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Sugar Pine and its Hybrids

By W. B. Critchfield and B. B. Kinloch

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Sugar Pine and its Hybrids

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Summary

Unlike most white pines, sugar pine *(Pinus lambertiana)* is severely restricted in its ability to hybridize with other species. It has not been successfully crossed with any other North American white pine, nor with those Eurasian white pines it most closely resembles. Crosses with the dissimilar *P. koraiensis* and *P. armandii*, both native to eastern Asia, have produced one and a few hybrids respectively. These Asian species are highly resistant to white pine blister rust *(Cronartium ribicola)*, and hybrids and hybrid derivatives of sugar pine × *P. armandii* show some enhancement of resistance to this disease.

Key words: Pinus lambertiana, white pines, blister rust, *Cronartium ribicola*, resistance.

Zusammenfassung

Anders als die meisten Kiefernarten der Sektion *Strobus* ist *Pinus lambertiana* in ihrer Fähigkeit, mit anderen Arten zu hybridisieren, stark eingeschränkt. Es gibt keine erfolgreichen Kreuzungen, weder mit irgendeiner anderen nordamerikanischen Kiefernart, noch mit den eurasischen Arten, denen sie am meisten ähnelt. Kreuzungen mit den unähnlichen Arten *Pinus koraiensis* und *Pinus armandii*, beide in Ostasien beheimatet, ergaben einen bzw. wenige Hybriden. Diese asiatischen Arten sind in hohem Maße gegen *Cronartium ribicola* resistent und Hybriden, sowie Hybrid-Nachkommenschaften von *P. lambertiana* × *P. armandii* zeigten eine erhöhte Resistenz gegen diese Krankheit.

Introduction

Among the white pines (genus *Pinus*, section *Strobus*), the least predictable in crossing behavior is sugar pine (*P. lambertiana* Dougl.), a valuable timber species native to the Pacific Slope of North America between central Oregon and Baja California. Within section *Strobus*, sugar pine is grouped with other American and Eurasian white pines having winged seeds and cones that open and shed their seeds at maturity. It has not been successfully crossed with any other member of this morphologically coherent and otherwise highly crossable group, however. Verified hybrids have been produced with only two other species, both white pines native to eastern Asia: *P. armandii* Franch. and *P. koraiensis* Sieb. and Zucc. (Stone and Duffield 1950). Shaw (1914), in his landmark monograph of the pines, used just two characteristics to segregate the white pines into groups: presence or absence of seed wings and opening or "indehiscence" of mature cones. Both Asian species differ from sugar pine in having wingless seeds, and the indehiscent cone of *P. koraiensis* has scales that fail to separate sufficiently to permit seed shedding. Shaw placed each of these species in a different group within section *Strobus:* sugar pine in *Strobi*, *P. koraiensis* in *Cembrae*, and *P. armandii* in *Flexiles*. This classification is still widely used, often with minor modifications (e.g. Little and Critchfield 1969), but the crossing behavior of sugar pine and its Asian relatives has helped to undermine the assumptions on which the classification is based.

The reproductive barriers that restrict or prevent crossing between species are quite different in the two principal groups of pines: the white pines of section *Strobus* and the hard pines of section *Pinus*. According to Kriebel (1972, 1975, pers. comm. Aug. 1981), there are no well-documented exceptions to the generalization that barriers between hard pines are expressed before fertilization and barriers between white pines after fertilization. Kriebel emphasized histological evidence in establishing the developmental stage at which reproductive processes break down, but routine crossing data (numbers of female strobili, cones, sound seeds, and hollow seeds) can also be used to determine whether breakdowns occur before or after fertilization. This is possible because the seeds of pines (Buchholz 1945), including sugar pine (Krugman 1961), reach their final size by the time of fertilization and develop hard seedcoats then or shortly thereafter. Thus pre-fertilization barriers, which cause the abortion of conelets or individual

ovules, reduce the numbers of mature cones or seed coats harvested. Post-fertilization barriers, which cause the abortion of embryo and female gametophyte within the seed coat, increase the number of hollow seeds without affecting the total number of seed coats extracted from a cone. Most crosses summarized in this paper resemble other white pine crosses in the timing of repreoductive breakdowns, but one species combination was blocked partly by a pre-fertilization barrier producing significantly high levels of ovule abortion.

Much of the impetus for hybridization of the white pines has come from efforts to develop or enhance resistance to white pine blister rust *(Cronartium ribicola* Fisch.) in sugar pine and two other economically important North American species in the *Strobi* group: eastern white pine *(P. strobus* L.) and western white pine *(P. monticola* D. Don). All three species are highly susceptible to blister rust, whereas *P. armandii* and *P. koraiensis* are among the most resistant of the white pines to this disease (Bingham 1972). The rust organism is also native to Asia, and Bingham (1977) has speculated that the high level of resistance in these Asian pines can be attributed to coevolution of host and rust. The hybrids of sugar pine and the two Asian species provide a possible bridge for the transfer of their higher level of resistance into sugar pine. A few hybrids and hybrid derivatives have been field-tested in a region of high natural rust infection, and the encouraging results are reported here.

