CHAPTER 19
MATING SCHEMES

We have discussed the benefits to be expected from breeding southern pines and how work objectives might be stated to provide orderly progress toward realization of expected returns from the investment in time and resources. Although the broad perspective of breeding projects must be considered and reviewed in planning, the key technical jobs in each successive step of the work may narrow down to a very small number.

As Allard (1960) points out, there are only two steps breeders can take to improve genetically variable populations. One of these is selection. This is the process by which the breeder decides which individual will be allowed to produce the next generation and, perhaps, how many offspring each might have. In the chapters on variation and inheritance in species of southern pines, the amazing range among individuals in important traits and the influence this imposes on the offspring are cited from many studies. The second alternative open to the breeder is to decide how the individuals they have selected will be mated to each other. The skill with which these two jobs are carried out governs the kind and amount of genetic gain as measured by the change in gene frequencies and the frequencies of different combinations of genes.

An exception to the combination of careful selection of breeding stock and controlled mating occurs in the seed orchard phase currently used in southern pine breeding. However, this may change as breeding programs and seed production projects become more refined. At present, seed orchard clones are carefully chosen but largely on a subjective basis because of the large number needed, the necessity for making selections in wild stands, and the requirement that many traits be considered. Once established in seed orchards, the clones cross-pollinate in a more or less random manner, with the exceptions imposed by different flowering periods and selfability. Considerable lack of uniformity among trees in stands can be expected as a result of these conditions. But this should not obscure the fact that seed orchards are the backbone of the pine breeding program.

An important job in evaluating results of various mating schemes on progeny is to define the range in variation for each trait among the sibs. The range in traits will guide the choice of the next mating system in recurrent selection or some other breeding system. For example, recurrent selection is a method for making stepwise changes in gene frequency within a population while maintaining sufficient genetic variability for continued selection (Penny *et al.* 1963). Thus, it is important to learn and to report, by using families of adequate size, what happens to the range in variation in each trait.

GENETIC CONSEQUENCES OF BASIC MATING SCHEMES

The five basic types of matings were defined and their effects on the population were described by Wright (1921) many years ago. They do not need to be discussed in detail except for consideration of their uses in pine breeding. A mating system is any of a number of schemes by which individuals are assorted in pairs leading to sexual reproduction (Allard 1960). The systems are in two broad groups: in one, mating is completely at random; the other deviates from random mating on a basis of mating like to like, or mating unlikes. The criteria for likeness or unlikeness are either relationship, such as ancestry, or appearance, such as phenotypic resemblance or distinction.

Random Mating

In this type of mating, it is assumed that each member of the population has an equal chance to produce offspring and that any female gamete is equally likely to be fertilized by any male gamete. Because these conditions are rarely met in plant breeding, in practice there is some modification of the system.

In the reference to seed orchards at the beginning of this chapter, there was random mating among clones within the limitations imposed by flowering characteristics and self-compatibility, but the parents were all selected clones. Thus, seed orchards definitely do not meet the first requirement and only partially meet the second. In reality, seed orchards and seed production areas are examples of random mating with selection. As we shall see, the results are quite different from those obtained if there was no selection of maternal and paternal parents.

With true random mating, the gene frequency will remain constant, the amount of genetic variability will not change, and the genetic relationship between individuals will remain constant. In contrast, random mating with selection will change the mean of the population in the direction of selection but will have little effect on population variance, homozygosity, or the genetic correlation between relatives.

The value of random mating with selection is demonstrated by results of polycross tests of seed orchard clones (LaFarge and Kraus 1967), in which significant improvement was obtained in height growth and tree form. However, improvement in resistance to fusiform rust, which may be a more complex character than vigor or tree form, was low. Roguing seed orchards on the basis of progeny tests is a highly refined method for selecting the clones to remain in the orchard as they approach full seed-producing capacity.

Genetic Assortative Mating

This mating system is usually referred to as inbreeding. The individuals to be mated are more closely related by ancestry than if matings were at random. The primary effect of genetic assortative mating is to increase the probability that offspring will inherit the same genes from both their parents. This fixes the characters, especially those of low heritability, that may be most important to the breeder.

