New Forests 4 : 325-342 (1987)

A conceptual framework for tree improvement programs

TIMOTHY L. WHITE
Department of Forestry, University of Florida, Gainesville, FL, 32611, USA

Received 11 may 1987; revised and accepted 28 August 1987

Key words: breeding strategies, genetic tests, mating designs, progeny tests

Application. The conceptual framework of tree improvement programs presented in this paper can be used by breeders, foresters and students to understand, describe and plan tree improvement activities and program strategies. For example, foresters can use this framework to more effectively schedule and manage genetic test plantations and seed orchards.

Abstract. Forest tree improvement programs have become quite complex and program strategies and intensities vary dramatically around the world. It is often necessary to examine the reasons for each activity separately in order to ascertain how all steps fit together in a strategy aimed at achieving genetic gain. This paper establishes a conceptual framework that explains the purposes of the various activities of tree improvement and allows complicated program strategies to be easily conveyed. This conceptual model, called the breeding cycle, stresses why, *not* how, each activity is conducted. The breeding cycle turns around one time for each generation of breeding and is composed of various types of plant populations. Each plant population serves a role in the tree improvement program and is created form a preceding population in the cycle by an activity of the breeder.

Tree improvement concepts are explained and the roles of genetic test plantations are described in the context of the breeding cycle. This conceptual model is useful for foresters responsible for implementing tree improvement programs, for students and breeders trying to understand and compare divergent program strategies and for managers responsible for making investment decisions.

Introduction

Genetic improvement is an integral part of reforestation and silviculture in forested regions around the world. Several authors have described factors to consider in developing a tree improvement strategy (Burdon & Shelbourne 1972; Libby 1973; van Buijtenen 1975, 1976, 1981; Fowler 1976; Kang 1979a, 1981) and it is a small wonder that differences in species biology, organizational goals, forest management intensity and economic considerations cause operational programs to vary dramatically in both program design and intensity. Differences in program strategies coupled with the large number of different activities in a single program, often make it difficult to understand the reasons for each step and to understand how different strategies are employed to achieve similar goals. Nevertheless, most programs are based on a common conceptual framework that involves successive cycles of selection and breeding. That is, various individual activities differ in practice among programs but serve common functions in the quest for genetic gain.

The goal of this paper is to establish a unified conceptual framework that depicts the various functions of the activities conducted as part of tree improvement programs. This conceptual model, called the breeding cycle, stresses why each activity is conducted and how each activity fits into the overall breeding strategy. As a teaching tool, the breeding cycle framework can be valuable to students of tree improvement, to foresters who must implement program activities, and to forest managers responsible for making investment decisions. The breeding cycle is also useful for comparing seemingly diverse programs in terms of different approaches to achieving genetic gain and for setting genetics research priorities by examining how answers to particular research questions will allow the cycle to turn faster and/or more efficiently.

The first section of this paper describes the plant populations and activities that are components of the breeding cycle. The second section deals with the functions and uses of genetic tests (progeny tests, etc.) that are often planted as part of tree improvement programs. Throughout the discussion, it is assumed that the species to be improved has been chosen. Also, for ease of understanding, the discussion emphasizes conventional programs that utilize sexual reproduction even though the same concepts apply to vegetatively propagated species.

The breeding cycle

General concepts

Most improvement programs of cross-breeding plants and animals can be described in general terms using the framework of the breeding cycle. The breeding cycle is best viewed as a potential set of activities and population types which can occur during a given generation of a tree improvement program (Fig. 1). The activities consist of, for example, selection, breeding, progeny testing and seed orchard establishment, while the populations consist of different groups of individuals which result from those activities. The core activities of genetic improvement programs are selection and breeding. Selection is based on the principle that the average genetic value of a group of selected individual trees chosen on the basis of superior outward appearance (called phenotype) will be higher than the mean genetic value of

