CHAPTER 18

SELECTION AND BREEDING FOR MULTIPLE TRAITS

Choice of parental stock is one of the most important steps in applying methods of breeding cross-pollinating plants, as discussed in the preceding chapter. Thus, the conditions under which selection is carried out and the principles involved for a few or several traits are of utmost significance.

In his book, *The Genetic Basis of Selection*, Lerner (1958, p. 5) proposed that selection be defined in terms of its observable consequences—"the non-random differential reproduction of genotypes" and in the lay sense of choice—"the actual procedure by which discrimination between individuals with respect of their reproductive rate is arrived at."

Lerner, in additional discussion, states that the basic purpose of artificial selection of metric traits is: (1) to modify its mean (directional selection); (2) to reduce its variability (stabilizing selection); and (3) to extend its range in one direction (directional selection to produce a record performance). In creative breeding, improved performance may be a result of a change in several traits; therefore, multiple-trait selection as well as single-trait selection may be necessary.

The importance of breeding for multiple traits and the kind of research data needed to do it well have been discussed by Dorman (1967), Stonecypher (1969b), Namkoong (1969), and van Buijtenen (1969b).

One of the early papers on variation and inheritance in forest trees stressed the importance of economic traits and used photographs of southern pines to illustrate good combinations of growth rate with stem and crown form and freedom from disease (Dorman 1952).

METHODS OF SELECTION

Three basic procedures for carrying out selection have been described by Hazel and Lush (1942): (1) Independent culling levels—trees are rejected in the field unless they meet a certain level required for a trait, (2) tandem selection—pressure in selection is applied to one character at a time or per generation, (3) index selection—a total score, based on values assigned to numerous individual traits, is the basis for selecting trees.

SELECTING SOUTHERN PINES

Some of the traits and combinations of traits that must be considered in selecting southern pines are illustrated by offspring of two different slash pine phenotypes (figures 198 and 199). Young trees are used as examples because most environmental factors probably have not exerted much influence on them and, what is more important, selection may be concentrated on young trees in future selective breeding programs. However, certain traits, such as seed production, cannot be evaluated by observation in young trees, and breeding plans should be prepared accordingly.

In breeding southern pine, such as selection of seed orchard clones in wild stands, a combination of selection methods has been used. First, the trees were culled on the basis of insect attack, disease attack, stem form, or stem straightness. After this step, the candidate trees were rated for 10 to 12 traits for total score by index selection. The trees with the higher scores were selected for cloning (Stonecypher 1969b). However, roguing of orchards is based on results of progeny tests, an additional level of selection. Theoretically, tandem selection is the least efficient and index selection the most efficient, according to Hazel and Lush (1942).

Index selection has merit and has been widely used to obtain clones for southern pine seed orchards, but construction of an index is not without problems. Selection indices for wood quality were discussed by Wilcox and Smith (1973), who concluded that no matter what combination of characteristics is desired, aggregate expected gains from index selection are always greater than from single-trait selection. Falconer (1960, p. 327) stressed the importance and complexity of selection by means of an index and concluded as follows: "But since selection has to be applied to economic value by some means, it seems better to use a selection index, however imprecise, than to base selection on a purely arbitrary combination of component characters."

In contrast to the conclusion that the index selection system is the most efficient, geneticists point out that the selection differential for each trait decreases as the number of traits increases for which selection is carried out. The latter principle is quoted as the basis for recommendations that selection be carried out for only one or two traits at a time. The most important disadvantage of selecting for one or two traits at a time seems to be that the method assumes that there are no undesirable traits in a species that can offset the gains made in the particular trait or traits chosen. In the southern

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Figure 198.—Open-pollinated offspring of a poor slash pine phenotype have combinations of a few good and several bad traits. Of the five trees at the edge of a plot, two are crooked, two have forked stems, two are infected by fusiform rust, and all are large branched and poorly pruned, but height growth is rapid and fairly uniform. Probably the two largest trees at the left end of the row will be the only ones to develop into average trees in a forest stand. The tree in the immediate foreground has made very good height growth, but stem and crown form are bad, and it is infected by fusiform rust. The tree at far left is of average height in a slow-growing family of a different phenotype. All trees are 5 years old. The maternal parent of the trees in the foreground is the fast-growing but poor-formed phenotype shown in figure 160.

pines there are several traits that would offset gains made by selecting for growth rate and one other trait, as described in the chapters on variation among trees.

Combining selection by independent culling level with the total score method when selecting plus trees for southern pine seed orchard programs was a good device for eliminating some of the disadvantages of each. Use of independent culling levels enabled tree breeders to reject trees that were diseased, forked, crooked, or unfruitful, or had other undesirable traits that could not be offset by good traits. This procedure reduced the number of trees and traits to which the total score method would be applied, and good traits such as stem volume, branch size, natural pruning, and others could be rated.