Genetic assortative mating is usually accompanied by selection. This decreases the genetic variance within families but might increase it among families, depending on the kind of selection practiced. Fisher (1949) in *The Theory of Inbreeding* discusses the importance of inbreeding in improvement of plants and animals.

Inheritance of good traits from both parents is very desirable, but as a result of mutations of some kind, all traits are not good. As shown by selfing studies in slash and loblolly pines (Squillace and Kraus 1963; Franklin 1969b, 1972), the load of undesirable mutations may be fairly high. Also, the higher the coefficient of inbreeding, the greater the loss in oleoresin yield, vigor, seed yield, and seed germination (Squillace and Kraus 1962; Gansel 1971). Height growth decreased approximately 4 percent for each 0.1 increase in inbreeding coefficient (Squillace and Kraus 1962; Gansel 1971). It must be noted that all individual trees do not react negatively to selfing, for some produce offspring of good vigor and oleoresin yield (Snyder 1968, 1972a; Greene *et al.* 1964; Gansel 1971). Progeny of one selfed slash pine all produced yellow-colored oleoresin, in contrast to the normal transparent type, and it was concluded that the yellow oleoresin trait was a recessive (Kraus and Squillace 1964a). None of the outcrossed seedlings produced yellow oleoresin. Selfed progeny of a plus shortleaf pine selected for resistance to littleleaf were more uniform in height growth and faster growing than certain open- and control-pollinated families of other trees, but two small selfed families were significantly different in height after 6 years (Bryan 1973). In Australia, selfed progeny of certain plus slash pine trees had outstanding vigor (Nikles 1966). Snyder (1972a) concluded, on the basis of his limited data, that selfing was of doubtful value for predicting breeding value of individual trees for several traits.

Inasmuch as the southern pines seem to be partially self compatible, a wide variety of selection and inbreeding combinations is possible. Careful work might produce highly vigorous but highly uniform offspring also. Thus, inbreeding combined with selection plus other systems of mating may prove of value. Even though data developed to date are not very encouraging, this type of mating cannot be discarded. Conclusions have been largely based on average results from a relatively small number of trees; in addition, selfing effects in progeny of plus trees selected for highly important traits are largely unknown. Seed yield and quality have been studied most frequently. Growth rate estimates have been based on young seedlings, with the exception of a few plantings in Australia.

All in all, close inbreeding does not seem promising for use in seed orchards at present, although it may have a place in highly complex and long-range breeding programs.

Phenotypic Assortative Mating

In this system, individuals are mated that resemble each other on the basis of phenotypic characteristics. The effects on one or two gene pairs can be computed rather easily, but for economically important characters, gene numbers are likely to be large. Also, heritability may be low. When gene numbers are large, mating like to like will probably exert the limit of its effects within a few generations and seldom produces any real fixation of type (Allard 1960). The resemblance between close relatives is increased, as is the extreme diversity in a population.

Inbreeding tends to fix intermediate as well as extreme families, while phenotypic assortative mating tends to concentrate the population at the extremes to the exclusion of intermediate types. If random mating replaces phenotypic assortative mating, these effects disappear rapidly except where selection that accompanies assortative mating has permanently altered gene frequencies.

In southern pine breeding, mating like to like trees has resulted in progeny with greatly increased yields of oleoresin (Squillace and Harrington 1968), and volume growth, tree form, and resistance to pests (Webb and Barber 1966) in slash pine, to cite specific studies. Similar results were obtained in Australia (Nikles 1966). Additional examples are given in the chapter on variation and inheritance in slash pine and need not be repeated here. Comparable results have been obtained for other southern pines, particularly loblolly pine.

The results of the studies cited here are examples of transgressive segregation. Transgressive segregation occurs when crosses of two parents produce populations exceeding those of both or one of the parents in the character under study (Briggs and Knowles 1967).

