ADVANCED GENERATION BREEDING

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Abstract.--Advanced generation breeding is discussed in the framework of the overall breeding strategy, with emphasis on the key decisions which need to be made, rather than on specific solutions for a particular species. Factors that should be considered in the formulation of a strategy include the biology of the species, the choice of breeding methods, the use of combined or separate breeding and production populations, the manner in which the advanced generations are to be produced and the extent to which inbreeding is to be minimized. Key questions in the evaluation of a breeding strategy are the gain per cycle, the cost per cycle and the duration of a cycle.

Additional keywords: Breeding strategy, family selection, choice of testers, genetic gain, economic return.

INTRODUCTION

As the introductory paper for this session, its objectives are to set the stage and provide an organizational framework. Advanced generation breeding cannot be discussed separately from the overall breeding strategy, since it is the very heart of it. I will therefore discuss advanced generation breeding from the point of view of breeding strategy. In doing so my main purpose will be to pinpoint the questions which should be asked and answered for any specific case. A discussion more specifically oriented towards southern pines was presented by Franklin (1975).

WHAT FACTORS SHOULD BE CONSIDERED IN THE FORMULATION OF A BREEDING STRATEGY?

For our purposes a breeding strategy may be defined as an ingenious combination of breeding methods to achieve specific goals. These goals may not necessarily be the same for every breeding program. Some common goals are improvement in growth rate, wood quality, disease resistance, form, the preservation of germplasm, the formation of an adequate basis for long range improvement and the provision of an adequate raw material for a particular product, range of products or industry. The major factors which have to be considered in formulating a breeding strategy are the biology of the species, the choice of breeding methods, the use of combined or separate breeding and production populations, the manner in which the advanced generations are to be produced and the extent to which inbreeding is to be minimized. All these factors are related to each other and affect advanced generation breeding.

Biology of the Species

The biology of the species can present some unique opportunities or pose

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some serious limitations.

Some of the major considerations are (1) is the species monoecious or dioecious? (2) is the species wind pollinated or insect pollinated? (3) can the species be readily propagated vegetatively either by grafting or rooting? (4) at what age does the species flower? (5) can the species be effectively propagated by means of controlled pollination? (6) what is the production of viable seed in terms of the yield from one cross and from one tree? (7) how much variation is present in the species? (8) is the genetic variation in the desirable traits largely additive or does a substantial amount of non-additive variance exist? (9) does the species possess the genes for the desired trait or is interspecific hybridization desired? (10) can the species be grown in plantations? (11) how long does it take to test for the desired properties?

Other factors may play an important role as well, but the factors listed above are the most common ones that have a bearing on the choice of breeding methods employed.

What Breeding Method is most Suitable?

The choice of breeding method is strongly influenced by the biology of the species and in turn determines the direction the advanced generation breeding will take. Following are some of the breeding methods most frequently used.

A. Clonal propagation. Clonal propagation has two different possible roles in a tree improvement program: (1) the establishment of seed orchards or scion banks for the production of seed for breeding purposes or for commercial production, (2) the establishment of plantations for the commercial production of wood.

In the latter case clonal propagation is a breeding method while in the former it is merely a means of producing seed in larger quantities. Clonal selection and propagation can produce extremely large gains as has been demonstrated particularly with cottonwood. To attain further genetic gains however, it will be necessary to cross the selected clones among each other to establish a new breeding population in which further clonal selections can be made. Taking the long range view therefore, the clonal method will always have to be used in conjunction with other breeding methods.

B. Selection. Selection is most suitable in those instances where substantial amounts of additive genetic variation are present. Selection can take the form of individual tree selection, family selection, or combined selection. Individual tree selection is most advantageous when heritabilities are relatively high. In contrast family selection is more effective when heritabilities are low. Combined selection is always as good or better than the other methods, but the difference is never very great (Falconer, 1960). For the great majority of tree species this is a method that appears to be very suitable and is therefore chosen by many tree breeders.

C. Hybridization. Hybridization could take several forms, three of which offhand appear potentially important in forest trees. If the species can be self-pollinated readily, one could develop hybrids between inbred lines much as has been done in corn. This method does not seem very useful in forest tree breeding now, but could become more important as more advanced generations are produced.

Secondly, hybridization could take the form of crosses among widely separated geographic seed sources. Namkoong (1974) has some rather interesting ideas on this. Local races do not always appear to be optimal for use as commercial forest trees. Instead there appears to exist an optimal environment where the best races occur for introduction to a certain area. Plotting the results of geographic seed source tests against climatic variables at the source, one may find that the optimum environment does not exist. In such a case a suitable combination of sources might produce a hybrid, which in a sense could be considered the result of a synthetic optimal environment. A study by Woessner (1972) has shown that such an approach might have promise.

