Hybridization - Then and Now?

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Technologies have a way of changing, if they remain important for human welfare and economic development. As new techniques and approaches are tried and adopted, old ones become outmoded. The outmoded approaches retain interest for the historically-minded, but occasionally they may be dusted off and put to use again - witness the dusted-off technology of wood-burning stoves.

I believe it is fair to state that species hybridization has ceased, at least for the present, to be an important approach in tree improvement. Many of today's workers probably ask themselves: "What was all the fuss about species hybridization thirty and forty years ago?" As one of those tree-climbers of forty years ago, I recall the circumstances, compulsions, and rationales that shaped our programs. Some of these considerations are no longer relevant: others, I believe may warrant a renewal of interest in species hybridization on the part of tree imporvement workers.

But first, why did tree improvers devote so much effort to hybridization in the past? It would be accurate to say that ignorance and naivete played a large part, but these are curable human failings, and the curing process is often quite interesting.

Let's start with Germany's, or more precisely Prussia's energy crisis of a century and a half ago. Biomass, as it was not then called, was one way out, and a professor of botany named Klotsch conceived the notion that if trees could be made to channel the products of photosynthesis largely or exclusively to wood production rather than diverting them to reproductive tissues, they would be much more useful. The conventional wisdom in Klotsch's day was that hybrids were generally sterile, so he proposed to produce sterile hybrids by interspecies crossing, and one of his trials was an attempt to cross *Pinus sylvestris* with P. *nigra.* He reported that he made the cross, one fine spring in the 1840's, and in the autumn of the same year collected the resulting seed, which duly germinated and produced plants which exhibited hybrid vigor. His work has been cited more frequently than it has been read with care, and as one of those who cited it has written: " - - no further experiments were made and his pioneer work fell into oblivion".

But species hybridization in forest trees did occur, if not by design, then by accident. The accidents occurred in botanical gardens and on large estates where allopatric species were brought together. Some ex-

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amples are the London plane (involving *Platanus orientalis* and *occidentalis*), the Dunkeld larch (*Larix decidua* and *kaempferi*) and the red horsechestnut (*Aesculus pavia* and *hippocastanum*). The latter eventually proved to be of exceptional interest since it was shown to be an amphidiploid and as such is more or less true-breeding. It is worth noting that two of these hybrids are horticultural successes; the London plane is widely used as a city and garden tree, but its parents must be sought in their native haunts. Red horsechestnut has not displaced *Aesculus hippocastanum* as a street and garden tree, but is nevertheless widely grown. The hybrid larch has been produced in large numbers by mass pollination, largely at the instigation of Syrach Larsen, and has been found valuable as a forest tree in Denmark.

These three examples, although of little direct relevance to forest tree improvement practice in this country, were among the stimuli to forest tree breeders here fifty years ago. Other stimuli were the *Salix* hybrids made by Heribert-Nilsson and the *Populus* crosses of Augustine Henry. These roused the interest of A. B. Stout of the New York Botanical Garden, who, with the assistance of E. J. Schreiner and the support of the Oxford Paper Company in Maine, started, in 1924, the first systematic tree improvement program in this country, concentrated on the genus *Populus*. This program, as a consequence of progress in pulping technology and economic stress in the 1930's, eventually gave rise to the forest genetics project of the Northeastern Forest Experiment Station under Schreiner's direction.

At the Northeastern Station, work with *Populus* continued at a reduced intensity, while the scope of the project was expanded to cover most of the enera, broadleaved and coniferous, native to the region. The project could not be accurately termed a tree improvement effort; it was rather, and quite properly, involved in exploring the reproductive biology of forest trees, the technology of control of parentage, and propagation. Species hybrids in *Acer*, *Betula*, and *Quercus* were produced before 1942, and after 1946 in Picea and Pinus.