In seed orchard programs, phenotypic assortative mating will be useful in producing extreme variants destined to become seed orchard clones. In other words, the F_1 plus trees in progeny tests of clones become the basis for the first system of mating discussed, namely, random mating with selection. This procedure is being demonstrated in the seed orchards for slash pine with high yields of oleoresin. In the first step, plus phenotypes were selected in widely separated natural stands and mated. The offspring were grown in progeny tests. Oleoresin-yielding capability was determined for each tree and family of trees under the relatively constant environment. In the second step, individual trees outstanding for oleoresin, stem volume growth, and tree form in general were chosen and established as clones in seed orchards. It is expected that plantations from seed orchard seed will produce about 2.5 times more oleoresin than wild trees and, in addition, will have above average growth rate and form.

Studies in breeding southern pines have disclosed many opportunities to use phenotypic assortative mating. To date, little is known about the limitations of the system. However, this situation may change as it is applied to more species and to additional traits. So far, it seems an outstandingly successful method for increasing gene frequencies and combinations of genes.

Genetic Disassortative Mating

Crossing strains, varieties, or species has played an important part in plant breeding in general. Allard (1960) agrees with Stebbins (1950) that hybridization has been more valuable in vegetatively propagated species (orchard or ornamental trees and shrubs) than in those produced by seed (forage, cereal, fiber, and oil crops).

Hybrid vigor, an important factor in hybridization, has been observed in crosses of certain forest tree species but not among southern pines.

Characteristics of species hybrids in the southern pines were discussed in the chapter on this subject. Species hybrids have been made among the southern pines that are compatible. Most of the attempts were made to test crossability rather than to produce offspring with specific traits. However, in recent years, interspecific hybrids of shortleaf and slash pines were made for testing against fusiform rust infection. Also, slash and longleaf pine hybrids are being tested for adaptability to specific site conditions within the range of the species. The most successful cross of southern pines is used in Korea for large-scale planting, and it combines the good growth and form of loblolly pine with the cold hardiness of pitch pine. The same hybrid has not found widespread use in the United States.

It has been found that the individual parent trees of each species may exert strong effect on the hybrid. Inasmuch as differences in certain economically important traits are greater among trees and geographic races within species than among species, it is to be expected that careful selection of parent trees is essential if a hybrid with a good combination of traits is desired. Should a typical hybrid of certain species be desired, an adequate sample of parental trees and races would be required to produce it.

In the future, species hybridization may have more usage than at present. As stated before, most of the southern pines have both good and bad traits, particularly in regard to pest resistance. Breeding programs designed to combine the good traits might require selection plus different mating systems for a few generations.

Production of first-generation species hybrids in seed orchards is difficult because of differences among species in flowering time.

Phenotypic Disassortative Mating

This system of mating involves mating of unlikes. It may be used to compensate for defects by choosing contrasting parents, each of which compensates for weaknesses of the other. It may be used when the desired type is intermediate and the existing types are too extreme in opposing directions (Allard 1960).

Phenotypic disassortative mating has not been employed in seed orchards of southern pines. It seems not to have been tried in breeding programs with specific objectives such as individual traits. The method has, however, been utilized in inheritance studies of individual traits. These studies have been reviewed in the chapter on variation and inheritance in various species.

General Considerations of Mating Systems

Each mating system has its advantages and disadvantages for particular purposes. They each may have their place, or they can be used in combination plus selection to reach goals established in creative breeding. The breeder should understand fully the principal features of each system as well as the genetic makeup of the southern pine species with which he works. A high order of skill is required to isolate the key factors involved in creative breeding and to merge them into an efficient plan of action. As Hutchinson (1958) pointed out after a review of plant breeding work in Africa, those projects with definite objectives in creative breeding usually achieved them. In contrast, a breeder who was willing to take a gain in anything could not produce evidence of a gain of any kind.

Much research is needed on the effects of various mating schemes as they might be used by the breeder. The work might be concentrated first on economically important traits, with the objective of improving them or making them more uniform, depending on the nature of each one.

COMBINATIONS OF MATING SCHEMES

The types of mating schemes and their genetic consequences have been discussed very briefly, although they are, along with selection, the method by which the tree breeder changes the population. A change in direction toward higher utility or value requires that changes by controlled. This places certain restrictions on the breeder in regard to choice of traits, number of traits, and the time required to carry out his plans. Furthermore, to be highly efficient, he should combine selection with mating scheme. Progeny testing must be conducted out of doors and for a period of several years. These are the components of the framework within which he must work.

