CHAPTER 20
METHODS OF TREE BREEDING AND THEIR CHARACTERISTICS

In addition to choosing among several objectives when tree breeding projects are established, decisions have to be made in regard to specific traits to be improved and, what is equally important, the method or methods of breeding to be used. Improvement in crop plants may be achieved in many different ways, but all methods of breeding do not apply equally well to southern pine problems, and the advantages of each method have to be balanced against the disadvantages. Also, the tree breeder may have an opportunity to use several methods simultaneously or to combine several methods. Methods of tree breeding must be evaluated on the basis of genetic and tree breeding principles and, most importantly, on the basis of the species and traits with which the work is to be done; cultural practices and forest products must also be considered. A good method of breeding, in general, may not be effective for a specific problem.

Most tree breeding projects have limited time and funds; thus, efficiency or simplicity of various breeding methods becomes very important, as pointed out in the chapter on research needs. The chosen method must not only work, it must work better than any alternative method. Execution of a breeding plan requiring four generations of an annual plant is far simpler than four generations of forest trees. Thus, the tree breeder will concentrate on achieving the greatest gain in each generation, rather than on only the results after a series of generations.

The individual tree breeding methods discussed here fit into the organization plan for the South described in chapter 16. Advantages and disadvantages of each method are discussed so that they can be used effectively at the proper time and place by the keyman in all this process, namely, the creative, applied tree breeder. Also, the more important technical subjects that should be used to enhance various breeding methods are given.

IMPORTATION OF NEW SPECIES

Introduction of new species of plants from different regions or different countries has been an important part of breeding programs for many species, and the same can be said of animal breeding. Nonlocal species have been used in two ways: to be placed directly into commercial production, or to be utilized in hybridization for the purpose of combining one or more desirable traits with local species. The success achieved by plant and animal breeders has led forest geneticists to devote considerable time to establishing arboreta and carrying out species crossability studies.

Introduction of forest tree species in the southern United States has long interested landowners and foresters. Zon and Brisco (1911) described the success and failures of planted eucalypts in Florida dating from about 1878. Gemmer (1931) outlined plans of the USDA Forest Service for testing introduced pines in Florida. Locations at which exotic species are tested have been listed in a survey of genetics and tree breeding research (Dorman 1966).

Many pine species have been test planted in the South and some survive, but overall performance has generally been unsatisfactory. Results of plantings in Florida were summarized (Kraus 1963), as were those in North Carolina (Barber 1953), Mississippi (Schmitt and Namkoong 1965), Louisiana (Grigsby 1969), Georgia (Jones 1966; Reines and Greene 1956–57), and Texas (Zobel, Campbell, Cech, and Goddard 1956; Long 1973).

All these publications describe survival and other information for imported pines in test plots in the southern United States. In no case did survival, form, height growth, or resistance to insects and diseases equal the general performance of native United States pines. Pines from the western United States such as lodgepole, ponderosa, and Monterey have been tried, as have pines from Mexico, British Honduras, Spain, Italy, China, Korea, and Japan. Expectations for many years were high, but results in this country have been virtually nil.

Exotics for Large-Scale Planting in the South

The successful uses of exotics in forest planting in South America, South Africa, Australia, New Zealand, and some places in Europe are often cited as examples of the value of this work. It has been pointed out by Thulin (1957) that in Australia insufficient high-quality trees of Monterey pine occur per acre to justify establishment of seed production areas. This may come as a shock to many foresters who like to point to this work as a prime example of what can be obtained by tree introduction. It is quite true that Monterey pine grows very fast in Australia, but a selective breeding program is still necessary to develop varieties of good quality. Form of southern pines planted in Australia was so bad that foresters started a tree selection program in 1938 as part of a seed procurement project to provide better planting stock. While introduction of softwoods has been successful in Australia, there have been no reports of the use of hardwoods to replace eucalyptus. From the standpoint of forest tree breeding in the southern United States, it is important to realize that, in general, pines exported to other countries on a large scale have been either southern pines or pines from southern latitudes. Monterey pine is native in southern California, and Mexican weeping pine is native to Mexico. Thus, the South already has or has test planted the species that are commonly imported by other countries. Introduction of the two nonsoutheastern pines, Monterey and Mexican weeping pine, have been unsuccessful in the South because of their susceptibility to insect pests and cold damage. Therefore, the introduction of species that are superior to the native southern pines does not, at this time, appear at all promising. Introduction of hardwoods might be possible, but the South is well supplied with these also. Arboreta planting is continuing. Certain young eucalyptus trees grow fast in south Florida. Something useful may show up in the future from this work, particularly as hybridization material for disease and insect resistance or adaptability to poor sites. It is for this reason that performance in arboreta should be carefully recorded so that records are obtained on form, wood quality, and susceptibility or resistance to specific pests. This has not been done in the past; therefore, no records are available to show why certain species failed or if they had certain valuable traits.

