Crossability and Relationships of the Closed-Cone Pines[1])

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Introduction

The 90 to 100 species that make up the genus Pinus are not an exceptionally crossable group of plants. Most pines have been successfully hybridized only with those few species that appear to be their closest relatives on the basis of morphological and chemical criteria, and the yield of hybrid offspring is sometimes very low. Within pine species, however, strong barriers to interbreeding between populations have not been encountered until recently. The closed-cone pine group is of unusual interest because it includes one of the most readily crossable combinations of species so far encountered in the genus and the only known instance in Pinus of a breeding barrier between populations of a species.

The three California closed-cone pines – Pinus radiata D. DON, P. *attenuata* LEMM., and P. muricata D. DON – are perhaps the best known group of species in the genus. Except for the insular forms, they are readily accessible to botanists, their restricted distribution is known in detail, and they have a comparatively rich fossil record. One of them, Monterey pine (P. *radiata)*, is economically important as a planted forest tree – especially in the Southern Hemisphere. The hybrid of Monterey pine and knobcone pine (P. attenuata) – one of the first artificial pine hybrids – has attracted attention because of its adaptability to climates and sites where Monterey pine is marginal or unsuitable. For these reasons, variability and evolutionary trends have been more fully investigated in the California closed-cone group than in most other groups of pines.

In most recent arrangements of the genus, the California closed-cone pines are grouped with those Latin American pines that sometimes have serotinous cones. The latter – P. *patula* SCHIEDE & DEPPE, P. greggii ENGELM., P. *oocarpa* SCHIEDE, and P. *pringlei* SHAW – together with the California species, make up DUFFIELD's group XIV (DUFFIELD 1952), and this is the group considered in this paper. This group has recently been named subsect. Oocarpae LITTLE and CRITCHFIELD (CRITCHFIELD and LITTLE 1966). The same seven species were grouped with P. contorta var. *latifolia* in section *Serotinos* by MARTÍNEZ (1948) in his classification of the Mexican pines. DUFFIELD's group XIV and MARTÍNEZ' section Serotinos are both made up of remnants of SHAW's group *Insignes* (SHAW 1914), which included all of the closed-cone pines in the genus.

DUFFIELD based his arrangement of the hard pines partly on the results of the program of interspecific hybridization in Pinus carried on at the Institute of Forest Genetics at Placerville, California, and partly on chemical and morphological evidence. At the time, elements of the three California pines had been successfully crossed with each other, but very few attempts had been made to hybridize the Latin American species. DUFFIELD considered his group XIV a tentative and unsatisfactory arrangement of the closed-cone pines. Since then, continued exploratory hybridization of the closed-cone pines at Placerville and elsewhere has provided additional evidence concerning the coherency of DUFFIELD's group XIV (subsect. Oocarpae).

This paper summarizes the results of interspecific hybridization in subsect. Oocarpae, describes an apparent barrier to interbreeding between populations of bishop pine (P. muricata), and relates these results to other recent investigations of these pines.

The Species of the Closed-Cone Group

The closed-cone group in its entirety extends from southern Oregon to northern Nicaragua. The ranges of the individual species are illustrated by CRITCHFIELD and LITTLE (1966). The northern species are separated from the exclusively Latin American species by a 400-mile gap between Cedros Island, off the west coast of Baja California, and the state of Sonora, Mexico.

Two of the California species – Monterey and bishop pines – are entirely maritime in their distribution. Monterey pine is confined to three localities on the coast of central California; a related form, P. radiata var. *binata* LEMM., grows on Guadalupe Island, about 150 miles from the Baja California coast. Bishop pine occurs in a string of seven disjunct populations or clusters of populations extending along the Pacific coast from Humboldt County in northern California to northern Baja California. A variant named P. *remorata* MASON grows on two of the Channel Islands: Santa Cruz and Santa Rosa. A third insular pine grows on the Mexican island of Cedros. It has been named P. muricata var. cedrosensis HOWELL, but has characteristics in common with the insular variants of both Monterey and bishop pines (HOWELL 1941, NEWCOMB 1959, FIELDING 1961 b).

Monterey and bishop pines, together with their island relatives, are the (dominantelement of the closed-cone pine forest. This community has been interpreted as a relict of an insular flora which was more widely distributed and more homogenous in late Tertiary and Pleistocene times, when much of coastal California was a series of islands (MASON 1934, 1949; LANGENHEIM and DURHAM 1963). Monterey and bishop pines now grow together only in a small ares on the Monterey Peninsula.

Knobcone pine differs from its coastal relatives in its distribution and ecology. It is scattered throughout much of montane California, extending north into Oregon and south to a single known locality in northern Baja California. It often grows on dry, submarginal forest sites, and approaches the coast in only a few places. Nowhere does it grow with bishop pine (the two are separated by only about a mile near the coast of Mendocino County), but in Santa Cruz and San Mateo Counties it is in contact with Monterey pine in a limited area near Año Nuevo Point. Its cones rarely open on the living tree, unlike those of its relatives, and fire has influenced its distribution.

Although all three of the California closed-cone pines are variable, bishop pine is uniquely polymorphic in certain characteristics. In his analysis of morphological variation

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[1]) Morphological analyses of some of the young hybrids were msde by J. L. HAMRICK. J. W. ANDRESEN, E. L. LITTLE, Jr., and T. W. WHITAKER made collections of pollen used in these crosses.

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in this species, Duffield[3] observed an abrupt morphological change in an almost continuous stand of bishop pine that extends from near Fort Bragg, in Mendocino County, south to Fort Ross, in Sonoma County. This stand is separated by a gap of more than 30 miles from the next stand to the south, on Point Reyes Peninsula in Marin County. About 15 miles north of Fort Ross, the bluish-green foliage of the more northerly stands is replaced by green foliage in all stands south of this point, including the insular relatives of bishop pine. Compared to the southern trees, the stomata of the northern trees have a more open epistomatal cavity filled with wax, and this feature gives the foliage its bluish color.

Another unique feature of bishop pine is its biochemical polymorphism. It consists of three distinct chemical races, defined by major qualitative differences in their turpentine composition (Forde and Blight 1964). Turpentine samples from the northern blue-foliaged populations consist almost entirely of α-pinene; in the two central California stands (Marin and Monterey Counties) the turpentine is predominantly (about 80 percent) Δ-3-carene; and in the mainland stands south of Monterey County the turpentine is mostly sabinene and terpinolene, with small amounts of α-pinene. The Channel Islands pine resembles the nearby mainland stands except that α-pinene is a third principal component.

