III. IMPROVEMENT THROUGH BREEDING AND HYBRIDIZATION

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POSSIBILITIES OF INBREEDING, SELECTIVE INTRASPECIFIC BREEDING, RACIAL AND SPECIES HYBRIDIZATION, AND POLYPLOIDY

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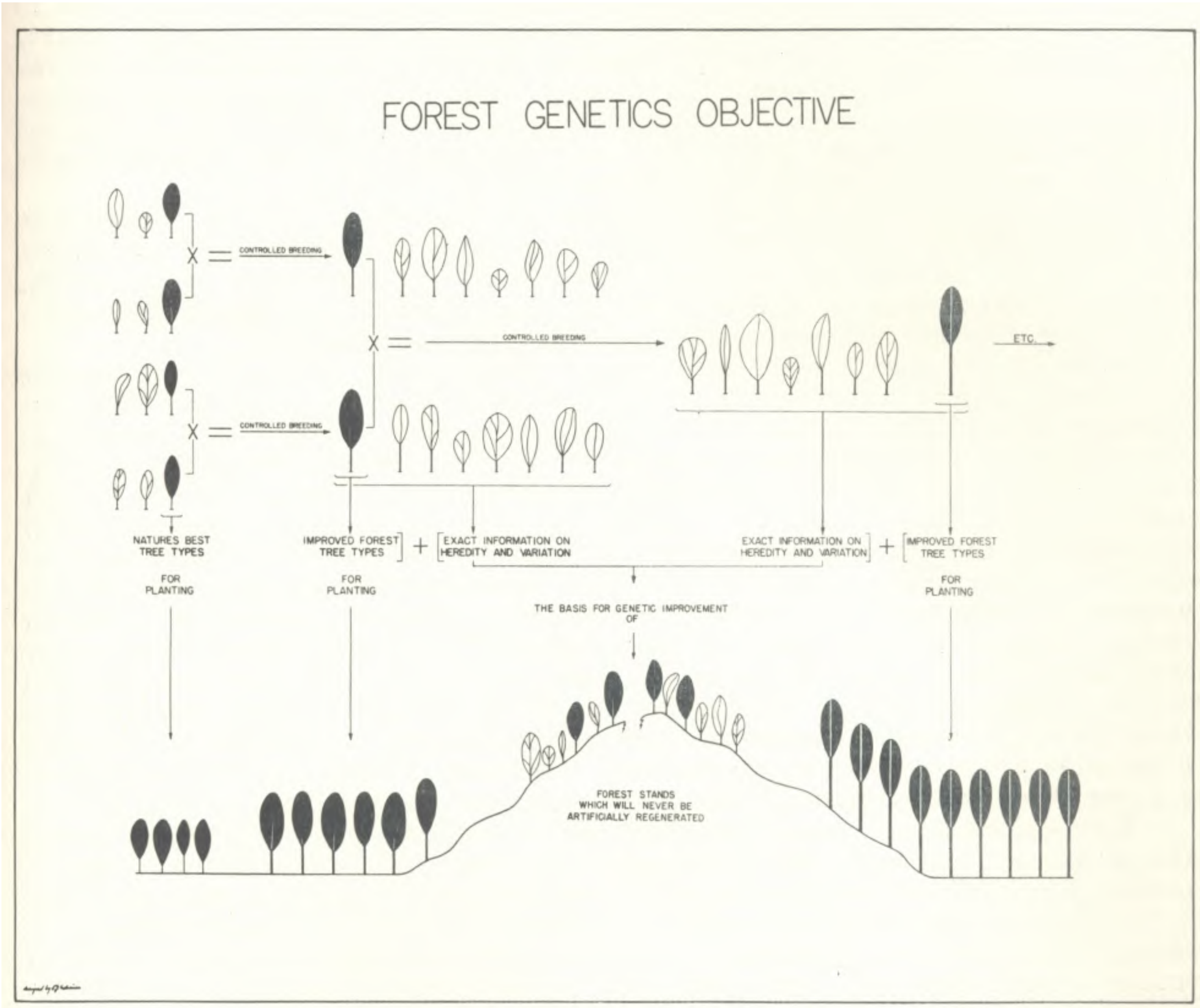
This must be a rapid surrey of a very broad field. As an introduction I wish to refer once more to objectives. Although our discussions have indicated that the specific objectives of forest genetics may be extremely diverse, genetics in relation to forestry implies two broad objectives. Since 1938 we have used this wall chart to picture the two-fold objective: 1. Production of improved forest trees for forestation. 2. Genetic improvement of native forest stands that are managed under a system of natural regeneration. The chart is intended to indicate that if we can make a better tree than Na-ture provides we may expect land owners to plant a little further up the hill of "inaccessibility". This hill represents the millions of acres of forests where we must depend upon natural regeneration. It is in those forests that we should apply genetical mass selection which will require exact information on the mode of inheritance. It is not enough to know that a character is inherited; we must also know what percentage of the progeny can be expected to inherit that character. Both of these objectives require controlled breeding experiments.