There are many ecological factors important in successful plant introduction work, and ignorance or disregard of these factors has been the cause of most of the failures. Nearly always, trees do best when planted on sites and in climates very similar to those of their origin. Seed should be obtained from the better individuals and races of each species. In the past, tree introduction has been most successful in Australia, New Zealand, South Africa, and parts of Europe where native species were few in number or species with wood of the desirable type—softwoods, for example—did not exist. Quite the reverse is true of the southern forests; in fact, we are blessed by nature with the best of the pines and have little chance of getting better from somewhere else.

Introduction for Breeding Stock

Use of non-native tree species to hybridize with local southern species may be of benefit in some tree breeding problems. This is the method used in breeding blight-resistant chestnuts, where species had to be chosen for disease resistance rather than suitability for forest planting. Undesirable traits such as poor form could be selected against in the F_1 and subsequent generations so that a few undesirable traits might not cause a species to be rejected for introduction, especially if it had a very important desirable trait such as resistance to a serious pest.

Complete testing of introduced species requires that they be planted on a variety of sites in each climatic zone in the South. Many years must pass before we can be certain what timber yield and wood quality will be and whether new species can withstand exposure to all types of weather conditions as well as all types of disease and insect pests. However, this process could be speeded up by using inoculation techniques or growth chambers to simulate climate conditions at various locations.

Advantages of Tree Introduction in the South

1. In principle, it may be quicker and cheaper to introduce a new species or variety if it exists than to create one through a selective breeding program with local species.
2. Even though not suitable for large-scale field planting, certain species may have genes or blocks of genes that can be transferred to a native species that is weak in some character such as susceptibility to disease or insect attack.
3. Introduced species may provide much wider latitude in the choice of paternal stock in hybridization than if only local species are used. For example, hybrid vigor may occur in crosses between distantly related species, races, or varieties of the same species, provided, of course, that they will cross.
4. It is advantageous in hybridization work to have parental stock readily available. Although pollen of some trees such as the pines can be shipped long distances, it is difficult to find competent people to correctly identify the species, collect the pollen, and ship it to the tree breeder.

Disadvantages of Tree Introduction in the South

1. It is costly and time consuming to test all the prospective tree species on a variety of sites in the South for an adequate period of time to insure reliable performance data.
2. There is only a slight chance that species growing faster and having higher value wood than local species will be found because there are a great number of southern tree species and many of them grow extremely fast. Also, they produce a wide variety of high-quality products. There are no large areas in which native species cannot be planted, although there are few species to choose from near

the north and west edges of the southern pine region.

3. Foreign species may not have inherent immunity or resistance to local diseases and insect pests.

4. Foreign species that have a wide geographic range may be composed of many strains or races which would be very time consuming and costly to test plant under a variety of conditions in this country.

RACIAL SELECTION AS A METHOD OF TREE BREEDING

Racial selection does not always insure use of a strain superior to local strains, because none may exist. In cases like this, selection of the local race is best because it preserves good genetic quality. It is well established in forest genetics literature that a substantial amount of variation in rate of growth and other traits is common in tree species, especially those with wide geographic ranges. However, in the South, except for species like loblolly and slash pines, we cannot go much beyond this point. We know variation exists, but we do not know exactly how much for each major and minor species or what the environmental factors are that are correlated with races. Neither do we know whether the difference in traits among races in all species is continuous or discontinuous. Furthermore, we do not know which are the better races of every species to plant or use as breeding stock in different areas.

As discussed in the chapters on geographic and racial variation, racial variation studies have been designed in accordance with different objectives, such as to determine: (1) the principles of variation in a species, (2) the better sources of seed to plant in specific geographic locations within the range, and (3) the better sources of seed to plant outside the natural range. Thus, the advantages and limitations of racial selection as a method of breeding should be evaluated on the basis of the problem to be solved.

Advantages of Racial Selection in Tree Improvement

1. Permits use of strains that may be more suitable for certain purposes than local stock. If racial selection is needed to obtain seed for planting outside the natural range, then it is good business to determine the best areas from which to obtain it.

2. If superior races are found, they can be used promptly in forest planting because a fairly large volume of seed would be available. Vegetative propagation to build up seed orchards for volume production would not be needed.

3. Racial variation occurs in most species, particularly those with wide geographic or elevational range. Environmental pressure is most effective in creating ecotypes where variation within the species is large.

4. Knowledge of racial variation will lead to better understanding of the inherent nature of the species.

5. A racial introduction is genetically variable and would not have some of the undesirable features of more genetically uniform strains if uniformity proves to be undesirable. Strains could be fairly uniform in traits, such as form, but genetically variable in resistance to pests.

