14. POSSIBILITIES AND LIMITATIONS OF HYBRIDIZATION IN PINUS

F. I. Righter, Forest Geneticist
Institute of Forest Genetics 1/,
California Forest and Range Experiment Station, Placerville, Calif.
Forest Service, U. S. Department of Agriculture

When I mentioned the title of my paper to Dr. N. T. Mirov, plant physiologist and biochemist at the Institute of Forest Genetics, he said. "Tell them that the possibilities are unlimited." It is easy and, perhaps, natural to take such a view. The pines exist in such diversified abundance that--given crossability among many of the species, fertility in the hybrids, the infinite future, and the consummate technical ingenuity of mankind--almost any reasonable objective can be attained through synthetic breeding in Pinus. In this, I am reminded of the first four verses of a sonnet to Vittoria Colonna by Michelangelo, a translation of which, as I recall, runs as follows:

"The master craftsman hath no thought in mind
That one sole marble block may not contain
Within itself; but this we only find
When the hand serves the impulse of the brain."

The genus Pinus, consisting according to Buchholz (1) of about 90 species, may well be likened to Michelangelo's all-encompassing marble block. Distributed circumpolarly in the Northern Hemisphere, it ranges from the equator to the Arctic Circle; and within that span, from sea-level to sub-alpine elevations and from swamplands to desert-edges. These facts imply, and the literature attests, that an enormous amount of genetic diversity--the raw material of breeding--is impounded in the genus. In the aggregate, the genus embodies, as no single species does, all the elements essential for synthesizing many different kinds of superior new products, adapted to numerous places and purposes.

1/ Maintained in cooperation with the University of California.

Synthesis in Breeding Analogous to Synthesis in Chemistry

The problem, however, is not one of artistic carving such as confronts sculptors, but rather one of synthesis such as confronts chemists, entailing the application of principles through appropriate techniques and procedures. I have long felt that interspecific hybridization, with selection standing at its stirrup, has much in common with chemical research, particularly, as I shall attempt to show, in its potential dynamism; and I daresay that, with pines at least, progress through such breeding will parallel progress in chemical research to a very considerable extent. It will be interesting and perhaps helpful, therefore, to enlarge on this aspect of the subject somewhat.

One of the first concerns of chemists was to discover and describe the elements. Regarding each species of a genus as an element, we may say that the jobs of discovery and morphological description have been well advanced by botanists.

The next step in dealing with the elements was to determine their affinities for other elements and describe the properties of the compounds they form with them. That, of course, is also a major objective of hybridization programs. Some elements, such as chlorine and oxygen, combine with many elements whereas others are inert. Similarly, various pines (P. attenuata, P. echinata, P. ponderosa, P. taeda for example) combine readily with various other species while others (P. sabiniana and P. resinosa, for example) appear to be relatively inert.

The number of substances that can be compounded from the 90-odd elements defies calculation. According to Conant (2), there are about 70 trillion isomers of $C_{40}H_{82}$ alone. Similarly, assuming that each individual that can be obtained from crossing P. echinata and P. taeda and their hybrids, for example, represents an individual isomer, the number of isomers or biotypes, as they are called, that are obtainable from crossing those species would, doubtless, be astronomical in magnitude.

Carrying the analogy further, it is possible to obtain hybrids in which genes of three or more species are represented. A half-dozen such crosses have already been obtained at Placerville; and doubtless many more will be obtained. Populations of such hybrids are likely to be highly variable. Nevertheless, in two instances at Placerville, they have surpassed two of their parental species in average growth-rate. Such populations abound with exceptional individualities that stand out in conspicuous contrast in nursery tests, and thus provide an abundance of materials in convenient array for selection.

As in chemistry, relatively few of the possible combinations will be of any great practical importance. Actually, relatively few of the possible combinations are likely to be investigated in the next 1,000 years; hence, we are presently concerned only with relatively few of the possible combinations. Nevertheless, even in that sense, "relatively few" may mean very many, indeed. And those that do prove to be important, are likely to be very important, indeed, at least over short periods of time.