Most attempts to cross sugar pine with other species have been made at or near the Forest Service's Institute of Forest Genetics (IFG), Placerville, El Dorado County, California. The IFG is located at an elevation of 823 m on the west slope of the Sierra Nevada, within the natural range of sugar pine. The results of all IFG crosses with sugar pine as either female or male parent are presented here, together with a progress report on its hybrids.

Previous Reports of Hybrids

Hybrids of sugar pine were first reported by Stone and Duffield (1950). They obtained seedlings of *P. lambertiana* × *armandii* and *P. lambertiana* × *koraiensis* by means of a modified "embryo culture" technique, after seeds from an earlier cross of *P. lambertiana* × *P. armandii* had failed to germinate in the nursery. They removed the seed coats and germinated the seeds under sterile conditions. The seedlings were tentatively identified as hybrids by the presence of secondary leaves on first-year seedlings and the absence of abaxial stomata on the secondary leaves.

The identity of these hybrid combinations was further documented in several papers. Keng and Little (1961) illustrated the leaf structure of *P. lambertiana* × *koraiensis* and both parent species. Little and Righter (1965) illustrated cones of *P. lambertiana* × *armandii* and both parents. Critchfield and Krugman (1967) illustrated seeds of *P. lambertiana* × *armandii* and parents. Saylor and Smith (1966) found that a *P. lambertiana* × *armandii* hybrid had more meiotic irregularities than representatives of the two parent species in one of two years, and more aborted pollen in both years.

A few putative hybrids of sugar pine and its Asian relatives have been produced in breeding programs outside California. *P. lambertiana* × *armandii* was duplicated by A. G. Johnson, according to Wright (1953, 1959), but the tree or trees were not described and their fate is unknown. Johnson also produced one or more putative hybrids from the cross *P. armandii* × *P. koraiensis* (Wright 1959). A cone-bearing graft from this cross growing at the IFG is not a hybrid, however. It is identical to *P. armandii* in several features that distinguish that species from *P. koraiensis* (Shaw 1914): glabrous twigs, dehiscent cones with long (3-cm) peduncles, apophyses that are not long and reflexed, a well-defined spermoderm confined to the dorsal (upper) face of the seed, and a poorly defined hilum. Pollen from *P. lambertiana* was used in hybridization attempts at Maple, Ontario (Heimburger 1972). Crosses with *P. armandii* yielded many hollow (100) and few sound (0.6) seeds per cone. Crosses with *P. koraiensis*, carried out on a much larger scale, produced few cones and few hollow seeds (1.5) but more sound seeds (2.3) per cone. No intraspecific crosses were included for comparison, and the putative hybrids were not described. One of them *(P. armandii* × *lambertiana)* is no longer recorded at Maple (L. Zsuffa, pers. comm. July 1980).

Materials and Methods

A total of 15 native sugar pines were used as female or male parents in these crosses. They grew in nine El Dorado County stands at elevations of 975 to 2255 m, mostly on the west slope of the Sierra Nevada but also near Lake Tahoe. Another 10 sugar pine parents growing in the IFG arboretum originated in southern Oregon (three trees), the extreme northern Sierra Nevada (three trees), or El Dorado County. Three pollen parents with a dominant gene for rust resistance grew in a natural stand north of Happy Camp. Siskiyou County, California, at 1280 to 1310 m.

Western white pine parents included 11 trees in three El Dorado County stands at 2135 to 2225 m, two arboretum trees of Montana and Washington origins, and four arboretum trees grafted from rust-resistant selections in a natural stand at 820 to 885 m in Benewah County, Idaho.

Other parents in natural stands were two trees of *P. balfouriana* (east side of southern Sierra Nevada, 2790 m), and single trees of *P. ponderosa* (El Dorado County, 1130 m) and *P. jeffreyi* (El Dorado County, 2285 m).

Other parent trees were in arboreta at Placerville or elsewhere. The origins of nine eastern white pine parents, most of them in the IFG arboretum, were Pennsylvania, Wisconsin, New Hampshire, Canada, or unknown. Four *P. flexilis* parents were from a seed lot that probably originated in Butte County, Idaho. The provenance of a single *P. strobiformis* pollen parent growing at IFG was the Chiricahua Mountains, southern Arizona. Two *P. koraiensis* pollen parents of unknown origin grew in arboreta in Denmark (Hørsholm) and Washington State (Wind River). Two *P. armandii* in the IFG arboretum are from the same unknown origin, and two *P. griffithii* parents originated in India. Single pollen parents of *P. parviflora* and *P. peuce* grew in arboreta in Denmark and Canada (Maple, Ontario).

The exploratory phase of sugar pine hybridization, begun in 1939 and continuing for about two decades, predated the more flexible breeding schemes made possible by the routine use of 1-year-old frozen pollen. Sugar pine is one of the most difficult western pines to use in breeding; regular cone production is delayed until the trees reach large sizes (Fowells and Schubert 1956), and it suffers heavy losses of immature cones to insects, birds, squirrels, and unknown causes. Despite these problems, it was commonly used as female parent for two reasons: many non-native white pines were unavailable as female parents, and sugar pine flowers late in the season, making possible pollinations with fresh pollen of other species.