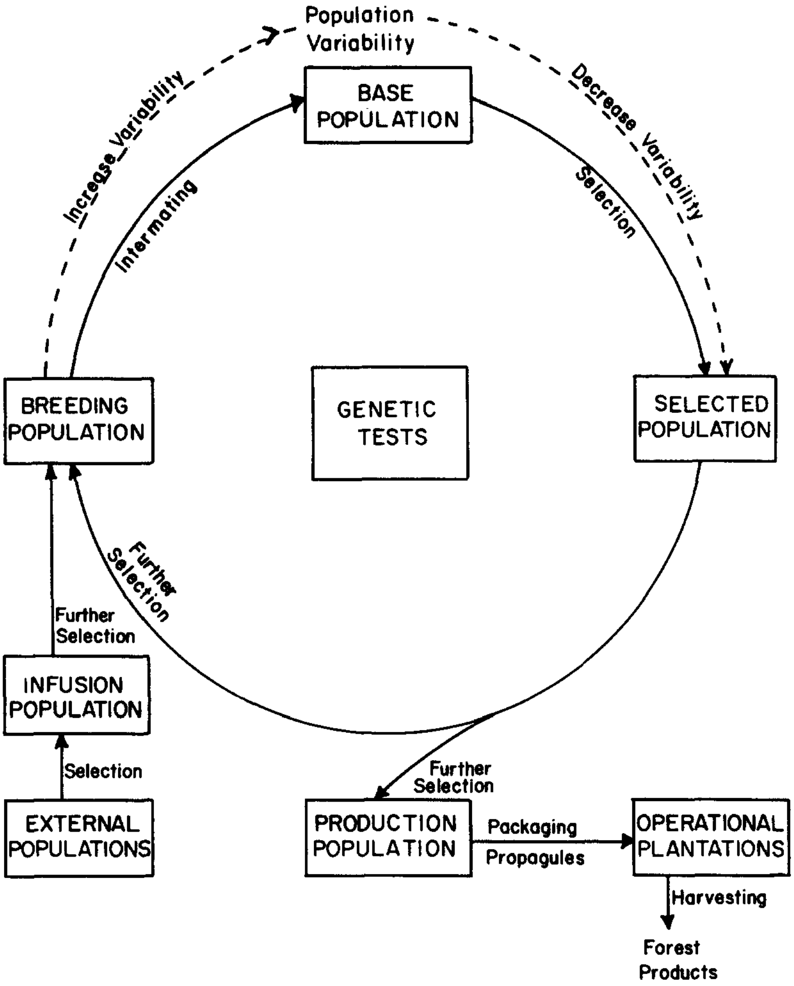

Fig. 1. Major components and activities of the breeding cycle of forest tree improvement programs. Each generation of breeding begins with the formation of a selected population. Each of three population types in the central part of the cycle (selected, breeding, base) are formed during a given generation in the sequence shown. The infusion and production populations may or may not be formed depending upon circumstances.

the entire population. For example, suppose the objective is to increase the resistance to a particular disease and disease-free phenotypes are chosen in natural stands heavily infected with the disease. If selection is effective in choosing superior genotypes (and not just phenotypes that escaped infection from the disease by chance or because of their microsite), then genetic gain in resistance will be made when seed from these selected disease-free trees is used for reforestation.

Most traits of economic importance are controlled by many genes with each gene having only a small influence on the phenotype. Every gene can have many forms (alleles) in the population, the different alleles for a particular gene having been generated by mutations over a course of many generations. Genotypes with favorable alleles tend, on the average, to form favorable phenotypes. The goal of selection is to increase the frequency of favorable alleles in the selected portion of the population. The effectiveness of selection will vary from trait to trait (e.g. yield vs disease resistance) being greater if selection is intensive (only the very best phenotypes are retained in the selected portion of the population) and if the trait is under strong genetic control.

Once selection has been applied, the selected trees are mated together to induce recombination of genes. Not all offspring from a given mating between two superior trees will be superior; there will be lots of variation. Because of the randomness of genetic recombination during sexual reproduction, some offspring will have a larger share of the better alleles from both parents and vice versa. This, combined with the fact that each tree develops on a different microsite will result in substantial phenotypic variability among offspring.

Selection is then employed again to choose the superior phenotypes and the breeding cycle begins for a new generation. If done effectively, the second generation of selection will result in still more genetic gain because, on the average, the second generation selections will contain better than average alleles from the first generation selections (which already were superior compared to the average of the original starting population). Thus, the breeding cycle is completed once per generation of selection and breeding and each cycle results in more genetic gain. The time between selection in two succesive cycles is called the generation interval.

This is an oversimplified description of tree improvement programs and there are many types of activities conducted as part of applied programs. The population types formed from these activities are useful conceptual constructs for understanding tree improvement programs (for example, van Buijtenen 1981; Kang 1982; Zobel & Talbert 1984) because each different activity leads to a different population type. However, in reality, population types are not always physically distinct from one another. That is, two different population types are sometimes designated as being different on paper but are housed in the same physical location: one physical group of trees serving more than one conceptual function in the program (and representing more than one population). In fact, it is this flexibility that leads to the diversity among tree improvement strategies. So, in this paper the breeding cycle is first explained as if all populations are distinct, then examples are discussed to depict how actual programs can combine population types.

One breeding cycle is completed per generation of improvement in the sequence shown (Fig. 1). Population types in the breeding cycle proper (the base, selected and breeding populations) are formed every generation from the preceding population type as a result of the activity given on the arrow connecting the population types. For example, the selected population is formed from the base population by the selection activity. Population types peripheral to the breeding cycle proper (production and infusion populations) may or may not be created each generation. For example in many crop species, a production population for the purpose of mass producing improved seed for operational use by farmers is created only once every several breeding cycles (generations). Genetic tests are an important but costly part of tree improvement programs. These are created by planting offspring from members of the various populations to provide the breeder with either material to select from or with information needed to make effective decisions.

Base population

The base population of a given generation consists of the group of individuals to which genetic improvement is applied. As the name implies, it is the foundation (founder population) from which an improved population will be developed and consists of all individuals available for selection (Zobel & Talbot 1982). The genetic quality of the base population improves after each turn of the breeding cycle if the selection of the past generation was effective.