Of the four Latin American closed-cone pines tentatively grouped with the California species by Duffield, three are confined to Mexico: *P. patula* in the east and south, *P. greggii* in the east and northeast, and *P. pringlei* in the south. The fourth, *P. oocarpa*, is the most widely distributed of the Latin American pines, ranging from northwestern Mexico to northern Nicaragua.

The Latin American species are a less coherent assemblage than the California closed-cone pines. They differ in a number of important respects from the California group, however. Their more symmetrical cones have less protruding apophyses, and the cones are tardy in opening rather than indefinitely serotinous (Martínez 1948, Loock 1950). They also differ from the California pines in having leaf resin canals that are variable in position, rather than always medial. In *P. patula* and the morphologically similar *P. greggii*, most of the resin canals are medial but some are internal. In *P. pringlei* internal canals predominate, but medial and septal canals are also present. And in *P. oocarpa* resin canals may occupy all four possible positions — medial, septal, internal, and external — even in a single leaf (personal observations in Honduras). This kind of variability in the placement of resin canals in the leaf is not encountered in any of the hard pines of the western United States, all of which have predominantly medial canals. But internal canals are common in a few other Mexican hard pines (Martínez 1948) and in many of the pines of the southeastern United States (see Harlow 1947).

Previous Reports of Natural and Artificial Hybrids

The knobcone × Monterey hybrids from a 1927 pollination at Placerville *(table 1)* are the first artificially produced interspecific hybrids in this group and the second in the genus. These hybrids were mentioned by Austin (1932) and fully described by Stockwell and Righter (1946). Since 1927 this cross has been made many times, and the hybrid is currently being produced on a large scale by the California Region of the U. S. Forest Service. The presence of natural hybrids between knobcone and Monterey pines was noted by Lindsay (1932), and the extent of natural hybridization was estimated by Stebbins (quoted in Bannister 1958).

The existence of natural hybrids between Monterey and bishop pines is less certain. Putative hybrids were noted by Mason (1949), and Stebbins (1950, p. 209) estimated that they constitute a fraction of one percent of the stand. Duffield[4] sampled several putative hybrids and illustrated the cones of one of them. But Forde (1964) failed to find any obvious intermediates in her investigation of natural variation in Monterey pine, and encountered no chemically intermediate trees in samples of Monterey pine (Bannister *et al.* 1962) or bishop pine (Forde and Blight 1964) from the Monterey Peninsula.

Two other verified artificial hybrids of the California closed-cone pines have been reported *(table 1)*: *P. remorata* × *radiata* from a 1942 cross and *P. attenuata* × *remorata* from a 1946 cross (Righter and Duffield 1951, Duffield and Righter 1953). A number of inconsistencies in the published record of these hybrids appear to be the result of confusion between *P. remorata* and *P. muricata*, which were treated as separate species in the two papers cited. *Pinus attenuata* × *remorata* is listed under that name and also under *P. attenuata* × *muricata* in tables 1 and 2 of the paper by Righter and Duffield (1951). Only the latter designation is given in the publication by Duffield and Righter (1953). The other hybrid, *P. remorata* × *radiata*, is listed by this name in table 1 of Righter and Duffield (1951), but in their table 2 it is designated *P. muricata* × *radiata*.

Table 1. — Verified interspecific hybrids of the closed-cone pines produced at the Institute of Forest Genetics, Placerville, and elsewhere.

Parents (*Pinus*-)		Pollination year first produced	Produced at:	First cited
Female	Male			
attenuata	*radiata*	1927	IFG, Placerville	Austin 1932
attenuata	*radiata* var. *binata*	1962	do.	This paper
attenuata	*muricata* (Sta. Cruz Island)	1946	do.	Righter and Duffield 1951
— — — — — — — — reciprocal — — — — — — —		1961	do.	This paper
muricata (Baja Calif.)	*attenuata*	1961	do.	This paper
muricata (Sta. Cruz Island)	*radiata*	1942[1]	do.	Righter and Duffield 1951
patula	*radiata*	1955	do.	Little and Righter 1965
patula	*greggii*	1950	Australia	Australia Forestry and Timber Bureau 1954
patula	*oocarpa*	1952?	South Africa	Union of South Africa 1954

[1] The trees from this cross are no longer in existence. They were cited as verified hybrids by Righter and Duffield (1951) and Duffield and Righter (1953). The cross was repeated in 1961, yielding three trees that have been tentatively identified as hybrids.

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[3] Duffield, John W. 1951. Interrelationships of the California closed-cone pines with special reference to *Pinus muricata* D. Don. Ph. D. thesis, Univ. Calif., Berkeley. 77 pp., illus.

[4] Op. cit., *fig. 8*.

Two other hybrid combinations of California closed-cone pines — *P. radiata* × *attenuata* and *P. radiata* × *muricata* — were erroneously reported by Schütt (1959), who cited Fielding (1950) as his source of information. Fielding mentioned "*P. radiata* × *P. attenuata*" and "*P. radiata* × *P. muricata*" growing at Placerville, and Schütt wrongly inferred that *P. radiata* was the female, rather than the male, parent in these combinations.

Two authentic hybrids have been reported between Latin American closed-cone pines *(table 1)*. A successful cross between *P. patula* and *P. greggii*, mentioned in the annual report of the Australia Forestry and Timber Bureau (1954), was later described by Fielding and Nicholson (1956) and Fielding (1960). A hybrid between *P. patula* and *P. oocarpa* (Union of South Africa 1956, 1958, 1959) has not been described, but cones and foliage sent to Placerville appear to be intermediate in morphology.

There has been a single report of a hybrid beween the California and Mexican closed-cone pines: *P. patula* × *P. muricata* (Union of South Africa 1954). This hybrid, referred to as showing "typical hybrid segregation", must be considered unconfirmed.

Several successful crosses of the closed-cone pines with species of other groups have been reported, but none has been adequately or convincingly described. Yablokov (1962) reported that heterotic hybrids between *P. sylvestris* and *P. muricata* had been obtained by another worker. The report of Schmidt (1956) that he had obtained hybrids between *P. sylvestris* and two closed-cone pines, *P. patula* and *P. radiata*, is doubtful and unverifiable; the trees died at an early age[5].

