MAXIMUM GENETIC IMPROVEMENT OF FOREST TREES THROUGH SYNTHETIC MULTICLONAL HYBRID VARIETIES

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INTRODUCTION

I have deliberately, and perhaps somewhat arbitrarily, chosen to present this paper here in Dunkeld Larch No. 19--at the end of a field tour during which the individual superiority of the named trees has been pointed out, beginning with the NORTHEAST and ending here with the GIANT in 19 (figure 1).

Look around you. There are few trees in this plantation of Dunkeld hybrids that approach the growth-rate and form of the GIANT., Perhaps this is fortituous. Since the GIANT is a seedling on a single micro-site, we cannot be sure that it is inherently superior to some of the fine trees in this stand. tut if as we suspect, the GIANT is an exceptional genotype, we cannot hope to use this tree as a parent for the production of genetically improved seed for commercial use without adulteration of its inherent potential,

My intent is not to discuss expected genetic gain in improved seed-reproduced varieties, but rather to point out once more that the multiplication of the rare and exceptional genotypes for commercial use WITHOUT DILUTION OF THEIR GENETIC POTENTIAL will require asexual propagation,

FOREST TREE BREEDING METHODS

Forest tree improvement programs too often have been narrowly oriented toward selection and breeding within a single native species. For forest trees it is not the species, it is the genus that--through selective interspecific hybridization--will provide the maximum diversity of genotypesneeded for maximum genetic improvement(Schreiner 1960, 1963a).The breeders of agricultural crops did not start with a single wild species; their foundation stocks were ancient mixtures whose ancestry is still open to debate. And to these stocks they are still adding wild types for improvement of particular characteristics.

Some system of pedigree breeding, including both intra- and interspecific crosses, will probably continue to be the method most generally used for the genetic improvement of forest trees. Inbreeding, where possible, usually provides the most rapid method to intensify and fix inherent characteristics and to determine the mode of inheritance, Backcross breeding also is highly effective for determining the mode of inheritance, and for transferring one or two simply inherited characters to an otherwise desirable type.

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However, it is becoming more and more apparent from practical agricultural crop breeding and from quantitative genetics that for maximum, long-term improvement of forest trees it will be necessary to initiate mass-pedigree breeding systems (appropriate to the genus) as soon as possible. This will not eliminate the need for individual-pedigree breeding (inbreeding, backcrossing, and so forth).

Figure 1.--Cooxrox Forest. The GIANT seedling in November, 1935. After 30 growing seasons, the tree is 14.4 inches d.b.h.; 76 feet tall. This is from Seed Lot E-207, an F_3 hybrid larch "from the original station, Dunkeld in Perthshire".

The scars on the tree to the left are the result of scraping from blow-downs during the great wind of 1950. (Photo by F.C. Chambers.)

IMPORTANCE OF CLONAL PROPAGATION

For many years I have stressed the importance of the clone for forest tree improvement, and the need for basic research to develop economical methods for clonal propagation of forest trees on their own roots (Schreiner 1939, 1957, 1960, 1963b, 1963c). The almost phenomenal economic importance of hybrid poplar in northern Italy exemplifies the advantages for rapid genetic improvement if superior genotypes can be utilized commercially as clones.

The introduction of the American cottonwood (*Populus deltoides*) into the Po Valley in northern Italy about 1790, and of the older European hybrids somewhat later, set the stage for extensive natural hybridization with the native black poplar (*P nigra*). By 1928, when epidemic spring dieback--and to a lesser degree leaf rust-- threatened to eliminate profitable poplar culture. innumerable natural hybrids were available throughout the Po Valley. This natural hybrid population, the product of a 100 or more years of natural cross-breeding, represented many kinds and degrees of intercrosses between hybrids and backcrosses, particularly to the originally abundant *P. nigra.*

The present profitable poplar culture in northern Italy is attributable in large measure to clonal selections from open-pollinated progenies of superior phenotypes of this natural hybrid population, made by the late Professor Piccarolo and his associates at the Institute for Poplar Research at Casale-Monferrato (Schreiner 1959). In the early years the Institute grew more than 20,000 seedlings per year for nursery selection. in some years as many as 100,000 The most vigorous seedlings that were resistant to spring dieback, leaf rust and other diseases were tested for rooting ability. After 2 years the very best from the standpoint of growth vigor, disease resistance, rooting ability and tree-form were planted in a selection arboretum and multiplied for 10- to 20-year clonal tests in plantations established by cooperators !private landowners) in various localities. Several ramets of a clone were planted in each test plantation, and as the trees reached merchantable size the best clones in these plots have been selected for commercial planting. It should be noted that these plantations have been a source of profit to the landowners while these clones were being tested.

