Integrating Progeny Testing with Forest Production[1]

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GENETIC IMPROVEMENT of forest trees is ceasing to be the exclusive preserve of the research worker and is becoming the active concern of the practicing forester. This development is most welcome to the research worker, who not only finds in it vindication of his activity, but sees in it opportunities for accelerating practical applications as well as for broadening and intensifying research.

This paper is an attempt to synthesize, from some recent work in tree improvement and from discussion with tree-improvement workers, a comprehensive procedure which makes forest tree improvement an integral part of forest production. As a synthesis, it borrows from the work and thought of many people. Yet it would be unfair to imply that any of these people would approve the form in which their ideas reappear. With this reservation, it is a pleasure to acknowledge the ideas, written, spoken, and published of R. Z. Callaham, R. C. Campbell, Carl Heimburger, Leo Isaac, F. I. Righter, Risto Sarvas, C. Syrach-Larsen, J. W. Wright, and Bruce Zobel as well as many practicing foresters in the Pacific Northwest.

The Forest Tree as a Special Problem in Genetic Improvement

Although the principles underlying genetic improvement are equally valid for all sexually reproducing organisms, distinctive features, such as longevity, size, economic value, reproductive biology, etc., must be considered in seeking the most effective means of applying genetic principles to practical tree-improvement problems.

Forest trees possess several features which appear to make them a special class as regards genetic improvement. Most conspicuous, at first view, is the length of generations, which seems to put trees in the same class as an

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organism notoriously unsuited to genetic manipulation. But length of sexual generation is perhaps not the most serious obstacle to genetic improvement of forest trees; the fact that many important properties of trees cannot be adequately evaluated until the trees are several decades old may be even more restrictive.

The restriction imposed by the length of time required to evaluate trees is not entirely inflexible. Juvenile-mature correlations can be used to achieve useful predictions and thus gain time. Nevertheless, plants are notorious for having an open system of growth, which tends to reduce the accuracy of predictions.

Length of test generations also tends to shift emphasis toward characters which may be evaluated in young plants. Examples are blister rust resistance in white pines, early seedling height growth, seedling drought resistance, resistance to soil-borne wilt in *Albizzia,* and resistance to atmospheric constituents in *Pinus strobus.* Selection for any one of these desirable characters is a useful or even indispensable step; it is, however, the first step in tandem or step-by-step selection, which is much less efficient than either index or independent culling-level selection. Nevertheless, the usual efficiency comparisons may not be relevant because time and mortality compel the tree breeder to adopt tandem selection, at least as a preliminary to more efficient procedures.

The other side of the coin is that the longevity—with clonal propagation, one might say the immortality—of a forest tree can be a great asset to the tree breeder. Syrach-Larsen (1956) has called attention to the advantages of working with durable plant materials.

Space may be as restrictive as time. A well-tended field of wheat will produce about 1.5 million mature plants per acre. A stand of Douglas-fir at 60 years, site index 140, carries 291 stems per acre 7″ d.b.h. and larger. Even if we do not need to grow our trees to the nominal rotation of 60 years we probably cannot crowd them much closer than 12 x 12 feet or 300 per acre. Thus our space requirement for a Douglas-fir in a test or breeding plot is about 5,000 times that for a wheat plant. This factor actually understates the difference in two respects. First, the area of soil occupied by a family of, say 40 wheat plants, is likely to encompass far less edaphic variation than the area occupied by a 40-tree family of Douglas-fir. This, as Wright and Freeland (1960) have pointed out, imposes different experimental designs on the tree breeder. Second, the area factor of 5,000 must, to be realistic, be multiplied by the number of years over which the tree must occupy the site before it can be adequately tested.

Another way of looking at the space-time dimensions of trees relative to annual plants is to compare the market value of a Douglas-fir and a wheat plant. Let us assume a yield of 70 bu./acre and a price of $2.50 per bu. to give a crop valued at $175 per acre. Dividing this by 1.5 million, the number of plants per acre, gives a value of .016 cent per plant. Douglas-fir on site index 140 (mid class III) yields 52 M b.f. international on trees 7″ d.b.h. and over. Assuming $15 stumpage, the value of the crop is $780. Dividing this by 291, the number of trees per acre, gives a single-tree value of $2.68, or 17,000 times the value of a price-supported wheat plant.

Just as space-time considerations may force the adoption of special procedures by the tree improver, so also may the fact that forest trees come to hand with a rather different genetic make-up than that presented to the agricultural plant breeder. The latter seldom encounters a truly wild plant. In most cases, the forest tree breeder starts with material shaped by natural selection to maximize its fitness to survive and reproduce in a specific environment. Whether this natural selection has narrowed the spectrum of heritable variation in characters of economic importance, as in red pine, or has left a bewildering array of types, as in Pacific coast Douglas-fir, depends on the evolutionary history of the species. If we take a species with wide heritable variation in characters of economic importance, like Douglas-fir, we find ourselves in a much different position than, for example, the corn breeder, who finds the variation in his species well sorted out by centuries of purposeful selection.

Not only does the forest tree breeder have wild material to start with, he finds his choice of materials and objectives dependent on technologies and markets dominated by tradition and yet increasingly subject to re-evaluation and change. This is particularly true of the Pacific Northwest, where forestry and the forest industries are new. Tree-improvement work has relevance to forestry only if artificial reforestation is widespread and effective. Techniques of artificial reforestation in our region are, at present, inadequate to justify substantial investments in tree improvement or, indeed, to support the testing essential to improvement. Markets currently seem to enforce concentration on Douglas-fir, to the neglect of numerous excellent species better adapted to management on particular sites in the region. But markets are notoriously subject to change enforced by competition or technological development.