The cross between *P. rigida* and *P. radiata*, made several times in Korea, has been reported more fully. Hyun (1956) stated that these two species were more easily crossed than *P. rigida* and *P. taeda*, one of the more compatible combinations of southern pines (Critchfield 1963). Subsequently, however, Hyun and Yim (1964) described a complete breakdown of the reproductive processes in this species combination. They found no pollen tubes in the nucellus of the ovule, and this absence was coupled with ovular collapse. In the same cross made the following year Hyun and Lee (1964) observed an occasional fertilization followed by zygotic or post-zygotic abnormalities.

The possibility of natural hybridization between *P. caribaea*, which is closely allied to some of the pines of the southeastern United States, and *P. oocarpa* has been mentioned repeatedly (Williams 1955, Denevan 1961, Barrett and Golfari 1962). Opportunities for crossing are plentiful where these two pines overlap in Central America, but the occurrence of natural hybrids has yet to be demonstrated.

Methods

Parent Trees

Except for a few individuals of knobcone pine, which grows naturally near Placerville, all female parents in the crosses summarized in this paper grew in the Eddy Arboretum at Placerville *(table 2)*. Many of the pollen parents grew elsewhere in planted or natural stands. Three of the Latin American species *(P. oocarpa, P. lawsonii,* and *P. teocote)* were represented by pollen collections made by E. L. Little, Jr., or J. W. Andresen in 1962-63. Many Monterey pines selected for their outstanding characteristics in plantations growing in Australia and New Zealand were used as pollen parents in crosses with knobcone pine. The single Guadalupe Island parent used in these crosses is planted at the U. S. Department of Agriculture's Horticultural Field Station at La Jolla, California[6].

Table 2. — Closed-cone and other pines used as parents at the Institute of Forest Genetics, Placerville.

Species	Number of trees	Geographic origin
attenuata	26	Calif.: Contra Costa, Eldorado Lake, Los Angeles, Nevada, Santa Cruz, and Shasta Counties (9 sources)
greggii	4	Coahuila, Mex.: unknown (2 sources)
lawsonii	1	Puebla, Mex.
muricata	3	Mendocino Co. (2 sources)
muricata	1	Monterey Co.
muricata	2	Santa Rosa Is. (2 sources)
muricata	8[1]	Santa Cruz Is. (3 sources)
muricata	4	San Vicente, Baja Calif., Mex. (1 source)
oocarpa	1	Guatemala
patula	4	Oaxaca, Mex.; Mexico (3 sources)
radiata	22	Calif.: Monterey and Santa Cruz Counties; unknown (Australia, New Zealand) (9 sources)
radiata var. *binata*	1	Guadalupe Island, Mex.
teocote	2	Michoacán and Puebla, Mex.

[1] Wind-pollinated offspring of three parent trees: one with *muricata*-like cones and two with *remorata*-like cones (C. B. Wolf collection numbers 2844, 2845 and 2843; herbarium of the Institute of Forest Genetics at Placerville). These eight trees all tend to have intermediate cone types.

Pinus remorata Mason is grouped here with *P. muricata*. Duffield[7] reduced *P. remorata* to a variety of *P. muricata* on the basis of their morphological similarity. Parent trees of these two types from Santa Cruz Island do not always breed true *(table 1,* and Mason 1949). And recent mass collections of all of the insular pines show that smooth cones — the definitive feature of *P. remorata* — are common in the other insular populations[8].

The breeding behavior of bishop pine has proved to be closely related to the geographic origin of the parent trees. For this reason details of parental origin are presented in *table 2*.

Monterey pine has rarely been used as a female parent at Placerville. It is the first pine to flower there in the spring (February), and only occasionally produces seed cones. It regularly produces abundant pollen cones, however, and is commonly used as a pollen parent. Bishop pine is the last of the California closed-cone pines to flower, and has often been used as a female parent. Some sources of bishop pine (Channel Islands, Baja California) have performed rather poorly as female parents, showing high levels of conelet and ovule abortion. Trees of these southern sources have been used as pollen parents in most crosses

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[5] Personal communication from Schmidt to R. Z. Callaham.

[6] This tree is one of several believed to have originated from seed collected on Guadalupe in the 1930's. Its binate fascicles and other characteristics bear out this identification: the large Monterey-like cones distinguish it from the other insular pines, and the numerous resin canals in the needles distinguish it from mainland Monterey pine, which invariably has two or less resin canals per needle (Forde 1964).

[7] op. cit.

[8] Personal communication from W. J. Libby and Y. B. Linhart.

Table 3. — Crosses of the closed-cone pines with other species at the Institute of Forest Genetics, Placerville, 1927—1963.

Other parent1)	Closed-cone parent							
	attenuata		*radiata*		*muricata*		*patula*	
	♀	♂	♀	♂	♀	♂	♀	♂
Sylvestres:								
silvestris		×				×		
thunbergii		×		×				
yunnanensis								×
halepensis			×	×		×		
brutia				×				×
pinaster	×							×
Australes:								
palustris	×							
pungens						×		
rigida				2)				
Ponderosae:								
teocote							2)	
lawsonii							2)	
Contortae:								
virginiana	×							
contorta				×		×		

× One or more unsuccessful attempts.

1) Species are grouped by subsection (Critchfield and Little 1966).

2) Germinable seed obtained. See text for further details.

within bishop pine because they flower about 10 days before trees of northern origins.

Only two of the Mexican closed-cone pines, *P. patula* and *P. greggii*, have been grown successfully at Placerville. *P. patula* produces pollen cones every year, but only sporadically produces seed cones. The flowering behavior of *P. greggii* is unique among the pines growing at Placerville. It is the only pine that regularly flowers twice a year: in November and again in June, when it is the last of the hard pines to flower. It behaves similarly in Australia (Fielding 1960). So far we have not succeeded in obtaining normal cones containing seed at either season at Placerville, and *P. greggii* has functioned only as a pollen parent.

Techniques and Terminology

The crosses described here were made during the pollinating seasons of 1927 through 1963. Many of the California species crosses were planned and executed in the late 1940's by W. P. Stockwell and H. L. Mason. Most other crosses between these species have been made since 1961. Other workers who helped plan and direct the hybridization program at various times were F. I. Righter, J. W. Duffield, and R. Z. Callaham. The breeding and seed-processing techniques used have been referred to elsewhere (Critchfield 1963).

The crosses between the closed-cone pines and species of other groups are reported only as failures or possible successes (*table 3*). Included in this listing are all crosses made between 1927 and 1963 that used fresh or year-old frozen pollen and yielded cones.