It is apparent, then, that synthetic breeding on the species level is roughly analogous to the work of chemists in producing new compounds. It differs chiefly, it seems to me, in that its conceptual basis lacks the high refinement that characterizes the conceptual bases underlying analogous work in chemistry. In short, to borrow an idea from Conant (2), the degree of empiricism in forest tree breeding is relatively high and will remain so for a long time despite the fact that genetic theory is highly developed. For that among other reasons, we must reconcile ourselves for the present to much less precision and consequently to much slower progress than is possible in chemistry. As we learn more about the hidden heredity of the various species, their affinities, the inheritance of their characters, and other pertinent facts, we shall be able to reduce the degree of empiricism in our work and breed for particular objectives with increasing precision and speed. The possibilities, however, are fairly similar, I believe, to the possibilities in chemistry.

Crossability of Pines

Those theoretical possibilities are, of course, contingent upon crossability among many species of a genus and fertility in the hybrids. With respect to the conifers, the possibilities were suggested incidentally by Muntzing (3) in 1933 and definitely emphasized somewhat later by Sax and Sax (5). Muntzing based his assumption of interspecific crossing and hybrid fertility among gymnosperms on the fact that a possible barrier to crossability and hybrid fertility, namely double fertilization, is lacking in the gymnosperms. The Saxes based their conclusion on the results of a study of certain cytological phenomena in conifers. Briefly, they observed relatively high uniformity within genera in chromosome number and morphology. As lack of uniformity in those phenomena is frequently a barrier to crossability and fertility among angiosperms, they concluded that species differences within coniferous genera are mostly genic; and hence, that differences between many species of a genus may be too small to prevent species crossing and fertility in the hybrids. Those contributions by great scientists, together with various other considerations, were responsible for the sudden shift of emphasis from selection to hybridization at Placerville in 1940.

The possibility envisioned by Dr. and Mrs. Sax is now a well-established fact so far as the pines are concerned. About 40 F_1 hybrids, many of which have already exhibited high fertility, have been produced at Placerville, some of them in considerable abundance. I have no doubt. that similar results will be obtained in most other coniferous genera.

Number of Hybrids Obtainable in Pinus

The practical possibilities obtainable from hybridization in Pinus, as in any other genus, are, in part, a function of the number of different hybrids that can be made. The more the crosses, the greater the possibilities! If all the 66 species recognized by Shaw (6) in his excellent classification of the pines could be crossed with each other, 2,145 F_1 hybrids, and a much larger number of hybrid progenies (F2's, backcrosses, tri-species hybrids, etc., could eventually be obtained. Such a prospect could generate a lot of fanaticism in pine-breeders, among some of whom there may already be too much. Unfortunately, only a small fraction of that number of F1's is likely to be obtained; for crossability is largely a function of closeness of relationship and the relationships between most of the pines are not close. Hence, it will be salutory to get back to earth and make an estimate of the number of crosses that we may reasonably expect to obtain.

Shaw's classification provides a good basis for such an estimate. It recognizes two sections, each divided into two subsections, each of which contains three or more groups of species. It is convenient to regard these groups as relationship groups because, on the basis of similarity in morphological characters, the species within a group are, by and large, more closely related to each other than they are to species in other groups. Assuming that this classification is accurate and that crossings can be obtained between all the species within groups but not between species in different groups, the possibilities would be as shown in Table 1.

The numerical possibilities shown in Table 1 are too high in my estimation. None of the southeastern members of Australes has been crossed to any of the western contingent of that group. Hence, the total for that group is much too high. All attempts to cross the Macrocarpae have failed; a number of crossings in both Lariciones and Insignes have likewise failed, and there is good reason to suppose that the two species in Leiophyllae will not cross. The total for Cembra probably is fairly accurate; for inter-group crossings in that subsection tend to compensate for intra-group failures in it. On the basis of Shaw's classification and our results to date, I should be satisfied with less than 200 crosses.