In first-generation tree improvement programs of native species, the base population includes all trees available for selection in both natural stands and plantations in the breeding unit. The breeding unit is the geographical area for which an improved variety will be developed and each different breeding unit has a distinct tree improvement program with its own base, selected, breeding and production populations. Improvement of exotic species may be based on stands in the native range or on genetic test plantations of the species planted outside the native range (such as in other countries). First-generation base populations typically contain a large number (millions) of individuals to select from and an immense amount of genetic variability.

Defining the base population and determining breeding unit boundaries are critical decisions in tree improvement programs. As two extreme examples of native species, consider the cases of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and slash pine (*Pinus elliottii* Engelm.) in the northwestern and southeastern portions of the United States, respectively. The Progressive Douglas-fir tree improvement program (Silen 1966) consists of 80 breeding units in Oregon and Washington (Wheat & Silen 1982). The average breeding unit size contains approximately 40,000 ha of commercial timberlands and the natural Douglas-fir stands within each breeding unit represent the base population from which an improved breed is being developed for that unit. There are 80 distinct tree improvement programs, each with its own breeding cycle and a different set of population types.

In contrast, the slash pine program (Goddard 1980) consists of a single breeding unit containing 4,000,000 ha of commercial timberlands (White et al. 1986). A single tree improvement program (with one set of population types) is being conducted for this breeding unit. The disparity in size between the Douglas-fir and slash pine breeding units reflects both milder climatic and topographic gradients in the southeastern U.S. and differences in breeding philosophy.

Advanced-generation (after the first complete turn of the breeding cycle) base populations consist of genetically-improved trees growing in genetic test plantations which were planted to allow the selection of still superior individuals. They form the foundation for further improvement cycles. Generally, advanced-generation base populations will be pedigreed; information regarding the geographic origin, history, parents and ancestors of each tree is kept to aid both selection and other aspects of the program.

Selected population

The breeding cycle begins each generation with the selection of superior individuals from the base population. We can expect genetic gains from forests planted with seed from the selected population of trees if their offspring are genetically-superior to offspring from the base populations; that is, if selection was effective.

In first-generation tree improvement programs, selection usually means mass selection of superior individuals (plus-trees) from natural stands or unimproved plantations. The criteria for selection as well as the selection method and intensity vary among programs. The comparison tree method employed by the North Carolina State University-Industry Tree Improvement Cooperative for loblolly pine involved rigorous, intensive screening and grading of candidate trees against their neighbors for superiority in volume, form, and straightness and freedom of disease (Zobel 1971). In constrast, the Progressive Douglas-fir tree improvement program (Silen 1966) entailed phenotypic selections of roadside trees which were visually-chosen (no measurements of the candidates or surrounding trees were made).

Because advanced-generation base populations for most tree improvement programs consist of pedigreed individuals, selection of superior trees uses information both on the individual's performance and on the performance of its parents and/or other relatives in genetic test plantations. The optimum age to make selections, as well as the best selection methods and traits to use, are topics of considerable current research in forest genetics (for example, Stonecypher & Arbez 1976; Lambeth et al. 1983; Cotterill 1984; Bridgwater & Squillace 1986; Talbert 1986).

However chosen, the selected population has substantially fewer individuals than the base population (hundreds or thousands of individuals *vs.* thousands or millions). Allele frequencies differ between the two populations both by intent and by chance. The breeder picks the more favorable phenotypes in an attempt to concentrate more favorable alleles in the selected population. This results in genetic improvement through selection. In addition, though, some alleles (especially uncommon ones) are lost by chance during the selection process because of the small population size (Kang 1979a, 1979b).

For a given generation, the selected population is a subset of the base population and is most economically left in place growing amongst the other trees in the base population of that breeding unit. Danger of loss of selected tress in natural stands or ease of management elsewhere may result in creation of gene or clone banks; selected individuals are transported (e.g. by grafting stem stegments into clone banks) to these localized clone banks where they can be preserved and/or managed for intensive flower production for breeding purposes. Regardless of its location, the selected population is, conceptually, that portion of the base population which is chosen to be carried forward in the breeding cycle. In most cases, each breeding unit has a completely distinct breeding program and therefore a distinct selected population; however, selected populations from several breeding units and of several species are often housed in the same clone bank for ease of management.

Production population

A given generation's production population is composed of some or all of the individuals (or their relatives) from the selected population. The function of the production population is to produce genetically-improved offspring (e.g. seed) for operational forestation. The increased yield from harvesting forests planted with these genetically-superior trees is the primary realized benefit of most tree improvement programs.

Seed orchards are the most common type of production population. In grafted seed orchards, all or a subset of the individuals in the selected population are grafted onto rootstock and then intensively managed for seed production. Further selection (Fig. 1) may be applied so that only the best say 10% of the individuals of the selected populaton are grafted into the production population (seed orchard). This ensures more genetic gain from the seed used for operational reforestation in the current generation without unduly restricting the number of individuals being used to breed for future generations.

Propagules (seed or plantlets) from the production population can be obtained for forestation in ways other than clonal seed orchards:

- Open-pollinated seed collected from selected individuals growing in the base population (e.g. collections from progeny-test-proven selections in natural stands as suggested by Silen & Wheat 1979).
- Seed from seedling seed orchard that are established with offspring from the selected population (in contrast to grafted orchards described above).
- Plantlets from seed orchard seed multiplied several-fold by tissue culture.
- Other vegetative propagules (e.g. rooted cuttings) from members of the selected population.

