CROSSABILITY AND RELATIONSHIPS OF THE CALIFORNIA BIG-CONE PINES

by William B. Critchfield[1]

In the genus *Pinus,* much of the information about species crossability that has accumulated during the past three decades has reinforced ideas about the relationships of pines based on other kinds of evidence. There are some conspicuous exceptions to this generalization, however, and the most thoroughly investigated of these exceptions is Jeffrey pine *(Pinus jeffreyi* Grev. & Balf.), an economically important forest tree of montane California and adjacent parts of Oregon, Nevada, and Baja California. Biochemically, this puzzling species is much like the Sabinianae Loud. (Macrocarpae Shaw), a group of big-cone pines endemic to California: Digger pine *(P. sabiniana* Dougl.), Coulter pine *(P. coulteri D.* Don), and Torrey pine *(P. torreyana* Parry). In its morphology, however, Jeffrey pine is very similar to ponderosa pine *(P. ponderosa* Laws.) and other members of the Ponderosae Loud.,[2] a varied assemblage of yellow pines of western and southwestern North America. In its breeding behavior Jeffrey pine links these two well-defined groups through its ability to cross with members of both groups --- *P. ponderosa* and *P. coulteri* — in nature and under controlled conditions.

The contradictory nature of the evidence concerning the relationships of Jeffrey pine led D field (1952), in his re-appraisal of the hard pines, to combine the Sabinianae and the Ponderosae into a single group (his group XII). Since 1952 bio-chemical investigations of the pines have been greatly extended, and several new hybrids invo ing Jeffrey pine or species of the Sabinianae have been produced at the Institute of Forest Genetics at Placerville, Calif. This paper summarizes the results that we have obtained from crossing Jeffrey pine and the Sabinianae with each other and with other pines, and re-evaluates the status of Jeffrey pine and its relatives in terms of this and other recent evidence.

The Species of the Big-Cone Group

The species included in the Sabinianae form morphologically and geographically coherent group (Lemmon 1888, Shaw 1914). They are not econo- ically important forest trees, but each species has unique features. Torrey pine has one of the most restricted ranges of any pine, and is the only ifornia hard pine with five needles per fascicle. Digger pine characteristically changes from a single leader to multiple leaders during devel ment, a change that produces the rounded, branchy crown of this species. Coulter pine is noteworthy for its large, heavy, spiny cones, the most massive in the genus. The members of the Sabinianae have in common a coarse branching habit, long coarse needles, several characteristics of the cones and

---

[1] *Geneticist, Institute of Forest Genetics, Pacific Southwest Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture, Placerville, Calif. During most of the period covered here, the hybridization program at the Institute was planned and directed by F. I. Righter, J. W. Duffield and R. Z. Callaham have also been concerned with the planning and execution of this continuing program. A preliminary analysis of the Digger pine hybrids reported here was made by Ben Burr. R. H. Smith has helpfully provided unpublished information on resin composition of several pines.*

[2] *The relationship groups of hard pines outlined by Duffield (1952) have recently been designated as subsections and their names have been brought up to date (Critchfield and Little 1966). The Ponderosae consists of all the species included in Duffield's group XII except the three species making up the Sabinianae (an earlier name of Shaw's Macrocarpae).*

seeds that distinguish the group from the Ponderosae, and paraffin hydrocarbons (heptane, nonane, undecane) in their wood oleoresin, a feature which they share with Jeffrey pine. Another biochemical characteristic that distinguishes the Sabinianae and Jeffrey pine from several members of the Ponderosae is the presence of alkaloids in the needles (Tallent *et al.* 1955).

With the exception of Torrey pine, which is geographically isolated from all related species, there is a high degree of sympatry among the Sabinianae, Jeffrey pine, and ponderosa pine (the principal California representative of the Ponderosae). In the upper part of its elevational range, Digger pine is commonly mixed with ponderosa pine. At a few places it meets the higher-elevation Jeffrey pine, usually in association with ponderosa pine as well.[3] Ponderosa pine is mixed with Jeffrey pine in many parts of California, and in the mountains of southern California both species occur with Coulter pine separately or together[4]. Coulter pine occurs with Digger and ponderosa pine in parts of the central Coast Ranges, and with Jeffrey and Digger pines in one locality (San Benito County). The distribution of these pines is shown by Critchfield and Little (1966).

Coulter pine has been exploited in the genetic improvement of Jeffrey pine. Young Jeffrey pines are sometimes badly damaged by the pine reproduction weevil *(Cylindrocopturus eatoni* Buch.), especially in plantations. Coulter pine has proven to be completely resistant to this insect under forced attacks (Miller 1950). Backcrosses of natural Jeffrey-Coulter hybrids to Jeffrey pine have also exhibited a high level of resistance under forced attacks (Miller 1950; Smith 1960) and in field tests (Hall 1959). This resistance of the backcross hybrids led Region 5 of the U.S. Forest Service to start producing them on a large scale several years ago (Libby 1958).