In 1925, the Eddy Tree Breeding Station, later to become the Institute of Forest Genetics, was established in Placerville, California. Its program was early concentrated on the genus *Pinus* and the first major activity was the assembling of a world-encompassing arboretum of pine species. Before this arboretum reached an age to permit a comprehensive program of species crossing, two hybrids were made on indigenous trees in 1927. The first was the *attenuata* x *radiata* cross, reproducing a natural hybrid found in at least one location in coastal California. The other was the *ponderosa* x *engelmannii* cross. Meanwhile, the emphasis shifted to assembling a comprehensive provenance collection of P. *ponderosa* and two open-pollinated progeny tests of *ponderosa* from a wide range of elevations in a restricted region of the central Sierra Nevada. By 1942, the program emphasis had reverted to species hybridization. Among the trees assembled in the arboretum at Placerville are several southern pine hybrids made by Phil Wakeley in the early 1930's.

From our present perspective, it is not too clear why forest geneticists of 50 years ago put in so much effort on species crossing and so little on selection in native population. To understand their reasoning, we have to remind ourselves of the "state of the art" (to use a current cliche) at the time. Much work in cytogenetics and plant breeding dealt with polyploidy and its artificial induction. It was thought that hybrids which combined the desirable properties of the parent lines or species could be made into true-breeding amphiploids by colchicine or other polyploidy-inducing treatments. It turned out that in the pines, at least, colchicine-induced polyploids were dwarfs of greatly reduced viability. At the same time, selection theory was barely off the pages of the works of Fisher, Wright, and Haldane and far from the practical application given impetus by Lush and others. It is true that improvement by selection is an ancient art, but the attention of forest geneticists of the 1930's was attracted by current and exciting work in cytogenetics rather than by applied plant breeding. Moreover, the few localitieswhere forest geneticists were at work provided little in the way of extensive even-aged stands of simple species composition. To be sure, one of the motivations of the tree hybridizers was that the variation to be found in F_2 and subsequent generations would be utilized in selection programs. Schreiner, for example, frequently wrote and spoke of "hybridization and selective breeding" as linked activities.

Then there was the expectation of realizing hybrid vigor. Indeed, embryological studies by Buchholz at the Institute of Forest Genetics demonstrated in the early forties that at least one pine cross (contorta x banksiana) resulted in embryos which developed faster than those resulting from open pollination of lodgepole pine. Eventually it became clear that hybrid vigor in forest trees, expecially in those cases where the parent species are allopatric, is difficult to define. Nevertheless, several species crossings in the white pines supported the notion that crosses between closely related but widely allopatric species are likely to result in vigorous offspring.

So far, I have attempted to give what might be termed the reasonable or respectable rationale for early programs of species crossing. There were other motivations as well. Simple minded as it may sound, success in producing recognizably hybrid progenies was an important validation of the techniques being worked out. Moreover, the plain delight at producing something new was a reward for the sometimes strenuous work involved. Both Schreiner and Righter enjoyed climbing trees - in Righter's case, the bigger the better, and in the Sierra Nevada, there are some big pines. Finally, the ability to exhibit hybrids readily recognized as such was used as a demonstration that forest trees, like agricultural plants, were subject to genetic manipulation by plant breeders. Because this notion was not at first widely accepted, these demonstrations were important in securing continuing support for programs. These "tree shows" as they were termed by Syrach Larsen, a master at the promotion of forest tree breeding, were short on experimental design, but long on audience appeal.

Species crossing in the pines has had one spin-off not directly relevant to tree improvement. As the number of recorded species hybrids in the pines increases, it appears that species crossability is one indicator of relationship, and this is of interest to pine taxonomists. Much remains to be done in quantifying degrees of pine species crossabilities along the lines laid down by Jens Clausen and his colleagues working with wild herbaceous plants in California, and summarized in his 1951 work on the Evolution of Plant Species.

So much for species hybridization as a curtain-raiser for present-day tree improvement activities. What part does it play today, and what role can it have in the future?

A most striking utilization of the strategy of combining useful properties of two species is the work of Hyun in South Korea, where thousands of hand pollinations in existing scrubby plantations of *Pinus rigida* produced operational quantities of *rigida* x *taeda* hybrids. These were of practical value in an environment where the seed parent contributed hardiness and the pollen parent good stem form. Recent reports from South Korea suggest that wind pollinated F_2 and back-cross progenies of the original F_1 are quite satisfactory in form and hardiness.