Information on the relative genetic value of members of the selected population such as that obtained from progeny testing can be used to create an improved production population so that genetically inferior individuals do not contribute genes to operational forestation. Two primary means are roguing inferior selections from seed orchards and creating "1.5 generation" seed orchards using only tested and proven selections (Weir 1980).

The real conceptual value in separating the production population from the main part of the breeding cycle (base, selected and breeding populations) is that the main part of the breeding cycle is concerned with achieving genetic gains and maintaining broad genetic diversity across multiple generations. However, the purpose of the production population is deployment of maximum genetic gains to operational plantations in a given current generation. These are very different objectives.

Breeding population

Some or all of the members (or their relatives) of the selected population are included in that generation's breeding population. These individuals are intermated to regenerate genetic variability through recombination of genes during sexual reproduction and the offspring from these matings are planted in genetic tests. By inducing recombination of genes among superior genotypes, we look for some of their offspring that exhibit the best attributes of both parents. These plantings are the base population of the next generation and we exploit the variation by including (by the selection process) only superior individuals in that next generation's selected population.

Though many mating designs have been used for crossing individuals in the breeding population (Zobel et al. 1972; van Buijtenen 1976; van Buijtenen & Bridgwater 1986), all have the common purpose of remixing genes together to create a variable base population for the further selection of superior recombinants. Once this base population has been formed, the whole cycle begins for the next generation.

In first-generation tree improvement programs, there has sometimes been a lag of 10 or more years between the initial selection process and the intermating of individuals in the breeding population. During this period, information from genetic tests can be used to rank selections so that only superior genotypes (say the top 50%) are included in the breeding population (further selection, Fig. 1). This delay can increase genetic gain because crosses will be among only the better genotypes; thus, there is more opportunity for creating superior recombinants in the new base population. However, this gain must be weighed against the opportunity cost of delaying that gain until progeny test information is available.

In intensive advanced-generation tree improvement programs, it has become common to turn generations over rapidly to maximize genetic gain per unit time. Intermating begins soon after the selections are made from the base population and no time is available to gain further performance information about the selected population. Therefore, all individuals of the selected population are included in the breeding population; the selected and breeding populations are identical.

Infusions

Many tree improvement programs periodically infuse trees from external sources into the breeding population. Infusion sources may include:

- Additional first-generation plus-trees from natural stands or unimproved plantations, e.g. disease-free selections of slash pine made in stands with high fusiform rust incidence to increase rust resistance in the breeding population (Weir & Goddard 1986; White et al. 1986).
- Proven (elite) individuals from breeding populations of other physiographic regions made available, for example, by breeding unit mergers, e.g. the potential use of elite North Carolina loblolly pine (*Pinus taeda* L.) selections in an Arkansas breeding program (Lambeth et al. 1984).
- Wide crosses within species e.g. crosses among loblolly pine from Maryland and Louisiana for the potential infusion of faster growth rate into the more frost-hardy Maryland population (Weir 1980).
- Interspecific hybrids, e.g. crosses between loblolly and shortleaf (*Pinus echinata* Mill.) pines for the infusion of fusiform rust resistance into loblolly (Dorman & Zobel 1973).

Infusions can either be aimed at improving a specific trait or at generally broadening the level of genetic variation to allow more intensive selection in future generations for a given level of inbreeding. In either case, care must be taken to evaluate the total effect of infusion to ensure that gains in some traits are not made at the inadvertent expense of other traits. For example, infusing rust resistance genes (above) from shortleaf pine into loblolly pine may concomitantly reduce growth rate. Members of the infusion population (or their relatives) can be carried along in the breeding cycle proper (closed circle in Fig. 1) until such time as their proven genetic value warrants inclusion in a production population.

Genetic test plantations

Genetic tests are central to most intensive tree improvement programs. The broad definition of genetic test used here is a planting of offspring from members of any population type in the breeding cycle. The plantings are usually located on a forest site, but also may be in, for example, a nursery, greenhouse, or growth room. Depending on its role in the breeding cycle, a given genetic test can be variously called a progeny test, base population, yield trial or research experiment. An explanation of mating and field designs used to create genetic tests is beyond the scope of this paper (see Libby 1973; van Buijtenen 1981; van Buijtenen & Bridgwater 1986; van Buijtenen & Namkoong 1983); rather, we concentrate on the purposes of genetic tests that directly advance operational tree improvement programs. In this regard genetic tests can provide:

- population-level information about a population type in the breeding cycle (e.g. the amount and type of genetic variation in a base population),
- information about specific individuals within a population (e.g. the relative genetic value of plus-trees in a selected population), and
- plant material for the construction of one population type from another (e.g. an advanced-generation base population in which to make selections).