An important factor in the successful use of index selection in southern pine breeding is that trees with several excellent traits can be located, although the selection intensity for certain traits is low (figures 200 and 201). Progeny test results discussed in the chapters on tree-to-tree variation show numerous families that have a higher percentage of wood yield per acre than the controls yet no loss of quality. Seed orchard clones contain numerous, extremely good, general combiners for volume growth, stem and crown form, and resistance to fusiform rust (Weir and Zobel 1972). If a low proportion of the trees, such as 10 to 20 percent, has an important defect, such as stem forking, stem crook, susceptibility to pests, low seed production, then selection can be carried out in the remaining 80 to 90 percent of the trees for growth rate, branch angle, branch size, natural pruning, and other traits. Additional examples of the relationship between kind and amount of variation among traits and the method of selection chosen will be given in the section on importance of phenotypic surveys in this chapter.

The principles of selection may be clearly stated, but they are generalizations; and in practice, selection methods or combinations of methods have to be chosen according to the characteristics of the par-

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Figure 199.—Open-pollinated offspring of a good slash pine phenotype have combinations of several good and a few poor traits. The branches are small, and natural pruning will be good; also, average height growth and uniformity of height growth are good. However, one of the trees has a forked stem, and one is infected by fusiform rust—offsetting the effect of the good traits. The trees are 5 years old. The maternal parent is shown in figure 156.

ticular tree species and the objectives of selective breeding to be attained. Some of the factors in southern pine breeding that influence the choice of selection methods are discussed in the sections that follow.

RESEARCH COMPARISON OF SELECTION METHODS

Selection is one of the most important activities in many plant breeding projects, but little effort has been made to compare methods. For example, Doolittle *et al.* (1972, p. 366) have the following statement in the introduction to a report on comparison of multiple trait selection in the mouse:

> The index selection method has been applied particularly in swine and poultry, and in the early 1960's several theoretical investigations of the method appeared (Harris 1961; Heidhues 1962). Not until 1964, however, was a comparison of index and other methods of selection in actual biological material published. Sen and Robertson (1964) compared index, tandem, and culling levels for simultaneous selection of two bristle traits in *Drosophila melanogaster*, chosen because of nearly equivalent heritabilities. No other report of an experimental comparison of methods for multiple trait selection is known to the authors.

In the study comparing selection methods in the mouse, Doolittle *et al.* (1972) selected for two traits: postweaning weight gain and litter size at birth. There was no significant difference in the amount of weight gain among lines in which index, culling levels, and tandem selection were used. Litter size increased equally in all three methods of selection in one replication, but in the second replication, index selection gave the greater increase. Thus, the differences from the three methods of selection were exceedingly small or nonexistent and, unfortunately, as the authors point out, caused by the fact that the traits, body weight gain and litter size, are positively correlated. Thus, research on relative effectiveness of three selection methods seems to be limited to only two traits each in the fly and the mouse. This is not an impressive amount of investigative work on a subject of such great importance.

The absence of hard research data on effectiveness of various selection methods points up the need for fundamental research on tree breeding methods. Work on breeding methods should be increased even though it might be at the expense of work on minor genetics subjects with minor traits.

USE OF SELECTED TREES

Inasmuch as trees are selected for different purposes, the objective to be gained will influence the choice of method. In research studies to last one generation, trees might be selected for one or two or a combination of traits according to a prearranged plan. Little importance would be attached to the remaining traits of plus or minus trees, whatever the case might be.

First-generation seed orchards should contain clones that give the maximum expectation of the best overall performance. It would be undesirable to include clones with certain minus traits such as poor form, low or zero seed production, or susceptibility to pests, all of which would affect gains by plus traits such as stem volume growth, good form class, good crown form, or good wood quality.

Selection for second-generation seed orchards would be more rigorous than for the first-

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Figure 200.—Slash pine 14.3 feet tall at 3 years of age growing in a progeny test. The tree has extremely fast growth and, in addition, a combination of several trunk and branch traits that are above average for the species.

