PROGRESS AND FUTURE NEEDS OF FOREST GENETICS RESEARCH IN THE SOUTH

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Abstract.--A broad view of forest genetics research in the South reveals some problems needing emphasis, and suggests some future directions. We need to improve delineation of breeding zones, incorporating climate, site factors, and pest problem areas. We should be avoiding monoculture and off-site planting. We may be selecting for too many traits. Second-generation breeding and selection techniques and progeny-test designs could be improved. Wild pollen contamination in seed orchards is a problem that needs attention. We must learn how to increase genetic gains as plateaus are attained, how to perserve germplasm, and how to breed minor species with minimum effort.

Additional keywords: Tree breeding, forest tree improvement.

My assignment is to take a broad look at past forest genetics research in the South and discuss problems needing emphasis. Aside from a few early special breeding programs, forest genetics research and tree improvement work began in earnest in the South about 1950. Accomplishments have been spectacular. Admittedly, this success was partly due to the strong demand for better seed by forest managers in the South. But it has also been due to the remarkably close cooperation and support of federal, state, and private agencies. Tree improvement programs in other regions have followed the southern mold, but never quite equaled it. Most of the research was oriented to solve practical genetics problems as they were encountered by the various tree improvement programs. These programs also stimulated research in related fields, especially entomology and physiology.

Dorman's recent book (1976) covers our achievements very well and I shall not elaborate on them. Rather, I shall point out some of the deficiencies and needs in our forest genetics research and take a brief look into the future. Topics are discussed in the sequence of major activities involved in tree breeding.

DELINEATION OF BREEDING ZONES

Delineation of breeding or planting zones is usually the first step in a breeding program. The breeder defines the areas and/or sites for which separate superior strains of trees are to be developed. Hopefully, each strain will perform well within all parts of the zone for which it was developed. But many mistakes in size and configuration are to be expected. The continuing refinements of the designated zones should be a normal ongoing part of

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forest genetics research and tree improvement work.

Establishment of breeding zones for our southern species has been rather haphazard. This was largely due to the multiplicity of organizations involved in tree improvement and to their varied and often overlapping forest land holdings. Some organizations having widespread holdings have delineated breeding zones for their own purposes. But because of the lack of needed information they were to some extent delineated arbitrarily and partly on the basis of political boundaries. Other organizations, having limited land holdings, felt no need for delineating breeding zones and this was often justified. But now that much experimental information is available, we can try to rectify this situation. Soundly-based breeding zones would almost certainly increase genetic gains, decrease costs, and help eliminate duplication of effort in the future.

The best information for delineation of zones comes from seed source studies and from analyses of climate and other environmental factors. In the South many seed source studies have been established for most of our commercially important pines, and some climatic studies have been made. It would be very desirable for researchers to analyze all old and new data for each species as a whole, to reconsider breeding zones, and to make recommendations for further tests. In most cases, only local tests may be needed because the broad patterns over species ranges have already been established. In some situations we are using non-native seed (such as the well-known Livingston Parish loblolly pine), and long-term studies may be required.

Some of our commercially important hardwoods and pines still need study. In planning new seed source studies, I recommend emphasis on local tests. The whole species range should first be divided into relatively broad zones, based on climatic and site factors. The size and configuration of such zones would vary greatly by species but a typical zone might encompass 10 to 20 counties.

Then seed should be collected from various portions of each zone and planted at different locations and sites within the zone. This approach will provide the most desirable data -- data on the magnitude of seed source x planting site interaction within each preliminary zone. With this information any need for subdivision of zones can be determined. To get a broad picture of variation over the species' range, some seedlots (possibly bulked from adjacent collections) could be planted at several locations on key sites.

Any seed source studies that are needed will have to be established very soon because the increasing number of plantations will soon prevent installation of reliable tests. Native trees will often be pollinated by trees in nearby non-native plantations. Where serious diseases or pests occur, the degree of hazard should be surveyed and mapped, as was recently done for fusiform rust damage. Such maps are very useful in delineating breeding zones.

