

1975. Symp. on Interspecific and Interprovenance
Hybridization in Forest Trees. [Ed] D. P. Fowler
and C. Y. Yeatman. Proc. 14th Meeting, Canad.
Tree Improv. Assoc., Part II

#32

INTERSPECIFIC HYBRIDIZATION IN PINUS: A SUMMARY REVIEW

W.B. Critchfield

*U.S. Forest Service,
Pacific Southwest Forest and Range Experiment Station,
Berkeley, California*

The pines and other groups of temperate forest trees often fail to conform to widely accepted principles of plant evolution that are based primarily on observations of herbaceous plants. For example, interpreters of plant evolution tend to equate the fertility or sterility of interspecific hybrids with the magnitude of the genetically controlled reproductive barriers limiting the production of hybrids. This tendency has been articulated by Grant (1958, p. 353): "This is assuming that incompatibility barriers and sterility barriers, two distinct phenomena in the physiological sense, tend to run parallel in most groups, an assumption which despite a few exceptions is generally supported by the facts." The common corollary to this assumption is that vigorous, fertile interspecific hybrids reflect the absence of well-developed barriers to hybridization. In *Pinus*, neither Grant's assumption nor its corollary is supported by the facts summarized in this paper.

Because of the economic importance of many pines, species hybridization has been explored more fully in this genus than in most other plant genera. This work has sought to establish the limits of genetic material available for the improvement of a wild species - the starting point of nearly all tree-improvement programs.

The first authentic pine hybrid was produced nearly 60 years ago, and the first continuing program of exploratory hybridization was begun in the late 1920's at the Institute of Forest Genetics (then the Eddy Tree Breeding Station) at Placerville, Calif. The results of the work done at Placerville, at the Northeastern Forest Experiment Station, at Maple, Ont., and elsewhere have been summarized by Wright (1962), Critchfield (1963b, 1966, 1967), and Bingham et al. (1972). The generalizations about pine hybridization advanced in this paper are based on these earlier summaries and on unpublished data of the Institute of Forest Genetics, at Placerville.

About four-fifths of the 95 to 100 species in *Pinus* have been involved in one or more hybridization attempts. Of the more than 4,500 possible combinations of species, an estimated several hundred have been attempted. From these attempts, about 95 successful hybrid combinations - a conservative estimate - have been produced (Table 1).

Pine species have proved to vary widely in their crossing ability. Some pines (e.g. *Pinus pinea*, the Italian stone pine) have not been successfully crossed with any other species, nor are they likely to be

TABLE 1. SUCCESSFUL INTERSPECIFIC HYBRIDIZATIONS WITHIN AND BETWEEN SUBSECTIONS OF *PINUS*.

Subsection(s) ¹	Number of species	Estimated number of hybrid combinations
<i>Cembrae</i> (white pines)	5	1
<i>Cembrae</i> x <i>Strobi</i>		2
<i>Strobi</i> (white pines)	14-15	18
<i>Cembroides</i> (pinyon pines)	8	6
<i>Balfourianae</i> (foxtail pines)	2-3	2
<i>Sylvestres</i> (Eurasian hard pines)	19	19
<i>Australes</i> (southern and Caribbean hard pines)	11	15
<i>Australes</i> x <i>Contortae</i>		2
<i>Contortae</i> (small-cone pines)	4	2
<i>Sabinianae</i> (big-cone pines)	3	2
<i>Sabinianae</i> x <i>Ponderosae</i>		2
<i>Ponderosae</i> (western and Mexican hard pines)	13-15	16
<i>Ponderosae</i> x <i>Oocarpae</i>		2
<i>Oocarpae</i> (closed-cone pines)	7	6

¹The eight species in the other five subsections have no verified interspecific hybrids.

without a major advance in the manipulation of reproductive processes. In contrast, some of the western and Mexican yellow pines, southern pines, white pines, and Eurasian hard pines can be crossed directly with as many as six other species and linked indirectly to still others.