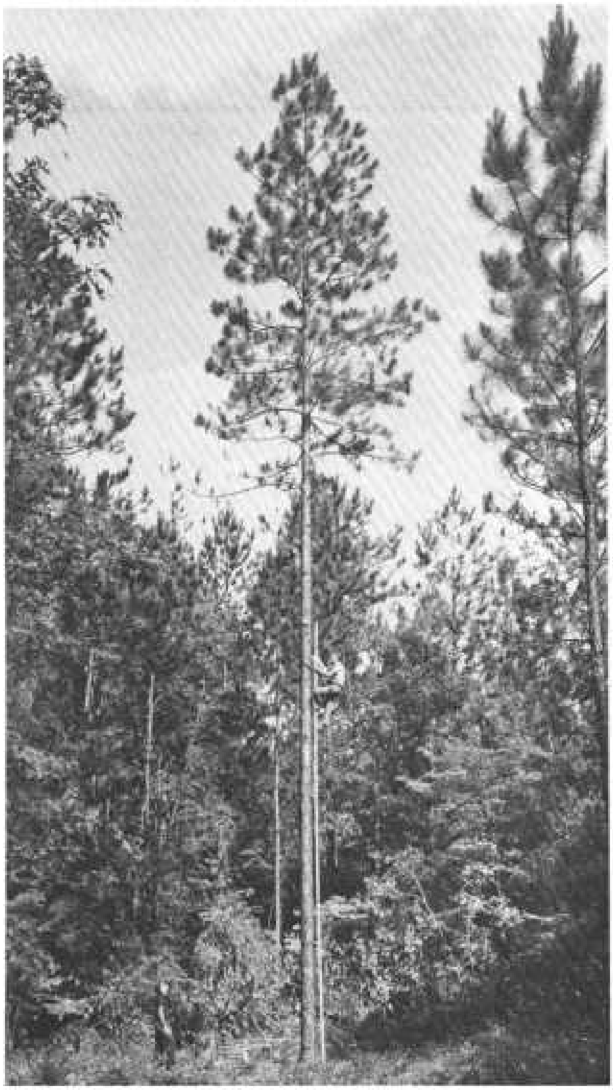

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Figure 201.—Slash pine phenotypes may have fast growth combined with straight and unforked stems, good natural pruning, small branch diameter, low branch angle, and other traits important in high-value, commercial-type forest trees. (Stephenson and Snyder 1969)

generation orchards. Trees in progeny tests, or wild trees that have been progeny tested, might be chosen, depending on whether phenotypic or genotypic recurrent selection is being used. Such trees would have a better combination of traits than earlier selections and would receive high scores under an index system. Some undesirable traits would have been bred out of some of the trees.

In a long-term plan of recurrent selection, large numbers of trees might be chosen, and they might have a range in traits. The objective would be to continue to select and cross to achieve the best combination of traits in the forthcoming generation.

If backcrossing is employed, trees with the required traits would be selected for mating. The objective would be to create desirable combinations of traits in the shortest possible time. A sufficient number of trees should be chosen in the initial crosses to provide breeding stock for all the generations that are required to obtain the results, based on the best estimate possible. Inasmuch as families will vary in the amount of inbreeding depression that they show, a small amount of inbreeding would not be harmful in certain clones.

Parents for hybridization among species should be selected for a combination of good traits. Inasmuch as most southern pine species have a few minus traits, these should be avoided while advantage is being taken of the good traits. The objective is to obtain hybrids with the best combination of traits possible. Morphological, chemical, and physiological traits of trees of the best races, stands, and individuals should be evaluated. Hybrids produced by crossing the best trees of species involved should be greatly superior to hybrids resulting from crossing a random sample of parental stock.

TYPE OF INFORMATION TO BE OBTAINED FROM SELECTED TREES

The basis on which results of selection are to be evaluated should influence choice of number and kind of traits chosen. If the objective of selection is to obtain the greatest genetic gain or loss in a single trait, selection should be for that trait to the exclusion of all the others. Tests of trees with extremes of a trait would be used in phenotypic disassortative mating or the mating of unlikes. It is possible, also, to select and mate trees that are alike for a trait—or phenotypic assortative mating. Mating phenotypes with plus values for a particular trait might be a desirable way to obtain estimates of genotypic variation among trees. The technique could be used in recurrent selection to obtain estimates of the number of generations required to reach a plateau for the trait. In recurrent selection, it is necessary to create variation in each generation as well as to improve average performance of each generation.

Crosses of trees selected for more than one trait would yield progeny on which estimates of gain or loss could be obtained. The results would apply only to the traits involved and not to overall performance of families or stands.

If the purpose of selection is to obtain the greatest economic gain in one trait, then parental trees would be selected for the trait with high economic importance, high heritability, and wide selection differential. Results would be based on performance expressed in wood yield or value for the families or stands of trees.

If the purpose of selection is to obtain the greatest increase in economic value of families or stands per acre, parental trees should be selected for the best possible combination of traits that can be found. The time or cost of selection surveys should be reasonable in relation to the size and importance of the breeding project. Results would be based on the value and amount of wood produced by families and unit area.

Clones for southern pine seed orchards were selected for a good combination of traits because the objective was to obtain the greatest economic gain possible, not the greatest genetic gain in one particular trait. As pointed out earlier in this chapter, selection by independent culling levels was the method selected in order to eliminate trees with obvious defects such as crooked stems, forked stems, insect and disease damage, and poor seed production. The remaining plus trees were then selected on the basis of an index system which assigned weights to 10 or 12 metrical traits.

If selection is part of a study to obtain classical heritability estimates, a random sample is necessary. It is more important to have a good sample than to have trees with the maximum range of variation for particular traits.

The kind and amount of variation in different traits are important factors in an economic analysis of yield increases from breeding. Some of the characteristic features of southern pine traits will be discussed in the following sections.

NATURE OF PINE TRAITS

In the literature, discussion of single versus multiple-trait selection has been largely theoretical because of the size and complexity of the problem. This is understandable because a principle that would apply in breeding everything from hay to horses would be rather broad.

Creative breeding is usually carried out with one species, or a very few at one location, and the traits of the particular species become the important consideration. Thus, it is important to consider in detail what is involved in selecting one or several traits in the southern pines. The information summarized here is based on data in earlier chapters about variation among trees. Information about variation among traits is more complete for certain species than others, and more complete for certain traits than others. Additional information is being acquired and should be used according to its value.