Table 1. — Crosses between sugar pine and other white pines in section *Strobus*, 1939—1959.

Parent			Minimum tree x tree combinations	Attempts producing sound seed	Female strobili pollinated	Strobili producing cones	Sound seed per cone (mean)	Total seed per cone (mean)
Female	Male	Attempts				Percent		
lambertiana	koraiensis	3	3	1	10	60	0.2	170.4
lambertiana	armandii	8	13	7	48	50	2.1	129.1
lambertiana	parviflora	1	1	0	5	60	0	203.3
lambertiana	griffithii	6	11	1	90	40	0.1	139.0
lambertiana	peuce	1	1	0	9	33	0	166.7
lambertiana	flexilis	4	13	1	28	25	0.5	164.3
lambertiana	strobiformis	4	4	1	58	45	0.4	146.5
lambertiana	strobus	5	6	2	95	51	1.4	137.2
lambertiana	monticola	6	7	0	44	68	0	164.0
strobus	lambertiana	1	1	0	6	50	0	11.0
monticola	lambertiana	11	19	2	195	60	1.9	42.0
lambertiana	lambertiana	3	3	3	14	86	128.2	159.3
lambertiana	(open-pollinated)	--	--	--	--	--	152.6	177.2

Very few of the early interspecific crosses *(Table 1)* were accompanied by intraspecific control crosses on the same parent tree. Without controls, no critical assessment can be made of two kinds of crossing barriers acting before fertilization: differential losses of strobili, expressed as percent of strobili producing cones *(Table 1)*; and differential losses of ovules, expressed as total seeds per cone *(Table 1)*.

In 1969 and 1972, another effort was made to cross sugar pine with western and eastern white pines *(Table 2)*, using as parents sugar pines known to carry a dominant gene for rust resistance and western white pines selected in the field for rust resistance. These crosses, accompanied by intraspecific control crosses, provide critical data on the expression of crossing barriers.

The crosses summarized in *Tables 1* and *2* are only a fraction of the total effort to cross sugar pine with other species. More than one-half (46 of 85) of all pre-1960 hybridization attempts on sugar pine females are omitted because they produced no mature cones. Crosses made with pollen stored in a refrigerator for 1 year (a common practice at IFG before 1961) produce variable but generally low numbers of sound seed (Callaham and Steinhoff 1966), and are omitted from *Table 1*. After 1961, most crosses were made with fresh pollen or pollen frozen for 1 year. Crosses with pollen frozen for longer periods are omitted except as noted *(Table 2)*. With these exceptions, *Tables 1* and *2* include all crosses for which we have complete data: number of strobili pollinated, cones harvested, and sound and hollow seed.

Before 1960, small lots of putative hybrid seed were often planted in the greenhouse rather than in the nursery. Sometimes the fate of this seed is not part of the permanent record, and it is no longer possible to determine whether the seed was sound and germinable, and whether seedlings survived until they could be studied. Included in this category are three presumably sound seeds from a 1950 cross of *P. lambertiana* × *P. griffithii*, and two *P. lambertiana* × *P. strobus* crosses (1940 and 1950) yielding seven and two sound seeds *(Table 1)*.

Standard breeding and seed-processing techniques are described elsewhere (Critchfield 1966). An attempt is the pollination during a single season of a female parent with pollen from a single male parent *(Tables 1* and *2)* or a mixture of pollen from two or more males *(Table 1)*. The minimum number of tree × tree combinations *(Table 1)* was estimated by assuming that two parents contributed to pollen mixes of unspecified makeup. Mean numbers of sound and total seeds per cone *(Tables 1* and *2)* were calculated from unweighted values for single attempts.

Results

Reproductive phenology and capacity. Sugar pine is one of the latest pines to flower in the IFG arboretum (Duffield

Table 2. — Crosses between sugar pine and western and eastern white pines, 1969 and 1972.

Parent			Attempts producing sound seed	Female strobili pollinated	Strobili producing cones	Sound seed per cone (Mean)	Total seed per cone (Mean)
Female	Male	Attempts			Percent		
lambertiana	monticola	8[1]	0	52	25	0	155.8
lambertiana	lambertiana	3	3	20	20	124.7	154.2
monticola	lambertiana	8	2	394	68	0.2	35.4
monticola	monticola	7[2]	7	175	87	62.1	80.7
strobus	lambertiana	1	0	49	86	0	20.2
strobus	strobus	2	2	9	78	18.7	58.3

[1] Pollen frozen for 2 years used in 4 of 8 crosses.
[2] Pollen frozen for 2 years used in 6 of 7 crosses.

1953). Over a 16-year period, the average pollination date of arboretum trees was June 1. In natural stands in El Dorado County, the earliest pollination date, at a low elevation, was June 15, and the latest, at a high elevation, was August 6. At middle elevations (1500 to 1800 m), the average pollination date was July 7, with a 23-day range. In the Klamath Mountains of northern California, 15 trees were pollinated between June 13 and June 29 in three seasons (C. R. SHARP, pers. comm., June 1978).