Although the exploratory hybridization of *Pinus* is incomplete, the available information provides a sufficient basis for several generalizations about the pines:

(1) With very few exceptions, there are no marked barriers to crossing between different races of a species. The Sierra Nevada and coastal races of lodgepole pine (*P. contorta*), for example, are fully crossable, although the morphological differences between them are so great that they are still occasionally regarded as different species.

A minor exception to this generalization is ponderosa pine (*P. ponderosa*). Crosses between its Pacific and Rocky Mountain races produce somewhat reduced yields of sound seed (Krugman 1970), indicating weak barriers to crossing. A more remarkable exception is bishop pine (*P. muricata*) of the California coast. Its northern and southern races are isolated by nearly absolute barriers to crossing (Critchfield 1967), although both can be crossed with a geographically intermediate race.

(2) With a few exceptions, pine species are partly or completely isolated from each other by genetic barriers. The magnitude of these barriers

can be expressed quantitatively as *crossability*: the yield of sound, germinable seed from crosses between two species, expressed as a percentage of the seed yield from within-species crosses.

The crossability of those pine species that have been successfully hybridized ranges from 100% to nearly zero. There appear to be no reproductive barriers between foxtail pine (*P. balfouriana*) and the western race of bristlecone pine (*P. aristata*), which have a crossability of close to 100%. The closed-cone pines *P. attenuata* and *P. radiata* have a crossability of 69 to 85% (Critchfield 1967). Examples of crossabilities approaching zero are the closed-cone pine cross *P. patula* x *P. radiata*, and the big-cone pine cross *P. sabiniana* x *P. coulteri*, each of which has yielded a single hybrid tree (Critchfield 1966, 1967). Most of the crossable combinations of pine species are in the lower part of the 0 to 100% range, with crossabilities of less than 40%.

(3) Crossing is usually impossible among the 15 groups of species (subsections) currently recognized as making up the genus. These groupings, reflecting ideas about relationships among the pines, are subject to continuing reevaluation as new morphological, chemical, cytological, and crossing data are accumulated. Such taxonomic groupings provide a necessary working hypothesis in the exploratory hybridization of a large genus like *Pinus*, with its numerous possible species combinations.

Shaw's (1914) monograph on *Pinus* supplied the working hypothesis for the early investigations of pine hybridization. The results obtained were the basis for Duffield's (1952) reappraisal of the hard pines (subgenus *Pinus*). His new groups, designated by Roman numerals, were more coherent morphologically, chemically, and geographically than the groups they replaced. Duffield's groups, with minor changes, have recently been named and more fully described by Little and Critchfield (1969).

The white pines (subgenus *Strobus*) have not received a recent reappraisal like that of the hard pines. One of the problems in this subgenus is the poorly defined subsection *Cembrae*, which is distinguished chiefly by its "indehiscent" cones. It may eventually be combined with *Strobi*, a group that includes nearly all of the familiar five-needled white pines (*P. strobus*, *P. monticola*, etc.). Two verified hybrids have been produced from *Cembrae* x *Strobi* crosses (Table 1), and other probable *Cembrae* x *Strobi* hybrids have been reported (Bingham et al. 1972). In this instance, the production of hybrids between species in different groups may reflect the unsatisfactory state of white pine taxonomy.

In other instances, hybrids between species in different groups may be true links between otherwise well-defined groups. Two successful *Sabinianae* x *Ponderosae* crosses (Table 1), both involving Jeffrey pine (*P. jeffreyi*), are an example of such a link. Jeffrey pine so closely resembles the more widespread ponderosa pine that field identification is often difficult, and both species are in the same subsection (*Ponderosae*). In its resin chemistry, however, Jeffrey pine is much more like the three big-cone pines in subsection *Sabinianae* (Mirov 1961). And in its crossing

behavior Jeffrey pine links the *Ponderosae* and *Sabinianae* (Critchfield 1966). It has been successfully crossed with several other species in *Ponderosae*, including ponderosa pine. It has also been hybridized with two big-cone pines, *P. coulteri* and *P. torreyana*. The problem posed by Jeffrey pine cannot be resolved taxonomically, and it seems best to consider the *Ponderosae* and *Sabinianae* as groups that have diverged somewhat less in the course of evolution than most of the other groups now classified as subsections.