CHOICE OF SPECIES AND TRAITS

Many people feel that we have concentrated too much on slash and loblolly pines. These are sometimes planted where they do not grow as well as other species that are better adapted to the site. Research on longleaf pine and other species should be encouraged to alleviate this problem. Going further, we should consider the possible advantages of growing mixed stands, especially where species grow naturally in mixture with others. Establishment of many small mixed-species plantations would be desirable to learn of the problems that might be involved.

I believe we tend to select for too many traits. Studies designed to determine which can be eliminated would be in order. Intentional or unintentional selection for heavy flowering, for example, might be eliminated. On the other hand, I believe that in view of impending shortages of oil and other energy sources, we should consider more research with high-density, short-rotation plantations as a source of energy and chemicals. Likewise, breeding of Eucalypts and other hardwood species for high oil content may be in order.

BREEDING STRATEGIES

In recent years forest geneticists have developed a number of advanced-generation breeding strategies. The more sophisticated ones usually entail 1) controlled breeding of original selections made in the wild, 2) establishment of base populations from the progeny, 3) selection of the best individuals to establish new seed orchards, and 4) roguing of previous-generation orchards on the basis of progeny performance. Here are some problems needing study.

In some programs, original selections from widely separated regions are incorporated into a single strain. The goal is to develop a broad gene base for broad adaptability (Zobel, 1974), but I believe that we should be cautious in this crossing. Genetic gains are reduced in trying to develop strains that will be suitable over wide areas and over a variety of sites. A broad genetic base can be maintained, even within a relatively small breeding zone, by insuring that selections come from various stands within the zone and by avoiding excessive inbreeding in subsequent generations.

The common practice of establishing dual-purpose base populations needs further study. For progeny testing, large plots are preferable, while for selection of trees for new orchards, small plots may be more efficient (Stonecypher and Arbez, 1976). In progeny tests, keeping individual tree ancestry is not necessary and wind-pollinated (or polycross) progeny are sufficient. Perhaps separate plantings would be in order.

Highly intensive and sophisticated breeding approaches may not be justified for our minor species. Later in this paper I propose a simple procedure which will meet other objectives as well.

Techniques for vegetative propagation of superior trees on a commercial scale will likely become available for at least some species. We should now begin to think about how this capability might affect our breeding strategies.

SELECTION TECHNIQUES

Techniques for selecting superior trees were relatively simple in the first generation. Selection in subsequent generations is complicated by the presence of known relatives and other factors. Immediate research is needed on several problems.

Selection techniques should take the following factors into account simultaneously: (1) individual tree performance for each trait of interest, (2) performance of known relatives, (3) heritabilities and economic value of each trait and correlations between traits and (4) degree of juvenile-mature correlations for traits that are selected prior to maturity. Research on this problem in France (Arbez et al. 1974; Baradat, 1976) should be examined for possible application in our work.

Many of our progeny tests show pronounced microsite variation in small patches or fluctuating gradients (Figure 1). Randomized blocks account for little of this type of variation. Techniques or better designs are needed for testing significance of family differences in such situations, as proposed by Wright (1978) and Swindel and Squillace[2/] (In press). Likewise, techniques are needed to account for such variation when selecting and evaluating individual trees within families. One possibility is to compare statistically each individual against its immediate neighbors.

Correlations between some traits are still not clear. For example, the correlation between growth rate and survival (adaptability) has received little attention because of the difficulty of studying this in the first generation of selection. However, now that we have progeny tests established this can be studied, using family performance. Also, we are still not clear about relationships of growth rates to fusiform rust resistance and flower production. Methods of expressing some traits can cause false correlations and these should be examined. For example, expressing wood characteristics on a dry weight basis can cause false correlations with wood density and even affect heritability (Franklin and Squillace, 1974).