Crosses between and within the closed-cone pines are more fully described (*tables 4 and 5*). Included in these tabulations are all crosses for which we have complete data: numbers of strobili pollinated, cones harvested, and sound and hollow seed. Since 1961 we have frozen all of our stored pollen, and crosses made with one-year-old frozen pollen are included. Crosses made with older frozen pollen, or with year-old refrigerated pollen, are omitted.

Table 4.—Summary of crosses among the California closed-cone pines at the Institute of Forest Genetics, Placerville, California, 1927-1963.

Male parent	Female parent				
		muricata			
	attenuata	Mendocino Co.	Monterey Co.	Channel Is.	Baja Calif.
attenuata	11(33)/11 105, 76 45.4/67.3	5(7)/0 291, 74 0/9.0	◇ 2(6)/1 45, 49 <0.1/12.8	◆ 3(7)/3 102, 46 3.4/6.5	◆ 3(7)/2 22, 36 8.1/22.6
radiata	◆ 32(66)/32 804, 65 38.4/62.0	4(6)/0 202, 68 0/29.6	◇ 2(4)/0 42, 48 0/8.2	◆ 1(3)/1 18, 6 4/26	3(4)/2 51, 18 0.2/1.8
radiata var. binata	◆ 2(2)/2 24/96 11.1/22.7	1(1)/0 20, 90 0/3.9	1(1)/0 15, 20 0/5.7	◇ [1]2(2)/1 42, 31 0.4/8.7	◇ [1]2(2)/2 25, 56 0.2/2.1
muricata (Channel Is.)	◆ 1(1)/1 51, 60 0.2/47.9	▨	▨	▨	▨

Legend:

◆ Verified hybrids

◇ Putative hybrids

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

Footnote:

[1] Putative hybrids killed by frost.

Table 5.—Crosses within the Pinus muricata complex.

	Mendocino Co.	Monterey Co.	Channel Is.	Baja Calif.
Channel Is.	2(4)/2 90, 71 0.1/30.7	1(3)/1 10, 80 0.1/12.6	5(7)/5 158, 36 4.3/6.1	
Baja Calif.	1(1)/0 23, 61 0/19.4	2(4)/2 58, 67 0.5/9.5	4(8)/4 46, 11 30.6/40.6	3(7)/3 18, 61 5.5/11.9

Legend: See table 4.

An *attempt* refers to the pollination during a single season of a female parent with pollen from a single male parent or with a mixture of pollen from several males. The minimum number of tree × tree combinations has been estimated by assuming that two male parents have contributed to pollen mixes of unspecified constitution.

Crossability in this paper refers to the ease with which two species or races can be successfully crossed, compared to crosses within the maternal species or race. It has been estimated in two ways: (1) If a series of attempts is accompanied by control (intraspecies or intraracial) crosses made on the same female parents at the same time, the crossability of a species or racial combination is the mean of the single-parent crossabilities. The crossability of a single parent is the yield of sound seed per cone expressed as a percent of the sound seed yield of the control cross. (2) If control-cross data are lacking, the crossability of a species or racial combination is the mean sound yield expressed as a percent of the mean sound seed yield within the maternal-parent species or race.

Control-cross information is mostly lacking for crosses made with bishop pine as maternal parent. Since 1961 most of the crosses intended as controls have been made with earlier-flowering trees of southern sources as pollen parents in combination with northern trees. From the failure of these intended control crosses has elements of possibility that the northern and southern elements of this species are almost completely isolated by reproductive barries.

Results

Crossing the Closed-Cone Pines with other Species

The inability of the closed-cone pines to cross successfully with other species was a major reason for their segregation into a separate group by Duffield (1952). Attempts to cross this group with members of other groups are summarized through 1963 (*table 3*). Most of these combinations have been tried only once or twice, but collectively they represent a substantial effort to hybridize the closed-cone pines with other pines. This effort has been unsuccessful, with three possible exceptions.

In these three instances germinable seed were obtained, but the seedlings either failed to survive or are too young to identify with certainty. After several unsuccessful attempts to cross *P. rigida* and *P. radiata* — the combination first reported by Hyun (1956) — we obtained from a 1958 cross 12 cones which yielded four germinable seeds. The seedlings showed some indications of intermediacy, but died at the end of their first growing season before they could be positively identified. Two 1963 crosses of a single *P. patula* with pollen from single trees of *P. teocote* and *P. lawsonii* yielded substantial numbers of germinable seed. The same pollen used on another *P. patula* failed to produce any sound seed. The seedlings are too young for a positive identification, but it is worth noting that *P. teocote* and *P. lawsonii* differ in several respects from the western yellow pines (*Ponderosae* Loud.) with which they were grouped by Duffield (his group XII). They have much smaller cones, and their leaf resin canals are internal occasionally (*P. teocote*) or predominantly (*P. lawsonii*), whereas medial canals prevail in the western yellow pines.

Crossing the California Closed-Cone Species with each other

This group presents remarkable contrasts in the ability of its members to cross with each other. Knobcone and Monterey pines, at one extreme, hybridize more readily than any other combination of pines so far investigated in any detail. At the other extreme is bishop pine, which is isolated and fragmented by strong inter- and intraspecific barriers to crossing.

All attempts to cross knobcone and Monterey pines have yielded sound germinable seed (*table 4*). The estimate of crossability based on all of these attempts is 85: knobcone and Monterey crosses yield 85 percent as much sound seed, on the average, as crosses between knobcone pines. Control crosses accompanied 11 of 32 attempts summarized in *table 4*. These 11 interspecific crosses yielded 69 percent as much sound seed as their controls, a significant reduction (*t* test, 5 percent). These high estimates of crossability indicate that the reproductive barriers between these two species are the weakest yet encountered between species in *Pinus*.

Knobcone pine crosses much less readily with bishop pine, its other maritime relative. All attempts to cross the Mendocino County sources of bishop pine with knobcone pine have failed (*table 4*). Two attempts involving the single Monterey County bishop parent have been nearly as unsuccessful, yielding a single putative hybrid seedling.

Bishop pines from the Baja California and Channel Islands sources behave quite differently than the Mendocino sources in combination with knobcone pine. Nearly all crosses involving these southern trees have been successful. The first crosses between knobcone pine and the Channel Islands pine, made in 1946, yielded large numbers of verified hybrids (*table 1*)[9]. Two 1961 crosses in the reciprocal direction and a 1961 cross between Baja California bishop pine and knobcone pine have all produced hybrids.