Interspecific hybridization might be useful in a number of cases. Perhaps the greatest application might be the introduction of disease resistance. The occurrence of true hybrid vigor is less common although frequent enough to be of real interest (Fielding, 1962). For the production of improved wood properties the method does not appear to hold much promise (van Buijtenen, 1970).

All forms of hybridization need to be combined with some form of selection and the maintenance of separate breeding populations if the process is to be continued for more than one generation. It will necessarily be a rather complicated system, but may have great merit especially in the case of resistance breeding.

D. Polyploidy. This method has been applied successfully to improve quaking aspen (Einspahr, 1972). Faster growth, greater fiber length and increased wood specific gravity have been the primary responses to increasing the chromosome number. For long range improvement however, it needs to be combined with selection or hybridization to maintain further gains. In the case of triploids this would mean maintaining and improving diploid and tetraploid populations for the production of triploids by crossing. The triploids then can be propagated vegetatively for mass production.

Are the Breeding and Production Populations the Same or Separate?

Namkoong (1974) examined this question and concluded that either approach can be appropriate. Maintaining separate breeding and production populations would necessarily entail extra cost and it would therefore be necessary to point to advantages otherwise not obtainable to justify this cost.

A strong argument for separating the two populations is to avoid the conflict between increasing genetic gain by increasing the selection differential (i.e., by selecting a very small number of trees) and maintaining an adequate genetic base for future breeding. By separating the two populations it is possible to maintain a broad base in the breeding population and yet get a greater gain by only using the very top families for the commercial production of improved seed or clonally propagated material. This is a key point that is often overlooked. Without a broadbased breeding population severe losses of germplasm can be expected.

A second argument for separating the breeding population from the production population is the effect of inbreeding. Exaggerating somewhat, one can say that no inbreeding can be tolerated in the improved seed harvested from the production population (the operational seed orchard), since any loss of vigor necessarily means a financial loss. In the breeding population on the other hand, inbreeding can be tolerated and actually may be desirable.

Production of Advanced Generations

The advanced generation population may serve many purposes (Burley, 1972; Andersson, 1960) such as: (1) evaluation of families for the purpose of roguin a seed orchard, or establishing a new orchard from the best clones; (2) provid ing the population for selection of the next generation; (3) providing estimat of genetic parameters such as additive and non-additive genetic variation, her abilities and gain prediction; (4) demonstration of realized gain; (5) production of commercial end product.

Although separate tests could be set up for each objective, limitations on cost and manpower generally require that the tests are combined in some way. Preferably one test should serve all purposes.

The number of selections to be made is a critical decision. By using a small number of highly selected individuals, it is possible to make the greatest genetic gains. On the other hand it is also desirable to have a large popu lation size to avoid losing too many genes from the population, which would limit the potential for future progress. Some compromise is called for. Twenty selections to establish a breeding population appears to be the absolute minimum. Approximately 1000 is the maximum attempted so far by a single industry or state organization.

An important point to be made is that the progeny test population does not need to be the same as the population in which advanced generation selections are made. As a matter of fact, a tester scheme of progeny testing is most effective when the worst possible parents are used as testers (Allison and Curnow, 1966). We therefore have potentially three distinct groups of trees to work with (1) the progeny tests (2) the breeding population - i.e., the plantation from which the new selections will be made and (3) the production population - i.e., the seed orchard. Following is a summary of some of the most common breeding syst ems.

A. Mass Selection. Allow the selections to mate at random, use all seed commercially and consider the entire production of seedlings as the next population. Although this system is simple, random sampling variations will cause some families to be overrepresented and others to be completely omitted, thus leading to a higher risk of inbreeding and loss of favorable ge nes.