The efficacy of including relatives in second generation orchards needs study. Inclusion of relatives increases the permissible selection intensity (and hence genetic gain) but results in a loss due to inbreeding depression (Squillace, 1973; Lindgren and Gregorius, 1976). We need to improve our esti-

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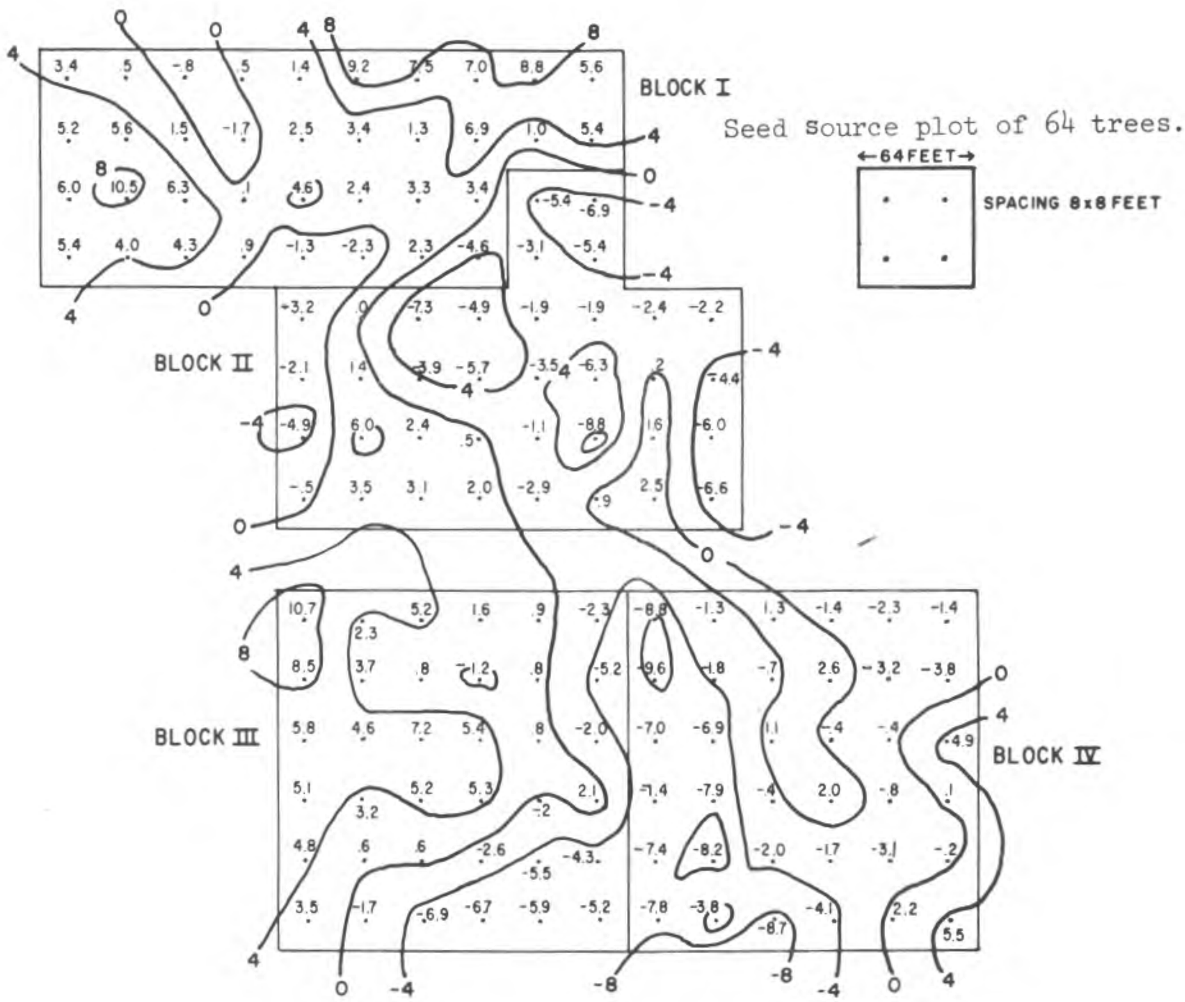
[2/] Manuscript entitled "A test for treatment effects in field experiments having severe microsite variation", by B. G. Swindel and A. E. Squillace.