Previous Reports of Natural and Artificial Hybrids

Although Jeffrey pine has generally been treated as a separate species in recent years, opinion concerning its status was divided in the past. Lemmon (1888, 1890) and Sudworth (1908) considered it a distinct species, but other botanists regarded it as a variety of ponderosa pine. Shaw (1914) noted: "Most observers discover many intermediate forms between this variety and the species," and Jepson (1910) stated, "... the transition forms in the intermediate region are quite as numerous and occupy as extensive an area as the Jeffrey Pine itself."

The findings of Schorger and others (see Mirov 1961) that the turpentine of Jeffrey pine is completely different in composition from that of ponderosa pine may have helped to define Jeffrey pine as a separate species. The first definite report of a hybrid between the two species was in 1929. A field survey in northeastern California turned up a single tree, intermediate in morphology, with turpentine consisting of both heptane, like Jeffrey pine, and monoterpenes, like ponderosa pine (Mirov 1929). At about the same time, the two species were crossed reciprocally at the Institute of Forest Genetics, then called the Eddy Tree Breeding Station (table 1).

The extent of hybridization between ponderosa and Jeffrey pines in several mixed populations was recently investigated by Haller (1962). Sampling more or less at random but including some variant trees, he found only a single putative F1 and a few possible hybrid derivatives, a small fraction of the sampled trees. He concluded that gene exchange between these two species is very limited.

Jeffrey and Coulter pines, because of their pronounced morphological differences, were not considered to be at all closely related until 1937, when a natural hybrid of these species was found in the mountains of southern California (Libby 1958). In 1939 this tree was backcrossed to Jeffrey pine, and a few years later the first artificial F1 hybrids between Jeffrey and Coulter pines were produced (table 1).

Natural hybridization between Jeffrey and Coulter pines was investigated by Zobel (1951), 5 who made an extensive search for hybrids in several mixed populations. He found five putative F1 hybrids, a few possible backcrosses to Jeffrey pine, and fairly numerous possible backcrosses in the other direction, grading more or less continuously into Coulter pine. Like Haller, Zobel concluded that natural hybridization has been ineffective in altering the characteristics of either species. A few years later, Libby located additional natural Jeffrey x Coulter hybrids (Libby 1958).

Verified hybrids have also been reported between Jeffrey pine and two other members of the Ponderosae: Washoe pine *(Pinus washoensis* Mason & Stockwell) and Montezuma pine *(P. montezumae* Lamb.) (table 1). An early report of a

[3] *Griffin, James R. Intraspecific variation in Pinus ponderosa Dougl. Ph.D. thesis, Univ. Calif., Berkeley. 254 pp., illus. 1962.*

[4] *Zobel, Bruce J. The natural hybrid between Coulter and Jeffrey pines. Ph.D. thesis, Univ. Calif., Berkeley. 114 pp., illus. 1951.*

[5] *See also, Zobel, Bruce J. The natural hybrid between Coulter and Jeffrey pines. Ph.D. thesis, Univ. Calif., Berkeley. 114 pp., illus. 1951.*

Table 1.--Hybrids of Sabinianae pines and Jeffrey pine produced at the Institute of Forest Genetics, Placerville

Parents (Pinus-)		Pollination year first produced	Year planted	First cited
Female	Male			
sabiniana	*coulteri*	1958	1960	This paper
sabiniana	*torreyana*	1958	1960	This paper [1/]
jeffreyi	*coulteri*	1944	1946	Righter and Duffield 1951
jeffreyi	*ponderosa*	1929	1933	Schreiner 1937
ponderosa	*jeffreyi*	1929	1933	Weidman 1947
jeffreyi	*montezumae*	1951	1953	Liddicoet and Righter 1960
jeffreyi	*engelmannii*	1955	1962	This paper
jeffreyi	*washoensis*	1948	1950	Liddicoet and Righter 1960 [2/]

1/ An earlier cross (1947), planted in 1949, was removed in 1953. These putative hybrids are mentioned in the unpublished Annual Report for 1949, California Forest and Range Exp. Sta., 1950, on file at Pacific Southwest Forest and Range Exp. Sta., U.S. Forest Serv., Berkeley, Calif.

2/ Also listed as verified hybrid in unpublished Annual Report for 1950, California Forest and Range Exp. Sta., 1951, on file at Pacific Southwest Forest and Range Exp. Sta., U.S. Forest Serv., Berkeley, Calif.

successful cross between Jeffrey and Montezuma pines (Duffield 1952) [6] appears to be in error; the earliest verifiable hybrids between these two species were produced by 1951 pollinations (table 1).

Two non-existent hybrid combinations involving members of this group are sometimes cited. One of these false reports appears to have had its origin in a statement by Austin (1927) that sound seed had been obtained from a 1926 cross between ponderosa and Digger pines. This seed, probably the result of pollen contamination during this first season of controlled breeding at Placerville, has been reported as a ponderosa x Digger pine hybrid by Richens (1945) and others. Richens also reported a hybrid between Coulter and ponderosa pines, but the source of this erroneous information is unknown.