Number of Traits That Vary

The southern pines are notable for the large number of traits that vary, in contrast to certain other pines such as red pine in the Lake States. Variable traits are found in the groups of morphological, physiological, and chemical traits of southern pines. Variation in many traits occurs among races, stands, and trees.

In regard to crown form, variation occurs in traits such as branch size, length and angle with the trunk, and the rate of natural pruning. Bark thickness varies among trees of the same growth rate. Volume of the stem varies widely among trees. Certain stems may be straight or have one or several forks or may be crooked. The wood varies in specific gravity, proportion of spring wood, and summerwood dimensions of tracheids, extractives content, and relationship of wood properties with age. The oleoresin varies in amount produced, the kind of chemical components in the turpentine, and in the amount of various components. Resistance varies to certain insects and diseases, also to drought and cold.

Consequently, in the southern pines, there is an opportunity to select among a large number of traits. Evaluation of economic gain, in contrast to genetic gain in one trait, must be based on the combined performance of all traits. Selection of seed orchard clones has been based on 10 to 13 traits, depending on the method used by various tree breeders (Cech 1959). Height, straightness, pruning ability, wood specific gravity, branch diameter, and freedom from insect and disease attack were included in five grading systems; volume, spiral, crown size, branch angle, and age were included in four systems; form point or class in three systems; ratio of bole volume to crown size in two systems; and ratio of basal area increase to crown size, seed production, and summerwood percent in one system. In all grading systems, strong emphasis has been placed on traits influencing volume growth, tree form, wood quality, and resistance to pests. Minor emphasis has been placed on traits of lesser importance.

Most of the traits can be evaluated by observation, but wood quality determinations must be made in the laboratory and wood volume determinations by tree measurement. Wood volume superiority is estimated by comparing the plus-tree volume with the average of five control trees. Wood volume comparisons are usually very weak because five trees is far from a sufficient number from which to compute an average for a stand. However, the grading systems provide only a means of comparing phenotypes. The genotype can be accurately evaluated later in progeny tests, and the test results can be used as the basis for roguing orchards.

Phenotypic variation occurs in growth rate and wood property patterns in relation to tree age. Height growth in certain trees may continue at a high and uniform rate for 30 years; but in other trees, it may be high while trees are young and decrease when they age, or it may be low while the trees are young and increase when they age, as reported by Wakeley (1971). Also, trees vary in seedling growth rate with month of the year (Ledig and Perry 1969) and date of growth initiation in the spring and cessation in the fall (Harkin 1962; Bassett 1966, 1969). Changes in certain wood properties, such as specific gravity, with tree age may be curvilinear, linear, or change little or not at all.

Genetic manipulation of growth patterns may be a productive method of increasing both volume growth and uniformity in southern pines. As Schultz (1972) found among slash pine clones 10 years old, volume growth of a vigorous clone was 3.7 times that of a slow-growing clone. Respective heights of the clones were 39 feet and 30 feet.

Variation throughout a tree in ring width, wood specific gravity, and tracheid length, for example, contributes to problems in wood utilization. If it were possible to improve wood quality by selection for such properties as pattern of wood development as well as for a particular level of specific gravity, it would be looked on with favor by industry.

Variation in growth patterns, such as height and diameter growth and annual rings, is high in priority for research. Much work needs to be done in accurately defining limitations and opportunities to guide selection for a combination of economically important traits in recurrent selection programs that are used in seed orchard projects.

Range of Variation in Each Trait

The range of variation is important in selection, as is the number of traits that vary. In a relatively uniform stand, such as an old-field plantation in the Atlantic Coastal Plain, certain trees may produce two times as much oleoresin as the average, some trees will have 70 to 80 percent or higher wood volume as the average trees, and some will have wood with about 20 percent higher specific gravity than the average. In stands or plantations of uniform spacing, certain trees will be well pruned, others very poorly pruned, certain trees will have nearly columnar crowns, others spreading crowns, and branching may vary from horizontal to a large angle with the horizontal.

Inherent range of each trait is difficult and expensive to determine, but some data have been obtained. Phenotypic surveys of trees in relatively uniform stands are of great value in estimating the kind and range of variation for various traits. The correlations between phenotypic and genotypic variation have been much higher in southern pines than predicted by geneticists. Obviously, it is of considerable importance to establish with accuracy the upper limit of variation for each economically important trait. Values for minor traits may be estimated rather broadly because major decisions may not depend on them. However, advantage should be taken of every opportunity to improve minor traits but not at the expense of gain in major traits.

Although much effort has been expended in determining the upper limit of variation in a trait—which governs the amount of genetic gain—some attention should be given to the lower end of the distribution curve. If trees at the lower end of the curve for a particular trait are acceptable for breeding programs or seed orchard clones, the trait might be omitted from an index to permit more emphasis on traits of high economic value. But if trees at the lower end of the scale are unusable, then the trait should be included in an index to insure that no minus trees will be selected. Seed-producing ability is a good example of the importance of recognizing variation of this type when planning selection jobs. In slash and loblolly pines, for example, seed production varies among trees, but a small proportion of trees produces very little, if any, seed. Certain longleaf pines are poor seed producers. If a group of plus trees was selected only for volume growth, crown form, stem form, resistance to pests, and wood quality, the group would contain several trees that would not produce seed and would be thus of no value to the tree breeder. If seed production had been included in the index, the poor producers would have been excluded.