The reproductive barriers between Monterey and bishop pines appear to be stronger than those separating knobcone and bishop pines. Like knobcone, Monterey pine has so far proved to be completely uncrossable with Mendocino County bishop pine (*table 4*). And crosses involving the

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[9] These crosses are omitted from *table 4* because of incomplete data.

Monterey County bishop parent have yielded only a single putative hybrid seedling[10]. Monterey pine crosses less readily than knobcone with the southern and insular sources of bishop pine, however. A possibly contaminated 1942 cross between Channel Islands and Monterey pines (omitted from *table 4)* was exceptional in yielding many offspring. At least some of them were considered authentic hybrids by Righter and Duffield (1951). A cone of one of the hybrids is illustrated by Duffield[11] and is deposited in the herbarium at Placerville. The trees were not outplanted and are no longer in existence. Repeated in 1961, this combination produced several hybrid seedlings. Crosses between Baja California bishop pine and Monterey pine have not yielded any hybrids to date.

The single Guadalupe Island pine parent has behaved much like mainland Monterey pine in crosses with the other closed-cone pines. It crossed readily with knobcone pine (crossability about 50 percent), but did not cross at all with the northern sources of bishop pine *(table 4).* Crosses with the southern sources of bishop pine (Baja California and Channel Islands) yielded a few putative hybrids, but these seedlings were killed in 1964 by early autumn frost.

Crossing within the Pinus muricata Complex

The Mendocino County bishop pines used in these crosses are almost completely isolated by reproductive barriers from the southern elements of this species complex. The crosses summarized in *table 5* have yielded a total of two seedlings — probably hybrids — which are the product of a Mendocino County × Channel Islands cross.

The ability of the single Monterey County parent to cross with the southern sources of bishop pine is somewhat greater. All crosses with Baja California and Channel Islands parents have yielded a few sound seed: 0.1 to 1.5 per cone. One seedling, from a Monterey County × Baja California cross, has been identified as a hybrid, but most of them are too young to identify with certainty.

Very different in their crossing behavior from the more northern sources, bishop pines from Baja California and the Channel Islands cross readily with each other. All combinations of these sources have yielded sound seed. The mean yield of sound seed per cone of the tabulated crosses — 30.6 — is much higher, in fact, than the sound seed yield of Baja California and Channel Islands within-source crosses. The very low seed set of the within-sources crosses may be partly an effect of inbreeding, since nearly all of these crosses were made between possible or known siblings. Despite the inadequacy of this control-cross information, it is evident that the Baja California and Channel Islands pines are highly crossable, much more so than any other combination of strains in bishop pine.

Crossing the Latin American Closed-Cone Pines with each other

Except for *P. pringlei,* the species of the Latin American group have been linked directly or indirectly through hybridization. From the fragmentary data available, these species appear to form a highly crossable group. Fielding and Nicholson (1956) reported the high yield of 58 germinable seed per cone in the first successful cross of *P. patula* × *P. greggii,* made in 1950. This yield of sound seed is much higher than we have obtained from *P. patula* in any combination at Placerville. Our successful 1953 cross between these species yielded only 8.7 sound seed per cone, but this compares favorably (more than 50 percent) with the sound seed yield that we have obtained from crosses within *P. patula.*

Pinus patula also appears to cross readily with *P. oocarpa.* Few details of the first hybridization of these two species have been reported (Union of South Africa 1956), but at Placerville we obtained abundant sound seed from two 1963 crosses between *P. patula* and *P. oocarpa* — more than 90 percent of the sound seed yield of the controls.

No attempts have been made to hybridize *P. pringlei* until recently. In February, 1965, I collected pollen of this species in the state of Oaxaca, Mexico, and we are currently investigating the ability of this little-known pine to cross with other species.

Crossing the California and Latin American Closed-Cone Pines

The California and Latin American closed-cone pines were not successfully crossed until 1955, when a *P. patula* in our arboretum was pollinated with a mixture of pollen from three *P. radiata* trees of Santa Cruz County origin. This cross yielded three cones and five seedlings. All but one of the seedlings died soon after outplanting, but the survivor is convincingly intermediate in its vegetative morphology (Little and Righter 1965). The composition of its resin confirms its hybrid nature. *P. patula* turpentine consists mostly of β-phellandrene, and *P. radiata* of β-pinene, with smaller amounts of α-pinene in both species (Mirov 1961, Bannister *et al.* 1962). The hybrid differs from its *P. patula* parent in its much higher β-pinene content and from *P. radiata* in its higher β-phellandrene content *(table 6).* It differs from both parents in its very high α-pinene content, suggesting an effect of age or the possible involvement of one or a few major genes.

A few other crosses between *P. patula* and *P. radiata* have not yielded any sound seed. Nor have crosses of *P. patula* with the other California closed-cone pines been successful. Four attempts involving *P. muricata* yielded 51 cones but no sound seed. Several other inconclusive attempts with *P. muricata* and *P. attenuata,* using old pollen, did not produce any hybrids.

Table 6. — Low-boiling-point constituents of wood oleoresin of *Pinus patula* × *radiata* and its parents[1]

Species or hybrid and tree number	Constituent			
	α-pinene	β-pinene	β-phellandrene	Other
		Percent		
P. patula × *radiata* (Pat R—2)	74.0	8.1	16.1	1.8
P. patula (Pat—V12)	10.0	0.2	83.6	6.2
P. radiata[2]				
R—184	13.1	84.9	0.7	1.3
R—185	33.2	64.5	1.0	1.3
R—186	15.9	82.0	1.1	1.0

[1] Percentages are based on constituents listed. Pentane solutions of resin were analyzed on an 8-ft. 10-percent β, β' oxydipropionitrile colmun under these conditions: injector temp. 140°C, column temp. 55°C, thermal detector temp. 165—170°C, filament current 170 ma, and helium vol. 63—71 ml per min.

[2] Three-tree pollen mixture used in cross.

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[10] The single successful attempt, made with two-year-old deep-frozen pollen, is omitted from *table 4.*

[11] Op. cit., *fig. 21.*

Discussion

The California closed-cone pines show several striking parallels in their variation patterns. In the mainland pines these trends are well documented (Bannister *et al.* 1962, Fielding 1961 a, Forde 1964, Forde and Blight 1964, Duffield[12], Newcomb[13]). The insular pines are not nearly so well known (Bannister 1958, Fielding 1961 b, Howell 1941, Mason 1930, 1949), but recent mass collections of these variants are now being described[14].