Parent Trees

Several of the species concerned in the crosses summarized here are native to the vicinity of Placerville, which is in Eldorado County in the central Sierra Nevada. About 20 Digger pines, widely scattered through the foothill zone of western Eldorado County, were used as parents. Nearly all of the Jeffrey pine crosses were made with about 55 trees growing at higher elevations in and near eastern Eldorado County, and most of the 60 or more ponderosa parents were in native stands in central Eldorado County. Arizona pine (*P. ponderosa* var. *arizonica* (Engelm.) Shaw), which is treated separately here, was represented by only three arboretum trees, all from the same collection in the Chiracahua Mountains of southern Arizona. The Washoe pine crosses involved six parent trees growing in two localities on Mount Rose, Nev.

The other species considered here were principally represented by trees growing in the arboretum. About a dozen Coulter pines were used, originating in several localities from San Diego to Contra Costa Counties. Torrey pine does not flourish at Placerville, and only about five trees were used as parents. The seven parent trees of Apache pine (*P. engelmannii* Carr.) originated from two seed collections in the Chiracahua Mountains. Durango pine (P. *durangensis* Martinez) was represented by a single tree from the state of Durango, Mexico. Ten trees of Montezuma pine were used most of them growing in the arboretum and originating from several different collections of Mexican or unknown origin. Three trees growing in natural stands in central Mexico were used as pollen parents.

Most of the crosses were made on Jeffrey and ponderosa pines, and crosses between these two species were usually made on the later-flowering Jeffrey pine. Digger pine was not used more often as a female parent because it flowers earlier than

[6] *See also U. S. Forest Service, Calif. Forest and Range Exp. Sta. Unpublished Report for 1950. On file at Pacific Southwest Forest and Range Exp. Sta., U. S. Forest Serv., Berkeley, Calif.*

any of the other species considered here except Torrey pine. Coulter pine produces abundant pollen from an early age at Placerville, but its cone production is rather limited there. Torrey pine and the southwestern and Mexican pines are unpredictable and generally sparse in their flowering in Placerville.

Methods

The results summarized here cover a 35-year period: the pollinating seasons of 1929 through 1963. The techniques used to control pollination in pines have been described by Cumming and Righter (1948). Numbers of sound and hollow seed were often determined by weighing the seed in the 1930's, but since then a Clipper Mill has been used for separating sound and hollow seed.

Many crosses involving these species have been omitted from this summary, including all crosses that failed to yield cones and all crosses for which data are not complete (numbers of strobili pollinated, cones harvested, and sound and hollow seed). Crosses that produced seed which was badly damaged by insects (more than 10 percent) have been omitted. Also omitted are nearly all of the crosses involving pollen that had been refrigerated for a year or more. Since 1961 we have deep-frozen all of our pollen at Placerville, and a few crosses utilizing year-old frozen pollen are included here. Also included are the crosses between Digger and Coulter pines, all of them made with year-old refrigerated pollen, since one of them yielded the single Digger x Coulter hybrid so far obtained.

With these exceptions, the data summarized here include all interspecific crosses involving the three species of Sabinianae, and all crosses of Jeffrey pine with members of the Sabinianae and Ponderosae. Also summarized are all intraspecific crosses of Coulter, Washoe, and Apache pines, and partial but representative data on intraspecific crosses of Jeffrey, ponderosa, and Digger pines. A comprehensive evaluation of interspecific crosses between members of the Ponderosae is outside the scope of this paper, but rough estimates of their crossability are presented as a basis for evaluating the status of Jeffrey pine in relation to the Ponderosae.

Several species combinations have produced sound seed but not verified hybrids. Single crosses of Washoe x Jeffrey and Jeffrey x Arizona pines have each yielded a single seed which failed to germinate. Three other species combinations (Jeffrey x Torrey, ponderosa x Coulter, and Washoe x Coulter) have yielded from one to a few sound seeds, but our records do not indicate the fate of these small seed lots.

An *attempt,* as used here, refers to the pollination of a single female parent with pollen from a single male parent or with a mixture of pollen from several male parents. The minimum number of tree x tree combinations attempted has been estimated by assuming that two male parents have contributed to pollen mixes of unspecified constitution. *Crossability,* as quantitatively expressed here, is the mean sound seed yield from an interspecific combination expressed as a percent of the mean sound seed yield of crosses within the maternal-parent species. In those few instances where two species have been crossed reciprocally (e.g. Jeffrey and Washoe pines), the two crossabilities have been averaged after weighting by the number of attempts.

Crossing the Sabinianae Pines

Despite the morphological similarity of Coulter and Digger pines, this species combination appears to be decidedly less crossable than Digger and Torrey pines. Crosses of Coulter x Digger have not yielded any hybrids (table 2), and the reciprocal combination has yielded a single tree.