Crown form, stem crook, and wood specific gravity are traits that may vary so widely that the minus trees would be worthless in breeding. Trees with minus traits would lower the economic value of the group of selected trees; hence, gains in volume growth would be offset by the loss in tree quality.

Variation in a particular trait is not unlimited in southern pines. Thus, selection differential increases as the number of trees observed increases, but only to a certain level. Trees above a certain level for wood specific gravity, stem volume, oleoresin yield, stem form, and other traits have not been found. For instance, in all the southern pine region, no pine has ever been found with a stem as large or the bark as thick as that of a mature redwood tree in the West. Thus, the best trees for a particular trait in a planted stand of several hundred trees may rank as high as the best trees in a stand of many thousands of trees.

Economic Value of Each Trait

Traits that influence volume growth, either directly or indirectly, generally have higher value than others. Vigor might influence growth per tree, but trees per acre may be affected by susceptibility to pests or drought. Certain diseases, such as hard pine gray blight of slash and loblolly pines, may have only slight effect, if any, on volume growth or economic value. Thus, growth per tree and wood yield per acre are both important. Economic value of a trait will vary according to the product or products for which trees are grown; for example, wood specific gravity might be important to foresters growing wood for pulp but not if the trees are to be used for lumber or poles. Similarly, resistance to fusiform rust in slash and loblolly pines and brown spot in longleaf pine may be of high economic importance at some geographic locations and of low or no importance at others. Wood volume growth, pest resistance, and tree form are given higher values in most breeding projects.

Moreover, the importance or economic value of a trait may be higher in certain species than others. Rate of natural pruning should receive higher priority in breeding sand and Virginia pines than in other species such as shortleaf and longleaf pines. If a group of sand or Virginia pines is selected for large stem volume, a large proportion would be rejected for poor pruning; but in longleaf, or other species, only a small proportion would have extremely poor pruning ability.

Economic value of a trait may vary over a long period of time, and this also must be considered in breeding plans to improve wood for a particular product.

Relationship Between Genetic and Economic Variation

Economic value may be directly related to changes in volume growth rate, but small genetic differences in branch size or natural pruning may have no effect on economic value.

Absence of a strong correlation between economic value and variation of a trait makes selection easier for multiple traits. For example, something less than "perfect" form could be tolerated without lowering economic value of a group of plus-tree selections that rated extremely high for volume growth and resistance to disease. Small differences among trees in branch diameter, branch angle, or natural pruning have no effect on economic value.

Traits such as forking or stem crook may vary in amount among trees that have the defect, but this is unimportant because no trees need to be selected in the group of forked trees as long as defect-free trees can be found.

RELATIONSHIP AMONG TRAITS

Correlation among traits can be positive (direct), negative (inverse), or zero. Correlation is used here in the broad sense as well as the narrow or statistical sense.

Positive Correlations

If the correlation among traits is positive, a change upward in one will automatically result in an upward response in another. For a group of trees, stem volume increases as crown size increases, oleoresin yield increases as stem diameter increases, and yield of pulp increases as specific gravity increases.

Negative Correlations

If the correlation among traits is negative, an increase in one trait will cause a decrease or change downward in the other. For example, an increase in growth rate from fertilizer application may result in a decrease in number of slash and loblolly pines free of fusiform rust. As diameter growth rate increases, wood specific gravity may slightly decrease, particularly in planted stands.

No Correlation

If there is no relationship among two traits, a change in one will not affect the other trait. The chemical composition of the oleoresin may not be related to any other trait. Seed production might not be related to crown size if all trees are open grown and have large crowns.

Relationship between pairs of traits are important, but in the final analysis the complex of all traits—the entire plant—must be evaluated from the standpoint of its culture and utilization. Also, this must be done from the standpoint of comparing performance of groups of plants, such as races or families, and for the purpose of selecting breeding stock. Methods of multivariate analysis are applicable to these problems (Seal 1964).

Variation Among Correlations

Although there is a phenotypic correlation between two traits, it might not be high. Thus, it would have no or very little effect on breeding. In certain studies there was a small but significant inverse correlation of stem specific gravity with tree diameter. However, the average specific gravity of trees averaging twice the volume of average trees may be about the same as average trees. Thus, it is possible to select for high, average, or low wood specific gravity among fast-growing trees. In slash pine, Perry and Wang (1958) found an average specific gravity of 0.535 for the outer wood at breast height in 97 trees growing 2.67 times as fast as the 10 nearest dominant trees of the same age. The wood specific gravity of 97 trees of normal growth rate was 0.532, not significantly different from that of the fast-growing trees. Among the 97 trees with 2.67 times the normal growth rate, wood specific gravity varied from 0.42 to 0.65, the same range as in the normal trees. Wood specific gravity of 0.65 is 22 percent above average. If trees of fast growth and high wood specific gravity are selected, the cumulative effect of both superior traits on yield of dry pulp per acre would be striking. Quality of pulp would be an important factor in certain breeding programs.