B. Single Pair Mating Schemes. Different systems have been reviewed by

Namkoong (1974), Cockerham (1970) and Kimura and Crow (1963). There appears to be an inverse relationship between the early avoidance of inbreeding and eventual inbreeding reached after many generations of following the same mating scheme. In an initial population of N individuals inbreeding can be avoided for k generations if N = 2k. Thereafter inbreeding increases rapidly. Systems studied include maximum avoidance of inbreeding, circular matings, and circular pair matings. The circular mating systems will develop inbreeding sooner (for N = 8 after 2 generations) but will lead to lower inbreeding levels in the long run.

c. Multiple Crosses Amon Parents. Crossing patterns which have been advocated include (1) a factorial mating design such as a four tester scheme in which all clones are tested with the same four tester clones. This will quickly lead to high levels of inbreeding. (2) A complete diallel or modified half diallel. The complete diallel would include all the possible crosses including reciprocals and selfs. The modified half diallel would omit the reciprocal crosses and the selfs. This would of course give the maximum amount of flexibility, but would also be the most costly. Especially in the case where many clones are involved, the number of controlled crosses needed would quickly getout of hand. Some organizations use a modified half diallel among the best parents (as proved by open pollinated tests) to produce the next breeding generation (Stonecypher, 1968). (3) A series of disconnected small diallels (Anon, 1973). This is also a very flexible system and fairly easy to handle in practice since each diallel can be handled separately. For the purpose of using the information for testing it may be somewhat at a disadvantage since parents involved in different diallels cannot be compared very accurately. (4) Other partial diallel schemes can also be used (Anon, 1972). These allow considerable flexibility but have some practical disadvantages in that it will be virtually impossible to complete the whole crossing scheme in a short time span. Consequently the crosses will have to be separated into different sets to be planted out at different times. This argument of course holds also for the tester schemes. Many of these crossing schemes allow the possibility of making alternate sets of single pair matings, so that one can take advantage Df family selection in addition to individual tree selection. In such a case some families will be eliminated and the rate of increase of inbreeding will)e greater.

HOW TO EVALUATE A BREEDING STRATEGY

To effectively evaluate a breeding strategy, it's necessary to simplify the evaluation by dividing the strategy into separate portions. One very natural portion to look at separately is the selection of the parental popuation, in other words the initial step of the breeding program. This phase s followed by the recurrent or recycling portion consisting of the advanced generations.

Since the advanced generations are really the crucial part of the long ange breeding program, it's advantageous to look at them first. Following re a number of questions that should be asked:

(1) what is the gain per cycle?
(2) what is the duration of one cycle?

(3) what is the cost of one cycle?
(4) what is the gain per year?
(5) what is the cost per year?
(6) what is the cost per unit gain?

For a given breeding scheme the cost per unit of gain will increase as the gain per cycle increases. This is so because the number of acceptable selections drops very rapidly as the selection intensity is increased. As a result the cost increases much more rapidly than the amount of genetic improvement obtained. This is nothing unusual and is to economists just another example of the law of diminishing returns. On the other hand, the cost of different breeding methods varies considerably and some are much more efficient than others.

The largest difference occurs between individual tree selection schemes and family selection schemes. Since we're generally dealing with characteristics of low heritability, the gain obtainable by individual tree selection is generally rather limited, perhaps about 10%. On the other hand, it is relatively cheap. Nevertheless, by the time that the 10% gain is reached you have arrived at the steep portion of the curve and additional gains become prohibitively expensive. Family selection is inherently much more expensive than individual tree selection but greater gains are possible. With the southern pines gains of 25 to 50 percent are obtainable with family selection,

After having made a decision on what kind of a breeding scheme to adopt for the recurrent portion, it is time to look back at the initial phase of selecting the parental population. The two main questions here are:

(1) what is the gain obtained in this portion of the selection scheme a
(2) how well does it lead up to the recycling portion.

EXAMPLE OF AN ADVANCED GENERATION BREEDING SCHEME

To illustrate these considerations it is perhaps useful to give a concrete example. The species considered is Hypoplatanus obtusa vB. — This particular example was chosen because it is fairly complex and shows the application of some ideas that so far have not regularly been incorporated into advanced breeding plans.

Biology of the Species

Hypoplatanus obtusa is an understory species growing under sycamore stands. It has a very dense wood and produces a fiber highly suitable for pulping. It can be grown on a coppice rotation of three years. Without any genetic improvement, it is capable of producing four tons of dry fiber per acre per year. The species is dioecious and flowers at age 3. The female flower can be readily hand pollinated and produces between 200 and 400 seeds per flower. The seeds are rather small and germinate readily with careful

2/ This is a very rare and as yet undiscovered species. Any resemblance with sycamore is purely coincidental.

treatment. One hundred sound seeds ordinarily are expected to yield about 50 plantable seedlings.

The species can be readily propagated from rooted cuttings by planting 8-inch cuttings in nursery beds about mid-February before they leaf out. The species has a rather thin bark and can be harvested as a whole tree without unduly adverse effects on pulp quality.