Coulter and Digger pines differ chiefly in cone and seed characteristics and wood-resin composition. The hybrid is too young to produce cones, but resin composition has proven to be conclusive in establishing its identity. The low-boiling-point fraction of Digger pine resin consists almost entirely of heptane, plus a small amount of nonane (Mirov 1961; Williams and Bannister 1962). The same fraction of Coulter pine resin is made up principally of α-pinene, β-phellandrene, and myrcene, with lesser amounts of several other compounds including the three paraffin hydrocarbons known to occur in *Pinus:* heptane, nonane, and undecane (Mirov 1961; Williams and Bannister 1962; Smith[7]). The resin of the hybrid tree, analyzed by gas-chromatographic techniques, is clearly intermediate. It contains large amounts of heptane and α-pinene, a lesser amount of β-phellandrene, and small amounts of several other constituents of Coulter pine resin (table 3). In other respects the tree does not differ greatly from young Digger pines.

In the few attempts that we have made, Digger pine combines much more readily with Torrey than with Coulter pine, although it differs from Torrey pine in cone form, number of needles per fascicle (usually three, compared to five in Torrey), and other characteristics. Three of the five attempts to cross these two species (table 2) have yielded 3 to 8 sound seed per cone. A large number of putative hybrids was obtained from the first of these, a cross made in 1947. These trees were judged to be nonhybrids at 5 years of age and were removed. The other two attempts were made in 1958, using other parent trees. Both crosses were made with pollen from a single Torrey pine.

[7] Smith, Richard H. Variations in the wood resin monoterpene composition of Pinus jeffreyi, P. washoensis, P. coulteri, P. contorta. In manuscript at Pacific Southwest Forest and Range Exp. Sta., Berkeley, Calif.

Table 2.--Summary of Institute of Forest Genetics crosses involving Sabinianae pines and P. jeffreyi, 1929-1963

Male parent	Female parent					
	sabiniana	coulteri	jeffreyi	ponderosa	washoensis	engelmannii
torreyana	5(6)/4 42, 69 2.1/60.4	4(7)/0 31, 29 0/122.3	3(6)/1 29, 48 0.4/71.9	3(3)/0 13, 77 0/42.1		
sabiniana	1/ 16(16)/16 80, 61 87.4/99.1	8(15)/0 85, 44 0/98.7	4(4)/0 23, 57 0/71.2	6(12)/0 42, 55 0/55.2		1(1)/0 10, 100 0/13.0
coulteri	2/ 8(12)/2 61, 41 0.1/45.0	1(3)/1 10, 70 86.1/106.9	29(41)/17 1112, 61 7.2/105.9	13(17)/2 290, 39 <0.1/48.2	4(11)/1 61, 36 <0.1/69.1	
jeffreyi			1/ 20(25)/20 164, 79 142.3/185.3	8(12)/2 83, 46 <0.1/49.4	3(9)/1 23, 57 <0.1/65.5	
ponderosa			32(36)/27 854, 40 4.1/134.7	1/ 29(43)/29 278, 45 52.1/57.8		
ponderosa var. arizonica			4(5)/1 127, 36 <0.1/141.0			
washoensis			1(2)/1 14, 71 3.4/172.8		3(7)/3 27, 52 65.6/110.6	
engelmannii			17(19)/6 367, 73 <0.1/158.6			2(3)/2 13, 85 46.8/54.3
sabiniana			3(1)/0 4, 75 0/75.3			
monticola		1(1)/0 4, 25 0/127	6(13)/3 199, 63 <0.1/116.5			

Legend:

Number of attempts — 0 (0)/ 0 — Minimum number of tree x tree combinations
Number of female strobili pollinated — 0, 0 — Number of attempts producing sound seed
Mean number of sound seed per cone — 0.0/0.0 — Percent of strobili producing cones
Mean total number of seed per cone

Successful interspecific cross (verified hybrids obtained)

Footnotes:
1/ Not all crosses included.
2/ Year-old pollen.

They yielded trees that have been identified as hybrids on the basis of their oleoresin composition. The low-boiling-point fraction of Torrey pine oleoresin consists mostly of limonene, with small amounts of heptane, nonane, undecane and other compounds (Mirov 1961; Williams and Bannister 1962). The resin of all five putative hybrids available for sampling contains large amounts of both limonene, like Torrey pine, and heptane, like Digger pine, plus small amounts of nonane, undecane, and other compounds (table 3).