Five different functions of genetic tests are delineated below and described in terms of their role in the breeding cycle (see also McKinley 1983). Offspring from members from various population types provide the seedlings for the establishment of genetic tests. Any one set of test plantings may have multiple objectives necessitating mating and field designs that do *not* maximize the attainment of any one objective. For this reason, we examine the objectives of genetic tests in terms of their functions in the breeding cycle. Then, competing objectives can be prioritized so that compromises in field and mating designs can be explicitly evaluated and directed toward accomplishment of the more important objectives.

1. Progeny testing

A progeny test is defined as a test of the value of a genotype (e.g. a selected individual) based on the performance of its offspring (Allard 1960). For example, progeny of first-generation plus-trees can be evaluated in randomized, replicated field tests in order to determine the genetic value of the plus-trees themselves. Where seed is the product of the production population, this is logical since seedling offspring will ultimately be used for commercial forestation. Where vegetative propagles (e.g. rooted cuttings) are the product of the production population, clonal testing replaces progeny testing and selections are ranked on the basis of the performance of their vegetative propagules. In either event, ''progeny' tests serve many useful functions in several different steps of the breeding cycle (Fig. 2). They are an integral part of most tree improvement programs and their many functions are briefly described below:

- *Further selection to upgrade the production population.* Progeny test field results can be used to exclude low-ranking members of the selected population from the production population. This upgrades the genetic quality of propagules from the production population. This can mean, for example, directing collections of seed in natural stands to proven superior plus-trees, or including only superior genotypes in or roguing inferior genotypes from seed orchards.

- *Deployment of production population.* Knowing the relative value of the members of the production population can be used for optimum deployment of the seed (or propagules) to specific planting sites. For example, many landowners in the southeastern US collect orchard seed and keep it in separate categories for deployment. For slash pine, seed from clones known to be fusiform rust resistant (based on progeny test data) is usually kept separated from that of rust-susceptible clones. The seed of ''rust-resistant'' genotypes is then deployed to field plantations which will likely experience a high level of exposure to the disease. Deployment strategies can be developed for other traits or to capture genotype x environment interaction and can become quite complex.

- *Further selection to upgrade the breeding population.* Low-ranking members of the selected population can be excluded from the breeding

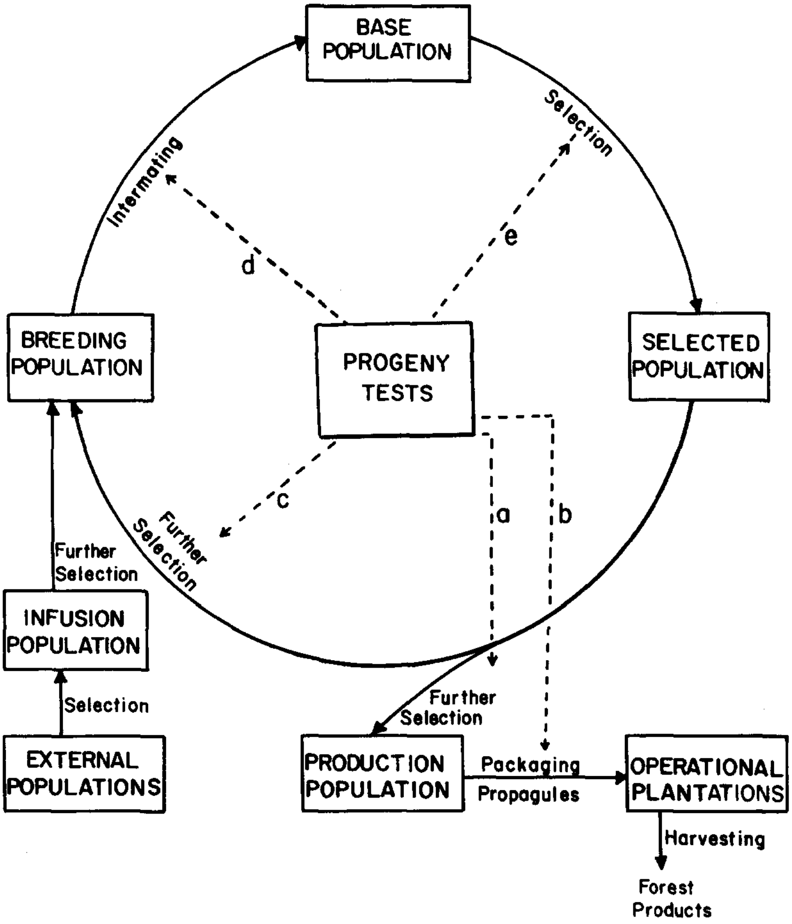

Fig. 2. When progeny test data are used to estimate the relative genetic values of the members of the selected population, this information (dashed lines) can be used in several stages of the breeding cycle to: (a) upgrade the genetic quality of the production population, (b) maximize gain from deployment of seed (or propagules) from the production population, (c) upgrade the genetic quality of the breeding population, (d) optimize mating designs for the breeding population, (e) provide information for next-generation selection.

population and their genes are thus excluded from subsequent base populations. For example, if the intermating activity is delayed until after progeny testing, the breeding population might be restricted to the top, say 50%, of the selected population. This type of further selection to upgrade the genetic quality of the breeding population has been employed in many first-generation programs and is planned in advanced-generations of a radiata pine (*Pinus radiata* D. Don) program in Australia (Cotterill 1984).