Figure 1.-- Microsite variation in tree height in a loblolly pine seed source plantation at Olustee, FL at age 10 years. Value at each point is 1/4-plot mean expressed as deviation from overall seed source mean.



mates of the extent of inbreeding depression for various traits, and to determine how much relatedness can be permitted. If it is to be excluded entirely, then perhaps single-pair mating schemes (Libby 1973) for establishing base populations should be used in preference to those that produce many related families.

MATING DESIGNS

Trees are usually mated either to determine the breeding value of selections for use in seed orchards or to develop advanced-generation base populations. Among the many designs available some are most suitable for one and some for the other of the purposes noted (van Buijtenen, 1976). However, we urgently need good experimental data to determine which designs are the most suitable, both from an economic and a statistical viewpoint.

PROGENY TEST TECHNIQUES

I often have qualms about our progeny test techniques. This phase of tree improvement is very costly, especially when it involves tree breeding and periodic measurement of traits. Perhaps wind pollinated seed or polycrossing should be used more frequently (Kraus 1971; Snyder and Namkoong, 1978). More information on juvenile-mature correlations is needed. Curves of trait performance over time would be helpful to determine the best time to measure progeny tests.

Franklin[3] recently showed that genetic and environmental variances of some traits change with age, following definite patterns possibly associated with changing degree of competition. Such effects could have a strong bearing on test designs and on when to measure traits. The matter should be studied further, especially to see if progeny grown at close spacings and under favorable conditions will provide reliable estimates of genetic and environmental variances.

PROPAGATING SUPERIOR STRAINS FOR COMMERCIAL USE

Several problems associated with seed orchards deserve quick attention. Recent work suggests that wild pollen contamination may be high in some situations (Squillace, 1967; Hadders, 1973; Squillace and Lone). More study is needed on this problem and on methods of alleviating it. Techniques, using monoterpenes or isoenzymes as gene markers, are available for studying contamination. Some work is underway to determine advisability of moving seed orchards southward, mainly to increase seed yields but to also reduce contamination. This type of research should be encouraged.

3/ Manuscript entitled "Model relating levels of genetic variance to stand development of four North American conifers", by E. C. Franklin, submitted to Silvae Genetica.

4/ Manuscript entitled, "Proportion of pollen from non-orchard sources", by A. E. Squillace and Ernest M. Long.

Seedling seed orchards seem to be gaining popularity. Planting designs and thinning procedures should be worked out to minimize inbreeding and maximize gains (Goddard and Brown, 1961; Rockwood and Kok, 1977).

Mass pollination techniques offer possibilities for increasing seed yields and genetic gains (Denison and Franklin, 1975). Research along this line should be helpful.

Recent work suggests that yield of selfed seedlings in slash pine seed orchards is probably no greater than in natural stands (Kraus, 1975). We need similar information on other important species.

The planting of vegetative propagules seems certain to become popular. We should be thinking about how best to utilize propagules in planting. For example, would interplanting of seedlings be desirable to stretch the limited supply of vegetative propagules?

ESTIMATING GENETIC GAINS

Many of our estimates of genetic gains are based on small plots in progenytests in which competition effects cause misleading results. More study is needed oncompetition effects and data are needed on yield per unit area rather than per tree.

Estimates of genetic gain are usually based on heritability. Nanson (1976) recently pointed out that the heritability concept suffers from many limitations in forest tree breeding and that it should be replaced by some measure of correlation. Although his proposal seems good in theory, some aspects of it need to be checked by experiments.

PRESERVATION OF GERM PLASM

Many people fear that in the process of breeding and extensively planting superior trees, we may lose germ plasm which although not presently desirable, may be needed in the future as environments or man's needs change. Storage of seed has been suggested as a means of preservation . However, such a technique would eventually require planting followed by recollection and storage. This procedure would have to be followed for collections made from various parts of the range of each species. Also, in the replantings we would have to avoid contamination of pollen from other sources.

