common in *Pinus*, but they have been encountered in at least one other species. The northern "blue" race of the Californian *P. muricata* D. Don is isolated from southern populations by reproductive barriers that are absolute or nearly so (Critchfield 1967). The more common situation in the genus, however, is exemplified by the absence of reproductive barriers between coastal and Sierra Nevada races of lodgepole pine, although these taxa are so different they are sometimes considered separate species (Critchfield 1980).

The hypothesis that Washoe pine is a geographically isolated off-

shoot of the Rocky Mountain race is based primarily on crossing behavior. Not only are the two taxa fully crossable, but in combination with the Pacific race they give almost identical results: 30% crossability for Washoe pine and 35% for the Rocky Mountain race. As an indicator of relationship, however, these results are inconclusive in the absence of comparable crossing data for the North Plateau race.

Morphological and biochemical characters provide only limited support for the hypothesis that Washoe pine derives from a Rocky Mountain-like ancestor. The closest similarities are in size (needles, pollen cones, and seed cones), and the most conspicuous differences in other kinds of characters: color (pollen- and seed-cone) and number (needles per fascicle and scales per cone). In several respects (resin composition; needle, seed-cone, and seed length; relative length of seed wings), Washoe pine resembles the geographically remote eastern populations of the Rocky Mountain race more than it does the populations in the eastern Great Basin (Table 4). This tendency suggests that involvement of the Rocky Mountain race in the ancestry of Washoe pine, if any, must have been remote in time, and in circumstances that have been obscured by subsequent displacement and migration.

The history of vegetation in the Great Basin region has been substantially revised in the past two decades, and the possibility that ponderosa pine migrated across the Great Basin in late Quaternary time is no longer tenable. This historical revision is based on radiocarbon-dated macrofossils recovered from hundreds of wood-rat (*Neotoma*) middens. The midden record is most complete for the Southwest and parts of the Great Basin (e.g., Thompson and Mead 1982, Van Devender and Spaulding 1979, Wells 1983), but it includes sites as far north as the central Rocky Mts. and southern Columbia Plateau (Wells 1983) and as far west as the Sierra Nevada (Cole 1983).

No aspect of Western vegetation history has been more drastically reinterpreted than the role of ponderosa pine. Fossil pollen data were the principal source of information before the midden work began, and one reconstruction of full-glacial vegetation mapped ponderosa pine forests across the southern Great Basin and throughout much of the Southwest (Martin and Mehringer 1965). This interpretation has been discarded as negative evidence from middens has accumulated. With two possible exceptions, macrofossils of ponderosa pine have not been found in any Pleistocene midden. Needles of either ponderosa or Jeffrey pine were recovered from full- and late-glacial middens in Kings Canyon, on the west side of the southern Sierra Nevada (Cole 1983). In the Southwest, "*Pinus* cf. *ponderosa*" was reported in Pleistocene middens in the Santa Catalina Mts. of southeastern Arizona (Thompson and Van Devender 1980).

The identity of this find has still to be established; ponderosa pine is present in the region today, but so are the closely similar Arizona pine (*P. arizonica* Engelm.) and Apache pine. The absence of ponderosa pine from the Pleistocene record of much of the interior West led Wells (1983) to speculate that in the late Pleistocene the species "must have been far south of its present range, possibly on the southern High Plains (Wells 1970) and in the mountains of the Southwest in and near northern Mexico."

The first postglacial record of ponderosa pine is from the Sheep Range in southern Nevada, where it was present in a midden dated 10,060 B.P. but absent from older middens at the same site (Van Devender and Spaulding 1979). The species was sparsely represented in the eastern Grand Canyon by 9070 B.P., but lacking in middens with dates of 20,630 to 9400 B.P. (Cole 1982). Ponderosa pine grew in Chaco Canyon, northern New Mexico, by 8300 B.P. (J. L. Betancourt, pers. comm., Nov 1982), and in the same region the fossil pollen record (identified to pine species) shows that it reoccupied the crest of the Chuska Mts. by about 5000 to 6000 B.P. (Wright et al. 1973). The species reached the Snake Range of eastern Nevada between 9180 and 6120 B.P. (Thompson 1979, Wells 1983), and the Rocky Mountain race, represented by two-needled fascicles, was in southeastern Wyoming by 4060 B.P. (Wells 1970). It is not known when this race reached its northern and northwestern limits in Montana, but a recent arrival is suggested by this sequence of dates and by the moderately abrupt transition between Rocky Mountain and North Plateau races in central Montana.

The anomalous absence of ponderosa pine from most of the interior West during the latter part of the Pleistocene virtually eliminates the possibility that eastern and western populations have been in contact across the Great Basin during the past 40,000 years—the span of radiocarbon time. And if the last glacial and present interglacial periods are representative of earlier glacial-interglacial sequences, the western Great Basin and the deserts to the south of it may have been a barrier to east-west migration of ponderosa pine for a much longer time, perhaps since the Tertiary.

Evidence of long-term separation between eastern and western segments of ponderosa pine strengthens the alternative hypothesis: that Washoe pine originated from North Plateau ponderosa pine. The close resemblance of Washoe pine to this race was first pointed out by Haller (1965a). At scattered localities in eastern Oregon, he found that occasional trees in predominantly ponderosa stands were within the morphological range of Washoe pine. He speculated that these variable populations might have originated from hybridization of local ponderosa pine with the Rocky Mountain race, and concluded that Washoe pine "could be a segregate from these hybrid populations, maintained in isolation in the south but only partially

differentiated in the north." He later found a stand consisting entirely of Washoe pines in south-central British Columbia, growing on Promontory Mountain (Fig. 1) at the relatively high elevation of 1460 m (J. R. Haller, pers. comm., Oct 1981). Haller now believes that Washoe pine originated in the interior of the Pacific Northwest and "migrated southward into California along the Sierra-Cascade crest, probably during one of the glacial phases of the Pleistocene" (J. R. Haller, pers. comm., Sept 1983).