Nikles, in Queensland, is reporting that on swampy sites, of which there are large areas, the cross between P. *elliottii* and *caribaea hondurensis* is outgrowing both parents. He is also finding that the nominal F_2 populations from seed orchards constituted of F_1 hybrids are quite usable even though somewhat inferior, in terms of variability, to the hand-pollinated F_1 populations.

What is common to these two instances is the fact that both parent species are exotic to the sites where the hybrids out-perform them. In a sense, as Nikles puts it, these hybrids are finding hybrid habitats hospitable.

At first sight, it appears that what we call the "southern pine region" is not likely to provide "hybrid habitats" for pines, since our commercial species are not exotic, and, in general terms this appears to be the case. But, on the ground, the "southern pine region" is not the homogeneous environment portrayed by the large green area shown on the maps. Moreover, foresters have found that some of the hardwood and mixed forest sites of the south can produce useful pine stands. It seems likely that as finer tuning is applied to the technology of suiting planting stock to site, reliance on the "big three" pines - loblolly, shortleaf, and slash - will become less pervasive, and that hybridization may be involved to some extent in the pedigrees of the planting stock.

There is a nagging practical question about the direct use of hybrids, namely cost of production. Hyun solved this problem by giving hordes of school children some healthy outdoor exercise, but one may speculate that this may have proven a short-term solution and certainly one hard to duplicate here. I suspect that despite the general effectiveness of southern pine seed orchards in producing seed, most seed orchard operators are less than completely satisfied with the practice of leaving the matchmaking to the vagaries of flowering times of individual clones and the weather. Moreover, it takes strong faith to believe that what goes on in a multiclonal seed orchard - or even a multi-family seed orchard - remotely approaches panmictic crossing. What I am suggesting is that, leaving aside for the moment the question of mass production of hybrids, single-species seed orchard technology will be greatly strengthened when the technology of mass low-cost artificial pollination is more widely used. Bruce Devitt in British Columbia has developed mass pollen handling techniques for supplementing the natural pollination in a Douglas fir seed orchard. When this technology, which should be much easier in the pines, comes into wide use, it will become a bit more practical to talk about the operational use of F_1 species hybrids.

There has been reluctance to use the nominal F_2 and backcross populations resulting from open pollination within F_1 populations. To some extent this reluctance derives from the observed variability in these F2 populations, but I suspect that it is also caused by consideration of the textbook examples of F_2 segregation following the original hybridization between established varieties or pure lines. The situation may prove to be less unfavorable in the case of wild species hybridization. To work both sides of the street, one may argue that considerations of cost of open-pollinated F_2 relative to controlled-pollinated F_1 seed, added to the silviculturally questionable value of a high degree of uniformity in forest stands, make F_2 and backcross populations worth considering in operational plantations.

In the west, at least, we hear a bit about the "clonal option", to use Bill Libby's phrase. To date, vegetative propagation techniques for our commercial conifers have not reached an operationally feasible stage, but the technology of producing container-grown seedlings in quantities and at costs competitive with bare-root nursery stock may soon be mated to rooting techniques to multiply hybrid - or other - clones for operational plantations. The clonal option is not new, even in forestry, as it has been the mode of operation in poplar plantation technology for at least a century in southern Europe. The disasters that plague poplar clonal monoculture are an object lesson one hopes will be heeded when the use of conifer clones becomes generally feasible.

The direct operational use of hybrids may be much less important in tree improvement, in the long run, than the use of hybrid derivatives to provide the materials for selection. So far, there seems to be no evidence that tree improvement programs in this country have started to run out of usable heritable variation within species, but it would seem prudent to get at the job of stockpiling species and provenance hybrids in various environments. After all, it is probably not accidental that most of our oldest and most indispensable agricultural crop plants have considerable hybridization in their pedigrees.