Fertilization took place a year after pollination in sugar pine at mid-elevations in the mountains of southern California (HAUPT 1941). It was observed the third week in June, and pollen shedding began 1 or 2 days later. At about 1280 m in the Sierra Nevada near Placerville, fertilization was in the last week of June (KRUGMAN 1961). By this time, the seed had reached its final size and the seed coat was fully formed.

Sugar pine cones open 14 to 15 months after flowering. In natural stands, cone opening began as early as August 21 at a low elevation (940 m) and as late as October 5 at a high elevation (2040 m). At elevations of 1200 to 1800 m, the average date for the start of cone opening was September 19. In one season, cone collections on an elevational transect extended from August 27 at 770 m to September 23 at 2195 m.

A female strobilus pollinated with sugar pine pollen has an estimated 40 to 50 percent chance of developing into a mature cone. In 12 controlled crosses made in 9 seasons on 10 sugar pines in El Dorado County stands and in the arboretum, 40.4 percent of 104 pollinated strobili produced cones. In a more extensive set of controlled crosses, made in 3 years on 15 trees in the Klamath Mountains, 40.0 percent of 783 buds containing female strobili survived to cone maturity (C. R. SHARP, pers. comm. June 1978). Data for open-pollinated strobili are limited, but of 60 female strobilus buds on a total of 7 Eldorado County trees in 4 years, 50 percent developed into cones.

These heavy losses have varied causes. On the Klamath plots, 18.5 percent of female strobili were lost during the first 5 to 12 weeks after bagging, and many aborted strobili showed no signs of insect or other damage (C. R. SHARP, pers. comm., June 1978). During the second season of development, cone borers *(Conophthorus lambertianae)* sometimes destroy most of the crop. Losses from this insect in one season ranged from 32 to 93 percent on six National Forests in northern California (HALL 1955). Damage by vertebrates is heaviest as the cones approach maturity. Of 1656 cones present in mid-August on 20 sugar pines in northern California, 54 percent were cut by pine squirrels *(Tamiasciurus douglasii)* and 34 percent destroyed on the tree by white-headed woodpeckers *(Dendrocopos albolarvatus)* (TEVIS 1953). Ripe seed released in mid-September was collected by chipmunks, mice, and several species of birds, and either consumed at once or cached. Seeds of sugar pine are large and heavy, and the seed cached by birds and small mammals may be an important means of dispersal for this species.

Cones that survive to maturity produce large numbers of sound seeds, with small or negligible losses to insects other than the cone borer (KEEN 1958). Cones collected in two seasons from a total of 210 trees in 13 stands in the central and northern Sierra averaged 150.4 sound seeds, with stand means of 112 to 171 and tree means of 34 to 257 sound seeds per cone. Open-pollinated cones collected in six seasons from 10 native trees used in intraspecific crosses *(Table 1)* averaged 152.6 sound seeds and 177.2 total seeds per cone (ranges: 103 to 199 and 134 to 212), with a mean of 86.1 percent sound (range: 67 to 99 percent). Seed yields from controlled crosses are usually lower *(Tables 1* and *2)*, but a total of 12 intraspecific crosses made in 9 seasons on 10 parents yielded 146.9 sound seeds per cone (range: 97 to 175) and 175.0 total seeds (99 to 226), with seed soundness averaging 84.2 percent (75 to 99 percent).

Crossing Sugar Pine With Other Species in Section Strobus. Among the interspecific combinations listed in *Tables 1* and *2*, only the crosses of *P. lambertiana* with *P. armandii* and *P. koraiensis* have produced verified hybrids. Crossability can be roughly estimated at about 2 percent for *P. lambertiana* × *P. armandii*, and less than 1 percent for *P. lambertiana* × *P. koraiensis*. All other combinations are probable or definite failures. Single crosses of *P. lambertiana* with *P. parviflora* and *P. peuce* produced no sound seed. One of four crosses between *P. lambertiana* and *P. flexilis* produced two sound but ungerminable seeds. As noted earlier, the fate of a few presumably sound seeds from crosses of *P. lambertiana* with *P. griffithii* and *P. strobus* is not recorded, and these combinations can be considered probable failures.

One of four crosses between *P. lambertiana* and *P. strobiformis* produced sound seeds and seedlings, and was listed as a hybrid at an early age *(P. lambertiana* × *ayacahuite*, in WRIGHT 1959). The parent species are similar in vegetative morphology, but at 20 years a surviving individual resembled its *P. lambertiana* maternal parent in its longer needles, scattered leaf serrations, and abaxial stomata extending nearly to the base of the needle. (The *P. strobiformis* parent had few serrations except near the needle tip, and abaxial stomata were restricted to the upper third of the needle.) This individual is probably not a hybrid, but its identity can be determined more reliably when it produces cones.