Subsection *Contortae* is another exception to the general rule that pines can only be hybridized with other members of their groups. This morphologically similar group of small-cone pines includes two northern species, lodgepole and jack pines (*P. contorta*, *P. banksiana*) and two southeastern species, Virginia and sand pines (*P. virginiana*, *P. clausa*). Lodgepole and jack pines hybridize naturally where they overlap in western Canada, and are readily crossable under controlled conditions (crossability about 30%). The two southeastern pines are also highly crossable (Critchfield 1963b). Efforts to cross the northern and southern species have failed to produce any verified hybrids. But sand pine has been successfully crossed with two southern pines in subsection *Austerales*: *P. elliotii* (Saylor and Koenig 1967) and *P. taeda* (Critchfield 1963b). The limits to crossing of the pines in *Contortae* have not been fully explored, but this group appears to be a notable exception to the rule that morphology and crossing ability tend to go together in the pines.

(4) The two major groupings in *Pinus*, the white pines and the hard pines (subgenera *Strobus* and *Pinus*), differ greatly in several aspects of species hybridization. The two groups are completely isolated from each other; the magnitude of the reproductive barriers separating them is reflected in high levels of conelet abortion and often in much reduced numbers of hollow seed when white and hard pines are crossed (Krugman 1970).

The most conspicuous difference between the breeding behavior of white and hard pines is related to geography. White pines of the Eastern and Western Hemispheres hybridize readily; half of the 21 species combinations in the *Cembrae/Strobi* (Table 1) are interhemisphere crosses. The most unusual example of this lack of association between crossing ability and geographical separation is sugar pine (*P. lambertiana*), a California montane species. Although it is a fairly typical white pine in its morphology, it has not been successfully crossed with any of the other American white pines. It has, however, been hybridized with two east-Asian white pines, *P. armandii* and *P. koraiensis*, both of them very different in morphology from sugar pine and from each other.

The hard pines, by contrast, exhibit strict geographic limits to crossing. The only successful Eastern x Western Hemisphere cross between hard pines is the difficult and as yet unrepeated *P. nigra* x *P. resinosa* (Critchfield 1963a). Among the North American hard pines, even crosses between species of different geographic regions are uncommon. The northern and southern species of *Contortae*, already discussed, are an example. Geographic limitations to crossing are also illustrated by two rather

similar groups of American hard pines: subsection *Australes*, of the southeastern U.S. and the Caribbean region, and subsection *Ponderosae*, of western and southern North America. Most of these pines were grouped together by Shaw (1914). They were segregated into two groups by Duffield (1951-52), partly because of the failure of all attempts to cross the eastern and western species.

The white and hard pines also differ in the nature of the reproductive failures that occur in species crosses. The genetic barriers between white pines are usually expressed relatively late in the reproductive process, after fertilization has taken place (Kriebel 1972). In crosses between hard pines, however, reproductive failures may occur at almost any stage, from the failure of the pollen to germinate to the development of the embryo (McWilliam 1959, Krugman 1970).

(5) Most interspecific pine hybrids are highly viable and highly fertile. Hybrid inviability is very rare, and the only two reported examples need to be repeated and verified. They are the southern pine crosses *P. taeda* x *P. clausa* and *P. elliottii* x *P. glabra*. These combinations have produced only seedlings (some of them albino) that died soon after germination (Critchfield 1963b). With these possible exceptions, the growth and development of pine hybrids show few major departures from the growth and development of nonhybrids.

The reproductive capacity of pine hybrids is also comparable to that of nonhybrids, although critical comparisons are mostly lacking. Hybrids do have generally higher levels of meiotic irregularities than do nonhybrids (Saylor and Smith 1966). Pollen abortion levels are definitely higher in some hybrid combinations, but most show the same low levels (0 to 5%) as nonhybrids. Many of the interhemispheric white pine hybrids studied by Saylor and Smith had fairly high levels of aborted pollen: 10 to 22%. The largest amounts of pollen abortion, however, have been found in some lodgepole x jack pine hybrids, one of the more crossable combinations of hard pines. Many individuals of one hybrid lineage produced 30 to 40% aborted pollen (Saylor and Smith 1966, and Saylor 1972 [personal communication]). Despite these sometimes high levels of pollen abortion, lodgepole x jack pine hybrids of the F₁ to F₃ generations produce large amounts of sound seed in most combinations.

