

CHAPTER 17

RESEARCH NEEDS IN SOUTHERN PINE BREEDING

NEED FOR DIRECT AND SIMPLE BREEDING METHODS

The southern pines may be easier to manipulate genetically than slower growing tree species in other regions, but this does not make them easy in comparison to ornamental shrubs or annual crop plants. The fact that they are trees places stringent restrictions on the kind and number of things that the tree breeder can do with them.

The breeder of southern pines cannot grow large populations—many progeny tests with large numbers of families and individuals. He cannot carry out a breeding plan requiring many generations of outcrossing, selfing, or backcrossing, or various combinations. He cannot irradiate hundreds of thousands of plants, seed, or pollen for many years with the expectation that by chance desirable mutants will appear. He cannot start with a large population of trees and selectively breed for one trait at a time over many generations and improve present planting stock. These are some of the restrictions imposed by the large size and long life of southern pines. There may be others because of their genetic makeup. Our pines are generally cross-pollinated, and although individuals may be self-fertile, it might be impossible to carry out a program of selfing for several generations in spite of the fact that this type of mating might be highly desirable for some purposes. Certain species hybridize rather easily, but not all the southern pines do so. Thus, we could not combine the best traits of all species, races, and individual trees, if such a grand breeding plan seemed desirable.

The period of time between generations is so long that it is more efficient to improve traits as much as possible in each generation than to do a few things in each of many generations.

There is a wealth of raw material—the gene pool is large—because the pines are highly variable genetically and grow over a large area and in many environments. This provides an opportunity for high selectivity in the choice of breeding stock and gives high genetic gain in only one or two generations—as is being proven by progeny tests, although many of the trees in them are still young.

In any event, breeding plans for southern pines must be very simple in many respects. Conversely, they must be highly technical in concept and skillfully carried out. The cost of each generation is so high that the thinking, planning, and execution of the plan for each should be done with great skill.

A strong frontal attack to reach specific breeding goals is often highly successful. Although very effective, this direct approach in breeding is constantly under attack on the grounds that more “basic” information is needed to guide the work. But a shortage of “basic” data has not noticeably encouraged research workers to supply the specific kind needed in creative breeding. Borlaug (1972) urged a direct approach in creative breeding and not an indirect approach emphasizing basic genetics. The direct approach would involve selecting, breeding, and testing large numbers of trees. One of the most valuable findings for southern pines has been the high correlation between genotype and phenotype. And these correlations were developed largely from applied breeding, not basic research.

This strong and direct approach has been very effective in certain instances. In Florida, phenotypic selection in slash pine for high oleoresin yield identified trees with two times the average yield, and their control-pollinated offspring averaged two times the average yield. Seed orchards were established with clones selected among the better families, and these seed are expected to yield strains with 2½ times the oleoresin yield of wild trees. Thus, application of a direct and simple program produced spectacular gains in yield. Impressive gains can be made in other traits—resistance to fusiform rust, resistance to brown spot, better natural pruning in sand and Virginia pines, etc.—while long-range and complex breeding programs are being conducted to produce better strains at some future date.

It is possible to see some lost opportunities by looking backward a little. For example, vegetative propagation could have been used to provide a clonal planting of trees selected for slow growth or fast growth combined with good or poor form, wood quality, or resistance or susceptibility to pests. As few as five trees per clone probably would have been sufficient to demonstrate the uniformity of traits within clones and the differences among clones.

A plantation of carefully selected clones would very early have demonstrated the general inherent range among trees in volume growth, tree form, wood properties, and resistance to pests. Furthermore, it would have been demonstrated that it is possible to combine fast growth with good tree and wood quality and with resistance to pests—a combination about which there is still some difference of opinion among geneticists today. After it was established that differences among trees were inherent,

tree breeders would have been encouraged to refine the information by following through the sexual cycle which is slow and very expensive but very important. Information would have been obtained on the yield gains derived by crossing trees with fast growth and other excellent traits—that is, breeding for multiple traits—and information about this subject is still lacking today.

Although breeding plans may be complex, it is possible to carry on several at the same time because of the long time between generations. This may be much more efficient than trying them in succession.

ADDITIONAL INFORMATION NEEDED IN BREEDING

Tree breeders will find no substitute for a sound knowledge of the principles of plant breeding. A rough classification system might separate breeding principles into administrative practices and biological factors. The administrative practices would include problems in laboratory or field test facilities, equipment, budgets, personnel, and all the other things associated with getting the job done.