Crosses of sugar pine and western white pine have been made on a larger scale than the other combinations listed in *Tables 1* and *2*. Sugar pine was female parent in 14 crosses involving at total of 96 strobili. None yielded any sound seed *(Tables 1* and *2)*. Western white pine is a more reliable and productive female parent than sugar pine. It produces larger numbers of more accessible strobili, and the chances of a strobilus developing into a cone are about twice as great (87 percent for intraspecific crosses: *Table 2)*. A total of 589 strobili were pollinated in 19 crosses on western white pines over a period of many years *(Tables 1* and *2)*. Four crosses on three trees produced sound seeds, sometimes in considerable quantities (0.8 to 19.7 sound seeds per cone). These trees were all crossed with sugar pine in more than 1 year; one produced sound seeds in 1 of 2 years, another in 1 of 4 years, and the third in 2 of 5 years.

All four progenies from western white pine × sugar pine crosses were considered to be nonhybrids. This conclusion was based primarily on subjective appraisals of gross differences in early height growth in the nursery. Sierra Nevada seedlings of western white pine are extremely slow growing, and sugar pine seedlings were 2.7 to 4.4 times as tall as western white and putative hybrid seedlings at the end of the first and second growing seasons. Two outplanted trees were studied more carefully at age 12. They resembled their maternal parent in their short needles (6.1 cm, compared with 8.2 cm for the sugar pine parent)

and, unlike sugar pine, they lacked stomate over much of the abaxial face of the needle.

Data from all interspecific crosses made on sugar pine females were generally consistent with the view that genetic barriers between white pines are expressed after fertilization. When interspecific combinations that produced no cones are added to the interspecific crosses in *Tables 1* and *2*, a total of 658 sugar pine strobili produced 196 cones. This yield (29.8 percent) is lower than intraspecific crosses (40 percent), but without adequate controls the reduction cannot be attributed to differential abortion of strobili or cones. Three species combinations *(P. lambertiana* × *P. armandii,* × *P. peuce,* and × *P. griffithii)* produced cones in less than one-half of all attempts, and only 1 of 10 crosses with *P. peuce* produced any cones.

Crosses made on sugar pine showed no indications of differential ovule abortion. Seed yields of all species combinations were within the range for sugar pine, with means of 129.1 to 203.3 total seeds per cone *(Tables 1* and *2).*

Western white pine females, in contrast, showed reduced yields of cones and total seed compared with intraspecific crosses when sugar pine was pollen parent *(Table 2).* Paired crosses were made in 1969 on six western white pines, using pollen from a sugar pine with a dominant gene for rust resistance and pollen from a western white pine. In 1972, one of the same female parents was crossed with the same sugar pine and one other carrying the dominant gene, and with a different western white pine. In both years, the chances of a strobilus developing into a cone were substantially reduced in interspecific compared with intraspecific combinations. The reduction was consistent between years (22 and 21 percent), but it was not statistically significant within years or in the pooled data (G-test, Sokal and Rohlf 1969). Differential reduction in the proportion of ovules developing into seeds, however, was pronounced and significant. In both years, interspecific crosses produced less than half as many total seeds per cone (41.6 and 45.5 percent) as intraspecific controls. When cone number : total seed ratios were compared for between- and within-species crosses, this reduction was highly significant in both seasons (G-test, $P \leq .01$).

Crossing Sugar Pine With Species in Other Groups. No successful crosses have been made between sugar pine and any species outside section *Strobus.* A 1940 attempt was made to cross it with *P. balfouriana,* a five-needled white pine in subsection *Balfourianae,* section *Parrya* (classification of Little and Critchfield 1969). Two *P. balfouriana* females crossed with a single sugar pine pollen parent produced a single cone with 10 hollow seeds from a total of 10 pollinated strobili. This low yield of cones and seed coats may be an expression of incompatibility; in crosses within *P. balfouriana,* control-pollinated strobili have an 85 to 93 percent chance of producing cones, and cones average 55 to 62 total seeds (Critchfield 1977).

Crosses between sugar pine and hard pines of section *Pinus* have also yielded much reduced numbers of cones and seed coats. A total of 28 strobili on two sugar pine females pollinated with the same *P. ponderosa* pollen, produced only one cone with 31 hollow seeds. Intraspecific pollinations of 17 strobili on the same two sugar pines yielded 3 cones and 63 to 172 total seeds per cone. On a *P. jeffreyi* female, two strobili pollinated with sugar pine pollen produced two cones with 98 hollow seeds per cone. Controls were lacking, but *P. jeffreyi* averages 185 total seeds per cone (Critchfield 1966).

Characteristics of Hybrids. The first *P. lambertiana* × *armandii* progeny, comprising 5 trees, was the product of a 1947 cross between a sugar pine growing at 1830 m in El Dorado County and a mixture of pollen from two *P. armandii* trees of the same unknown origin in the IFG arboretum. The seeds were germinated without seed coats under laboratory conditions, but seeds of the same hybrid produced a few years later germinated in the nursery without special treatment. The first progeny was outplanted at close spacing at 3 years of age. One tree was suppressed by its neighbors and died at 18 years. Another tree was naturally dwarfed; it reached at height of 1 m at 20 years and died shortly therafter. The other three hybrids grew rapidly from the outset, and at 18 years the tallest was about 10 m in height (Critchfield and Krugman 1967, *Fig. 1).* At 28 years, the trees were 13.4 to 17.1 m tall, in the midrange of heights for unrelated sugar pines of this age in the arboretum. These hybrids are parents of all hybrid derivatives so far produced.