6. Racial selection is needed to insure that full advantage is taken of the opportunity to use the best strains occurring naturally. Thus, racial plus single-tree selection and hybridization within species might be productive of significantly better tree types. A knowledge of racial variation is essential to proper selection of stock in species hybridization.

Disadvantages of Racial Selection in Tree Improvement

1. Races may not exist that are better than local stock, particularly if the area is located within the optimum range of the species. Local selection would preserve the best strain, but it would not give local tree planters any improvement. The benefit of racial selection may not be the same over all parts of the range of a species.

2. Testing an introduced race is expensive, because much the same procedure is required that is needed for an introduced species. Also, if the species concerned is widespread geographically, many sources must be tested, each on several sites. Fairly long periods of time are required for good test of resistance to climatic factors and pests.

3. Test designs are complicated because of the large number of seedlings required for a good sample of a racial strain, as compared with those of a plus tree or a hybrid, particularly if intraspecific variation is large. Tree breeders have not been able to establish many racial variation studies where all sources of variation (tree-to-tree, stand, and race) are under control.

4. Racial variation may not exceed tree-to-tree variation, especially if the species is inherently variable and geographic range is small. Racial variation in vigor, for example, may be much less in slash pine than in shortleaf or loblolly pine.

5. Tree-to-tree variation may be large within a race; thus seed collection without consideration of maternal parent may produce seedlings with a mixture of genotypes ranging from desirable to undesirable. Uniformity of good phenotypes would be

lacking, particularly if selection is desired for several traits other than vigor, such as oleoresin yield, wood specific gravity, form, tracheid length, and chemical properties. Certain traits may be negatively correlated, or they may be positively correlated. The difficult problem lies with those that are negatively correlated, such as rapid growth and susceptibility to cold injury. For example, loblolly pine of southern origin grew rapidly in Ohio but was highly susceptible to cold injury (Woerheide 1959). Shortleaf pine planted in Pennsylvania gave similar results (Aughanbaugh 1950).

STAND SELECTION IN TREE BREEDING

Stands of forest trees may form a deme or a genetically different unit within species or races, as described in the chapters on stand and racial variation. Geographic location within species or race may be an important factor in creating differences among stands. In Texas, progeny of maternal parents in stands on ridges and upper slopes were more drought resistant than offspring of trees in stands on lower slopes. Evidently, moisture supply is critical in this area, and there is strong selective pressure for drought resistance. In contrast, slash pine seedlings from trees on wet and dry sites did not differ in a Florida study, where summer rainfall is high.

It is difficult at this time to set up detailed requirements for stands to be converted to seed production areas, but the same general procedures can be followed that are used when selecting plus trees. Stands with an unthrifty appearance, trees of generally poor form, and with a fairly high incidence of pest attacks are poor candidates for seed production areas. To ignore signs of questionable inherent quality might very well defeat the purpose of the project, which is to designate a stand of as high genetic quality as possible, a stand to be managed for seed production.

Inasmuch as little is known about stand selection as a discrete method of breeding, no attempt will be made to give advantages and disadvantages listed for other methods.

SINGLE-TREE SELECTION IN TREE BREEDING

Selection is defined as choosing certain individuals with desirable traits from a population. It is the system by which use is made of the best types produced naturally, either for commercial production or for further selective breeding. Sometimes, natural variants differ sufficiently from average trees to be placed in production as clones without further modification. Many horticultural varieties of fruit and ornamental plants are of this origin (Miller 1954). Other selections are crossed directly or used in multiple crosses to obtain further refinement in combinations of desirable traits. Lerner (1958) discussed many aspects of selection in his book on this subject. Hayes *et al.* (1955) and Allard (1960) have given selection extensive treatment in their books on plant breeding.

Breeding Cross-Pollinating Species

Mode of reproduction of plants is important in evaluation of breeding methods because it controls the manner in which plants can be crossed, and also, it influences variability among individual plants. In general, self-pollinating plants are homozygous, whereas cross-pollinating plants are heterozygous. However, as stated by Hayes *et al.* (1955), differences are not clear and sharp, and plants can be divided into major subdivisions on a basis of mode of reproduction, such as (1) naturally self-pollinated, (2) often cross-pollinated, (3) naturally cross-pollinated, and (4) dioecious (male and female plants).

The southern pines, as shown in the chapter on sexual reproduction, are naturally cross-pollinating species, although a small amount of natural selfing occurs in stands. Controlled selfing is possible, but self-compatibility and inbreeding depression vary widely among individual trees. Thus, methods for breeding cross-pollinating species are most important for pines, but those for self-pollinating species should not be overlooked. Individual trees may be strongly male or female, and dioecism may be a factor in breeding, particularly in selection of individual trees.

Ways of breeding cross-pollinating plants are: (1) mass selection, (2) selection of seed orchard clones, (3) recurrent selection, (4) synthetic varieties, (5) backcrossing, and (6) nursery selection. Each method is briefly described and the more important technical aspects given.