One conspicuous trend is a definite increase from north to south in within-population variability; southern stands of the closed-cone pines tend to be more variable than northern stands. This increase is especially pronounced in cone morphology because of the appearance — and in some instances the prevalence — of a type of cone that is distinctly different from the cone types exemplified by the three mainland species. Cones of this type are more symmetrical, and have relatively flattened apophyses and less well-developed umbos than representative cones of the mainland species. This cone form is common on Cedros and Guadalupe Islands, and is the *"remorata"* extreme of the Channel Islands pine. It is present in the southern bishop pine stands on the mainland, and the southernmost knobcone pine stand, near Ensenada in Baja California, also tends strongly in this direction. Another geographical trend in the closed-cone group is the greater number of resin canals in the needles of southern stands — both mainland and insular — compared to northern stands.

This tendency of the southern closed-cone pines to converge in cone and needle characteristics is responsible for most of the taxonomic complexities in the California closed-cone group. The insular pines, all of them taxonomically difficult, form a nearly complete morphological series that connects Monterey and bishop pines. Trees with typical bishop pine cones grow on Santa Cruz Island, and trees with typical Monterey pine cones grow on Guadalupe Island. But in both places they are one extreme in a continuous array that includes trees having smooth *"remorata"* cones. The relatively smooth-coned Ensenada population of knobcone pine is so different from the rest of the species that Newcomb[15] excluded it from both of his subspecies.

Despite their geographic isolation, the island pines appear to be relatively crossable elements of the closed-cone complex. Channel Islands pine is the only member of the closed-cone group that has been successfully crossed with all other members (*fig. 1*), and it is doubtful whether there is any appreciable reproductive barrier between it and Baja California bishop pine. Our results with a single Guadalupe Island pine suggest that it too is a relatively crossable member of this group. The third insular form, Cedros Island pine, crosses readily with Monterey pine, and behave much like Monterey pine in combinations with the other closed-cone pines[16].

The crossing behavior of the island pines provides a basis for evaluating the relationships of these pines with each other and with the mainland pines. The failure of the Channel Islands and Guadalupe pines to cross readily does not support the view that there is a close evolutionary link between the two. The similarity of Channel Islands pine and Baja California bishop pine in their ability to cross with the other closed-cone pines, and the ease with which they cross with each other, do not support the views of Mason (1949) or Newcomb (1959) concerning the origin of Channel Islands pine. Newcomb suggested that this island pine might have evolved from some introgressive combination of mainland bishop pine and Cedros Island pine. Mason considered the Channel Islands pine a distinct and ancient lineage in the process of losing its identity — at least on Santa Cruz Island — through hybridization with invading *P. muricata.* The crossing behavior of Channel Islands pine suggests a third alternative: that it is a variant of bishop pine that has not appreciably diverged in its breeding behavior from southern mainland stands of that species.

The most puzzling element of the California closed-cone pine complex is the blue-foliaged northern race of bishop pine. Duffield made mass collections in the narrow zone where blue- and green-foliaged trees intermingle, and in stands not far north and south of this zone[17]. He did not find any marked morphological differences between these samples except in the stomata. In his taxonomic appraisal of bishop pine he included the green-foliaged Sonoma County stands in his northern variety. Recently Forde and Blight (1964) have suggested that the change in turpentine composition from nearly all α-pinene in the northern stands to mostly 3-carene in the isolated Marin and Monterey County stands might be correlated with the change in stomatal type, and this has now been demonstrated by Mirov *et al.*[18]. In the mixed stand on the Sonoma County coast they found only a few putative hybrids combining, or intermediate in, the stomatal and oleoresin characteristics of the two parental strains. They did not encounter any indications of hybridization at a short distance from the mixed zone. This coincidental change in two unrelated characteristics — stomatal form and turpentine composition — suggests that the reproductive barriers which isolated the Mendocino County blue-foliaged parents in the crosses at Placerville may be operative in keeping the blue- and green-foliaged strains distinct at the place where they meet. This hypothesis is now being tested. The Placerville crossing results indicate, however, that this is not the only reproductive barrier to intercrossing geographic strains of bishop pine; the single Monterey County parent also failed to cross readily with other strains of bishop pine. At Placerville we have begun a series of crosses to explore in more detail the system of reproductive barriers between these and other elements of bishop pine.

The reproductive isolation of the Mendocino strain of bishop pine is unique among those pines whose crossing behavior has been investigated. In *Pinus ponderosa* Laws. and *P. contorta* Dougl., for example, even long-isolated and morphologically divergent segments of the species do not show any appreciable reduction in their ability to cross with each other. The closest parallels to the situation in bishop pine appear to be the sibling species — morphologically similar but reproductively isolated populations — which are common in some groups of animals (Mayr 1963) and plants (Grant 1964).

The California closed-cone group is a striking exception to the general rule in *Pinus:* that crossability and morpho-

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[12] Op. cit.

[13] Newcomb, Gene B., 1962: Geographic variation in *Pinus attenuata* Lemm. Ph. D. thesis, Univ. Calif., Berkeley, 191 pp., illus.

[14] Personal communication from W. J. Libby and Y. B. Linhart.

[15] Op. cit.

[16] Personal communications from J. M. Fielding and A. G. Brown.

[17] Op. cit.

[18] Mirov, N. T., Zavarin, Eugene, Snajberk, Karel, and Costello, Kathleen: Further studies of turpentine composition of *Pinus muricata* in relation to its taxonomy. Phytochemistry 5: 343—355 (1966).

logical resemblance tend to reinforce each other as indicators of species relationships (Duffield 1952). Knobcone pine is sharply separated from the maritime species in its fossil history (Mason 1949), morphology, ecology, and distribution, but it is only weakly separated by reproductive barriers from most of the other elements of the group. By contrast, Monterey and bishop pines — although they are two extremes in a nearly continuous morphological gradient — are strongly isolated by reproductive barriers. Possibly these barriers have evolved during their long association in the closed-cone pine community. And the separation of knobcone pine from the coastal closed-cone pines early in their history may account for the absence of strong reproductive barriers between it and most other members of the group. But the history of the closed-cone group offers no such explanation for the apparent reproductive isolation of the northern bishop pines used in these crosses from the rest of the group.

The low crossability of bishop and Monterey pines raises further questions concerning the existence of natural hybrids between these species. The reproductive barrier between them is reinforced by a large difference in flowering time. At Placerville, Monterey pine flowers almost two months before bishop pine trees of central and northern origins, and a few observations indicate that the difference is about the same in natural stands. Either of these isolating mechanisms would greatly restrict natural hybridization, and together they make it a remote possibility. By comparison, knobcone and Monterey pines are highly compatible and differ in flowering time by only a month or six weeks. Yet natural hybrids between the two are not common, and neither species appears to have been affected by introgression from the other (Forde 1964, Newcomb[19]).