- *Improve efficiency of mating designs.* Information from progeny tests can be used to construct more efficient designs than simply randomly mating members of the breeding population. One example is that disease resistant parents might be mated with fast growing parents. Two other examples, relatively new in tree improvement, are assortative mating (Cotterill 1984; Foster 1986; Lindgren 1986) and greater use of known-better parents (Lindgren 1986). Assortative mating entails first ranking the parents and then mating parents of similar rank. Greater use of better parents means that highly ranked parents are used in more crosses than parents of lower rank. Both of these design efficiencies increase the potential genetic gain that can be made from the next round of selection.

- *Improve efficiency of selection from future base populations.* The above four functions of progeny tests serve to increase genetic gain in the current cycle (generation) of breeding; however; information on parental performance from progeny tests can be combined with individual performances of the base population members to improve effectiveness of selection in the next generation. For example, selection of the best individuals from a field planting of a second generation base population (created by intermating members of the first generation breeding population) can be based not only on the performance of the individuals and their parents in that test, but also on the performance of the parents in prior progeny tests. Selections can be made among offspring of known-better parents. In fact, the performance information from progeny tests may serve as ancestral information about potential selections for many future generations.

2. *Evaluating offspring of intermatings*

After completion of intermatings among the breeding population members, the progeny are planted in the field to evaluate which specific trees of which crosses appear superior. These genetic tests are the base populaton for the next generation of selection and the objective is to provide a field planting in which to select the very best phenotypes from some or all of the crosses.

3. *Defining genetic architecture*

The strategies of tree improvement programs rest on a presumed genetic architecture of the populations in the breeding cycle (see Libby 1973 for a complete list of types of genetic architecture studies). We must either estimate or assume relative and/or absolute amounts of genetic variation due to:

- geographic origin of seed,
- general and specific combining ability,
- genotype x environment interaction, and
- juvenile-mature relationships.

Estimates of these parameters gained from genetic tests, along with other information, are used to determine size and location of breeding units, mating and field designs, and selection procedures most effective in achieving genetic gains while still maintaining adaptability. Genetic architecture tests are critical to the soundness of long-term breeding strategies and for predicting genetic gains from selection programs.

4. Evaluating infusions

Potential infusions are often evaluated in field progeny tests either before or after inclusion in the main-line breeding population. This ensures that hard-won genetic gains are not reduced by inclusion of poor performers in subsequent production populations. For example, progeny-test-proven plus-trees from an adjacent breeding unit should also be progeny tested for adaptability and growth on a range of sites in a new breeding unit into which they are being infused. Outstanding individuals from superior families can then be selected from these tests for inclusion in the breeding population of the new unit.

5. Evaluating realized gain

Evaluation of the actual (realized) gains is achieved by testing the yield and product quality of improved vs. unimproved plantations. For statistical reasons, the other types of genetic tests (described above) use plots containing only one to a few members of a given family in one block. Yield trials, on the other hand, generally need to use large plots in order to achieve the kind of competitive conditions that exist as stands mature. For example, large plots of first-generation seed orchard seedlings compared in a replicated manner with plots from commercial (unimproved) seed lots would test the superiority of orchard seed. Due to the length of tree life cycles and plantation rotations, information from yield trials often measures progress from a point in the program which has been far surpassed. Nevertheless, these serve a useful function validating gains on a per-unit-area basis in large plots treated in a truly operational manner. Some organizations in the southern United States are employing family block plantings where entire reforestation units are planted with seedlings from a single mother clone wind-pollinated by surrounding males in the seed orchard (Gladstone 1981). Operational experiments (genetic tests) comparing large plots of different families and commercial unimproved seed lots both evaluate which families are best on which sites and also provide realized genetic gain estimates of the family blocks against the unimproved lots (Gladstone et al. 1987).

Discussion

In order to reduce costs in some applied tree improvement programs, one physical plant population serves multiple functions in the breeding cycle. For similar economic reasons, breeders often try to meet several objectives with a single set of genetic tests (Zobel et al. 1972; van Buijtenen 1976; Burdon & Shelbourne 1982; van Buijtenen & Bridgwater 1986). This may make it difficult to delineate the exact functions of a given plant population or genetic test in the context of furthering the breeding cycle. However, delineating and prioritizing the objectives of a given population or test plantation become even more critical for multi-purpose populations or genetic tests. That is, a single combination of mating design, field design and cultural management regime will probably *not* maximize attainment of all objectives. So, by prioritizing objectives and considering constraints, the appropriate compromises can be found. Two examples of multi-objective plantings are discussed below.

In the early 1960s a controversy ensued over the relative merits of clonal (vegetative) vs. seedling seed orchards (see Toda 1964). In general, clonal seed orchards are established by grafting (or rooting) some or all of the members of the selected population into a single area which is intensively managed for the production of genetically-improved seed. The clones in the orchard form the production population which is managed for a single purpose, seed production.