The growth rate and wood specific gravity relationships found in slash pine probably occur in other southern pines. For example, wood specific gravity of trees selected for seed orchard clones, based on growth rate, straightness, crown size, branch size, and branch angle, was about the same as that of comparison trees in loblolly, longleaf, sand, shortleaf, slash, and Virginia pines (Saucier and Taras 1969). For 300 outstanding fast-growth and excellent-form loblolly pine trees selected for industrial seed orchards, the average specific gravity was 0.55, while that for the somewhat slower growing check trees was 0.54 (Zobel and McElwee 1958a).

Somewhat the same situation occurs with regard to crown form and resistance to fusiform rust. Stands of above-average growth may have larger crowns or higher rust infection than the average, but certain individual trees will have large volume and, in addition, good form and will be disease free (Barber 1964, 1966; Barber and VanHaverbeke 1961).

Importance of Noncorrelation Among Traits

Results of nursery selection studies illustrate the absence of a correlation among certain traits. Seedlings selected for superior height growth in nursery beds cannot be classified for other traits, and no gain is expected for the additional traits. At 10 years of age, volume of selected loblolly pine seedlings was 3.4 times and slash pine seedlings 1.8 times the volume of controls, but there was no improvement in resistance to fusiform rust, crown form, or stem form (Hatchell *et al.* 1972).

The economic gain of offspring or overall performance—seedlings from seed orchard seed—may not be equivalent to the genetic gain in one or a few traits. The genetic gain in volume growth, stem form, and seed production might be high, but the economic gain might be low or even minus if the offspring were more susceptible than average to fusiform rust or to some other disease or insect pest.

Some of the problems in breeding for a combination of anatomical factors with the aim of developing strains for high-quality pulpwood are discussed by van Buijtenen (1964).

The importance of traits that are not correlated in individual trees is illustrated by the photograph of slash pine clones in the chapter on variation among trees. As a general rule, stem diameter is correlated with tree height; but in two clones of the same height, stem volume is greatly different. Thus, selection based on height alone would not always identify phenotypes with superior stem volume. Certain slash and loblolly pine stands with higher growth rate than other stands may have a larger number of fusiform rust infections per tree, but within fast-growing stands many highly vigorous trees may be disease free. Thus, the generalized conclusion that rust infection is correlated with growth rate does not apply to individual trees.

Cumulative Effect of Traits

When variation in the number of economically important traits and the range of variation are both wide, as in southern pines, the cumulative effect of all the traits on wood yield and quality becomes an important factor in choice of selection methods. The value of forest products per acre depends on both volume and quality. Wood volume is a function of number of trees, height, diameter, and, for certain products, stem taper. Tree quality traits include those related to branch size, angle, natural pruning, stem straightness, stem forking, and, for certain products, various wood properties.

To obtain maximum increase in wood yield per acre, selection efforts should be concentrated on individual traits contributing most to volume per tree and number of trees, such as resistance to disease and resistance to insects and drought. To increase tree quality, preference should probably be given to such traits as straight and unforked stems and good natural pruning.

Estimates of inheritance and heritability are computed for individual traits, but the best estimates of gains from breeding are based on the cumulative effect of many traits on per-acre wood yield and quality.

Selection for three or more traits may result in a lower selection differential than for two traits, but the cumulative effect may cause a greater net gain. Selection for increased volume growth and improved form would increase the value per tree, but it would not increase the number of trees per acre if the trees were to be planted in an area of high fusiform-rust damage. If resistance to fusiform rust were added to the selection criteria, the increase in volume growth because of greater numbers of trees per acre may more than offset the slightly lower volume growth per tree and tree quality. Thus, the tree species, traits, and geographic location influence selection techniques.

Discussion of selection techniques is largely academic unless the cumulative effect and economic importance of the traits are considered. Multivariate statistical analysis is used to arrive at an estimate of the combined effect of many traits. However, it may be difficult to obtain the basic data on which the analyses are based. The tree breeder is more concerned with fairly large differences among tree groups, which may be rather obvious, than with small differences even if they are accurately computed.

Errors in Selection for Single Traits

Many traits vary in southern pines, and selection for a single trait might be in error because of the effect of a different trait. For instance, a tree of large stem volume may have an average-sized crown but high efficiency, and, consequently, it would be a good tree for a seed orchard clone. A different tree may have large stem volume but, at the same time, an exceptionally wide and long crown; thus, high stem volume might be a result of a poor trait or poor natural pruning, rather than crown efficiency, and the tree would be unsuitable for seed orchard cloning. If this latter tree were chosen, there might be only slight genetic gain under intensive forest management, and this would be offset by a large decrease in tree quality which would lower economic value of the clone for certain forest products.

Because of the effect of other traits, the correlation of genotype with phenotype will probably be fairly low for southern pines selected strictly for one or two traits.

Importance of Phenotypic Surveys

Lack of knowledge about phenotypic variation, as a result of limited surveys of southern pine stands and overemphasis of theoretical relationships, has led to some exaggeration of the problems in selecting for multiple traits. Results of phenotypic surveys have been given in the chapters on tree-to-tree variation in each pine species and should be used to guide selection in southern pines.