In the South, the genetics of the southern pines is the item of supreme importance, of course, but this truism is harder for tree breeders to accept than one might think. One of the reasons for this is that the broad subject-matter classification system (such as *selection*, *hybridization*, *mutation*) becomes a habit fostered by educators, editors, and convention planners, with the result that emphasis on the broad subject blurs the emphasis on individual species and their specific problems. The hard facts are that most breeders work with problems of one species in one locale and must reject conflicting ideas or theories that come from research with other species at other places.

The situation in loblolly pine in which trees and races of trees vary in resistance to rust (which itself also shows racial variation) is an example of the complexity of breeding and amount of detailed information needed in creative breeding to improve only one trait of one species.

Research Needed on Longleaf, Shortleaf, and Minor Southern Pines

Much has been learned about most of the subjects important in southern pine breeding, as we can conclude from the extensive literature review. But more has been learned about slash and loblolly pines than all the others together. Moreover, it is not enough to know, as we now do, that important racial differences occur in pines in general. The problem of racial selection in connection with selec-

tion of seed orchard clones or hybridization requires much more specific data for each geographic location and each pine species if the breeding and seed orchard project work is to be kept on a high technical level. Somewhat the same situation exists in regard to tree-to-tree differences, resistance to pests, and other important traits: it is not enough to know that inherent variation occurs when the essential step consists of combining resistance with many other traits to create a group of genetically improved seed orchard clones of a particular species.

The pattern of investigation that has developed seems to be first a general survey to estimate the correlation among traits, such as was done for wood specific gravity and growth rate. This might be followed by some effort to establish the range in variation among individual trees in a constant environment for both growth rate and wood specific gravity. Next, the researchers obtained estimates of the inheritance or heritability of the traits, or they bred individual trees to create offspring with the desired combination of growth rate and wood quality.

Estimates of Inheritance and Heritability

In theory, heritability estimates, usually expressed in percentage, have an important place in tree breeding, and much effort has been expended in accumulating an impressive list of estimates. More useful in breeding practice, however, are estimates of inheritance expressed in units such as cords of wood, pounds of pulp, pounds of oleoresin, trees free of disease, and other units to which dollar values can be directly attached. The requirements for classical studies in heritability are rather rigid and all inclusive; thus, it is nearly impossible to meet them all. Furthermore, in specific breeding projects in which individual parent trees are carefully chosen, there is a serious question about the usefulness of heritability estimates obtained by standard methods. A discussion of heritability for breeders has been given by Hanson (1963).

It is nearly impossible to sample all the environments important in forestry, and yet the environmental variance strongly influences estimates of heritability and may be responsible for a wide range of heritability estimates for the same trait. Heritability estimates may apply to populations of different size, but much tree breeding is done with individual trees. As Robinson (1963, p. 609–610) has pointed out in a discussion of heritability, "It is well known that proportions are difficult to deal with statistically, and that there is a loss of information when one considers a single number, i.e., the ratio, as opposed to its two components."

If the above conclusions about the limitations of

Limitations of Heritability Estimates

heritability estimates are correct, then inheritance data become highly important. This is borne out by results of crossing trees for high oleoresin yield, fast growth, and resistance to pests. Thus, it is often more important to know the results from crossing the exceptional trees among a distinctive group than the average for the group. Because breeding is the process of applying great pressure in a series of steps to change gene frequencies or combinations of gene frequencies, it is important to know in detail the breeding characteristics of small numbers of trees, rather than the average for a large group.

Inheritance and heritability estimates from a regression of offspring on either parent or the midpoint of both are particularly useful. Visual inspection of a graph of the data indicates the range among parental trees in the trait tested, and the scatter of points around the regression line indicates the range in performance among progeny of families of parents of similar phenotype. If the range among families of similar phenotypic parents is wide, careful progeny testing of seed orchard clones as a basis for roguing might significantly increase the quality of seed from the orchard. Similar phenotypes may have different combining abilities or breeding values, and if the difference is great, the possibility should be recognized and provision made for making use of it in breeding plans or seed orchard specifications.

Trees of similar phenotype might produce families that differ in performance because of differences in combining ability; but if we use the offspring as a standard for judging the parents, it could mean that the estimate of the genotype was in error. In this instance, the genotype-phenotype correlation is low. Errors in estimating the genotype are easier to make for some traits than one might think, partly because environmental effects, such as exposure to insects and diseases or other pests and soil conditions, are extremely hard to evaluate with the same level of accuracy in different environments.

