

ADVANCES IN GENETICS AND TREE BREEDING

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GENERAL

Tree improvement has progressed rapidly during recent years to the point that major decisions must be made and major changes employed. Early tree improvement efforts were "simple" in that they essentially consisted of learning the biology of the species and variation patterns, selecting for the desired characteristics, "packaging" them into suitable individuals and mass-producing the packages for operational planting. This "simple-minded approach" has proven to be very effective and in some areas such as in the southern United States, parts of Australia and New Zealand, parts of South America and in Europe, it is time to move on into more advanced and genetically complicated breeding methods.

LONG-TERM BREEDING

The activities required to obtain the greatest gain and still maintain a viable long-term breeding program are many; because of restrictions of time and space I will emphasize only a couple of them. Among the full list of needs is included (1) developing the most suitable advanced-generation breeding methods to obtain the greatest gains possible, (2) keeping the genetic base as broad as possible while at the same time keeping it narrow enough to maximize gains, (3) making every effort to conserve the gene base available and expand it as possible. Many specific breeding problems are related to the three listed above; I will be able to discuss only a few of these.

It is sufficient to say that a "revolution" in activities and methodology is coming in tree improvement as advanced breeding programs develop. But one must be careful not to be carried away with the wonder and technical developments of the new approach. The organisms we work with are still trees and have the same biological responses as always. There are biological and economic limitations inherent in any approach. For example, I have seen predictions of possible gains through speeding up generation turnover that are completely unrealistic. Even if the researcher could obtain the genetic gains he visualizes, the law of limiting factors will prevent the 200 to 300% improvements visualized. Except in unusual instances, the growth rate of trees will be restricted by limited water, nutrient imbalance, shallow soils or many other factors of the environment. As one gets into the more advanced breeding phases, the need for a complete coordination between genetic and silvicultural factors becomes of increasing importance. Even in the first generation, when the genetic potential was often the limiting factor, we repeatedly warned and emphasized that maximum gains could not be obtained without

combining genetic improvement with the best silvicultural practices. This has been proven to be a solid rule; for example, no matter how good the genetic potential, growth will not be satisfactory on an excessively wet site without drainage or bedding. No matter how superior the potential of a strain, its full genetic benefits will never be obtained unless proper stocking control is practiced, including a thinning regime that is meticulously planned and applied.

No matter how advanced the genetic potential that might be developed, it is necessary for every tree improvement program to have two phases. The first, the operational or use phase, has as its objective the maximization of gain for commercial forestry. It requires the use of only the very most outstanding genotypes to obtain the greatest genetic differential possible by having a large selection differential. There is need to keep only a broad enough base to be reasonably safe in operational planting. Many errors are made in not recognizing this fact, and much gain has been sacrificed by using hundreds of individuals in a seed orchard instead of the few best genotypes. It encompasses the old "game" of gain versus risk, common to all applied breeding programs. In the sense of advanced-generation breeding, this operational phase is essentially dead end. The second phase is what I call the breeding or research phase. The objective here is to keep the genetic base as broad as possible and to create as many combinations of genotypes as possible. It is similar to the gene conservation program we hear so much about but differs in that it is active and ongoing. Not only are genotypes preserved but they are actively recombined to form new genotypes which are then tested. The new and advanced-generation production or operational programs are then developed from intensive selection among the best performers of the new genotypes.

Advanced tree breeding is therefore different, but yet in many ways similar to the initial programs. The success of advanced-generation activities is dependent upon the initial programs because without the proper long-term planning, advanced programs will be limited and slow. It is essential to remember that time is an integral factor and must be built strongly into any advanced breeding program.

PROBLEMS IN ADVANCED BREEDING PROGRAMS

Because of space and time limits it is not possible to do more than mention some of the things that will be critical in an advanced-generation breeding program. Below are a few examples of the types of problems that must be aggressively attacked if tree improvement is to make the greatest gains possible.