Stand tables show that in planted and natural stands of about 700 trees per acre, there are a few trees with twice or more the average volume (Nelson 1964; Clutter and Bennett 1965). If the 3 largest trees on each acre of a 100-acre plantation are marked, we would have a total of 300 phenotypes with 100 percent greater than average volume growth. If 10 percent are forked, we still have 270, and if 30 percent of these have crook, the total is reduced to 189 (Mergen 1955b). Among the 189 phenotypes of superior volume growth and good stem form, we can select first for the traits of greatest economic importance, such as resistance to pests or wood specific gravity, if these traits are important to the particular project. The next round of selection would concentrate on traits of lower economic importance such as branch size, branch angle, natural pruning, stem taper, seed production, or others. There are good prospects that we would identify sufficient trees for a small seed orchard and that the trees would be outstanding in all of the most important traits and above average or acceptable in the less important traits. It should be kept in mind that, in this theoretical example, we started selection in a relatively small area and with a small number of trees compared with the resources or stands that are available.

A few examples indicate that the above estimates may not be unreal. Among 4,050 slash pine in a 20-year-old plantation, two trees were found with 2 and 2½ times the normal volume growth and 1½ and 2½ times the normal oleoresin yield; in addition, both had good stem and crown form (Squillace 1966a). Among slash pine seed orchard clones, several were found that had exceptionally high oleoresin yield, and it was concluded that it was possible to have clones with good volume growth, gum yield, and stem and crown form (Peters 1971). As summarized in the chapter on variation among trees, one- and two-parent progeny tests demonstrate that offspring inherit combinations of good traits.

In southern pines, the magnitude of gains from the use of simple breeding methods, including selection for multiple traits, is extremely high as compared with certain other crops. Much work is usually required—for instance, to improve grain yield a few percentage points or to make the crop less susceptible to disease.

Accuracy of Phenotypic Selection

Probably the influence of environmental factors on tree growth, form, resistance to pests, etc., has not been greatly exaggerated for southern pines, but the problem of estimating the genotype in selection has been grossly distorted. In the early years, it was not wrong to say that selection of plus trees would be inaccurate in stands where age, spacing, soil, moisture, and exposure to pests differed widely. But it was wrong to extend this conclusion to include stands that were relatively uniform for age, spacing, soil, moisture, and exposure to pests. The key factor in the breakdown of logic seems to have been a failure to recognize that if various environmental factors cause phenotypic variation, then in a uniform environment there would be little phenotypic variation. If there was no variation in environmental factors, the external appearance of trees was, and is, a relatively accurate expression of the genotype.

In a study of the laws governing fluctuation of intraspecific variability in trees, Mamaev (1968) found that the extent of variability was determined by the genetic characteristics of a species and was little influenced by ecological factors. Mamaev computed coefficients of variation for 17 morphological, 9 anatomical, and 10 physiological or biochemical characteristics in Scots pine. He examined spruce and fir and five hardwood species also.

Surveys of phenotypic variation have been of great importance in guiding selection in southern pine breeding, and phenotypic selection has produced large gains in wood yields.

The accuracy of phenotypic selection should not be underestimated, but, at the same time, it should not be overestimated. Progeny testing is necessary for additional refinements in estimating the genotype and suitability of clone performance in relation to other clones in a particular seed orchard. There is always the possibility of some error in selection because "relative uniformity" of stands is not easy to estimate with precision, and, also, there may be differences in genetic levels between plantations or stands at different geographical locations. Thus, plus trees with about the same selection index rating may not have similar genotypes, although both would be greatly superior to average for the species at a particular geographic location.

NUMBER OF TRAITS SELECTED DEPENDS ON PURPOSE

Inasmuch as selection is carried out for several different research purposes as well as to obtain seed orchard clones, there is no single answer as to which is best—single-trait or multiple-trait selection. Multiple-trait selection is best to make the largest economic gain—which is the objective of seed orchard projects. Single-trait selection is best if the objective is to make the largest genetic gain in a particular trait without consideration of economic value of the whole tree. Selection for an individual trait can be used in studies of variation and inheritance or of effects of various mating schemes, or in long-range breeding programs not involving seed production in interim stages. These studies would be separate from seed orchard projects.

Large-scale projects to create new strains by recurrent selection may include several methods of selection from generation to generation as well as different mating schemes. Also, several such carefully planned breeding systems might be conducted concurrently. Selection methods and mating schemes would be used according to the families and individual trees that were available. It is helpful in making decisions to have the merits and disadvantages of multiple-trait selection listed in brief form, as in the sections that follow.

Plant and animal breeders have acquired much experience in breeding for multiple traits. As Lush (1945, p. 161) has pointed out in connection with animal breeding, "The fact that several things must be considered lowers the intensity of selection possible for each of them, but there is no escape from that so long as all those things have something to do with the net desirability of the animal to the breeder or to his customers." Also, he says that it is not correct to compare the gains made in one of a group of traits in one generation with those made in breeding for just that one trait alone. If 12 traits are involved, results after 12 generations of breeding in each generation for all traits should be compared with those after 12 generations of breeding for only 1 trait in each generation.