Merits of Heritability Estimates

1. Provide an evaluation of the relative strengths of inheritance versus environment.

2. Give a figure for genetic gain in percent when multiplied by an estimate of variability such as the standard deviation.

3. Are useful for ranking importance of each trait in cross-breeding programs.

4. May indicate importance of sexual versus vegetative propagation if it is feasible to use either in pine breeding programs. Broad-sense heritability may be much higher for certain traits than narrow-sense heritability.

1. Each estimate is strongly influenced by the component for environmental effect, and "environment" is exceedingly difficult to define, duplicate, or sample in the depth necessary to provide all data needed.

2. Must be used in connection with estimates of variation, and these must then be determined for each trait and condition where they vary, such as with age, site, spacing, geographic location, or other factor for each tree species.

3. Must be available for all economically important traits and environmental conditions before they can be effectively used in planning breeding programs. Also, all the various estimates must have about the same degree of accuracy.

4. May seriously underestimate strength of inheritance for a trait if "environment" effects are overestimated. The usefulness of a ratio, for certain purposes, is impaired because it is composed of two values.

5. Estimates in the amount and degree of accuracy required for economic analyses are exceedingly difficult to obtain for southern pines, or any tree species, because of the years required for each study and the difficulty and cost of using highly sensitive study designs under field conditions. The problem is not so complex for plants grown in greenhouses, for example.

6. Although advocated because they provide a mathematical basis for making decisions, much subjective judgment is required in using heritability estimates because they are not available in the kind and amount needed in intensive breeding of southern pines. This situation may improve if new research provides answers needed by breeders.

7. They are based, by mathematical computation, on inheritance of the trait in field tests, that is, the actual performance of individual trees; but, for certain traits and breeding programs, demonstrated performance of trees themselves may be far more important than a heritability "estimate."

8. Procedures are not available for computing heritability estimates for certain traits such as resistance to insects and diseases or for the seed production of southern pines—traits of great economic importance or value in creative breeding.

9. They are difficult to use if field performance such as wood production per acre is dependent on cumulative effects of many individual traits, such as seedling survival, tree growth, resistance to pests, tree form, or wood quality. If cultural treatments are to be applied to stands, these may be factors of importance in influencing wood yields also.

10. It is very difficult to obtain in advance of need the estimates required to guide breeding

programs such as recurrent selection, backcrossing, or species hybridization. Nearly all estimates obtained to date are based on parent trees in wild stands, and yet the great need in seed orchard programs is estimates for breeding for second and succeeding generations, where estimates from wild trees may not apply.

Genotypic Variation

In the discussion of basic mating schemes and their genetic consequence, the key factors were the characteristics of parental stock and the performance of the offspring. This gives us a clue as to the type of basic research needed as a foundation for efficient applied breeding. We should have complete information about the range of variation in the traits of all the breeding stock available. This would include single traits and combinations of traits. Also, it includes tree species and all the classifications thereof, such as geographic races, stands, and individual trees. Polyploid and mutant forms are included. The economically important traits rank the highest in importance and should be defined first.

Inheritance of Important Traits

The consequences of mating trees possessing a wide range of traits and combinations of traits constitute the most important research problem of all to the tree breeder. Whether the mating is under natural conditions, as in seed orchards or seed production areas, or is controlled, this is the means by which the breeder changes the population in the desired direction. Just as in studies of variation, which provide a guide to selection, studies in inheritance should concentrate first on important traits, either singly or in combination. There is a need, of course, to study other traits that may increase in importance later, particularly as training and teaching devices, where there are limitations of time, cost, and facilities and where the objectives of research are different.

Emphasis on important traits places no restrictions on the researcher; in fact, the factors that motivate most of them—the thrill of discovery, adulation by their associates—apply to the work with major as well as minor traits. In the eyes of most people, a solution to a major problem gives a researcher more prestige than solving a minor one. Often the research on an important trait or subject is far more difficult than on a minor one and presents a strong challenge to the most ambitious researcher. Problems in the genetics of growth rate of wood yield per acre or growth rate in combination with tree form and resistance to diseases and insects are some good examples of difficult subjects.

Breeding Highly Vigorous Strains

Researchers in tree breeding and forest genetics should be taking a hard look at the long-range job ahead. We are already using in some current seed orchard programs the best geographic races and individual trees from natural stands. Having used the natural, available variation, our problem soon will be how to find or create better clones. This corresponds to the trend toward increasing intensity of silviculture in general.

We need to breed strains that will respond to intensive silvicultural treatments. These treatments include the relationships among trees as a stand, in addition to those affecting the site, such as cultivation, fertilization, irrigation, and control of competing species.