Table 1. Crossing possibilities in Pinus by Shaw's relationship groups

Section	Subsection	Group	Number of Species			Number of F_1 Hybrids Possible		
			Group	Subsection	Section	Group	Subsection	Section
Haploxylon (soft pines)	Cembra	Cembrae	3	-	-	3	-	-
		Flexiles	2	-	-	1	-	-
		Strobi	7	-	-	12	-	-
			-	12	-	-	25	-
	Paracembra	Cembroides	3	-	-	3	-	-
		Gerardianae	2	-	-	1	-	-
		Balfourianae	2	-	-	1	-	-
			-	7	-	-	5	-
			-	-	19	-	-	30
Diploxylon (hard pines)	Parapinaster	Leiophyllae	2	-	-	1	-	-
		Longifoliae	2	-	-	1	-	-
		Pinea	1	-	-	0	-	-
			-	5	-	-	2	-
	Pinaster	Lariciones	12	-	-	66	-	-
		Australes	11	-	-	55	-	-
		Insignes	16	-	-	120	-	-
		Macrocarpae	3	-	-	3	-	-
			-	42	-	-	244	-
			-	-	47	-	-	246
Total for the genus								276

Mass Production of Products of Breeding

Practical possibilities are also contingent upon the ease and speed with which products can be produced in abundance. Mass production of F_1 hybrids, whether from seed or through vegetative propagation, presents a problem of no little apparent difficulty. The magnitude of the difficulty will vary from case to case, regardless of method. As the rootability of hybrid-pine cuttings remains to be studied, there is no point in dwelling on the possibilities in that field just now. Results obtained at Placerville on the number of sound seed obtainable per pollination bag are of immediate concern. It varies greatly from cross to cross. The maxima obtained for a number of crosses are shown in Table 2.

Table 2. Maximum sound seed produced per pollination bag, Institute of Forest Genetics

Hybrid	Sound seed per bag
P. ayacahuita x *P. griffithii*	75
P. echinata x *P. caribaea*	229
P. echinata x *P. taeda*	432
P. jeffreyi x *P. coulteri*	109
P. jeffreyi x *P. ponderosa*	101
P. monticola x *P. strobus*	184
P. contorta x *P. banksiana*	54
P. ponderosa x *P. engelmannii*	175
P. ponderosa x *P. montezumae*	152
P. rigida x *P. taeda*	130
P. strobus x *P. griffithii*	81

Whether or not such yields would be worthwhile, even if they co could be obtained on the average, depends on numerous relationships which time does not permit me to discuss. Average yields of such magnitudes, however, probably would be highly profitable in some cases.

Nevertheless, production of hybrids from hand pollination could supply only a very small part of the seed needed for planting in the South in the immediate future. Perhaps the main benefit to be expected from planting relatively small numbers of Fl hybrids will be in the large amounts of seed that can be obtained from them. Last fall, we obtained 11,500 sound seed from a single, 16-year old hybrid between shortleaf and loblolly pines.

The Potential Dynamism of Systematic Hybridization

In the foregoing discussion, I have suggested that hybridization is an exploratory process, having highly dynamic potentialities, capable of effecting continuous improvement in products; and I venture to say that, in consequence, some very substantial improvements may be rendered obsolete before they can be utilized on a large scale, just as the dynamism of industry often renders its newest products obsolete almost as soon as they can be marketed. An example of such dynamism may be illustrated by a comparison of several hybrids of ponderosa pine.

The hybrid between ponderosa and Apache pines outgrows ponderosa pine in the habitat of the latter (4). Its superiority is manifested in height- and diameter-growth, foliage production, and probably in root-development as well. The hybrid between ponderosa and Montezuma pines, which was produced later, outgrows the ponderosa-Apache hybrid by a considerable margin in height, but it lacks the early diameter-growth and root-development of the latter. Figure 1 shows a comparison of the hybrids at 2 years.