Although the data summarized in Table 4 confirm the overall similarity of Washoe pine and the North Plateau race, they do not support the degree of taxonomic congruence suggested by Haller (1965a). In Wells's (1964) analysis of seedling traits, Washoe pine was unique in its distinctness from the other western populations. It differed significantly from most or all North Plateau provenances in five seedling traits: height at two years, for example, was only 41–65% of seedling height in North Plateau samples. In resin composition, North Plateau populations approach but do not equal Washoe pine's high frequency of trees with high carene and low limonene. In other adult characteristics, Washoe pine was distinct from 43 of 45 North Plateau populations in a combination of needle traits and from 33 of 34 populations in length of seed cones. The exceptions were all upper-elevation populations: two in eastern Oregon (1430 and 1800 m) and one in southeastern British Columbia (1000 m). In limited data on length of pollen cones, all Washoe pines differed from all western ponderosa pines. Seed traits are less discriminating; the only North Plateau populations that differed significantly from Washoe pine were in the eastern part of the region (Idaho, western Montana). None of the North Plateau populations was identical to Washoe pine in an array of characters, although some may have included individuals within Washoe's range of variation.

Haller's observations in the Northwest suggest the following speculative reconstruction: Washoe pine is better adapted than ponderosa pine to the harsh climates that prevailed in the periglacial environments of the interior Northwest, and is most likely to have evolved from an isolated fragment of the North Plateau race during the Wisconsin or an earlier glacial period. Near the end of the Pleistocene, Washoe pine comprised a string of scattered populations extending from eastern Oregon to the Mt. Rose region. It was geographically separated from ponderosa pine, and grew at lower elevations than it does today. In the warmer climate of the early Holocene, it migrated north on to deglaciated terrain in southern British Columbia as the ice receded from its full-glacial limits in northern Washington. In the south it moved to higher elevations where suitable sites were available, and it still occupies some of these sites. Most remnants of Washoe pine in the interior Northwest were replaced or absorbed by the North Plateau race as the latter expanded

throughout the region from unknown refugia, but at least one population (Promontory Mountain) may have survived intact on a high-elevation site in British Columbia.

The late Quaternary vegetation history of the interior Northwest provides one piece of evidence supporting this reconstruction. This history is based entirely on fossil pollen, and in most studies of radiocarbon-dated sequences the pollen of *Diploxylon* pines (lodgepole and ponderosa in this region) is lumped (e.g., Mack et al. 1979). An exception is Alley's (1976) analysis of Kelowna Bog, in the Okanagan Valley of southern British Columbia (Fig. 1). A forest dominated by *Diploxylon* pine occupied the site before 8400 B.P., and may have been contemporaneous with ice in the nearby valley bottom. Alley identified the *Diploxylon* pollen as ponderosa pine, using a combination of morphological and size characteristics. Mack et al. (1979) questioned Alley's identification on ecological grounds, because of lodgepole pine's well-documented role as a pioneer on deglaciated terrain in parts of the Northwest. Washoe pollen has not been studied, but if it falls within the range of ponderosa pine in size and morphology, this taxon, rather than ponderosa or lodgepole pines, may have been the early postglacial *Diploxylon* pine in the Okanagan region. The influence of Washoe on ponderosa pine is more marked in southern British Columbia than in any other part of the North Plateau region except eastern Oregon (J. R. Haller, pers. comm., Oct. 1981), and the Kelowna Bog site is only 100 km east of the Washoe pine stand on Promontory Mountain.

According to this reconstruction, Washoe pine is the product of major displacements that occurred during the Pleistocene, and may have originated as recently as within the past 100,000 years. A more direct estimate of its antiquity is based on an immunological investigation of differences in seed proteins (Prager et al. 1976). Washoe pine from Mt. Rose had an antigenic distance of 0.6 from Sierra Nevada ponderosa pine (seed origins from IFG files). This was greater than the distances of Jeffrey and Digger pines from ponderosa (0.4, 0.5), but less than the values for Coulter and Apache pines (0.8, 1.0). Rough estimates of rates of protein evolution based on these and other values suggest that the lineages represented by Washoe and Pacific ponderosa pines separated long before the Pleistocene, possibly as much as 20 million to 30 million years ago. This estimate does not conflict with the hypothesis that Washoe pine is a recent derivative of the North Plateau race, however, if it actually estimates the time of divergence between North Plateau and Pacific races of ponderosa pine.

A recent origin is in better agreement with other attributes of Washoe pine, which are suggestive of a brief and unsuccessful experiment in speciation. This taxon exists as a distinct entity only in a narrow range of forest sites, on which it retains a precarious hold.

And if the low seed production of the Mt. Rose population is characteristic of other populations, Washoe pine is poorly equipped to survive even in these limited habitats. The consistency of poor seed yield from year to year appears to preclude an environmental explanation, such as the production of functionally impaired pollen under harsh climatic conditions. A genetic basis is more likely, but the available data are insufficient to discriminate among alternatives. If low seed production is restricted to Mt. Rose, it may be related to the near-destruction of this population in the 19th century. If the population regenerated from a few closely related seed parents, a high level of inbreeding could account for large reductions in seed yield. An alternative is that Washoe pine has accumulated unusually high frequencies of deleterious genes, many of them acting to produce embryo death. Critical genetic tests (interpopulation crosses, selfing) are lacking, and either genetic explanation is compatible with the increased yield of sound seed when Rocky Mountain ponderosa pine are used as pollen parents.

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