Inbreeding.--Where self-pollination is practicable it usually provides the most rapid method for intensifying and fixing inherent characteristics. Crossing of such inbred lines can provide a uniform and vigorous hybrid pro. geny. This is the method used for commercial production of hybrid corn seed. Inbreeding is also the most rapid procedure to determine the mode of inheritance for many characteristics.

In forest trees the possibilities for inbreeding will be limited by self-incompatibilities in many species, but there is evidence of some degree of self-compatibility in at least some trees of larch, spruce, pine, hemlock, yellow-poplar, birch, elm, and alder. In most cases the sell-compatibility is very low and the selfed progenies grow very poorly. Inbred lines of larch, spruce, birch, and alder are being studied in Europe. We have one selfed line of yellow-poplar. Although the possibilities appear to be limited, we should continue to seek out self-compatible individuals and develop selfed lines in as many species as possible.



<u>Selective intraspecific breeding</u>. --Controlled breeding of selected individuals of the same species is generally the easiest method to maintain, combine, or intensify the desirable characteristics of the selected parents. It can provide improved types for planting, and will provide the information on mode of inheritance which is needed for the application of mass selection in our forests.

The use of elite, so-called "plus" trees in clonal seed orchards was covered in the preceding discussion on selection of wild types. Since trees of the same species usually cross easily and produce abundant fertile seed, selective intraspecific breeding will often be the most certain method for the early production of improved seed in commercial quantities. Plantings of selected intraspecific progenies of native species also involve a minimum risk for the forest owner. The progenies of local selections particularly can be expected to be well adapted to local environmental conditions. The need for progeny tests to determine the breeding quality of the selected clones used in seed orchards have been mentioned. Information on the blooming habit, cross-compatibilities, and fruitfulness of the parent clones will also be required. Even a small difference in blooming time could prevent natural crossing between selected parents. Selective intraspecific breeding is a safe and fairly certain improvement procedure, but hybridization offers greater possibilities, particularly for maximum increase in growth rate.

Hybridization.--As used here the term hybridization will be limited to racial and species crosses. During the discussion of objectives I called attention to the present and continuing importance of inherently rapid growth. There is evidence that in some of our most important forest genera hybridization is the shortest and most effective route to this goal.

Races of the same species are usually interfertile. Since racial hybrids may possess hybrid vigor it is possible that some of the reported vigorous progenies derived from intraspecific crosses between selected trees, particularly selections from different parts of the natural range, represent such racial hybrids. Racial hybridization will be relatively easy. In addition to possible hybrid vigor it may be expected to give the same type and degree of improvement, through intensification or combining of desirable characters, as selective (intraracial) breeding. Species hybridization appears to offer the maximum improvement possibilities, particularly for the production of faster growing types. Hybrid vigor has been reported for some species crosses in many forest tree genera. There is evidence from poplar and other hybrids that species hybridization can combine hybrid 'vigor with such characteristics as timber form, hardiness, disease and insect resistance, literally in one step. It can also produce new characteristics, (apparently even new wood qualities) as a result of combinations of germplasm never before combined in nature.

First-generation species hybrids can be sufficiently uniform to permit mass production of seed and seedlings for commercial forestation. Hybrid planting stock of the European aspen (Populus tremula) and the American aspen (P.tremuloides) are being produced on a commercial scale in both Denmark and Sweden. Seedlings of intraspecific crosses between selected (plus) trees of Populus tremula have also been available in Sweden on a commercial scale. At present there is practically no demand for the plus-tree progenies because the growth rate of the species hybrids has been so much better. There is also evidence that a naturally regenerated, second-generation hybrid stand can equal the growth rate of the parent hybrid plantation. The Institute of Forest Genetics reports that although there is great variation in the F_2 progeny of the hybrid Pinus attenuradiate, a sufficiently large number of these trees (approaching 50 percent are as good as the F_1 hybrids. This percentage of vigorous trees is more than ample for natural restocking.