Marx (1973) has pointed out that certain plant species are two to three times more efficient than others at the photosynthetic fixation of CO₂ into useful organic compounds. Inasmuch as photorespiration is the most important factor affecting photosynthetic efficiency, it was suggested that productivity of plants could be improved by breeding for lower than normal rates of photorespiration. Ledig (1969) has given a broad discussion of the possibilities in the physiological analysis of growth. The problem of breeding for increased photosynthetic efficiency might be reduced to improving one or a very few physiological or chemical traits rather than the whole complex of traits affecting tree growth.

As part of the program in developing intensive silvicultural systems, we should be collecting information about advantages and disadvantages of genetically uniform stands or mixtures of clones or strains. The strains would be created by using a combination of a mating scheme with vegetative propagation or haploid breeding.

Perhaps the most important problem in research for the future is how to create more vigorous strains. These should be not only individual trees but trees that produce high volumes of wood in forest stands. If we reach a plateau in vigor of growth by means of natural crossing combined with selection as now used in seed orchards, which of the other mating schemes can be used to create still faster growing strains without loss in other traits? How far can we go in increasing growth rate with genetic or phenotypic assortative mating? Are there limitations in the effectiveness of these mating schemes, and if so what are they? A large amount of basic research effort should be concentrated on the genetics of vigor and how to increase it in pines.

Creating strains with not only increased rate of growth but more uniform growth is desirable. The frequency distribution curves of commercial forest plantations and full sibs in progeny tests show great

variation among trees in volume growth. Certain individual trees may produce 2½ times as much wood as the average or even greater amounts. This range in variation is usually consistent from family to family or plantation to plantation, and it cannot be considered a random occurrence. Some of the variation is environmentally caused, and susceptibility to certain pests is often a factor. However, the damage by pests can be seen in many cases, and variation in growth independent of pests is evident. The range in volume growth among trees is far too wide to attribute all of it to variation in soil fertility.

If a large amount of the tree-to-tree variation in growth is genetic, it becomes obvious that most of the trees are not utilizing the available soil, water, and light to the fullest. Can this situation be improved? What mating scheme can be used to improve uniformity of growth without loss in variability of physiological traits for protection against pests or other unforeseeable environmental influences?

Volume Growth in Combination With Other Traits

In the early work in breeding southern pines, there was some concern about the negative correlation of volume growth with other traits. The most important traits involved were wood characteristics, tree form, seedling survival, and susceptibility to certain diseases such as southern fusiform rust. Reservations against going too far in breeding for increased growth are given in the chapters on variation and inheritance. Progeny tests have shown that, in some instances, there is an undesirable relationship in the broad sense between growth rate and some of the traits. The progeny tests have shown, too, that the relationships may not be strong or that they do not hold for individual trees, families, or races. Also, the relationship was so low in some cases that it was within the tolerance acceptable to foresters and the wood-using industry. Nevertheless, the overall performance of strains is the standard by which they should be judged, and fast-growing strains must have many other good traits, also.

For the future, there is a need to develop methods of selecting and breeding for multiple traits. The subject is so important that a later chapter is devoted to a discussion of current thinking and information about methods applicable to southern pines. There has been an extremely small amount of research on the subject of selection methods in relation to the great importance of the subject.

Creative breeding requires extensive field areas for progeny tests and also requires the training of

employees to measure trees. To insure that individual trees with a good combination of traits occur, more and larger families of trees must be produced than are generally necessary for forest genetics research.

Time Between Generations

Research on the genetic factors that reduce time between generations is desirable. Studies in early sexual maturity would be a part of this work. A more important objective would be to determine the factors genetically controlling growth patterns. This would form the basis for estimating juvenile-mature correlations leading to a reduction in length of progeny tests.

Although it might not be possible to predict mature performance with a high degree of accuracy for long periods for all traits, it would be helpful to know the amount of error involved for particular traits at different time intervals so that the tree breeder can make proper allowances in evaluating interim progeny test data.

Designing long-term progeny tests for a few traits is much easier than for many traits; thus, it is important to know those on which to concentrate. This is part of the much larger subject of progeny testing southern pines that should be treated as a distinct and important research project, but the important thing here is to focus attention on the genetic factors involved. Do growth relationships with age follow a fixed pattern, or are they strongly influenced by environmental factors as well, and if so which ones and how much?