The Breeding Cycle

The advanced generation breeding cycle consists of a ten-year cycle (table 1). In year one of the cycle, the selections are made in the advanced generation population. At that time, clonal tests are established of these selections and a small clonal orchard is established from rooted cuttings.

Table 1. Advanced generation breeding cycle of *Hypoplatanus obtusa*

Year	Breeding Population	Test Population	Production Population
1	Selections in F_n Generation	Establish Clonal Lines of Selections	
2		Cross Selections with Polymix of Worst Trees	
3			Establish Unrogued Seed Orchard
4		Field Plant Progeny Test	
5		Field Plant Clonal Test	
6	Make Single Pair Matings of Best Selections	Evaluate Progeny Test	
7		Evaluate Clonal Test	Rogue Orchard or Start New Orchard
8	Field Plant Seedlings		
9			Produce 10 Best Clones Commercially
11	----------------- START NEW CYCLE -----------------		

Since the species produces abundant seed, this will produce all the seed that will be required. A number of crosses are made for the purpose of progeny testing by pollinating the selections with a mixture of pollens from the worst trees available. In the following year, seed is collected and in year four a progeny test is established. The progeny test is evaluated after two years in the field and single pair matings are made among the parents of the best families to produce the following generation of the breeding population. These are field planted in year 7. At year 7 the clonal orchard can be rogued to the best clones and at age 9 of the cycle, rooted cuttings of the ten best clones can be mass produced for commercial planting purposes. In year 11 new selections are made in the breeding population, which constitutes the beginning of the next cycle.

Expected Gains and Economic Considerations

Based on the admittedly rather limited experience with this species gains were calculated for the three different production populations: the unrogued seed orchard, the rogued seed orchard and the rooted cutting nursery. These are alternatives and would not necessarily all have to be done. For this reason it is important to look both at the gains possible and the economics.

In the calculations it was assumed that in year one of the breeding cycle, one hundred initial selections were made. These would be the ten best trees of each of the ten families formed by single pair matings among the best 20 selections of the previous generation. Two hundred trees per family are raised every generation.

A summary of the comparisons is given in Table 2. The unrogued seed orchard would produce a gain of only 5%. This would be obtained as a result of individual tree selection within the families. The total cost discounted to the beginning of the breeding cycle at 8% interest would be $17,700.

Table 2. Cost and economic returns for the three kinds of production populations of Hypoplatanus obtusa

Year	Production Population	Gain %	Total Cost,$	Cost/acre of Plantation,$	Cost/ton of Fiber,$
3	Seed Orchard	5	17700	23	5
7	Rogued Seed Orchard	20	14700	24	5
9	Rooted Cuttings	40	28600	40	4.30

Assuming that the coppice plantations are established with 5000 plants per acre, the cost per acre for tree improvement will be $23. It is assumed further that these coppice stands will be harvested every three years and will be cleared and replanted to improved stock after 3 rotations. On this basis the cost per ton of fiber obtained as a result of genetic improvement will be $5. In other words this is the "marginal" cost necessary to produce an additional ton of fiber with genetic improvement over and above the basic cost of growing the 4 tons annually from unimproved stock.

The rogued seed orchard will be established at age 7 and the gain will be 20%. Total cost will be $14,700 and the cost per acre $24. The cost per ton of fiber due to genetic improvement will again be about $5. Although the genetic gain has been increased the economics are unchanged because of the delay of four years in obtaining this gain.

The rooted cuttings will produce a gain of 40%. The total cost will be $28,600, and the cost per acre of improved planting is $40. Despite the further delay in availability, the cost per ton of fiber due to genetic improvement is reduced to $4.30 because of the substantial increase in genetic gain.

Comparing these three alternatives the rooted cuttings would appear to be the best choice. The reason for this is not only the somewhat lesser cost per ton of fiber but also the fact that the additional gain will be available about 8 years sooner than otherwise would be the case. This is so because during the following cycle the seed from a rogued seed orchard would be equal in quality with the rooted cuttings of the previous cycle assuming the genetic progress remains constant from one generation to the next.

CONCLUSIONS

The above example was merely used to illustrate the principles involved in developing and evaluating a strategy for advanced generation breeding.

The most important ingredient in developing such a strategy for a new species is an open mind willing to explore the unique opportunities the species offers rather than following conventional procedures.

The most crucial decisions are the choice of breeding method and whether the breeding plantation, the progeny test plantation and the plantation producing the seed (or rooted cuttings) are kept separate or are combined in some way.

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