Obviously, hybrid vigor is not the sine qua non for all forest tree improvement. Some promising hybrids have been reported (particularly in Pinus and Betula) that are intermediate in growth rate between the parent species. Between 1937 and 1940 we obtained hybrids between grey birch (B. populifolia) and paper birch (B. papyrifera). At five years the average height of the hybrids was intermediate (5.5 feet) between that of the parents but 40 percent better than paper birch (3.8 feet). There is the possibility that we can combine the aggressiveness of a commercially worthless pioneer species (grey birch) with the wood quality of the paper birch in hybrids that grow 40 percent better than this valuable parent species.

Essential improvement is also possible through hybridization, without any increase in growth rate over that of a valuable native species, by com the widely different characteristics of individual species. Promising hybrids produced at the Institute of Forest Genetics indicate that the growth rate and timber form of our eastern or western white pines can probably be combined with the blister-rust resistance of the Balkan white pine.

Time does not permit a recitation of all the promising species and racial hybrids that have been produced in this country and in Europe. From the standpoint of forest tree improvement they presently outnumber and excel the results of selective breeding.

On the basis of our present knowledge, the possibilities of species hybridization appear to be limited for some forest genera such as ash and oak. Admittedly hybridization must not be our only approach to forest tree improvement. My colleague, Jonathan Wright, reminds me at least once a week that for every promising hybridization we can find a hundred failures. I agree; the odds may be even higher. But for many species the greater, and in some cases immediate improvement possibilities through species (and racial) hybridiz ation as compared to selective intraspecific breeding, warrant a higher risk of failure. There is additional justification in that the odds may be no better for economically important improvement through selective breeding.

The commercial use of hybrids which have not been tested for at least one complete rotation will involve a higher risk to the grower than the use of similarly untested types derived from selective breeding within local races. In their commercial use of aspen hybrids, Danish and Swedish foresters are accepting this risk because of the rapid growth (anticipated shorter rotation) of the hybrids.

The use of hybrids in practice is very simple if vegetative propagation from cuttings is possible; excellent new hybrids can be multiplied and used immediately as clones. Hybrid aspen seed can be commercially produced on cut branches in a greenhouse. Parent species which bloom at the same time can be established in seed orchards for natural hybridization, but differences in blooming time will limit the use of such "hybrid" seed orchards. At present many hybrid combinations seem impractical. Some of them may never he economically feasible, but practical uses will surely be developed for most of the really excellent hybrid combinations that are discovered.

Polyploidy. --Many valuable types of cultivated plants have arisen through an increase in the number of chromosomes. Polyploidy, duplication of the chromosomes in multiples of the basic number, occurs naturally and can be induced artificially by various means. Polyploidy may result in greater vigor, larger cells, new variations, and--in special cases--true-breeding types.

The natural triploid aspens (three sets of chromosomes) which were found in Sweden are more rapid-growing than the normal diploids (two sets of chromosomes). Triploid aspen seedlings have been produced on a large scale in Sweden by crossing diploids with tetraploids (four sets of chromosomes). These triploid progenies have been extremely variable in growth rate; some in dividuals are practically dwarf types. Although the best individuals of these diploid x tetraploid progenies are as vigorous as the European-American hybride their average growth is not sufficient to bring them into competition. with the species hybrids. These preliminary results in Sweden do not rule out the possibility of usable seed progenies of triploid aspens. Uniform triploid progenies have been produced in cultivated plants and probably can be produced with forest trees. Clonal propagation would provide an immediate solution. A cheap method of vegetative propagation is needed for multiplication and immediate use, not only of the best triploid, but also of the best hybrid aspens.

Since the chief product of the forest is wood we must consider the effect of increased cell size that usually results from polyploidy. An increase in fiber length and diameter, and a decrease in wood density may be expected in rapid-growing polyploids. This will enhance the wood quality for some uses and depreciate its quality for others.

Polyploidy offers early improvement in growth rate in aspens and possibly in several other important genera such as maple, birch and ash. There is, however, no good assurance that commercial planting of new, untested polyploids of a native species will involve less risk than racial or species hybrids involving a native parent.

In conclusion I wish to point out that there is no best procedure for the improvement of all our important forest trees. For some species all of the above breeding methods will be useful, for other species only one approach may be practical.