Axelrod (1958) includes the California closed-cone pines in the Madro-Tertiary flora, which originated in Mexico and migrated to west-central California in the late Tertiary. Although the basis for their inclusion is not clear, their morphology and crossing behavior lend some support to this possibility. A Mexican origin would help explain the tendency of southern elements of the three California species to resemble each other in cone morphology and leaf resin-canal number. Possibly the hypothetical migrant had these characteristics, and they have persisted in the isolated southern fragments of the California species. This possibility is consistent with the morphology of the present-day Latin American closed-cone pines. Their cones lack the extreme asymmetry and well-developed apophyses of the cones of the California mainland species, and two of them (*P. oocarpa* and *P. pringlei*) have numerous resin canals in their needles. However, their resin canals are often internal — unlike the California closed-cone species. Future crosses between southern elements of the California complex and the Latin American species may help to clarify the relationships of these two groups of closed-cone pines, which are now tenuously linked only by the single *P. patula* × *radiata* hybrid produced at Placerville.

Although three of the four Latin American closed-cone species have been successfully crossed, the affinities of the Latin American group are not at all clear. A link with the western yellow pines through *P. teocote* and *P. lawsonii* is a possibility *(fig. 1)*, and persistent reports of natural hybrids between *P. oocarpa* and *P. caribaea*, and artificial hybrids between *P. rigida* and *P. radiata*, suggest that the closed-cone group may be incompletely isolated from the southern U. S.-Caribbean pines. We are now establishing an arboretum of Latin American pines in a climate milder than that of Placerville, and when these trees begin to flower we plan to expand our exploratory hybridization of these species.

Summary

The long-term program of species hybridization at the Institute of Forest Genetics at Placerville, California, has helped to clarify the relationships of the closed-cone pine group, which includes three closely allied California species and a heterogeneous group of Latin American pines. *Pinus radiata* and *P. muricata*, two long-associated species of the California coast, are difficult to cross artificially, and it is doubtful whether they cross in nature. The third California species, *P. attenuata*, differs from the others in its inland distribution and fossil history, but it crosses readily with some elements of *P. muricata*, and the ease with which it crosses with *P. radiata* makes this one of the most compatible combination of species so far encountered in *Pinus*. At the other extreme is *P. muricata* of

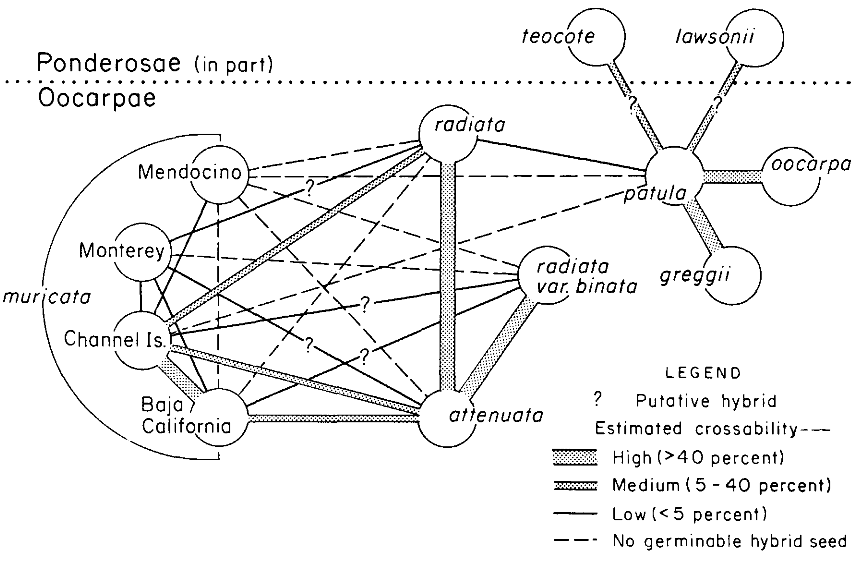

Fig. 1. — Crossability of the closed-cone pines.

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[19] Op. cit.

Mendocino County origin, which is almost completely uncrossable with all other closed-cone pines — the first instance of a strong reproductive barrier between populations of a pine species. The California species are weakly linked to the possibly ancestral Latin American group by a single *P. patula* × *radiata* hybrid. Some of the Latin American species cross readily with each other, but little work has been done with these pines.