The need for cheap methods of clonal propagation of all agricultural plants has been strongly advocated by Twamley and Christie (1964). The following quotations from their paper are most pertinent to this discussion:

> "One of the most exasperating and frustrating experiences that plant breeders the world over commonly encounter is their inability to capitalize fully and cheaply on the really superior germplasm that passes through their hands. This situation is confined to no one crop and to no one breeding method but rather is common to all."

Their example of alfalfa a cross-pollinated perennial in which the very best germplasm is not being utilized should be of particular interest to us as we sit here and observe the few superior individuals in this hybrid larch plantation, particularly the GIANT

> "Not only in alfalfa but in all crops belonging to this breeding type, the situation is even more exasperating. Rare indeed must be the forage breeder who in the course of his work has rot run across a few individual plants which stood out among their fellows as a giant among men. The plant breeder's frustrating inability to capitalize on this unique germplasm lies in two sources The plant owes its outstanding superiority to a rare combination of genes many of which are in the heterozygous state. In the

process of meiosis this superb combination is broken up, probably never again to be reconstituted. In addition, the plants with which this outstanding individual is forced to mate for the production of offspring are bound to be inferior to it. And so, instead of being able to capitalize fully on the really superior germplasm at his disposal the forage breeder is forced first to shatter it and then to dilute it He thus ends up with a variety containing a population that is variable in yield, maturity, persistence, disease resistance, seed production, etcetera, and not particularly outstanding in any one of them."

"When the technique of inducing apomixis at will is developed--as it will be by someone in the not too far distant future--the revolution that occurred in corn production with the advent of the double cross system will be repeated, not in one species, but in every crop species in existence and in some synthetic species not yet in existence. When this happens, when our superior germplasm is utilized instead of dissipated, two plant breeders' dream will come true."

SYNTHETIC MULTICLONAL HYBRID VARIETIES

At present there are few forest trees that can be propagated as clones for commercial planting. Nevertheless, I predict that we can and will develop practical methods for clonal propagation of our important forest trees in order to speed and maintain maximum improvement through what I have called "synthetic multiclonal hybrid varieties" in a summary paper for the Proceedings of the NATO and NSF Advanced Study Institute on Genetic Improvement for Disease and Insect Resistance of Forest Trees, held at The Pennsylvania State University in 1964 (Schreiner 1966). These are analogous to, but genetically different from the mulilineal hybrid varieties" and the "synthetic corn varieties.

A synthetic multiclonal hybrid variety would be a <u>mixture of many genetically superior hybrid clones</u> sufficiently similar in their growth requirements to be grown in random mixtures. The breeding system to obtain multiclonal hybrid varieties should follow the same general pattern of selective intraspecific breeding, species hybridization, controlled sib- and backcrosses, and recurrent mass selection as for the development of synthetic varieties to be propagated by seed. But there would be a difference in the nursery procedure and the progeny tests.

The selected seedlings (F_1 and later generations) would be released from competition and grown in the nursery beds, or preferably in a transplant nursery, long enough to produce enough ramets for replication of at least 2-tree clonal plots in several regional progeny tests. This would increase the size of the progeny test plantations, but they would then become not only progeny tests but also clonal tests, and by proper roguing, gene pools of superior genotypes. These gene pools would be the source of superior clones for use in the synthetic multiclonal hybrid varieties and for continuing individual- and mass-pedigree breeding.

When necessary, the clones in a multiclonal hybrid variety could be changed on very abort notice, because the breeder could multiply superior genotypes for commercial use <u>without adulteration of the genotype, and without determining their combining ability to transmit the desirable qualities or characteristics.</u> When individual clones in a synthetic multiclonal hybrid variety began to lose their value, due to increasing disease or insect susceptibility, lack of local adaptability, decline of general fitness due to long-term climatic changes, or to change in industrial use requirements, they could be replaced by new clones selected from the appropriate regional gene pool.

The genetic improvement of clones selected for commercial use can be estimated directly from the clonal means broad sense heritability (clonal heritability) is not needed. If the clones are to be used for controlled breeding to establish new lines, then heritability in the narrow sense may be useful.

ESTIMATE OF TIME REQUIRED FOR GENETIC IMPROVEMENT

Following is an estimate of the time required to complete one breeding cycle in the production of synthetic seed varieties, and to produce first-cycle ortets for commercial propagation of synthetic multiclonal hybrid varieties.