The failure of meiotic irregularities and pollen abortion to seriously depress the reproductive capacity of pine hybrids may be related to the reproductive system of pines. Although a pine seed usually contains only a single embryo at maturity, the ovule from which it develops can accommodate several pollen grains and ordinarily contains several eggs. With this margin for reproductive failures, it seems probable that only high levels of reproductive disturbance would significantly influence the reproductive capacity of pine hybrids.

In conclusion, *Pinus* does not appear to be very different from many other plant genera in the ability of its species to cross with one another. In most instances crossing is possible only between those species

that resemble each other most closely, although the exceptions have been emphasized in this paper. *Pinus* does differ from many herbaceous plant genera, however, in that most interspecific hybrids are vigorous and fertile. Reproductive sterility is sufficiently common among herbaceous plant hybrids to have been used by Clausen, Keck, and Hiesey (1940) as a major criterion in defining their still widely used biosystematic categories of ecotype, ecospecies, and coenospecies. These categories are not applicable to *Pinus* and similar woody genera, in which hybrid sterility is both uncommon and seemingly unrelated to the magnitude of crossing barriers between species.

REFERENCES

- Bingham, R.T., R.J. Hoff, and R.J. Steinhoff. 1972. Genetics of western white pine. USDA Forest Serv. Res. Pap. WO-12. 18 pp.
- Clausen, Jens, David D. Keck, and William M. Hiesey. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Inst. (Washington) Publ. 520. 452 pp.
- Critchfield, William B. 1963a. The Austrian x red pine hybrid. *Silvae Genet.* 12:187-192.
- Critchfield, William B. 1963b. Hybridization of the southern pines in California. Pages 40-48 in South. Forest Tree Improv. Comm. Publ. 22.
- Critchfield, William B. 1966. Crossability and relationships of the California big-cone pines. Pages 36-44 in USDA Forest Serv. Res. Pap. NC-6.
- Critchfield, William B. 1967. Crossability and relationships of the closed-cone pines. *Silvae Genet.* 16:89-97.
- Duffield, J.W. 1951-52. Relationships and species hybridization in the genus *Pinus*. *Z. Forstgen.* 1:93-100.
- Grant, Verne. 1958. The regulation of recombination in plants. Cold Spring Harbor Symp. Quant. Biol. 13:337-363.
- Kriebel, H.B. 1972. Embryo development and hybridity barriers in the white pines (section *Strobus*). *Silvae Genet.* 21:39-44.
- Krugman, Stanley L. 1970. Incompatibility and inviability systems among some western North American pines. Proc. Sex. Repro. Forest Trees (IUFRO Sect. 22 Work. Group) vol. 2. 13 pp.
- Little, Elbert L., Jr., and William B. Critchfield. 1969. Subdivisions of the genus *Pinus* (pines). USDA Misc. Publ. 1144. 51 pp.
- McWilliam, J.R. 1959. Interspecific incompatibility in *Pinus*. *Am. J. Bot.* 46:425-433.

- Mirov, N.T. 1961. Composition of gum turpentine of pines. USDA Tech. Bull. 1239. 158 pp.
- Saylor, L.C., and R.L. Koenig. 1967. The slash x sand pine hybrid. *Silvae Genet.* 16:134-138.
- Saylor, LeRoy C., and Ben W. Smith. 1966. Meiotic irregularity in species and interspecific hybrids of *Pinus*. *Am. J. Bot.* 53:453-468.
- Shaw, George R. 1914. The genus *Pinus*. Arnold Arbor. Publ. 5. 96 pp.
- Wright, Jonathan W. 1962. Genetics of forest tree improvement. FAO, Rome. 399 pp.