P. armandii, although its survival and growth are poor in California, flowers at an early age at Placerville. One *P. armandii* parent is known to have produced pollen at age 13, and this early-flowering trait was inherited by the hybrids of *P. armandii.* One hybrid began pollen production at 11 years and produced female strobili a year later. By age 14, all nondwarfed hybrids were producing pollen, and within a few years were regular and prolific producers of male and female strobili.

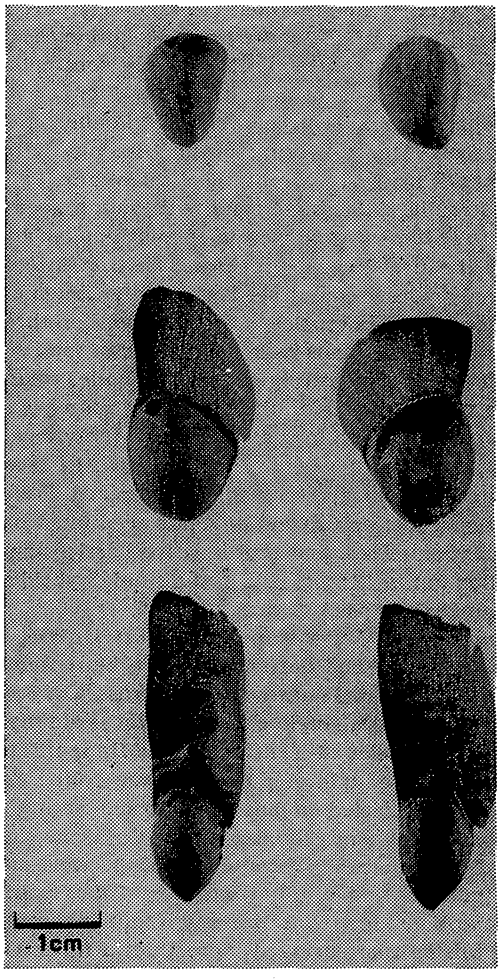

Fig. 1. — Seeds of *Pinus koraiensis* (top row), *P. lambertiana* × *koraiensis* (middle row), and *P. lambertiana* (bottom row). Upper (dorsal) face on right, lower (ventral) face on left.

The first and only *P. lambertiana* × *koraiensis* hybrid was produced in the same year on the same female parent as the first *P. lambertiana* × *armandii* progeny, and the single sound seed was germinated under the same conditions. *P. koraiensis* rarely survives to reproductive age at Placerville, and the pollen for this cross was supplied by C. Syrach Larsen from a tree in Denmark. The hybrid was slower growing than its *P. lambertiana* × *armandii* half-sibs on the same site, and its height at 28 years (11.3 m) was near the lower limit for sugar pines of the same age in the arboretum. The hybrid did not produce a female strobilus until it was 25 years old, and 5 years later was still producing few male or female strobili. The hybrid cones were intermediate in length between the parent species, but resembled sugar pine cones in opening fully at maturity.

These hybrid combinations may be the first products of winged-seed × wingless-seed pine crosses to reach reproductive age. The seed wing of sugar pine, measured from the tip to the nearest end of the seed, is 1.5 to 2 times as long as the seed proper *(Fig. 1)*. Both kinds of hybrids have well-defined wings shorter than the seed *(P. lambertiana* × *armandii* : Critchfield and Krugman 1967, *Fig. 16; P. lambertiana* × *koraiensis: Fig. 1,* this paper). *P. lambertiana* and *P. koraiensis* also differ in extent of spermoderm, the outermost layer of the seed coat. In the former it is mostly confined to the exposed upper surface and is continuous with the seed wing. The spermoderm of *P. koraiensis* is unique among the pines in covering almost the entire surface of the seed except the hilum, where the darker stony layer of ste seed coat is exposed. Apart from its short wing, seed of *P. lambertiana* × *koraiensis* is much like that of *P. koraiensis,* with a nearly continuous spermoderm and conspicuous blackish hilum *(Fig. 1)*.

Attempts were made to backcross *P. lambertiana* × *armandii* soon after flowering began. A single cross with *P. armandii,* using as parent the first hybrid to produce female strobili, yielded one cone with hollow seeds. Backcrosses to *P. lambertiana* were made with pollen from four trees of the first hybrid progeny. The first attempt produced only a few sound seeds, but later attempts were more successful. Six crosses in three seasons on three sugar pines in different stands gave a low yield of total seeds per cone (68 to 145), suggesting that some ovules aborted. An average of 26 percent of the seed was sound, compared with 88 percent sound in control crosses. Individual crosses ranged from 19 to 39 percent sound seed. In crosses accompanied by controls, crossability averaged 29.8 percent. This large reduction in yield of sound seed must be due to a combination of residual reproductive barriers and abortive pollen (up to 12.9 percent in the single hybrid studied: Saylor and Smith (1966).