Mass Selection

This method involves making a choice among trees for purposes of seed collections. Only the maternal parent of the seed is known. Trees are chosen for high vigor plus good stem form, good crown form, and freedom from attack by pests. Collection of seed from trees in seed production areas, natural stands or plantations, and desirable geographic locations is a form of mass selection.

Mass selection is an improvement over no control of the maternal parent. Seed of poor maternal and racial phenotypes is avoided, but gains in wood yield and quality are lower than those from more intensive breeding methods. Reliable estimates of gain are difficult to obtain because of the difficulty of choosing adequate control stock, numerous environmental factors that influence yield and vary from year to year, and rigor of selecting trees; also, the large number and combinations of traits to be evaluated cause difficulty. Wide variability among plantation trees is maintained from seed obtained by mass selection, but there should be fewer trees of poor form and high susceptibility to certain pests. Mass selection should be used when small amounts of seed are needed or until seed orchards come into production. It can, moreover, be used in countries unable to conduct tree improvement projects. Mass selection insures use of the best seed known, but no controlled crossing or creative breeding is involved.

Application of mass-selection techniques in each tree species requires a knowledge of subjects such as phenotypic variation, geographic variation, tree selection, racial selection, and random mating.

Selection of Seed Orchard Clones

Selection of stock for seed orchard establishment is perhaps one of the quickest and most effective ways of gaining genetic improvement in a few important traits in southern pines on a large scale in a short time. Trees developing from grafted stock cross-pollinate with others and produce offspring with a higher level of genetic uniformity than those obtained through mass selection. The offspring will not be uniform to a high degree as would clonal plantations, but this is quite desirable from the standpoint of maintaining genetic diversity in resistance to pests as insurance against epidemics. There is little reason to fear that uniformly straight-stemmed trees with well-formed crowns and wood of desirable quality will not be genetically diverse in regard to pest resistance or adaptability. While genetic diversity is important, it is not complete protection against pests. One must remember that genetic diversity has not protected native American tree species from chestnut blight, white pine blister rust, or disastrous outbreaks of various insects.

Recurrent Selection

The method consists of selecting parents and crossing them or their selfed progeny to produce populations for reselection (Penny *et al.* 1963). Additional or recurrent cycles of selection can be made as long as satisfactory improvement continues. Stonecypher (1969a) discussed the general use of recurrent selection in tree breeding and outlined the steps in phenotypic and genotypic recurrent selection (fig. 202).

Recurrent selection is the most important and effective method of breeding for southern pines. Highly important gains in wood yield per acre plus improvement in individual traits, such as stem and crown form, natural pruning, wood specific gravity, and resistance to pests, have been obtained. Large expenditures for clonal seed orchards in the Southern States were justified on the basis of evidence from crossing carefully selected plus trees of various species.

Additional improvements in performance seem possible because the upper limits to selection and hybridization have not been reached. Much research in creative breeding techniques is needed in this subject to guide practice, which is becoming highly intensive.

In intraspecific hybrids, family means are improved, but for certain economically important traits, wide differences remain among full sibs. Since the genetic base narrows with each generation, a very broad base is needed at the start if the process is to continue. Just how broad we cannot say until the effects of inbreeding in relation to selection and crossing are known. Also, the number of clones required for a seed orchard should be estimated before breeding starts.

Breeding by recurrent selection makes use of information from subjects such as tree selection, racial selection, breeding for multiple traits, genetic disassortative mating, and phenotypic disassortative mating.

Synthetic Varieties

A synthetic variety is made up of genotypes which have previously been tested for their ability to produce superior progeny when crossed in all combinations. This method differs from other breeding methods that are defined on the basis of how populations are created. Allard (1960, p. 47) writes, "A synthetic variety is one that has been synthesized from all possible intercrosses among a number of selected genotypes; thereby, a population is obtained that is propagated subsequently from open-pollinated seed." In mass selection, the next generation is propagated from a composite of the seed from phenotypically desirable plants selected from the source population, according to Allard (1960).

The term *variety* is used to indicate trees with special characteristics but may not be named or "taxonomic" varieties. Southern pine breeding is leading toward a gradual and sustained improvement in performance rather than production of named varieties—unlike farm crops that are reproduced true to name in order to maintain uniformity and meet seed certification requirements.