There are many variations on the seedling seed orchard theme (Wright 1959). In the classical open-pollinated seedling seed orchard, open-pollinated seedlings from the members of the selected population are used to establish a single planting which serves two functions: progeny test and production population. Measurements of important traits are made at a fairly young age and the best families (parents) thereby determined (progeny test function). Then, the planting is converted into a seed orchard by rogueing out individuals from the poor families and managing for seed production. This is successful if management of a single planting for both seed production and parent evaluation are compatible.

A second example of multi-function plantings is that some second generation breeding strategies (e.g. see Weir 1980) employ a single series of genetic tests (based on one mating and field design) to serve both as progeny tests and to evaluate intermated offspring (i.e. create a third generation base population in which to make selections). In this approach, the testing and breeding activities begin simultaneously with no information available from prior testing to exclude poorer individuals in the selected population from the breeding population. Thus, the selected population and breeding population are identical. The members are mated together and the cross-pollinated offspring planted in a randomized, replicated field design. The tests are measured and first, the data are used to rank the parents (i.e. members of the breeding population). Second, the plantings are used as the third generation base population from which the best seedlings in the best families are selected to carry on the program.

A different approach used by some programs (e.g. see Lowe & van Buijtenen 1981) is called complementary mating designs. Here two different sets of mating and field designs are used; they are chosen separately to optimize the two different objectives: progeny testing and forming a base population for selection. The mating and field designs for progeny testing are chosen to effectively rank parents and must be statistically sound (e.g. the field designs must be randomized and replicated). Designs for establishing the base population are then chosen to maximize gain from selection (for example by using assortative mating in the mating designs and by employing large, but poorly replicated plots of offspring from each cross).

Both approaches (single vs. complementary mating designs) can be very effective, but complementary mating designs are especially useful when the objectives of progeny testing and base population formation are *not* both effectively met by one set of plantings of a single design. For example, the use of assortative mating to maximize gain from selection is usually not compatible with ranking the parents used in the crosses. Also, the use of complementary mating designs allows (if warranted) the separation in time of the testing and breeding activities and individuals with poor test performances can be eliminated from the breeding population and thus not used in crosses. This is especially useful when short-term progeny test data are reliable. Thus, by using two sets of designs, one for testing and one for selection, both objectives may be better accomplished.

The breeding cycle is a useful conceptual construct for quickly identifying the purposes of the various activities being conducted as part of tree improvement programs. As many programs move into advanced generations and become more complicated, foresters and breeders may benefit by using simple constructs such as this to understand *complex* strategies, help delineate program needs, and assess the efficacy of combining multiple objectives into single populations and plantations.

Acknowledgments

Journal series No 8388 of the Florida Agricultural Experiment Station. I thank Tom Adams, Bruce Bongarten, Floyd Bridgwater, Lauren Fins, Greg Leach, Don Lester, Bill Lowe, and John Pait for their suggestions on various versions of this manuscript.

References

Allard, R.W. 1960. Principles of Plant Breeding. John Wiley and Sons, New York, NY.

Bridgwater, F.E. & Squillace, A.E. 1986. Selection indexes for forest trees (pp.17-20). In: Advanced Generation Breeding of Forest Trees. Southern Coop. Series Bull. 309. Louisiana Ag. Exp. Stn., Baton Rouge, LA.

Burdon, R.D. & Shelbourne, C.J.A. 1972. Breeding populations for recurrent selection: Conflicts and possible solutions. N.Z. J. For. Sci. 1:174-193.

Cotterill, P.P. 1984. A plan for breeding radiata pine. Silvae Genet. 33:84-90.

Dorman, K.W. & Zobel, B.J. 1973. Genetics of loblolly pine. USDA For. Serv. Res. Pap. WO-19, Washington, D.C.

Foster, G.S. 1986. Making clonal forestry pay: Breeding and selection for extreme genotypes, (pp. 582-590). In: Proc. IUFRO Conf. on Breeding Theory, Progeny Testing and Seed Orchards. October 13-17, Williamsburg, VA.

Fowler, D.P. 1976. Genetic variation influences tree improvement strategies. Pulp Pap. CAN 77:65-69.

Gladstone, W.T., Bean, P.M., Hughes, J.H. and Talbert, C.B. 1987. A challenge for tree improvement, (pp. 1-7). In: Proc. 19th South. For. Tree Improve. Conf. June 16-18, College Station, TX.

Gladstone, W.T. 1981. Customize or compromise - An alternative for loblolly, (pp. 200-204). In: Proc. 16th South. For. Tree Improve. Conf. May 26-29, Balcksburg, VA.

Goddard, R.E. 1980. The University of Florida Cooperative Genetics Research Program, (pp. 31-42). In: Proc. 15th North. Amer. Quant. For. Genet. Group Workshop. August 6-8, Coeur d'Alene, ID.

Kang, H. 1979 a. Designing a tree breeding system, (pp. 51-66). In: Proc. Seventeenth Meeting Canadian Tree Improvement Association. August 27-30, Gander, Newfoundland.

Kang, H. 1979 b. Long-term tree breeding, (pp. 66-72). In: Proc. 15th South. For. Tree Imp. Conf. June 19-21. Mississippi State Univ., Starkeville, MS.