Susceptibility of Hybrids to Blister Rust. Only *P. lambertiana* × *armandii* and derivatives have been field-tested. Small-scale trials of *P. armandii,* backcrosses of F_1 hybrids to sugar pine, and a single cloned F_1 were established between 1964 and 1968 at a test site near Happy Camp. The trials also included a large number of sugar pine progenies from parents selected in heavily infected natural stands for apparent resistance to blister rust. Epidemic conditions for the disease, naturally chronic at this site, were augmented by interplanting of alternate host *Ribes* spp. Under these conditions, few white pines without inherent resistance to blister rust survived more than a few years. The environment of the site, experimental design, and procedures for evaluating resistance were described by Kinloch and Byler (1981).

Twenty *P. armandii* seedlings grown from seed collected in Shansi Province, China, were planted on the site in 1967. Their poor adaptation to this environment was evident in their slow growth, poor form, and needle shedding after one or two seasons. Perhaps for this reason, symptoms of rust infection were atypical and difficult to evaluate. None of the suspected infections sporulated, and most lacked the typical symptoms of sugar pine infections: bark discoloration, swelling, and infestation with *Dioryctria* spp. *larvae.* The unexpectedly high degree of apparent infection after 6 years (70 percent: *Table 3)* may thus be overestimated, but it was still considerably lower than infection levels in unselected sugar pine. Four ramets of a *P. armandii* clone of unknown origin, grafted onto sugar pine rootstocks, were more thrifty than the seedlings and also lacked typical symptoms of the pathogen.

After 6 years on the test site, infection in the backcross progenies ranged from 67 to 100 percent, and rust-associated mortality from 44 to 100 percent. More extensive backcrosses were later produced on 11 sugar pine females selected in natural stands for freedom from rust. Pollen from the same four hybrids was used--presumably in a mix, although records are incomplete. These backcross progenies were compared to progenies from the same sugar pine parents crossed with other sugar pine selects. Both sets of progenies were evaluated after 6 years for cumulative rust infection and associated mortality, and for infection rate (r). A more sensitive index of susceptibility than cumulative infection, infection rate was used to demonstrate apparently quantitatively inherited resistance in sugar pine (see Kinloch and Byler 1981). The backcross progenies were substantially less susceptible than their sugar pine siblings *(Table 3)*.

Four rooted cuttings of a single F_1 hybrid were planted on the test site in 1971. The trees were well adapted to the site, and their growth and form were excellent. No symptoms of rust were observed for 5 years, although 90 percent of the sugar pine controls outplanted at the same time became infected and died. During unusually severe epidemic conditions that followed, many sugar pines known to carry the dominant gene for resistance were infected for the first time (Kinloch and Byler 1981), and it was established that the new infections were caused by a race of the the rust virulent to this gene (Kinloch and Comstock 1981). By 1978, all four ramets of the hybrid sustained typical and multiple infections, many of which later sporulated.

Table 3. — Blister rust infection on progenies of *Pinus armandii, P. lambertiana* × *(lambertiana* × *armandii), P. lambertiana* parents selected for resistance, and susceptible *P. lambertiana* controls.

	Type of cross (No. of parents)	Cumulative infection (mortality) after 6 years	Infection rate (r)[1]
		---------Percent---------	
1.	*P. armandii* (bulk seed lot)	70.0 (20.0)	.220
2.	*P. lambertiana* selects (11) x (lambertiana x armandii)	83.6 (37.0)	.436
3.	*P. lambertiana* selects (11)[2] x *P. lambertiana* selects (various)	92.5 (58.8)	.756
4.	*P. lambertiana* controls (4 unselected seed lots)	95.7 (62.0)	1.098

[1] See Kinloch and Byler 1981.
[2] Same parents as in (2).

Discussion

The core group of white pines in which sugar pine is usually placed is notable for the ease with which its members can be crossed with each other. This is the only group of pines in which species native to Eastern and Western hemispheres can be successfully crossed, and in many combinations inter-hemisphere crossabilities are moderately high (Bingham 1972, Wright 1976). Against this background, it is all the more remarkable that sugar pine cannot be hybridized with any other North American pine. Within *Pinus*, the crossing behavior of sugar pine and its Asian relatives is the outstanding exception to a positive correlation between morphological resemblance and the possibility and ease of hybridization. This lack of correlation is due partly to the characters used to classify the white pines of section *Strobus*. Accumulating evidence suggests that wingless seeds and indehiscent cones have evolved more than once in response to seed dispersal by birds (data of Turček and Kelso 1968, and Lanner 1982). The poor agreement among the kinds of data that bear on white pine relationships underlines the need for a critical reappraisal of species groupings within section *Strobus*.