Breeding synthetic varieties utilizes trees and clones produced under other breeding methods

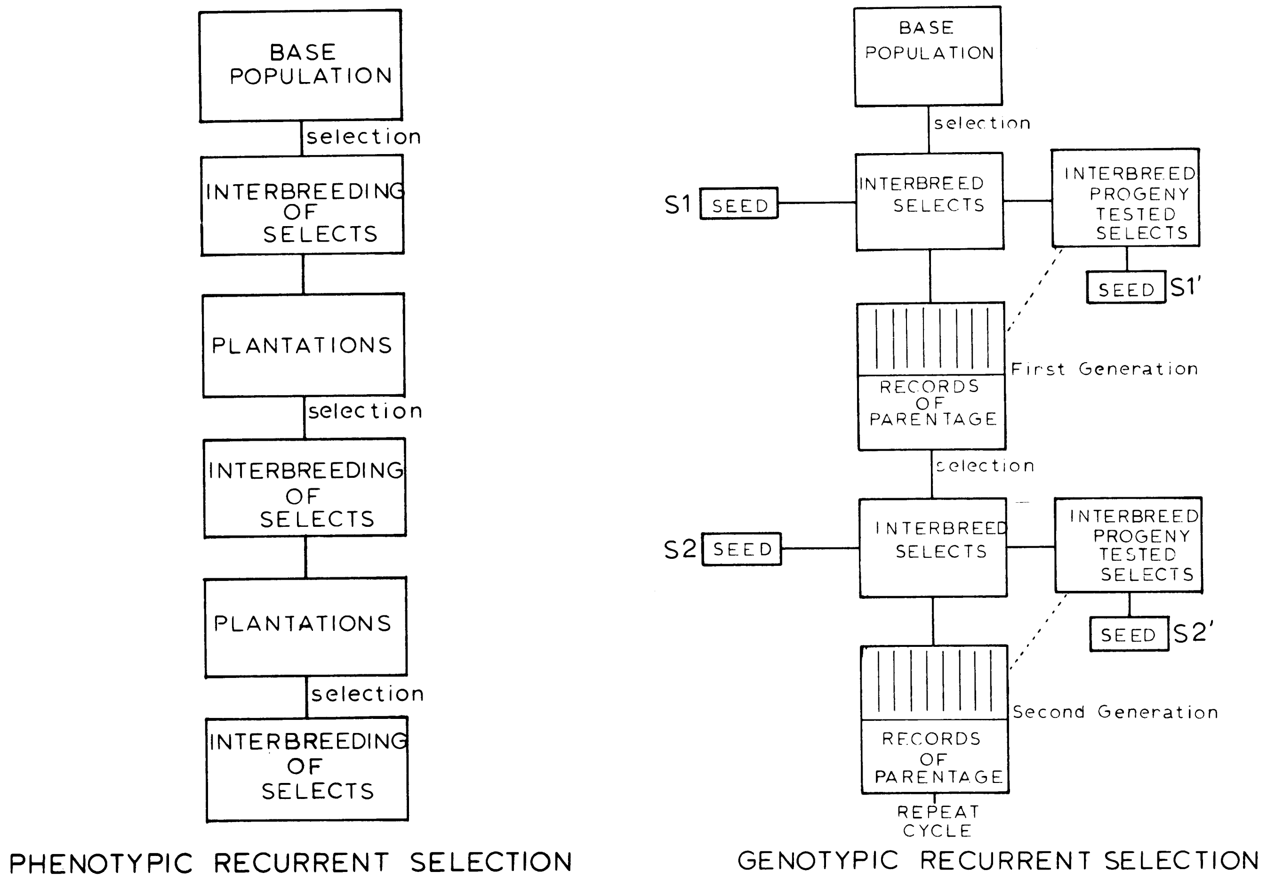

Figure 202.—Diagrams of recurrent selection breeding methods. In phenotypic recurrent selection, the selections are recombined and are the base for the next cycle. In genotypic recurrent selection, records of parentage are required, and selections are based on performance of relatives. (Stonecypher 1969a)

such as backcrossing and hybridization. Involved in breeding synthetic varieties are tree selection, racial selection, phenotypic assortative mating, and genetic disassortative mating.

Backcrossing

The method consists of recurrent crossing of offspring to the more desirable parent while selection is practiced for the characters being transferred from the donor parent. Thus, it may be a form of species hybridization but could be used with trees within species if there were no true species to serve as donor parents. Backcrossing has been little used in pine breeding but could become important as the use of intensive breeding schemes and systems develop. The method would produce trees with a very good combination of traits, but it would at the same time narrow the genetic base. The method might be useful in transferring traits of vigor to low-vigor trees that possess the asset of high cold resistance, such as pitch and shortleaf pines in the northern part of the southern pine region. It could also transfer pest resistance to strains that have high vigor and good form.

Backcrossing requires a knowledge of tree selection, racial selection, species selection, genetic disassortative mating, breeding for multiple traits, and inbreeding.

Nursery Selection

This method involves careful inspection of large numbers of seedlings while still in the nursery bed and also involves outplanting the most vigorous for use as breeding stock or for seed orchards. The method has several advantages as well as disadvantages, although actual tests have not developed to the point where we can be certain about many of them.