In other respects the Digger-Torrey hybrids are nearly indistinguishable from young Digger pines. In number of needles per fascicle, a characteristic that might be expected to differentiate the hybrids from both parent species, Digger pine is partly dominant. In a 10-fascicle sample of each of the 5 hybrids listed in table 3, 2 had exclusively three-needled fascicles and the other 3 had mixtures of three- and four-needled fascicles. None had any five-needled fascicles. Thus all of the hybrids are within the range of Digger pine itself, which often has more than three needles per fascicle.8 This

8 *Griffin, James R. Intraspecific variation in Pinus sabiniana Dougl. Ph.D. thesis, Univ. Calif., Berkeley, 274 pp., illus. 1962.*

Table 3.--Low-boiling-point constituents of wood oleoresin of Pinus sabiniana x coulteri, P. sabiniana x torreyana, and their parents 1/

Tree No.	Parentage of hybrids	Constituent (percent)										
		hep-tane	nonane	α-pinene	un-decane	cam-phene	β-pinene	3-carene	sabin-ene	myr-cene	limon-ene	β-phell-andrene
						P. coulteri						
C1-V30 2/	--	2.4	1.5	40.3	4.3	0.4	2.1	tr	1.5	21.0	3.9	22.5
						P. sabiniana x coulteri						
SC1-1	S-Eld-13-1 x C1 (V28 + V30)	34.8	1.8	43.0	4.5	0.3	1.8	0.8	tr	0.3	0.3	12.4
						P. sabiniana						
S-Eld-13-1	--	93.3	6.7	--	--	--	--	--	--	--	--	--
S-Eld-13-2	--	96.0	4.0	--	--	--	--	--	--	--	--	--
						P. sabiniana x torreyana						
STo-17	S-Eld-13-2 x To-V27	43.9	5.9	2.8	7.8	--	0.3	0.6	--	2.1	36.6	--
STo-21	Do.	45.4	1.4	4.2	4.3	--	tr	tr	--	1.4	43.3	--
STo-27	S-Eld-13-1 x To-V27	56.0	1.2	1.9	4.7	--	--	1.2	--	1.5	33.5	--
STo-29	Do.	23.1	1.4	11.2	7.0	--	--	--	--	1.4	55.9	--
STo-32	Do.	26.6	1.6	2.4	5.7	--	--	--	--	1.6	62.1	--
						P. torreyana						
To-V27	--	3.2	2.4	1.8	7.7	--	tr	--	--	2.7	82.2	--

1/ Percentages are based on constituents listed. Pentane and acetone solutions of resin were analyzed on an 8-ft. 10-percent β, β' oxydipropionitrile column under the following conditions: injector temperature 140°C, column temperature 55°C, thermal detector temperature 165-170°C, filament current 170 ma, and helium volume 63 to 71 ml per minute.

2/ Data supplied by R. H. Smith. The other P. coulteri used in pollen mix (C1-V28) was removed in 1960.

may have been true also of the putative hybrids from the 1947 cross, which were evaluated when resin analysis of young trees was not yet possible, and for this reason the 1947 cross has been included in the summarized data.

With the notable exception of Jeffrey and Coulter pines, all attempts to cross the Sabinianae with other pines have failed (table 2). Most species combinations have been tried on a rather small scale, but collectively they show that there is a strong degree of isolation between the Sabinianae and the Ponderosae, so far bridged only by Jeffrey pine. One combination attempted on a fairly large scale, ponderosa x Coulter pine (13 attempts yielding 290 cones), has produced a few sound seed on two occasions. Although the fate of these seeds is unknown, further trials of this combination may be warranted.

Crossing Jeffrey Pine with the Sabinianae an Ponderosae Pines

All crosses between Jeffrey pine and Digger and Torrey pines have been unsuccessful. These crosses, which have not been tried on a large scale, also show a marked reduction in the yield of cones and total seed compared to intraspecific crosses (table 2). These measures of incompatibility are difficult to evaluate in the absence of control crosses, however.

In contrast, crosses between Jeffrey and Coulter pines have averaged 7.2 sound seed per cone. This is a higher yield of sound seed than any other species combination involving Jeffrey has produced (table 2). It is heavily biased, however, by repeated crosses made on an otherwise unremarkable Jeffrey pine. This tree, unlike its neighbors in the stand, has consistently yielded 20 to 50 sound seed per cone irrespective of the Coulter parent. It has produced more than four-fifths of the sound seed obtained in the Jeffrey x Coulter crosses summarized here. A less biased estimate of the average sound seed per cone for Jeffrey x Coulter — 3.4 — includes only the first cross made on this tree.

With the exception of the Jeffrey x Coulter combination, crosses between Jeffrey pine and species of the Ponderosae have been on a much larger scale than other attempts to cross this species (table 2). Although four different hybrid combinations have been obtained in all (table 1), the genetically controlled reproductive isolation of Jeffrey pine from Southwestern U.S. and Mexican representatives of the Ponderosae appears to be almost complete. Only three Jeffrey x Montezuma hybrids have been produced, and only a single Jeffrey x Apache hybrid.

The ability of Jeffrey pine to cross with the sympatric ponderosa pine is considerably greater. The relatively few attempts in which ponderosa pine has been used as a female parent have not been very successful, but much larger scale attempts in the opposite direction have yielded an average of 4.1 sound seed per cone (table 2). This

compares favorably with the corrected average of 3.4 sound seed for Jeffrey x Coulter combinations.