Although relationship in section *Strobus* are obscure, the group as a whole is unambiguously distinct from other pines. Its members are unique among the pines in having cone scales with terminal umbos, and they share other distinctive features such as five-needled fascicles (Shaw 1914). The group is also genetically isolated from all other pines. Its members are unique among the pines in having production are often disrupted. Cessation of pollen-tube growth, conelet abortion, ovule collapse, or reduced numbers of hollow seeds are all common in crosses made in both directions (Hagman 1975, Krugman 1970, this paper). Crosses with species of *Balfourianae*, the only other group of five-needled white pines, are also unsuccessful but much less disruptive of the early stages of reproduction. High yields of cones and hollow seeds from most combinations (Critchfield 1977) show that the barriers between these white pine groups are mostly expressed after fertilization, just as they are within the groups.

Crosses between sugar pine and western white pine provide an uncommon exception to the generalization that reproductive barriers between white pines are expressed after fertilization. Levels of conelet and ovule abortion were not unusually high when crosses were made on sugar pine females, but western white pine females had consistently higher levels of conelet and ovule abortion with sugar pine pollen than with western white pine pollen. The increase in conelet abortion was not statistically significant, but it exceeded 20 percent in both years the crosses were made. The level of ovule abortion, however, was highly significant in both years: less than half as many seed coats developed in sugar pine crosses compared with intraspecific controls. Too few parent trees were involved to establish whether early reproductive breakdown was associated with individual trees or whether it is characteristic of this species combination.

The reproductive barriers between sugar pine and its Asian relatives strictly limit potential numbers of F_1 hybrids, but even the few existing hybrids provided an effective bridge between the parent species. Limited field-test data have established that improvement of blister rust resistance in sugar pine by transfer of genes from *P. armandii* is biologically feasible, if practically difficult. The consistent and relatively smooth gradient of increasing susceptibility from *P. armandii* through the backcrosses to selected and unselected sugar pines *(Table 3)* suggests that these white pines share a common mechanism of resistance under polygenic control. Differences between progenies were unspectacular, but a wider range of variation might be expected from a broader base of *P. armandii* than the two parent trees used in these tests.

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Neue Ergebnisse des II. Internationalen Lärchenprovenienzversuches von 1958/59 nach Aufnahmen von Teilversuchen in 11 europäischen Ländern und den USA

Von R. Schober

Schriften aus der Forstlichen Fakultät der Universität Göttingen und der Niedersächsischen Forstlichen Versuchsanstalt, Band 83

164 Seiten mit 45 Abbildungen und 24 Tabellen
Kartoniert DM 27,—

Zur Prüfung von Wuchsleistung und Resistenzeigenschaften verschiedener Lärchenherkünfte wurde 1959 von Forschern verschiedener Länder ein neuer, der II. Internationale Lärchen-Provenienzversuch von 1958/59, vereinbart.

Dieser enthält 67 Provenienzen der wichtigsten Rassen- und Herkunftsgebiete der europäischen Lärche und eine Japanlärche. Mit 70 Teilanlagen in 14 europäischen Ländern und den USA ist dieses Forschungsvorhaben die bisher umfangreichste Versuchsserie dieser Baumart. Die der Iufro-Arbeitsgruppe S 2.02-07 angehörenden Versuchsteilnehmer beschlossen 1978 bei der Osloer Iufro-Tagung die gleichzeitige Aufnahme ihrer größeren Versuche im Bestandsalter 20 nach einheitlicher Methodik. Neben den regionalen Berichten über die Versuche in den einzelnen Ländern wurde auch eine alle Beobachtungen zusammenfassende Betrachtung in Aussicht genommen. Ihr Ergebnis wird hier mitgeteilt.

Die zentrale Auswertung konnte auf die breite Grundlage der Daten von 46 Versuchen gestützt werden. Von diesen sind 26 Anlagen etwa im Alter 20 nach einheitlicher Methodik aufgenommen. Aus den Daten dieser und weiterer Versuche konnten Streuung und mittleres Niveau der Provenienzleistungen in vielen Versuchen errechnet werden.

Die zusammenfassende Interpretation zahlreicher Versuchsergebnisse läßt für die einzelnen Provenienzen — im gegenseitigen Vergleich — sehr unterschiedliche Wuchs- und Resistenzeigenschaften erkennen. Diese differenzierten genetischen Anlagen erweisen sich nicht nur als provenienzspezifisch sondern auch als (herkunfts-) gebietsspezifisch: für mehrere Provenienzen des gleichen Herkunftsgebietes ergibt sich — im Vergleich zum Versuchsmittel — meist ein ähnliches Leistungsniveau.

Eine kritische Würdigung der charakteristischen, oft stark differenzierten Herkunfts-Eigenschaften läßt die grundlegende Bedeutung richtiger Provenienzwahl für einen erfolgreichen Lärchenanbau der Praxis erkennen. Für diesen werden Provenienzen empfohlen, die sich in den Anlagen des II. Internationalen Lärchen-Provenienzversuches und früheren Versuchen in wichtigen Eigenschaften besonders bewährt haben.

J. D. SAUERLÄNDER'S VERLAG, FRANKFURT AM MAIN