Literature Cited

Austin, Lloyd: Tree breeding for timber production. Proc. Sixth Int. Congr. Genet. 2: 387—388 (1932). — Australia Forestry and Timber Bureau: Annual report for the year ended 31st December, 1953. 40 pp. (1954). — Axelrod, Daniel I.: Evolution of the Madro-Tertiary geoflora. Bot. Rev. 24: 433—509 (1958). — Bannister, M. H.: Evidence of hybridization between *Pinus attenuata* and *P. radiata* in New Zealand. Trans. New Zeal. Roy. Soc. 85: 217—225 (1958). — Bannister, M. H.: Specimens of two pine trees from Guadalupe Island, Mexico. New Zeal. J. Forest. 7: 81—37 (1953). — Bannister, M. H., Williams, Allette L., McDonald, I. R. C., and Forde, Margot B.: Variation of turpentine composition in five population samples of *Pinus radiata*. New Zeal. J. Sci. 5: 486—495 (1962). — Barrett, Wilfredo H. G., and Golfari, Lamberto: Descripción de dos nuevas variedades del "pino del Caribe" (*Pinus caribaea* Morelet). Caribbean Forest. 23: 59—71 (1962). — Critchfield, W. B.: Hybridization of the southern pines in California. Proc. Forest Genet. Workshop, Macon, Ga., October 25—27, 1962: 40—48. Sponsored Pub. 22, South. Forest Tree Impr. Comm. (1963). — Critchfield, W. B., and Little, Elbert L., Jr.: Geographic distribution of the pines of the world. U. S. Dep. Agr. Misc. Pub. 991, 97 pp. (1966). — Denevan, William M.: The upland pine forests of Nicaragua. Univ. Calif. Pubs. Geogr. 12: 251—320 (1961). — Duffield, J. W.: Relationships and species hybridization in the genus *Pinus*. Z. Forstgenetik 1: 93—100 (1952). — Duffield, J. W., and Righter, F. I.: Annotated list of pine hybrids made at the Institute of Forest Genetics. U. S. Forest Serv., Calif. Forest and Range Exp. Sta. Forest Res. Note 86, 9 pp. (1953). — Fielding, J. M.: The Institute of Forest Genetics. Austral. Forest. 14: 43—46 (1950). — Fielding, J. M.: *Pinus patula* × *greggii*. Austral. Forest. 24: 99—102 (1960). — Fielding, J. M.: Provenances of Monterey and bishop pines. Austral. Forest. and Timber Bur. Bull. 38, 30 pp. (1961 a). — Fielding, J. M.: The pines of Cedros Island, Mexico. Austral. Forest. 25: 62—65 (1961 b). — Fielding, J. M., and Nicholson, D. I.: A hybrid between *Pinus patula* and *P. greggii*. Austral. Forest. 20: 104—105 (1956). — Forde, Margot B.: Variation in natural populations of *Pinus radiata* in California. Parts 1—4. New Zeal. J. Bot. 2: 213—257, 459—501 (1964). — Forde, Margot B., and Blight, Margaret M.: Geographical variation in the turpentine of bishop pine. New Zeal. J. Bot. 2: 44—52 (1964). — Grant, Verne: The biological composition of a taxonomic species in *Gilia*. Advances in Genetics 12: 281—328 (1964). — Harlow, William M.: The identification of the pines of the United States, native and introduced, by needle structure. N. Y. State Coll. Forest. Tech. Bull. 32, 19 pp. (1947). — Howell, John Thomas: The closed-cone pines of insular California. Leafl. West. Bot. 3: 1—8 (1941). — Hyun, S. K.: Forest tree breeding work in Korea. Inst. Forest Genet., Suwon, Korea. Inst. Pap. No. 1, 16 pp. (1956). — Hyun, S. K., and Lee, Bo Sik: A study of fertilization in the crosses of *Pinus rigida* with *P. taeda* and *P. radiata*. Office Rural Develop., Korea, Res. Rep. 7 (2): 53—61 (1964). — Hyun, S. K., and Yim, K. B.: On the fertilization in the crossings of *Pinus rigida* with *P. taeda*, *P. radiata*, and *P. elliottii*. Proc. World Consult. Forest Genet. and Tree Impr., Stockholm, Swed., 23—30 August 1963, v. 1., sec. 2 b, no. 3, 10 pp. (1964). — Langenheim, Jean H., and Durham, J. Wyatt: Quaternary closed-cone pine flora from travertine near Little Sur, California. Madroño 17: 33—51 (1963). — Lindsay, A. D.: Knobcone pine (*Pinus attenuata* Lemmon). Commonwealth Forest. Bur. Leafl. 14, 4 pp. (1932). — Little, Elbert L., Jr., and Righter, Francis I.: Botanical descriptions of forty artificial pine hybrids. U. S. Dep. Agr. Tech. Bull. 1345, 47 pp. (1965). — Loock, E. E. M.: The pines of Mexico and British Honduras. Union of South Africa Dep. Forest. Bull. 35, 244 pp. (1950). — Martínez, Maximino: Los pinos Mexicanos. 2nd ed. 361 pp., México, D. F., México: Ediciones Botas, 1948. — Mason, Herbert L.: The Santa Cruz Island pine. Madroño 2: 8—10 (1930). — Mason, Herbert L.: A phylogenetic series of the California closed-cone pines suggested by the fossil record. Madroño 2: 49—55 (1932). — Mason, Herbert L.: Pleistocene flora of the Tomales formation. Carnegie Inst. Wash. Pub. 415: 81—179 (1934). — Mason, Herbert L.: Evidence for the genetic submergence of *Pinus remorata*, pp. 356—362. In: Genetics, Paleontology and Evolution, ed. G. L. Jepsen, E. Mayr, and G. G. Simpson. Princeton, N. J.: Princeton Univ. Press, 1949. — Mayr, Ernst: Animal species and evolution, 797 pp. Cambridge, Mass.: Belknap Press of Harvard Univ. Press, 1963. — Mirov, N. T.: Composition of gum turpentine of pines. U. S. Dep. Agr. Tech. Bull. 1239, 158 pp. (1961). — Newcomb, Gene B.: The relationships of the pines of insular Baja California. Proc. IX Int. Bot. Congr. 2: 281 (1959). — Righter, F. I., and Duffield, J. W.: Interspecies hybrids in pines. J. Hered. 42: 75—80 (1951). — Schmidt, Werner: Kreuzungsversuche zur Erzielung von Kiefernhybriden. Forsch. und Beratung: Forstwirtschaft, Heft 2: 134—146 (1956). (Nordrhein-Westfäl. Landesausschuß landwirt. Forsch., Erzieh., und Wirtschaftsberatung). — Schütt, P.: Züchtung mit Kiefern. Teil II: Kreuzungen, Resistenzzüchtung und Zytologie. Mitt. Bundesforschungsanstalt Forst- und Holzwirtschaft, Reinbek bei Hamburg, No. 42, 40 pp. (1959). — Shaw, George R.: The genus *Pinus*. Pub. Arnold Arboretum 5, 96 pp. (1914). — Stebbins, G. Ledyard, Jr.: Variation and evolution in plants, 643 pp. New York: Columbia Univ. Press, 1950. — Stockwell, Palmer, and Righter, F. I.: Pinus: the fertile species hybrid between knobcone and Monterey pines. Madroño 8: 157—160 (1946). — Union of South Africa: Annual report of the Department of Forestry for the year ended 31st March, 1953, 36 pp. (1954). — Union of South Africa: Annual report of the Department of Forestry for the year ended 31st March, 1955, 43 pp. (1956). — Union of South Africa: Annual report of the Department of Forestry for the year ended 31st March, 1956, 34 pp. (1958). — Union of South Africa: Annual report of the Department of Forestry for the year ended 31st March, 1957, 34 pp. (1959). — Williams, Allette L., and Bannister, M. H.: Composition of gum turpentines from twenty-two species of pines grown in New Zealand. J. Pharm. Sci. 51: 970—975 (1962). — Williams, L.: *Pinus caribaea*. Ceiba 4: 299—300 (1955). — Yablokov, A. S.: Wide hybridization in silviculture and greenbelt work. Survey and prospects, pp. 48—61. In: Wide hybridization in plants, Tsitsin, N. V., ed., 1960, Moscow, Akad. Nauk SSSR (Engl. transl. OTS 61-31214, Israel Program for Sci. Transl., Jerusalem, 1962).