How do these two species combinations — Jeffrey x Coulter and Jeffrey x ponderosa — compare in other measures of compatibility? A larger proportion of attempts to cross Jeffrey x ponderosa has yielded sound seed: 84 percent compared to 59 percent for Jeffrey x Coulter. And the Jeffrey x ponderosa crosses have also yielded appreciably higher total numbers of seed per cone: 135 compared to 106 for Jeffrey x Coulter and 185 for within-Jeffrey crosses. But the level of conelet abortion is lower in Jeffrey x Coulter combinations. They produced cones from 61 percent of the strobili pollinated, compared to only 40 percent for Jeffrey x ponderosa crosses and 79 percent for within-Jeffrey crosses. These data are not critical, but in conjunction with the sound seed yield they indicate that the compatibility of Jeffrey pine with Coulter and ponderosa pines is of the same order of magnitude.

The interspecific hybrids of Jeffrey pine are highly fertile, like most other pine hybrids but unlike interspecific hybrids in many other groups of plants. Meiotic irregularities during microsporogenesis were about equally uncommon in trees of the parent species and in representative Jeffrey-Coulter and Jeffrey-ponderosa F1 hybrids in Saylor's analysis.[9] The production of aborted pollen grains by these Jeffrey pine hybrids has not been critically investigated, but routine observations indicate that they are generally few. This was not the case in the first natural Jeffrey x Coulter hybrid used in breeding; about half of its pollen aborted (Libby 1958). Many of its wind-pollinated and backcross offspring growing at Placerville also show high levels of pollen abortion.

The ability of these Jeffrey pine hybrids to yield sound seed in backcrosses is also remarkably high, considering the comparatively strong reproductive barriers that separate Jeffrey pine from other species. A Jeffrey x ponderosa hybrid used as female parent in backcrosses to unrelated individuals of ponderosa and Jeffrey yielded only about 10 sound seeds per cone with ponderosa but a remarkable 95 sound seeds per cone with Jeffrey. The Jeffrey x Coulter F1 hybrids began producing pollen only a few years ago, and the backcrosses that have so far been made to Jeffrey pine have suffered heavy seed losses from insects. But one set of crosses involving three Jeffrey female parents and a mixture of pollen from three hybrids produced an average of 133 sound seed per cone, 93 percent of the control-cross seed yield. Other backcrosses, heavily damaged by seed insects and not involving pollen mixtures, have yielded much less sound seed — from 0 to 66 per cone.

[9] *Saylor, Leroy C. Chromosome behavior and morphology in species and interspecific hybrids of Pinus. Ph.D. thesis, N. C. State Coll., 128 pp., illus. 1962.*

Discussion

Although most of the California pines considered here are associated in natural stands, only two hybrid combinations have been encountered in nature: hybrids of Jeffrey with Coulter and ponderosa pines. Ponderosa, Digger, and Coulter pines are all partly sympatric, but they are apparently prevented from hybridizing by strong reproductive barriers reinforced by differences in flowering time. Near Placerville, native Digger pine flowers more than 3 weeks before native ponderosa pine and about a month before planted Coulter pine. Phenological differences of this magnitude probably do not eliminate the possibility of cross-pollination between species, but they must reduce it to the level of an uncommon event.

The limited crossability of Jeffrey pine with Coulter and ponderosa pines helps to explain the rarity of natural hybrids between these species. In both cases the reproductive barriers that restrict crossing are accompanied by differences in flowering time. At Placerville native ponderosa pine flowers a little more than 2 weeks before planted Jeffrey pine, and Haller (1962) noted a difference of 2 weeks to a month in pollen-shedding time in natural stands. Planted Coulter pine flowers only 9 days before planted Jeffrey pine at Placerville, but a few observations suggest that the difference may be somewhat greater in nature. It is impossible to compare the frequency of these two natural hybrids of Jeffrey pine because of the differing approaches to sampling taken by Zobel (1951) and Haller (1962). Zobel's sampling was oriented around natural hybrids that had been located after an extensive search, whereas Haller sampled mixed stands nearly at random. However, Zobel's observation that he found no indications of natural hybridization in many mixed stands, compared to Hailer's finding that all three of his sample areas showed indications of natural hybridization, suggests that hybridization between Jeffrey and ponderosa pines may be more common in nature.

The anomalous characteristics and crossing behavior of Jeffrey pine have produced a considerable diversity of recent opinion concerning its relationships. Mirov (1961), impressed by the chemical similarity of its turpentine to that of the Macrocarpae (i.e. Sabinianae) pines, transferred it from the Australes of Shaw (which includes the Ponderosae) to the Macrocarpae. He noted, however, that he considered it to occupy an intermediate position between the Macrocarpae and the western Australes (i.e. Ponderosae). An opposing view was expressed by Zobel in his study of Jeffrey and Coulter pines and their hybrids (1951). He left Jeffrey pine in the Australes and re-emphasized the distinctness of the Macrocarpae and Australes groups. Still a third viewpoint was adopted by Duffield (1952) at a time when the only hard pines

known to have paraffin hydrocarbons in their resin were the Macrocarpae and Jeffrey pine. He considered the morphological similarities of Jeffrey and ponderosa pines too great to warrant transferring Jeffrey pine to the Macrocarpae, but on biochemical and crossability grounds he eliminated the Macrocarpae and provisionally grouped these species with the western Australes. At the same time he observed, "... the group Macrocarpae is coherent biochemically, geographically, and morphologically."