Treatment of Natural Stands

There are large areas of natural pine stands such as farm woodlands that are being converted to plantations of genetically improved strains. If genetic improvement could be achieved, through modification of regeneration or improvement cuts, total wood yields might be increased because the methods could be applied over large areas. The problem should be analyzed and a research program, if needed, outlined in cooperation with silviculturists.

INFORMATION NEEDED ON SUBJECTS RELATED TO BREEDING

Applied tree breeding draws on information from many fields besides genetics, plant breeding, and silviculture. Specialists in plant physiology, forest products, wood technology, entomology, pathology, and statistical methods can make and are making

major contributions by working out modifications or refinements of a technical subject or a technique. The coordinated and cooperative work should continue.

Resistance to Pests

Intensive study is needed of inherent resistance to each specific insect or disease pest. We should establish a base, if it is biologically feasible, for the genetic solution to pest control. This is extremely timely because of the public concern about the use of chemical or biological controls. Pathologists, entomologists, and physiologists should determine whether inherent resistance occurs, such as within species, between individual trees or races, and in species hybrids. If inherent resistance is demonstrated, much work may remain for the tree breeder to incorporate the traits into breeding plans to mass-produce resistant strains with good growth rate, tree form, and wood quality. Lack of basic data on inherent resistance to common pests such as fusiform rust and brown spot delayed for years action programs in breeding for resistance.

Relation of Growth to Age, Site, and Density

There is a need to determine the relationship of growth to age, site, and stand density in pine strains bred for fast growth, slender crowns, and accelerated natural pruning. The relationships established for wild trees may not apply to improved strains; also, we need to determine the effects of fertilization and irrigation on inherently fast-growing strains instead of only for wild trees.

Wood Properties of Fast-Growing Strains

A large amount of research is needed in the wood and tree quality aspects of pine breeding, particularly in relation to improved growth rate. Uniformity of growth is an important part of the research subject. It is in the field of wood quality that the vast, complex relationships of pine genetics, silvicultural practices, and utilization for various products come together. The formation and support of the Forest Biology Committee of the Technical Association of the Pulp and Paper Industry by foresters, tree breeders, and wood technologists is sound evidence of the importance of wood quality and wood property problems. The subject of wood quality is composed of so many individual research problems that research programs must be well defined and executed to cover the full range of the subject. Research in wood quality and genetics should be oriented within the presently accepted utilization standards and, in addition, to the evaluation of entirely new combinations of tree and wood properties that creative tree breeders produce for

research purposes in contrast to commercial production. Breadth of wood quality studies should extend from the species and population level to smaller units, such as strains for commercial production and individual trees for research purposes.

Vegetative Propagation

A rapid and highly effective method of vegetative propagation for southern pines would facilitate establishment of new seed orchards and the updating of present orchards. Also, it would be useful in research on genetics, tree improvement, pathology, entomology, physiology, and wood quality to produce genetically uniform trees. For example, if needle bundles would root and begin height growth in a period of a few weeks, clones for seed orchards or research studies could be produced in a relatively small space and would be ready for planting at the beginning of the growing season. Problems relating to grafting in the nursery or field, transplanting fairly large plants, and incompatibility of stock and scion would be eliminated. Expensive facilities with controlled moisture, temperature, carbon dioxide, and light, plus the care required to handle the little trees, would be justified because of increased overall efficiency. The man who perfects a simplified, mass-production method of rooting needle bundles or cuttings will make a great contribution to the whole southern pine industry.

Field Test Designs

The principles of field test designs are well known among research workers, but there is a need to refine them to fit southern pine traits, combinations of traits, soils, and environmental factors. Progeny testing is expensive, and great skill is required to do it efficiently. Design of field tests for various purposes is a problem in quantitative genetics, and available data derived from past experience should be used as a basis for developing efficacious methods with reasonable costs. Improved techniques for progeny testing are needed for research studies involving a relatively small number of traits of a few parent trees and, in addition, for a large number of traits and many trees, as is required in testing several hundred seed orchard clones. A few specialists, such as McKay (1958), Stern (1964), and LeClerg (1966), have addressed themselves to progeny testing problems with trees, but in a rather general way. There should be less effort in attempting to make southern pines fit standard field test designs and more effort in refining techniques specifically for problems in testing southern pine progeny.