The tree breeder cannot attack each problem separately at the same time or at different times. Thus, the simultaneous interaction of all factors may be the most difficult technical problem he faces. Choice of environment for progeny testing is difficult because of the wide variety in the southern pine region. The tree breeder usually uses the most typical because it makes the results applicable to the largest area. An alternative is to choose, for initial tests, the two or three most important in forest production. Subsequent tests can be made at other locations.

Progress in breeding is greatest when all the factors involved are controlled in such a manner that they complement each other to the maximum amount. If the basic principles are adhered to, none of the methods chosen should be antagonistic. However, the range between completely antagonistic methods and fully complementary methods leaves a vast area within which judgment may be exercised. The large number of factors to be manipulated simultaneously by the tree breeder shows why creative breeding is more complicated than many studies in genetics.

The importance of the basic principles of plant breeding is recognized by several authors. Certain subjects such as selection (Lerner 1958), inbreeding (Fisher 1949), population genetics (Li 1955), and quantitative genetics (Falconer 1960) have been given book-length treatment—to cite a few of the more recent publications. These are all very fine works, but the tree breeder in the final analysis is left with the responsibility for welding the plan of action. In his plan, he rarely has a choice of omitting certain steps that have been inadequately researched. He has "to do" or "not to do"; there is no middle ground.

Detailed study of reproduction, propagation, variation in the full sense of the subject, and inheritance may seem like unnecessary refinement, but these must all be merged successfully into one action program. It may be that the one or two exceptions to the general rule (but which are specific for this particular tree species) may be the very Nemesis to bring a vast and elegant plan to nought.

Recurrent selection, as now used in many southern pine seed orchard programs, must be carried out to achieve a genetic gain in each generation without losing the variability among trees upon which gains in the following generation are dependent. Different mating schemes may be required in order to reach these goals.

REPRODUCTION SYSTEMS AND CHOICE OF MATING SCHEMES

Mating schemes important to breeding obviously act through the reproduction system of the trees in the population. If the system is highly versatile, there will be no restrictions in choice of mating scheme; but if it is limited, there might be important restrictions regardless of how promising the system might be from a theoretical standpoint. In their book on plant breeding, Hayes *et al.* (1955, p. 66) devote a chapter to mode of reproduction and define its importance as follows: "Knowledge of the methods by which plants reproduce is of primary importance from the standpoint of plant breeding."

The two commonly used divisions of reproduction are *asexual* in which vegetative parts of the plants are utilized to produce new plants and *sexual* in which gametic fusion occurs to produce a seed.

Asexual Reproduction

There are various forms of apomixis (which is a substitute for sexual reproduction) such as the formation of seedlike bulbils in onions, which serve the purpose of seed production. Stebbins (1941) has summarized the subject of apomixis and described various cases. Asexual reproduction also includes use of larger vegetative organs, such as buds, stems, twigs, or bulbs, and is the system with which most foresters are familiar.

Apomixis may occur in the reproduction of southern pines, but it has not been confirmed. It is definitely not important enough to influence choice of mating schemes or breeding methods.

Vegetative reproduction such as production of haploid plants by culturing pollen grains has not been perfected for southern pines.

Vegetative propagation by grafting, air layering, or cutting was discussed in the chapter on this subject. Although not easy, propagation by several methods is possible. For research purposes, propagation of own-rooted plants by cuttage has been demonstrated for most species, and graftage with rootstock of the same or different species is possible with several variations of conventional methods. For seed orchards and large-scale use, twig grafting on rootstock of the same species is the most common method.

Managers of southern pine seed orchards utilize the system of natural mating with selection. The ability of the tree to be vegetatively propagated, although somewhat expensive, makes possible the use of this system. It is the most powerful tool tree breeders have developed to date to upgrade the genetic quality of seedling planting stock now being produced annually by the millions.