Since 1952 the biochemical argument for associating Jeffrey pine with the Sabinianae pines has lost some of its force. Paraffin hydrocarbons have been found to occur sporadically in several members of the Ponderosae. Mirov (1961) reported that ponderosa pine growing in Santa Cruz County, Calif., has a small amount of undecane in its turpentine; Montezuma pine growing in the state of Chiapas, Mexico, has a substantial amount of heptane (8 percent) ; and P. *oaxacana* Mirov, a weakly segregated relative of the Mexican P. *pseudostrobus* Lindl., has both heptane (21 percent) and undecane (1.3 percent) in its turpentine. It should also be re-emphasized that neither Coulter nor Torrey pine turpentine contains more than 10 to 15 percent of the paraffin hydrocarbons; their turpentine consists predominantly of monoterpenes.

Arguments for associating Jeffrey pine with the Sabinianae on the grounds of crossability have also lost some of their persuasiveness in the past decade. The coherence of the Sabinianae has been strengthened by successful crosses in two of the three possible combinations. At the same time, Jeffrey pine has been more firmly linked to the Ponderosae by successful crosses with four members of the group. Finally, additional attempts to cross species of the Sabinianae and Ponderosae groups have been unsuccessful, and the two groups are still bridged only by the ability of Jeffrey and Coulter pines to cross (fig. 1).

The strongest arguments for retaining the Sabinianae as a separate group, and for excluding Jeffrey pine from it, are the numerous morphological features that distinguish Coulter, Digger, and Torrey pines from Jeffrey pine and the species of the Ponderosae. Some of these were mentioned by Shaw (1914) : the long stout leaves, the large cones, and the basally thickened seed wing. Unifying features noted by Lemmon (1888) are the long stout conelet peduncles and the very thick, hard seed coats. Other definitive characteristics of the group are the delayed and gradual cone opening, the persistence of the cones on the tree, the large seeds, and the numerous cotyledons (Sudworth 1908; Jepson 1910). The density of Torrey pine cones has not been investigated, but both Coulter and Digger pines have very dense cones; cone specific gravity averages 0.70 to 0.85 in Digger pine

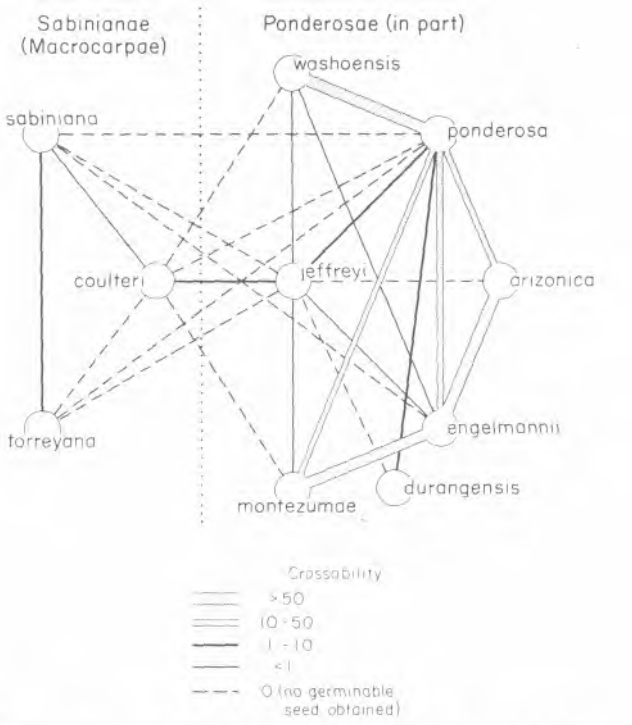

FIGURE 1. — Crossability of the Sabinianae and Ponderosae pines.

and 0.93 in Coulter pine, compared to an average of 0.55 for Jeffrey pine (Zobel 1953; Griffin 1964).

The distinctness of the Sabinianae and the species included in it suggests that this may be a very old group. The restricted ranges of these pines, especially the very limited and discontinuous range of Torrey pine, lend some support to this suggestion, and so does the extreme genetic isolation of these species, compared, for example to the Ponderosae (fig. 1) or the southern pines (Critchfield 1963). The relative uniformity of Digger and Coulter pines (Griffin 1964; Zobel 1953) also suggests that these are old species. The fossil record of the group is not extensive, but cone scales and seeds of pines not unlike the present-day Sabinianae have been found in Pliocene deposits in southern California (Dorf 1933; Axelrod 1937).

Although there are good morphological and other grounds for associating Jeffrey pine with the Ponderosae, it should be emphasized that this species occupies a unique and isolated position in the Ponderosae. It is separated by strong reproductive barriers from the rest of the group, in marked contrast to the relative ease with which most of the other species of the Ponderosae can be crossed with each other (fig. 1).