Correlation of traits between juvenile growth stages and mature trees is important in reaching

decisions about duration of field tests and thus becomes part of testing techniques. Analyses of data must be specifically for use in creative tree breeding, genetics, research, or silviculture because the requirements of each subject will differ. For example, selection of plus trees for fast growth would depend upon growth relationships for large seedlings only, and not for average or below-average seedlings. But, estimates of growth for families or per acre would require estimates of relationships for all seedling sizes. Much information can be obtained from current tree breeding and silvicultural studies that have been underway for many years. In addition to knowing the correlation between young and mature trees, it is important to know the correlation between young trees and those at intermediate ages; also, we should determine the kind as well as the amount of error that may occur so that results can be used accordingly in field testing. Anything that can be done to shorten progeny and other field tests will be very helpful. From a strictly statistical standpoint, certain errors may seem large; but they may be a result of certain factors that do not limit usefulness in breeding but do permit a large saving in time and expense. A correlation may be fairly low for a group of trees but high for certain individuals.

Among the southern pine species, variation in certain traits is continuous but discontinuous in others; some traits vary widely and others narrowly; some have high economic importance and others low; some are greatly affected by the environment while others are not; some can be evaluated early in life and others only when trees are mature. Furthermore, and probably most important, the effect of certain groups of traits is cumulative, while other groups of traits may contain some bad ones that cancel the effects of good traits. In addition to the variation in traits to be tested, the tree breeder has to contend with the variation in soil fertility, competition from ground cover, variable survival, and other environmental factors within and among planting locations. All of these conditions add to the complexity of designing efficient progeny tests specifically for southern pines. Evaluation of various sources of experimental error might be a good place to start the study of methods for improving field test designs.

Combined Breeding and Progeny Testing

There is a need, also, to develop techniques for combining creative breeding with progeny testing. In certain tests, the number and size of families should be large enough to permit choice of breeding stock for further generations of recurrent selection, backcrossing, or hybridization. Several objectives rather than just one should be considered in judging

the "efficiency" of various experimental designs. Much more is involved in progeny testing than estimating the mean of a family or group of families.

Economic Analyses

Information is needed that is suitable for economic analyses of seed orchard programs for each tree species, combination of traits, and geographic location. Tree breeders or geneticists should obtain most of this information because they can do it with higher accuracy than anyone else. Estimates of gains do not have to be extremely precise or of great scope, but they should meet the needs of people responsible for preparing cost-and-return estimates.

Foresters are extremely fortunate, at present, in being able to bypass the highly technical and expensive step of creating new trees before placing them in seed orchards; they can begin by selecting plus trees in wild stands, then propagate clonal lines, establish orchards in which the clonal lines cross-pollinate, and produce improved seed. Thus, foresters are insured of a genetic gain, but they do not know how much because the clonal lines have not been progeny tested. In the future, they will need good estimates of costs and returns.

Another reason for evaluating genetic selections is to determine the cumulative effect of selecting for a few or several traits. Estimated gains for each individual trait usually cannot be added to indicate the overall gain. Moreover, it is necessary for the breeder to decide what combination of good traits he accepts in plus trees. Total gain from increased resistance to pests, increased growth rate, and product value may be very great and will be largest at locations where losses to the pest have formerly been greatest. Conversely, total gain will decrease as the importance of any particular pest decreases over large geographic areas.

An additional reason for determining gains is to insure that investments in seed orchards are adequate. The danger of overestimating returns on investments is well known, but there is a need to consider the possibility of losses from underinvesting. What about the loss from *not* increasing growth rate? In southern pine breeding, estimates by specialists have been increasing, which indicates early estimates were too low. As breeding advances, estimates of gain will become more reliable because figures will become available from early seed orchards, but we need estimates before new orchards are planned. Estimates of overall gain are not extremely difficult to obtain.

Inability to test all clones in all combinations of geographic area and trait is not adequate justification for testing none. Research people may dislike

to be involved in preparing estimates of economic factors because of the shortage of performance data. This attitude is commendable from a certain viewpoint, but research specialists need have no fear if they are generating information that silviculturists and foresters can interpret according to the needs of their own particular organization.

DISCUSSION

The subject of forest genetics research may be broken down into smaller fields of work such as genetics, applied genetics, tree breeding, and applied tree breeding. Work is needed in all four subjects to increase yields of southern pine stands.

Simple and direct breeding methods are needed because pines are large in size and time is long between generations, in comparison with annual crop plants. Variation and inheritance data for the economically important traits are of great importance, but strictly mathematical heritability estimates may have limited usefulness. Development of techniques for breeding highly vigorous strains without loss of tree or wood quality is a major need and requires use of inheritance data for many traits plus the proper mating scheme. Tree breeders need information from men working in pathology, entomology, silviculture, forest products, vegetative propagation, field test design, and economic analysis.