Preparation of economic value estimates does not end with construction of the selection index to use at the beginning of a seed orchard project. Estimates of overall performance based on wood yield and quality must be computed for families in progeny tests to guide the roguing of clones in seed orchards. The objective will be to prepare a system to rate clones so that those low on the scale can be removed. Defining small differences between individual clones will not be of major importance.

Barber (1964) showed that young open-pollinated progeny of slash pine inherited the combinations of good or bad traits for which the parents were selected. He ranked 15 families and 4 control lots of trees for eight characteristics. Certain groups of seedlings ranked high and others ranked low for all the traits according to the combination of several poor traits in certain parents and the combination of good traits in other parents. Although the trees were young, they had reached an age nearly one-half a rotation of 20 years, which some foresters consider the span for slash pine pulpwood.

Although statistical methods, such as canonical analysis, are available for evaluating complexes of traits, their effectiveness depends on the availability of a large amount of the appropriate biological and economic data. Thus, as was stated in the chapter on organization of tree breeding, there is a need to prepare long-range research plans and carefully select the kind and number of studies needed to carry them out and obtain data of the kind and amount needed.

There is no very good reason why selection and breeding for multiple traits should be easy and inexpensive, and before we recite all the problems involved, we must consider the alternatives. If we do not select and breed for multiple traits, the alternative methods involve long, expensive, and complex crossing and progeny testing programs that have not yet been charted by research.

It is important to remember, also, that the most important evaluation of seed orchard clones is on the basis of progeny tests. Selection schemes are not an end in themselves.

MERITS OF MULTIPLE-TRAIT SELECTION

1. Identifies trees with composite traits of greatest total economic value for specific products or breeding objectives. In seed orchard clones, the amount of gain in economic value may be of greater importance than maximum genetic gain in one or two traits. It is more important to obtain the greatest gain now from use of improved planting stock for commercial planting than to delay seed orchard establishment for many years in the hope of achieving larger genetic gain.
2. Permits selection against trees with one or more undesirable traits even though they may rate very high for one or two desirable traits. This is important in southern pine species because they have several bad traits, and any one may cancel the gain from several exceptionally good traits. Independent culling levels can be used to exclude from consideration those trees made unfit for seed orchards by one or more undesirable traits.
3. Procures a group of clones that will produce offspring with uniformly good traits because no clone or clones will have one or more highly undesirable traits. The possibility is reduced that the selected trees will produce offspring with a combination of undesirable traits.
4. Identifies a group of clones with an excellent combination of traits that can be used for breeding stock in subsequent generations of recurrent selection or selective breeding with various mating schemes.
5. Provides an opportunity in each generation of recurrent selection to vary the weight assigned to several individual desirable traits whose economic value may have changed with the years, and this can be done most effectively if bad traits do not occur in the same trees.
6. Traits such as stem crook, stem forking, large branches, or poor seed production may be bred out of the strain in one generation. Thus, selection can concentrate on a smaller number of traits in subsequent generations, which should produce rapid genetic gain.

DISADVANTAGES OF MULTIPLE-TRAIT SELECTION

1. Does not permit selection for the greatest genetic gain in the single trait with the highest economic value. This may be an important handicap when selecting within small groups of trees such as full-sib families but less so in large populations such as natural stands.
2. Requires complex techniques to arrive at a realistic value for a group of traits that vary in degree, heritability, and economic value. Evaluation of traits is particularly difficult in species such as southern pines that have wide variation in many traits.
3. Manipulation of several traits in each generation makes planning difficult for several generations in advance. This is an important problem if information about heritability and combining ability is lacking for various traits.
4. May not permit use of the most effective mating scheme or combination of mating schemes to obtain the most rapid advance in improving specific important traits. This is an important factor if utilization of heterosis is being attempted.
5. Maximum uniformity among selected trees may be difficult to obtain for the few traits of greatest economic value.
6. Large genetic gains as a result of cumulative effects are difficult to obtain if economically important traits are negatively correlated.
7. Continued selection for uniformity may result in inbreeding depression and lower performance in certain traits while attempts are being made to improve other traits.
8. Rating trees for economic importance is difficult if there is strong genotype-environment interaction for some traits.
9. Because of errors in estimating the genotype from the phenotypic expression, the range of genotypic variation among selected trees may be greater than anticipated. This situation would result in wider than expected range of variability among trees from seed orchard seed, but it should not reduce the amount of genetic gain.
10. High expenditures for field surveys may be necessary to locate the required number of trees with an excellent combination of traits if they are to be used for seed orchard clones.

DISCUSSION

Selection is the procedure by which discrimination between individuals is carried out. Classic methods are selection by independent culling levels, tandem selection, and index selection. If the goal of selection is the greatest genetic gain in one trait, tandem selection is best. If the goal is greatest economic gain, such as in selecting seed orchard clones, independent culling levels plus the index methods are best. These conclusions are based on the facts that, in the southern pines, many traits vary, magnitude of variation differs among traits, the kind of variation differs among traits, certain traits are correlated, and many traits are not correlated. Selection for multiple traits by use of an index has numerous advantages as well as disadvantages, which are listed; intensive study of goals and methods should be made before work begins.