This catalog of perplexities besetting the tree improver is not offered as a rationalization for inaction. It is, rather, an attempt to describe the framework within which tree-improvement objectives must be set and procedures developed.

To bring these concepts down to earth, we must speak in terms of concrete facilities. These may be divided into seed-producing and progeny-testing facilities.

The terms seed-production area and seed orchard, should, at this date, need no further elaboration. These are the principal recognized seed-producing facilities in these days when we are at least talking about disemploying the squirrel and the casual cone collector. I should like to add to this list the clone or scion bank, because it seems likely that for certain suitable species, among which I should include Douglas-fir, the clone bank may effectively double as a source of seed, if not for quantity production, at least for extensive testing.

Seed orchards are already, in the major forest regions of this country, being established largely by administrative rather than research personnel, although the latter are usually deeply involved as advisers. The same is true of seed-production areas. These are often considered to be temporary expedients which may be used only until seed can be secured from grafted seed orchards based on a much higher intensity of selection. I have suggested elsewhere (Duffield, 1962) that seed-production areas can have other uses as well. They can, for instance, provide the opportunity for phenotypic evaluation of large numbers of trees over a period of several years before resources are committed on a large scale to installing small numbers of clones in grafted seed orchards. Some of the tree properties which require this long-term evaluation are flowering and fruiting habit, graftability, and stock-scion compatibility, features of crucial importance to the effectiveness of a grafted seed orchard.

These seed-producing facilities are not yet part of the herd or flock; they cannot be expected to contribute directly to forest production, except perhaps in the case of the seed-production area which is eventually logged. Even so, at least with Douglas-fir, it seems unlikely that the repeated harvesting of cones and the production of usable volumes of wood will be compatible uses of the same tree. The breeding and production herd concept takes over when the seed from these facilities is sown in the nursery. Because of the virtual impossibility of maintaining parentage records, direct seeding cannot be included as a reforestation technique in this procedure.

The nursery is the first test facility, in which information on the performance of progenies is fed back to start the process of selective elimination of the less desirable parents. The work of Callaham and Hasel (1961) has shown that for ponderosa pine, second-year height growth in the nursery has good predictive value for 15-year height of planted trees. It is likely that this may be true for many species provided nursery practices are such that seedbeds are fairly homogeneous. Moreover, with the trend toward using larger planting stock, it is likely that the nursery may be available as a test facility for the first three years of the tree's life. This offers the opportunity to select parents which produce fast-starting progenies, a property which seems particularly important in regions where animal damage takes a heavy toll of young plants and where competing vegetation is lush.

In the nursery it is quite practical to use agronomic designs which may not be suitable in outplantings, for the reasons already detailed. Not only is it physically practical to use such designs, but because the nursery is a single central location, the personnel trained to use such designs can be employed effectively.

Anyone who has moved pedigreed plants from a nursery to a plantation laid out in a formal design will appreciate the costs in labeling, layout, mapping, record keeping, and supervision. These strongly restrict number and size of tests. If, as Wright and Freeland (1960) have suggested, formal field designs can be abandoned in favor of single-tree plots in numerous replications, it becomes possible to reduce or eliminate many of these items of cost. The key to such a scheme is a satisfactory system of labeling individual plants so that their parentage can be determined after they have been moved to the plantation. This permits either complete or some restricted form of randomization which can be performed at the nursery, thereby avoiding the extra costs of layout, mapping, and special supervision at the planting site. If the labels are permanent, so attached as to allow growth of the plants, and each with a unique number, they can serve for many years to identify the growing trees for successive inspections and measurements. The scheme is essentially analogous to ear-tagging livestock.

The additional costs involved are almost entirely chargeable to the nursery phase of the operation. Hence, the scheme is applicable to routine production plantations, provided the level of routine planting technology is sufficiently advanced.

Selective elimination can begin at any time, can be applied to families or individuals, and can continue as long as labeling of trees is maintained. The results of measurements and observations may be fed back to guide selection in seed orchard or seed-production area. Moreover, as the plantation reaches the age of cone production, scions from selected plantation trees of known parentage can be moved into clone banks and seed orchards.

This scheme transfers much of the cost of testing to production plantations, and much of the work to administrative routine operations. It requires a more effective plantation technology than is common in some of our forest regions, for fairly high survival and freedom from animal damage are needed to provide adequate test data. It will require the development of special analytic procedures, based on sampling schemes rather than on formal layouts.

Experience with this type of testing is meager. We have found numbered leg bands, as used in game bird studies, unsatisfactory, and have since adopted heavy aluminum foil bands, serially numbered and wrapped spirally around the transplants in the nursery. These appear to be satisfactory so far. Adequacy of planting varies widely from one operation to the next. Some of our existing test plantations will have no value because of poor planting, poor microsite selection, domestic livestock grazing, and neglect of early plantation care. These causes of early loss and poor growth should not be tolerated in any planting program, regardless of its involvement with a tree-improvement scheme. Indeed, it seems likely that the close scrutiny, which the use of individually marked trees enforces, will be in itself beneficial to the planting technology of our region.

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