One advantage of nursery selection is that a large number of plants can be examined in a short time, as compared with that required to make surveys for superior trees in wild stands or plantations. And the seedlings selected for outstanding vigor may be inherently superior. If the nurseries are large, several hundred individual seedlings may be selected in a short time. Studies of the relationship between seed weight or size and seedling growth show that seed weight has some effect on seedling size (Brown and Goddard 1959) but that it is quite small compared with other factors. Thus, seedlings apparently have different inherent growth capabilities that may continue for many years, as shown by results of studies in grading nursery stock. Tests now being made will show what proportion of these continue their habit of rapid growth (Ellertsen 1955; Zobel *et al.* 1957).

One disadvantage of nursery selection is the fact that environmental factors in the nursery, such as early germination, soil differences, or other conditions, may be about equally responsible for the rapid growth of certain seedlings; thus a large error is involved in selecting plants that are truly outstanding in vigor. Another disadvantage is that, as yet, we cannot estimate stem or crown form characteristics of mature trees from young seedlings. Since undesirable features, such as stem crook, high branch angle, long branch length, poor natural pruning, and probably stem taper, vary in the species and are under rather strong genetic control, the method involves an important weakness. Also, no estimate of wood quality such as specific gravity, fibril angle, or cellulose content can be made without sacrificing the seedling. In some breeding programs, such considerations would be very important; in others, they would not. The same objection would apply to selection for disease resistance. In addition, even though some outstanding seedlings may be selected, several years of growth must accumulate before the tree breeder can be sure he has chosen a desirable genotype. So, unless selection is highly accurate, several years of testing are required for rating the individual trees, just as are required for estimating the genotype of mature trees. Our inability to accurately predict tree growth and areawise wood volume yield is an important factor in progeny testing.

Advantages of Single-Tree Selection in Tree Improvement

1. Since most species vary genetically, especially southern pines, use of the best stock occurring naturally offers an opportunity to obtain an improvement over wild stock. The improvement in some traits is more than in others; the variation in some species is greater than in others.
2. Single-tree selection can easily be used by silviculturists, since pollen handling and controlled pollinations may not be required for simple selection methods such as seed collection from plus trees, seed production area establishment, and seed orchards establishment with open-pollinated seedlings of plus trees.
3. Single-tree selection plus hybridization within the species permits increasing one or more traits without introducing undesirable traits that may occur in a separate species.
4. Single-tree selection, or recurrent selection, enables the tree breeder to obtain improvement where no superior races occur or where there are no suitable species with which to hybridize.
5. Improvement is possible in traits that are difficult to evaluate economically—branch diameter, for example—by including the trait along with others in selection criteria.
6. Progeny of single trees, or trees in stands established with seed from seed production areas, should be of fairly good quality.

Disadvantages of Single-Tree Selection in Tree Improvement

1. Some important traits may not vary within the species or not vary widely enough to permit selection for improved varieties. For example, resistance to tip moth in loblolly or shortleaf pines is nonexistent or so low that it does not appear to be feasible to select for it.
2. Rigid selection may lead to loss of vigor through inbreeding, and losses to pests might increase because genetic diversity is reduced.
3. Selection for a large number of traits is very difficult because of the survey work required to find individuals outstanding in a great many traits. However, this obstacle applies to interspecific hybridization, too.
4. Selection for a combination of certain traits may be difficult because they are negatively correlated.

SPECIES HYBRIDIZATION AS A METHOD OF TREE BREEDING

Hybridization of species has been a powerful tool for the plant breeder. Genera composed of closely related but varying species have permitted the plant breeder to create an almost unlimited number of combinations of traits in different varieties. Thus, collection of species and varieties, although they are distributed worldwide, followed by cataloging their traits, has been an important part of many plant breeding programs. This technique has been particularly effective in breeding cereal grains and other important crops. Hybrid vigor, the goal of many plant breeders, is not fully understood, as indicated by Gowen (1952) in *Heterosis*, and does not appear to occur in southern pine hybrids.

The term *hybridization* has been used, in general, to denote crossing between plants of different species. A very well known exception to this is hybrid corn, which is not crossed between species but between different lines. As Duffield and Snyder (1958) point out, interspecific hybridization refers to crosses between species, intraspecific hybridization to crosses between individuals within a species, and interracial hybridization to crosses between members of populations within species. These are very useful terms and are needed to describe fully the work that has been done in hybridization of forest trees.

Hybridization work with poplars (Schreiner 1958), with pine (USDA Forest Service 1948a; Righter and Duffield 1951; Wright and Gabriel 1958; Wright 1959), and with spruce and other species (Wright 1953) seems to be based largely on random crossing of all different species. This approach provides a pattern of crossability that will be very useful in future work. Also, it is highly commendable from the statistical point of view because it is certainly an unbiased sample—all species being crossed. However, yield of improved strains for wide-scale commercial use has been low. Many species of some genera are not important commercially, and crosses between them, or between them and more valuable species, cannot be expected to yield anything very useful.