Cutting or air layers of certain individual southern pine trees root with extreme difficulty or not at all. Scions from some trees are highly incompatible with seedling stock of the same species, and this may be the basis for rejection from the seed orchard regardless of even a very high index rating. However, the percentage of clones that must be rejected is about 10 percent and is not an insurmountable obstacle to the seed orchard program—as it is in Douglas-fir.

Sexual Reproduction

Fusion of the sperm and the egg, male and female gametes, is the most common form of reproduction in southern pines. The system is similar in all species.

The reproduction system and seed characteristics are highly favorable to intensive as well as extensive breeding methods. The southern pines reach sexual maturity at a later age than certain species, but many other species mature even later. Most trees eventually flower freely. Trees are cross-pollinated, but certain ones can be selfed. Cones are large with many seed, facilitating controlled pollinations and seed procurement for nurseries. The seed are large and easy to handle. The seed stores well and germinates readily, except that relatively simple methods of stratification are required by some species for uniformity of germination.

Plants can be classified on a basis of modes of pollination of major importance as follows: naturally self-pollinated, often cross-pollinated, naturally cross-pollinated, and dioecious (Hays *et al.* 1955). The first group (naturally self-pollinated) generally have less than 4 percent of cross-pollination. In the second group, self-pollination is more frequent than cross-pollination. The names of the other two classifications are self-explanatory.

As a group, flowering in the southern pines is dichogamous and protandrous, that is, the sex and time of ripening differ. Since classification of individual trees is not rigid, the exceptions may strongly influence use of individual trees in seed orchards or inheritance studies. Weather conditions cause important differences from year to year.

Most trees of each species are monoecious, and fecundity may be high for both male and female flowering parts. Individual trees are inherently variable in total amount of seed produced and in the proportion of male and female parts produced. Certain trees may be rejected for seed orchard clones because of poor flowering characteristics. In this respect, some trees approach dioecy.

Southern pines are naturally cross-pollinated, but inbreeding and selfing are possible with some trees. Selfing results in a loss of vigor and low production in flowering and seed traits, but this is not constant among trees. The importance of selective fertilization is unknown, but some tree breeders are concerned about the amount and effect of selfing in commercial seed orchards.

The flowering characteristics of the southern pines are such that any of the basic mating schemes can be applied within certain limits. There will be minor exceptions or restrictions for individual trees which cannot be selfed, and certain species crosses may not be possible, but this has small effect on the almost unlimited opportunities available. This potential is certainly one of the outstanding features of southern pine breeding, in contrast to the situation applying to other pine species or forest regions.

The fact that numerous mating schemes are possible might be given as a reason that slow progress is being made in research with a particular scheme. However, in the long run, the fact that many alternatives are available to apply to a variety of specific situations will be a great advantage. The tree breeder has enough problems and unknowns in selecting traits and working with their inheritance, without being handicapped by restrictions imposed by flowering characteristics.

EFFECT OF SPECIES AND BREEDING OBJECTIVE ON CHOICE OF MATING SCHEME

Species of southern pines cannot be readily crossed in all combinations. Thus, the tree breeder cannot use species hybridization to obtain certain combinations of traits however desirable this might be to reach his breeding objectives. On the other hand, it might be possible, with certain species, to find individual trees that will hybridize and provide an opportunity for additional crossing among individual trees of various families.

If the breeding objective is to increase growth rate per tree, crossing among fast-growing trees within species is more promising than selfing or crossing among species. Resistance to disease or certain pests might be improved by crossing pest-free trees within species or trees of the susceptible species with a resistant species, if one is available. Oleoresin yield can be increased more by crossing within slash pine than by crossing slash pine with longleaf pine. Yield of wood per acre can be increased by crossing trees selected for a combination of good traits within species or among species, providing seed production is not a problem in perpetuating the species hybrid. These examples illustrate the alternatives in choice of mating schemes to achieve certain objectives. Opportunities of improving wood yields are good because of the wide range in breeding material within and among southern pine species.

DISCUSSION

Choosing among the five basic mating schemes reviewed is an essential element in the creative tree breeding of southern pines. The method to be used must be picked on the basis of the reproductive system of the individual trees, the characteristics of the species being improved, the traits involved, and the breeding objective. It may be advantageous to use different mating schemes in successive generations in large breeding projects.