1. The effect of relatedness. Until we know the effect of half-sib, full-sib and other related matings, progress in tree breeding will be slow. Because of the tendency for a few parents to be good general combiners, many of the advanced-generation trees will have common ancestors. Should only a few of these best trees be used, along with somewhat poorer trees, in order to avoid relatedness? Or can a certain number of related matings be tolerated? Answers to these questions are not now available. There has been criticism of the early programs because they did not generate such data. Although the problem of relatedness has been long recognized and much discussed, tests could not be made until enough families with a known pedigree flowered. Such studies are started and many more are needed, but answers to the effects of relatedness are still some time off.
2. Maintaining a suitable genetic base. As seed orchards mature and advance-generation orchards come into heavy seed production, the orchard manager is faced with the problem of how many clones may be rogued, how many kept. The same problem is faced when vegetative propagation is used in operational planting. One common answer is "The more, the better." This is foolish! The objective of a tree improvement program is to obtain genetic gain. And a major part of the gain formula is the selection differential. The too conservative answer of many clones is irresponsible. One seed orchard I know about has 360 clones; for that species and condition, I feel 15 clones are sufficient for an operational orchard. By adding 345 more clones, the genetic gain has been reduced to less than half of what would be available with 15 clones. Is it good sense to reduce gain that greatly over hundreds of thousands of acres just because someone thinks larger numbers of clones might be needed? It is essential to know the minimum number of clones that can be tolerated in operational planting to get the greatest gain with a risk of acceptable magnitude.
3. Vegetative propagation. An expanded use of vegetative propagation, whether through rooted cuttings or tissue culture plantlets will radically change forest genetic thinking. Gains will be larger, manipulation will be easier, and especially hybrids can be used operationally. As methods of vegetative propagation develop, such as for the eucalypts, the total breeding strategy will be altered. In my opinion the widespread use of vegetative propagules operationally is going to greatly expand and we need to be ready for it.
4. Pest resistance. As forestry becomes more intensive, pest attacks will become more serious. Some of the losses can be partially avoided by breeding against the pest. A success

in this area is breeding against fusiform rust in the southern pines; an area of pest attack urgently needing attention is the spruce budworm. Pests should not be able to dictate forestry practices. As time goes on, more exotic species will be planted. A truism is that exotic plantings will be attacked by one or more kinds of pests, be it one year or ten years after introduction. Breeding for pest resistance must be considered as a routine part of a tree improvement program.

5. Adaptability. As the need for food increases, forests are being pushed from the better to the poorer sites. Many of the poor sites are marginal or submarginal for economic production of forest products. To be suitable for timber production, new strains of trees need to be developed to grow on the poor sites. Breeding for adaptability has been very successful and will increase greatly in the future.
6. Improved statistical techniques and indices. Continued breeding without the use of suitable selection indices is not efficient. We have much of the genetic information in hand but intensive work is needed to develop suitable economic data. Developing good indices requires skills and information that we now have but did not have in the past.
7. Balance between conifers and hardwoods. As competition for timber increases, a better balance is needed between utilization of conifers and hardwoods. This means giving the hardwoods more emphasis in breeding and regeneration. As the use of wood in energy and for organic chemicals increases, hardwoods will become of increasing importance, especially for short rotations.

SUMMARY

1. Tree improvement activities are becoming more complex as we go into advance generations. The original "simple" approach of selecting for desired characteristics, packaging them into desired individuals and mass-producing them for operational planting must be expanded.
2. Common sense must be applied in determining potentials from a tree improvement program. The law of limiting factors always comes into place and some gain predictions are not reasonable. There needs to be complete coordination between genetic improvement and silvicultural management.
3. All tree improvement programs must have an operational phase whose objective is to mass-produce better stock and a research phase in which the genetic base is kept wide and new material developed for future generations.

4. Tree improvement always entails an assessment of gain from increased selection differential against added risk from a reduction in the genetic base.
5. A series of special problems in advanced breeding were outlined; the effect of relatedness, maintaining a suitable genetic base, vegetative propagation, pest resistance, adaptability and improved statistical techniques and indices are all urgent if advanced-generation tree improvement is to develop as it should.

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The term applied by a former student and ardent admirer