When using hybridization, knowledge of such subjects as selection of trees, races, or species is important, as are compatibility, phenotypic assortative mating, genetic disassortative mating, inheritance, heritability of traits, and breeding for multiple traits.

Advantages of Hybridization in Tree Improvement

1. An extremely large number of genic combinations is possible because variation among species is often greater than among trees or races within species. Furthermore, species not only vary but may be composed of many races and individual trees with outstanding traits. This permits a very wide selection of material.
2. Hybrid vigor may occur in species crosses.
3. It may be possible to obtain progeny with traits that do not occur in either parent.
4. Hybrids of many tree species are fertile.
5. It may be possible to cross incompatible species by using still other species as a bridge, thus transferring genes of blocks of genes.

Disadvantages of Hybridization in Tree Improvement

1. Crossing is limited to compatible species, and in some cases this may limit the number of combinations possible.
2. Compatible species and species adapted to a specific geographic area may not vary widely in a large number of economically important traits. Thus, improvement is limited—wood quality characteristics among southern pine species, for example, do not vary widely.
3. Although various species may be compatible, some may have undesirable traits; thus, first- or second-generation hybrids are not suitable for planting, and several generations of trees may have to be produced before the desired combination of traits is obtained. This means that improvement would be very slow. Hybridization requires manipulation of all the traits, good as well as bad, of two species, which is more difficult than improving traits of a single species.
4. Seed set in some hybrids may be very low.
5. Seed may be difficult to produce in large quantities because species may bloom at different times. Seed orchards of vegetatively propagated material from the F_1 or F_2 generation, however, may be feasible.
6. Species may be only partly compatible, and many undesirable individual trees may be produced that cannot be identified until after they have been outplanted several years. Loblolly × slash hybrids in Georgia, for instance, have many aberrant forms.
7. Segregation in the F_2 or subsequent generations after outplanting may result in the establishment in the forest of vigorous trees with undesirable traits.
8. Hybrids of species or races that occur in different geographic areas or climatic areas require a fairly long period of observation before their resistance to climatic factors and pests can be ascertained for the specific areas in which they are to be grown. Wide variation within species broadens the opportunities for hybridization, but it complicates the testing of hybrids as well.
9. Insufficient evidence on heritability of traits is available upon which to base estimates of characteristics of a hybrid of certain species. Eventually, we will know more about traits that are dominant, intermediate, or recessive, which will aid greatly in making proper choices of parental stock.
10. Performance of a hybrid may be strongly influenced by the individual maternal or paternal parents that were used; hence, duplication of results may be difficult unless the race and genotype of the parents are given.
11. Silviculturists who have no special training in pollination techniques will find hybridization difficult.

POLYPLOID AND MUTATION BREEDING

The effects of multiple sets of chromosomes (polyploidy) and heritable changes in genes or chromosomes (mutations) on growth and morphological traits were reviewed in an earlier chapter. Changes such as these may occur naturally, but they can also be induced artificially and, consequently, can be classed as methods of plant breeding.

Methods of Inducing Mutations

Mutations may be induced by several methods having different effects (Briggs and Knowles 1967). One group of materials brings about changes as a result of ionizing radiation, the types most commonly used being X-rays, gamma rays, neutrons, beta particles, alpha particles, and protons or deuterons. Ionizing radiation can cause gene mutation; chromosome, chromatid, or subchromatid aberrations; changes in chromosome number; inhibition of cell division; induction of mitotic activity; death of nuclei or cells; partial or complete sterility; retardation or stimulation in growth rate; and the induction of abnormal growth. An additional type of mutagenic agent is ultraviolet radiation; and compared with X-rays, ultraviolet radiation produces more gene mutations relative to chromosome aberrations. The last group of materials is made of chemicals such as alkylating agents, urethane, the alkaloids, the peroxides, formaldehyde, and substances related to nucleic acid and nitrous acid.

It is apparent that mutation and polyploid breeding are complex methods because of the large number of agents, difficulties in using them, differences in effects, differences in genetics of various plants, and the large number of parts of the plants to be treated (pollen, seed, twigs, buds).

Mutation Breeding in Trees

Mutation breeding with forest trees has followed the general methods used with other crops but without notable success. As Gustafsson (1960) and Khoshoo (1959) point out, polyploidy and mutants are rather rare in gymnosperms but more frequent in angiosperms. In Russia, it has been pointed out that polyploid conifers occur very seldom in nature and with rare exceptions are of low vitality (Matskevich 1959). In his review of breeding methods for forest trees, Brewbaker (1967) was not optimistic about the possibilities of induced polyploids or mutations, and neither was Cech (1963).