In view of these problems, a more practical procedure might be to establish a number of small natural areas, over the entire range of each species. The feasibility and techniques for doing this need study. Germ plasm could also be preserved in seed production areas in which modest genetic gains could also be made. This possibility is discussed in the next section of this report.

A LOOK INTO THE FUTURE

It is very likely that eventually we will run into a plateau of superiority for the traits we are trying to improve -- maybe sooner than we think. I am confident that we can continue to increase growth rate, for example, for several generations, but the gains are likely to decrease with time. In addition to simply running out of genetic variation in growth rate there is very likely a physiological limitation on how fast trees can grow and still be resistant to the rigors of environment. Too, there is the possibility that environments may change. The fusiform rust pathogen, for example, might mutate and become capable at attacking resistant strains of pines. Finally there is a likelihood that human needs, such as products desired from trees, may change.

How are we going to continue to make improvements in the face of these probable events? One possibility is to decrease the size and nature of our breeding zones greatly and develop separate strains for each zone. This approach would not only increase genetic gains but also maintain a large gene pool -- trees bred for different sites or different parts of the species' range would likely be genetically different. This admittedly could also be very costly, and would also eventually encounter thresholds of gains.

In a recent study of the problem of depleting genetic resources, Namkoong (1974) noted that we can attempt to achieve an optimum balance between immediate exploitation (large early genetic gains) and a slower utilization of such resources providing for future gains. This proposal can well be studied further.

What are we going to do about minor species, for which intensive and sophisticated breeding procedures cannot be justified? Here is a suggestion that may be considered for minor species and possibly also for special situations.

1. Divide the entire species range into many planting zones (say from 20 to 40), using the best knowledge available on climate, site factors, and pest problems.

2. Pick at least two phenotypically good, young stands (or good native plantations if available) in each zone. Thin them, using the best selection techniques available, for conversion into seed production areas.

3. Collect seeds from these areas and plant them only in their respective planting zones.

4. As soon as these plantings reach fruiting age, establish new seed production areas for each zone.

5. Collect seeds from the new seed production areas as soon as possible, dropping the old ones.

6. Repeat the process indefinitely, or initiate sophisticated breeding procedures when and if justified.

Note that under this procedure, although the breeder has imposed some degree of artificial selection, natural selection will also occur for adaptability and resistance to adverse environmental factors of the breeding zone. If the environmental factors change with time, so will the population of survivors change. Further, I doubt that the breeder would have to face inbreeding problems, the problem of deterioration of some traits at the expense of others, or genotype-environment interactions. Finally, I believe that, although some degree of artificial selection is imposed, a wide genetic base will be maintained by preserving stands in many widely separated areas.

This proposal is not really new; the seed production area has been frequently used in the past. The only added features are that the whole species range is systematically covered and that the process of mass selection is continued. The procedure could probably also be used in special situations such as in high fusiform rust hazard areas, where genetic differences in the pathogen may occur over the species range or change with time.

Although forest genetics researchers of the South have made remarkable achievements in providing the bases for developing superior trees, there is room for improvement. We could have done a better job in some areas, such as in studies of geographic variation, delineation and refinement of breeding zones, and techniques for comprehensive preservation of germ plasm. Such studies require consideration of the entire range of each species and therefore need highly centralized planning and coordination to avoid duplication and to obtain maximum information. Deficiencies in this regard were partly due to the mixed ownership patterns of forest lands and the multiplicity of research organizations. This situation has been considerably alleviated by the coordinating efforts of such organizations as the Southern Forest Tree Improvement Committee and the Regional Tree Improvement Project S-23. Both should be strongly supported.

Some of the deficiencies in our work were due simply to the newness of our endeavor -- we sometimes were groping in the dark. Also, new problems keep cropping up, as might be expected in any endeavor of this type. But with continued excellent support and cooperation as obtained in the past, these new problems can be solved.

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