Synthetic Varieties for Propagation by Seed

Depending on the growth rate and reproductive habit of the species, the inherent characteristics or qualities to be improved, and assuming the availability of a sufficient number of parent trees. the time required for reasonably effective selection of parents for the first controlled sibbing and backcrossing (one breeding cycle) might be approximately as follows:

From original pollination to seed	1 to 2 years
Nursery screening	1 to 4 years
Evaluation of progenies and individuals in the regional progeny tests	8 to 20 years
Total time required for completion of one breeding cycle SELECTION OF PARENTS FOR FIRST CONTROLLED SIBBING AND BACKCROSSING, OR FOR MASS-PEDIGREE BREEDING	10 to 26 years

Synthetic Multiclonal Hybrid Varieties

On the same assumptions as above, the time required to produce improved, locally adaptable, ortets for commercial propagation as multiclonal hybrid varieties from the first breeding cycle might be approximately as follows:

From original pollination to seed	1 to 2 years
Nursery screening and propagation of selected ortets for 2-tree clonal plots in regional progeny tests	3 to 7 years
Evaluation of clones in the regional progeny tests	6 to 15 years
Total time required to produce FIRST-CYCLE SYNTHETIC MULTICLONAL HYBRID VARIETIES FOR COMMERCIAL PROPAGATION	10 to 24 years

URGENT NEED FOR BASIC RESEARCH ON VEGETATIVE PROPAGATION

The possibilities of multiclonal hybrid varieties for early improvement through the use of unadulterated superior genotypes, and for continuous, practically annual, flexibility of the clonal mixtures to meet changing conditions, bring me again to the need for research on the vegetative propagation of forest trees

Plants can be propagated vegetatively in many ways such as graftage, cuttage, and various layering methods including air-layering All forest trees can be grafted, and they can be propagated with varying success to produce plants on their own roots. Clonal propagation (including grafting) is still considered too expensive for the production of forest planting stock of all but a very few commercially important timber trees, For a specialty crop such as Christmas trees, the use of grafted planting stock may be economically feasible (Schreiner 1963b).

Grafted stock has been used for various aspects of forest tree improvement research. If grafted trees are used either for research or for commercial forest planting, there must be assurance that the rootstock does not have a direct or indirect effect on the scion, There are many references in the plant science literature on the effect of the stock on the scion. Awad and Kenworthy (1963) have reported that significant differences in leaf composition between trees on different rootstocks were obtained for K, P, Ca, Mg, and Cu Young and Olson (1963) from their studies on eight scion-rootstock orchards exposed to a severe freeze in January 1962 in the Rio Grande Valley, reported that certain mandarin rootstocks induced more cold hardiness than other rootstocks when used for four citrus clones.

For both research and practice we need to develop economical methods for clonal propagation of all important forest trees on their own roots. I am convinced that this will be possible, but I doubt that the answer will come by continuing the past and much of the present empirical approach; this problem requires fundamental research.

For the pines the answer may come through rooting needle fascicles. This method is not new: an old propagator at The New York Botanical Garden, who was rooting fascicles in the early 1920s, told me that he learned the method as a young apprentice in Europe. A primary difficulty in production is the dormancy of the buds below the terminal fascicles. This dormancy is being investigated in several countries.

The production of cuttings (or scionwood) poses a problem for clonal propagation of conifers to which experience with shearing of Scotch pine Christmas tree plantations to produce multiple shoots may provide an answer. Annual shearing of widely spaced mother trees could provide at least 50 to 100 cuttings (or scions) per year at 6 to 10 years of age; 100 such trees would produce 5,000 to 10,000 per year. If, eventually, needle¯fascicles are used as cutting-stock for clonal propagation, small, clonal "mother-blocks" will supply a large amount of propagating material.

And as a final recommendation for basic research on clonal propagation of genetically superior forest trees, I urge investigation of methods to utilize apomixis (agamospermy), reproduction by seed without fertilization. Although a large amount of literature on apomixis in plants has accumulated during the past 100 years, very little of this has concerned forest trees. Two broad avenues of approach should be investigated: (1) the induction of agamospermy in forest trees that normally reproduce sexually; (2) an intensive search for genes that could be used in breeding for agamospermy.

The second approach is being followed most intensively by forage breeders. They have had considerable success with buffelgrass in the development of breeding systems utilizing genes for apomixis that will permit the economical production of apomictic F_1 hybrid varieties,

On the basis of present knowledge, the second approach, the search for apomictic individuals for use in forest tree breeding appears more promising, particularly for our broadleaf species, than induction of agamospermy Our breeding work with birch in the late 1930s indicated such possibilities, Allen (1942) reported that although his data was limited it did indicate that parthenogenesis , although uncommon, is possible in Douglas-fir.

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