The techniques of breeding haploids have been reviewed by Brown (1967), but the work has not sufficiently advanced so that the advantages and disadvantages can be compared. The method requires growth of gametophytic tissue followed by chromosome doubling and the formation of complete plants. As a result, a homozygous line would be established that could not otherwise be created without many generations of selfing that might be extremely costly and technically difficult to produce. Nei (1963) recommended haploid breeding for forest trees. The suggestion was based on the assumptions that heterosis was possible in crosses of inbred lines and that less time was required to produce the inbred lines by the haploid method than others. But these assumptions are questionable. Burk *et al.* (1972) demonstrated that homozygous, true-breeding tobacco (*Nicotiana tabacum*) strains could be created in one generation. They cultured anthers of hybrids to produce haploid plants and then doubled the chromosomes of the haploids by colchicine treatment. Progenies of doubled plants of the same clone did not differ in traits. Although the authors claimed that the results show the effectiveness of the method for creating homozygous lines, they tested it only with tobacco. In tobacco, it is extremely easy not only to grow haploid plants but to double them by colchicine treatment. Thus, practicality of results with tobacco may differ sharply from those obtained with other species. Kimber and Riley (1963) concluded from a review of the subject of haploids that the greatest obstacle to their use was the lack of techniques for creating them when needed. Stettler and Howe (1966) described problems encountered in producing haploids in *Populus*. Haploid breeding required that a choice be made among wild trees or individuals in families for trees with which to begin the process. Thus, a knowledge of variation among trees is essential.

Advantages of Polyploid and Mutation Breeding

1. Plants with unusual numbers of chromosomes or changed genes or chromosomes may differ greatly from natural trees in valuable traits.
2. Combinations of traits such as resistance to several pests may have to be induced because no resistant stock exists, and, thus, there are no opportunities for breeding.
3. Highly uniform strains of plants may be produced by haploid breeding.

Disadvantages of Polyploid or Mutation Breeding

1. The processes cannot be directed; thus, an

Table 9.—*Estimated relative effectiveness of tree-breeding methods such as racial selection, single-tree selection, and hybridization in improving various traits in major southern pines*

Traits to be improved	Method of breeding		
	Racial selection	Single-tree selection	Hybridization
Oleoresin yield	Poor	Good	Poor
Wood specific gravity	Poor	Good	Poor
Rate of growth	Good	Good	Good
Tracheid length	Poor	Good	Poor
Stem straightness	Poor	Good	Poor
Natural pruning ability	Poor	Good	Poor
Crown form	Poor	Good	Poor
Resistance to drought	Good	Fair	Poor
Resistance to fusiform rust	Good	Good	Good
Resistance to littleleaf disease	Good	Good	Good
Resistance to glaze damage	Fair	Fair	Fair

extremely large number of plants must be treated and grown in test plots.

2. Costs of evaluating treated plants or tissue are very high.

3. Most changes are harmful rather than beneficial, which reduces the chances of creating improved trees but improves the chances of creating deformed trees.

4. Since vegetative propagation in southern pines is not easy, a few chance individuals would not be very useful.

5. The methods seem very low in productivity per unit of time and effort in comparison to alternative approaches to breeding, such as selection and hybridization, because of the presence of a very large amount of natural variability within and among the southern pine species.

6. The absence of useful variants in natural populations is evidence that producing them artificially might be very difficult.

7. Techniques for using various methods on a large scale have not been developed enough so that tree breeders can use them without an investment of time and expense in developing them.

8. Highly uniform strains of forest trees might not be silviculturally desirable because of the risk of losses to pests, but their value in comparison to costs should be studied by researchers.

DISCUSSION

Tree introduction, racial selection, stand selection, single-tree selection, and hybridization have a number of advantages and disadvantages. At the present time, it can be said that selective breeding within species combined with racial selection is the most effective method for obtaining improved strains of softwoods and hardwoods. Of the two methods of breeding, selection and crossing within species will give more improvement than selection of races. This comparison is based on results of studies to date showing that tree-to-tree variation is greater in economically important traits than is racial variation in certain species, and that tree introduction and hybridization are not very promising at present for general use. Hybridization for specific objectives will be of value in the future.

On a basis of the results from variation and inheritance studies to date, the relative effectiveness of the three main methods of tree breeding for improving some of the various traits in southern pines is given in table 9. Similar tables could be prepared for each species and for various types of racial selection, single-tree selection, or hybridization.

From the discussion in the sections on variation and inheritance in southern pines and on methods of tree breeding, it is apparent that great diversity in genetic material occurs in southern tree species and that, under certain conditions, various methods of breeding can cause dramatic changes. It is apparent, also, that methods of breeding cannot be applied indiscriminately; consequently, the great need now in southern tree breeding is to define carefully the specific problems and bring to bear on them the most specialized and effective method or combination of methods to fit the particular case.