The tri-species hybrid, which was produced still later by crossing the ponderosa-Apache hybrid with Montezuma pine, equals the ponderosa-Montezuma hybrid in height and, as Figure 2 shows, has greater diameter, to boot.

In Figure 3 are shown a plot of the tri-species hybrid paired with a plot of ponderosa pine.

In Figure 4 are shown the largest ponderosa pine in the entire nursery growing beside the largest of the tri-species hybrids, also at 2 years.

Thus, through a series of crossing, two suggesting a third, we have apparently succeeded in combining the exceptional height-growth of Montezuma pine with exceptional early diameter-growth of Apache pine in seedlings which, presumably, possess some of the local adaptability of ponderosa pine. This tri-species hybrid seems to be highly superior in important respects to two previously-obtained hybrids of ponderosa pine, each of which was sufficiently superior to the ponderosa pine to justify its use in place of that species in at least part of its range. We may well expect many additional instances of such dynamism in hybridization work.

Figure 1.-- From left to right: Pinus montezumae, P. ponderosa x P. apacheca, P. ponderosa x montezumae, P. ponderosa.

Figure 2.--From left to right: Pinus ponderosa, (p. ponderosa a P. apacheca) x P. montezumae, P. ponderosa x P. montezumae, P. montezumae.

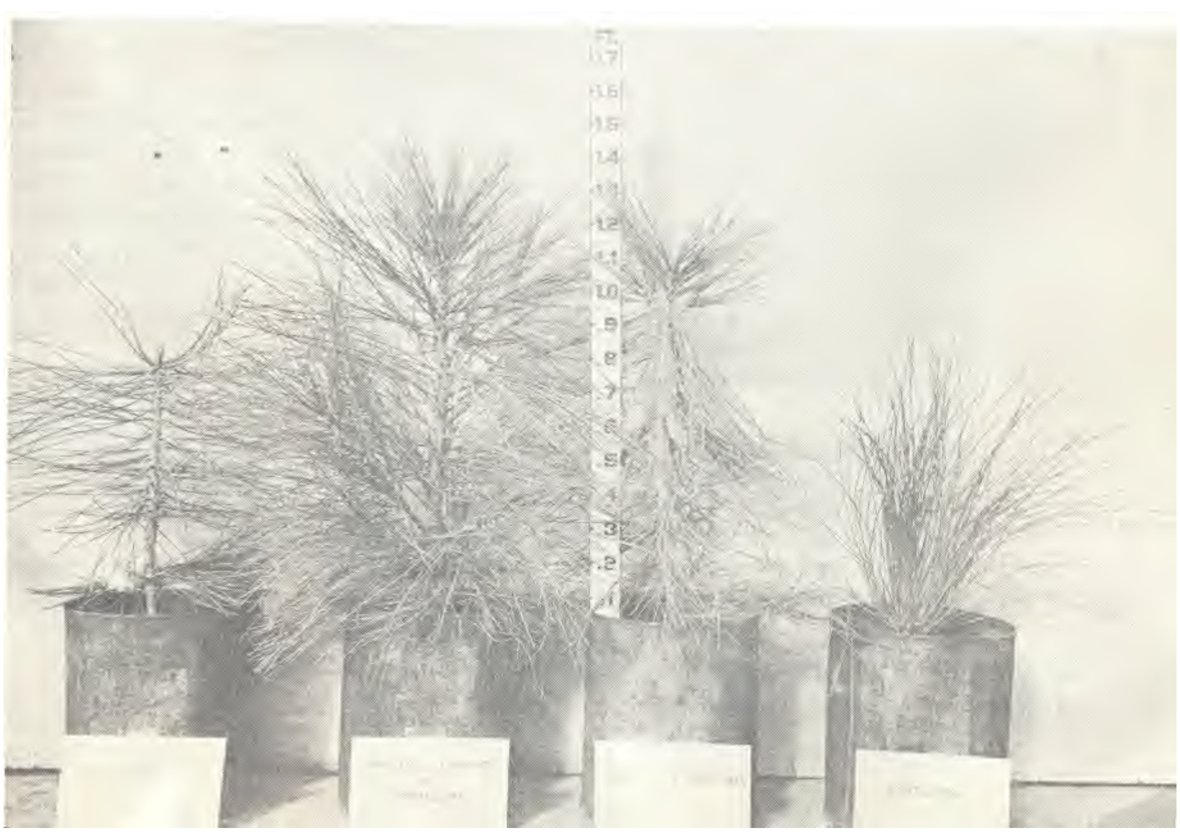

Figure 3.-- Front row: P. ponderosa; Rear: (P. ponderosa x P. engelmannii) x P. montezumae; Age :two years. At one year, there was no difference between the two progenies in height, but the hybrid had a highly significant advantage in diameter.

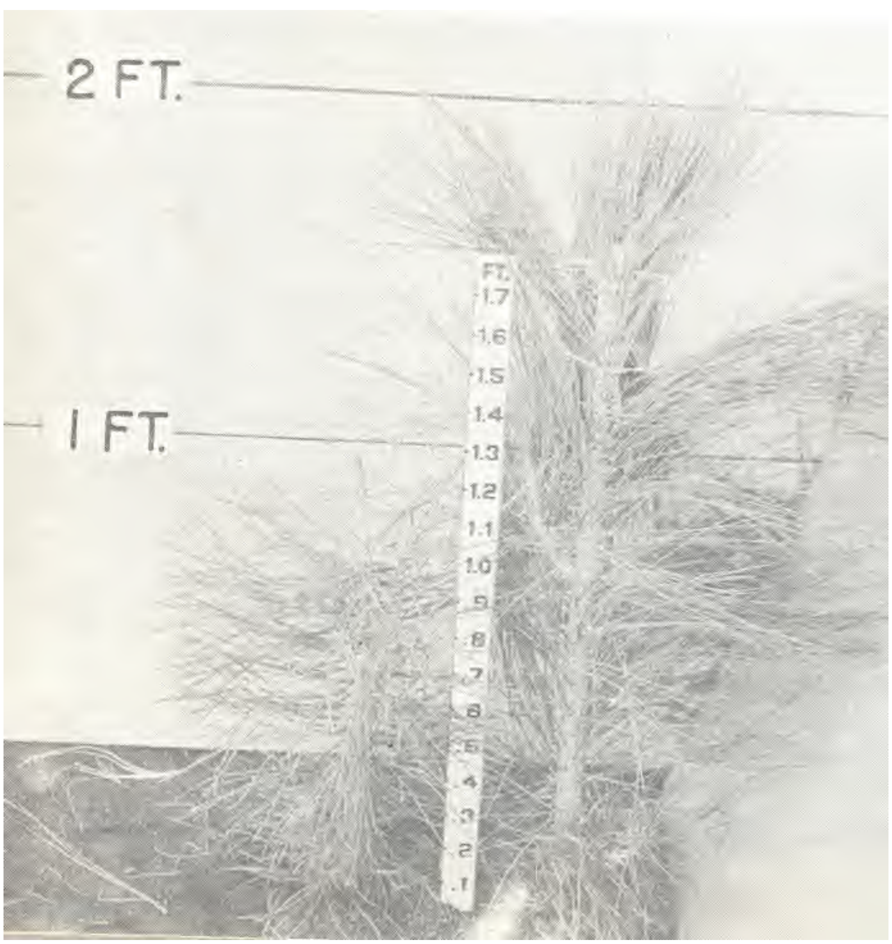

Figure 4.--
Left: Pinus ponderosa;
Right: (Pinus pondersosa x P. engelmannii) x P.montezumae

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