Kang, H. 1982. Components of a tree breeding plan, (pp. 119-135). In: Proc. IUFRO Conf. On Breeding Strategies Including Multiclonal Varieties. September 6-10, Sensenstein, West Germany.

Lambeth, C.C., Dougherty, P.M.. Gladstone, W.T., McCullough, R.B. & Wells, O.O. 1984. Large-scale planting of North Carolina loblolly pine in Arkansas and Oklahoma: A case of gain versus risk. J. For. 82:736-741.

Lambeth, C.C., van Buijtenen, J.P., Duke, S.D. & McCullough, R.B. 1983. Early selection is effective in 20-year-old genetic tests of loblolly pine. Silvae Genet. 32:210-215.

Libby, W.J. 1973. Domestication strategies for forest trees. Can. J. For. Res. 3:265-276.

Lindgren, D. 1986. How should breeders respond to breeding values?, (pp. 361-372). In: Proc. IUFRO Conf. on Breeding Theory, Progeny Testing and Seed Orchards. October 13-17, Williamsburg, VA.

Lowe, W.J. & van Buijtenen, J.P. 1981. Tree improvement philosophy and strategy for the Western Gulf Forest Tree Improvement Program, (pp. 43-50). In: Proc. 15th North Amer. Quant. For. Genet. Group Wrokshop. August 6-8, Couer d'Alene, ID.

McKinley, C.R. 1983. Objectives of progeny tests, (pp. 2-13). In: Progeny Testing of Forest Trees, Southern Coop. Series Bull. 275. Texas A & M Univ., College Station, TX, 77843.

Silen, R.R. & Wheat, J.G. 1979. Progressive tree improvement program in coastal Douglas-fir. J. For. 77:265-276.

Silen, R.R. 1966. A simple, progressive tree improvement program for Douglas-fir. USDA For. Serv. Res. Note PNW-45. Pac Northwest. For. and Range Exp. Stn., Portland, OR 13p.

Stoneycypher, R. & Arbez, M. 1976. Methods of selection, (pp. 31-46). In: Proc. IUFRO Conf. on Advanced Generation Breeding. Juny 14-18, Bordeaux, France.

Talbert, C.B. 1986. Multi-criterion index selection as a tool for operational tree improvement, (pp. 228-238). In: Proc. IUFRO Conf. on Breeding Theory, Progeny Testing and Seed Orchards. October 13-17, Williamsburg, VA.

Toda, R. 1964. A brief review and conclusions of the discussion on seed orchards. Silvae Genet. 13:1-4.

van Buijtenen, J.P. & Bridgwater, F. 1986. Mating and genetic test designs, (pp. 5-10). In: Advanced Generation Breeding of Forest Trees. Southern Coop. Series Bull. 309. Louisiana Ag. Exp. Stn., Baton Rouge, LA.

van Buijtenen, J.P. and Namkoong, G. 1983. Mating designs, (pp. 7-13). In: Progeny Testing of Forest Trees. South. Coop. Series Bull. No. 275. Texas A&M Univ., College Station, TX.

van Buijtenen, J.P. 1975. Advanced Generation Breeding, (pp. 63-72). In: Proc. 13th South. For. Tree. Improve, Conf. June 10-11, Raleigh, N.C.

van Buijtenen, J.P. 1976. Mating designs, (pp. 11-27). In: Proc. IUFRO Joint Meeting on Advanced Generation Breeding. June 14-18, Bordeaux, France.

van Buijtenen, J.P. 1981. Strategies for advanced generation orchards, (pp.121-129). In: Proc. Eighteenth Meeting of the Canadian Tree Improvement Assoc. August 17-20, Duncan, BC, Can.

Weir, R.J. & Goddard, R.E. 1986. Advanced generation operational breeding programs for loblolly and slash pine, (pp. 21-26). In: Southern Coop. Series Bull. 309. Louisana Agric. Exp. Stn., Baton Rouge, LA, 70903.

Weir, R.J. 1980. North Carolina State Industry Cooperative Tree Improvement Program, (pp. 57-70). In: Proc. 15th North Amer. Quan. For. Gen. Workshop. August 6-8, Couer d'Alene, ID.

Wheat, J. and Silen, R. 1982. 1982 Progress Report for IFA-PNW Cooperative Tree Improvement Programs. Industrial For. Assoc., Portland, OR . 97295.

White, T., Flinchum, M., Rockwood, D., Kok, H. & Powell, G. 1986. Twenty-eighth Progress Report, Cooperative Forest Genetics Research Program. Dept. of For., Univ. of Florida, Gainesville, FL.

Wright, J.W. 1961. Progeny tests or seed orchards?. Recent Adv. Bot. 2:1681-1687.

Zobel, B. J. & Talbert, J. 1984. Applied Forest Tree Improvement. John Wiley and Sons, New York, NY.

Zobel, B.J., Weir, R.J. & Jett, J.B. 1972. Breeding methods to produce progeny for advanced-generation selection and to evaluate parent trees. Can. J. For. Res. 2:339-345.

Zobel, B.J. 1971. The genetic improvement of southern pines. Sci. Amer. 225:95-103.