Literature Cited

Austin, Lloyd. 1927. A new enterprise in forest tree breeding. J. Forest. 25: 928-953.

Axelrod, Daniel I. 1937, A Pliocene flora from the Mount Eden Beds, southern California. Carnegie Inst. Wash. Publication 476: 125-183, illus.

Critchfield, William B. 1963. Hybridization of the southern pines in California. Forest Genet. Workshop Proc., Macon, Ga., Oct. 25-27, 1962: 40-48, illus. Southern Forest Tree Impr. Comm. Publication 22.

_____ and Elbert L. Little, Jr. 1966. Geographic distribution of the pines of the world. U. S. Dep. Agr. Misc. Publication 991, 97 pp., illus.

Cumming, W. C. and F. I. Righter. 1948. Methods used to control pollination of pines in the Sierra Nevada of California. U. S. Dep. Agr. Circ. 792, 18 pp., illus.

Dorf, Erling. 1933. Pliocene floras of California. Carnegie Inst. Wash. Publication 412: 1-112, illus.

Duffield, J. W. 1952. Relationships and species hybridization in the genus *Pinus*. *Z. f.* Forstgenet. u. Forstpflanzenzuchtung 1: 93-100, illus.

Griffin, James R. 1964. Cone morphology in *Pinus sabiniana*. Arnold Arboretum J. 45: 260-273, illus.

Hall, Ralph C. 1959. Field tests of the resistance of hybrid pines to the pine reproduction weevil. U. S. Forest Serv. Pacific Southwest Forest and Range Exp. Sta. Tech. Paper 33, 21 pp., illus.

Haller, John R. 1962. Variation and hybridization in ponderosa and Jeffrey pines. Univ. Calif. Pubs. Bot. 34: 123-165, illus.

Jepson, Willis Linn. 1910. The silva of California. Univ. Calif. Mem. 2, 480 pp., illus.

Lemmon, J. G. 1888. Pines of the Pacific Slope. *In* Calif. State Board of Forestry 2nd Bien. Rep. for the years 1887-1888, pp. 67-140, illus.

_____. 1890. Revision of broken-cone pines. *In* Calif. State Board of Forestry Third Bien. Rep. 1889-1890, pp. 196-201.

Libby, W. J. 1958. The backcross hybrid Jeffrey x (J effrey x Coulter) pine. J. Forest. 56: 840-842, illus.

Liddicoet, A. R. and F. I. Righter. 1960. Trees of the Eddy Arboretum. U. S. Forest Serv. Pacific Southwest Forest and Range Exp. Sta. Misc. Paper 43, 41 pp., illus.

Miller, John M. 1950. Resistance of pine hybrids to the reproduction weevil. U. S. Forest Serv. Calif. Forest and Range Exp. Sta. Res. Note 68, 17 pp., illus.

Mirov, N. T. 1929. Chemical analysis of the oleoresins as a means of distinguishing Jeffrey pine and ern yellow pine. J. Forest. 27: 176-187, illus.

_____. 1961. Composition of gum turpentine of pines. U. S. Dep. Agr. Tech. Bull. 1239, 158 pp., it

Richens, R. H. 1945. Forest tree breeding and genetics. Imp. Agr. Bur. Joint Publication 8, 79 pp.

Righter, F. I. and J. W. Duffield. 1951. Interspecies hybrids in pines. J. Hered. 42: 75-80, illus.

Schreiner, Ernst J. 1937. Improvement of forest trees to U. S. Dep. Agr. Yearbook 1937; 1242-1279, illus.

Shaw, George R. 1914. The genus *Pinus*. Arnold Ar boretum Publication 5, 96 pp., illus. Cambridge, Mass.

Smith, Richard H. 1960. Resistance of pines to the pine reproduction weevil, *Cylindrocopturus eatoni*. Econ. Entomol. 53: 1044-1048, illus.

Sudworth, George B. 1908. Forest trees of the Pacific Slope. 441 pp., illus. Forest Serv., U. S. Dep. Agr.

Tallent, W. H.; V. L. Stromberg; and E. C. Horning 1955. *Pinus* alkaloids. The alkaloids of P. *sabiniana*, Dougl. and related species. Amer. Chem. Soc. J. 6361-6364.

Weidman, R. H. 1947. Trees in the Eddy Arboretum U. S. Forest Serv. Calif. Forest and Range E Sta. Forest Res. Note 53, 8 pp.

Williams, Allette L. and M. H. Bannister. 1962. Composition of gum turpentines from twenty-two spec of pines grown in New Zealand. J. Pharm. Sci. 51: 970-975, illus.

Zobel, Bruce. 1951. The natural hybrid between Coulter and Jeffrey pines. Evolution 5: 405-413, illus.

_____. 1953. Geographic range and intraspecific iation of Coulter pine. Madrono 12: 1-7, illus.