RECURRENT SELECTION IN FOREST TREE BREEDING

BY

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INTRODUCTION

The rapid development of applied tree breeding programs in the South has concentrated much of our earlier work on problems related to selection and establishment of sources for the production of improved seed. It seems appropriate, now that many of the original goals have been reached, that our attention should turn to thoughts of further cycles of selection in tree breeding programs.

This paper will discuss the use of recurrent selection in crop breeding programs and relate this use to tree breeding. It should be pointed out in making a comparison between crop and tree breeding programs, however, that in the latter the commercial production of seed has been customarily considered as an inseparable portion of the breeding program. While the goal of the crop breeder is like the tree breeder commercial production of improved material,in many crop plants the breeding program is considered somewhat apart from the commercial production of seed. It would appear that such a separation might have merit in certain tree breeding programs and will probably evolve as subsequent generations of select material become available.

While it is not the purpose of this paper to present all-inclusive details of breeding procedures available to the tree breeder, it is hoped that the paper will be useful in providing a coherent framework within which the breeder can operate.

Classification of Breeding Systems

Classification of plant breeding systems has been traditionally based on methods of reproduction. The three major categories are: Self-Pollinated, Cross-Pollinated, and Asexually-Propagated.

Sprague (1967) has provided an alternate classification of breeding systems by use of the terms "population improvement" and "hybridization." As defined by Sprague, population improvement includes all operations within a system designed to yield a sexually-propagated improved type whether this be a random mating population or pure line. Hybridization, on the other hand, was defined to include all aspects of a system designed for the commercial production of F_1 hybrid seed.

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Note that the above definition of population improvement does not include the use of asexual reproduction. Since, however, continued improvement of vegetatively propagated material generally involves the use of sexual reproduction, the production of vegetatively propagated material resembles the development of pure lines. The difference lies in the fact that genetic homozygosity if not required for the mass production of desirable genotypes which can be vegetatively propagated.

Sprague's system of classification appears to have merit for categorizing tree breeding programs. Drawing heavily on quantitative genetic principles, and providing a framework within which tree breeding systems can logically be included, the two categories seem to be well adapted to classifying forest tree breeding programs.

Recurrent Selection Defined

The term recurrent selection was first used by Hull (1945). According to Hull (1952), "recurrent selection was meant to include reselection generation after generation, with interbreeding of selects to provide for genetic recombinations." Note that, in applying the above definition to a selection program, the program is not recurrent until the selects have been interbred and a new cycle is initiated. Non-recurrent selection programs have been referred to as "pick the winner" selection (Cockerham, 1961).

RECURRENT SELECTION IN BREEDING PRACTICE

The interest in recurrent selection first arose in maize breeding programs because of general disappointment with the performancies of second-cycle hybrids (Hull, 1952).

As Penny et al. (1963) have pointed out, recurrent selection is a method for improving populations where the ultimate goal is the development of a superior population for commercial production. In addition, it is also a means for developing commercial hybrids. In fact, recurrent selection programs were first suggested as a means for developing improved inbred lines for the production of hybrids in maize.

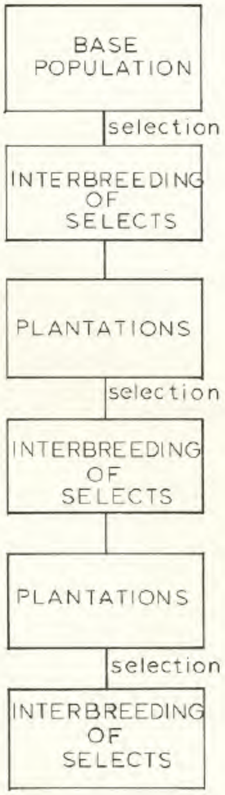
It would appear that recurrent selection is receiving more emphasis in forest tree breeding from the stand point of developing superior populations for commercial production per se. Although much hybridization work has been carried on in forest genetics work, a relatively small amount of this crossing has involved systematic selection or testing of the parents which were involved in the production of these hybrids. Such an oversight is most unfortunate.

The developments which follow in this paper are concentrated on the use of recurrent selection as a method for producing improved populations. The use of this breeding system, however, should not be overlooked as a means for producing potentially valuable racial or species hybrids from existing selected forest tree material.

Theoretically, recurrent selection is a breeding procedure for increasing the frequency of desirable genes within a population while maintaining sufficient variability for continued selection (Penny et al., 1963). The importance of such considerations to tree breeding programs is obvious.

Phenotypic Recurrent Selection

Phenotypic recurrent selection is defined as recurrent selection in which the phenotype of the individual plant serves as the basis for selection (Penny et al., 1963). Such a system is shown in Figure 1.



PHENOTYPIC RECURRENT SELECTION

Figure 1. Diagrammatic representation of phenotypic recurrent selection. Note that the selections for a given cycle are recombined and. are the base for the next cycle.

An example of phenotypic recurrent selection in forest tree breeding would be selection of trees in the forest followed by interbreeding of selects with subsequent selection and interbreeding of selects from the first generation. (See Figure 1)

Genotypic Recurrent Selection

Genotypic recurrent selection will be assumed to include types of recurrent selection in which identity of families is possible; i.e., a system of matings is used to develop relatives (Figure 2). The important distinction between phenotypic and genotypic selection is that in the latter additional information from phenotypic values of relatives often provides a more reliable guide to the breeding value of an individual than the phenotypic values alone (Falconer, 1960).

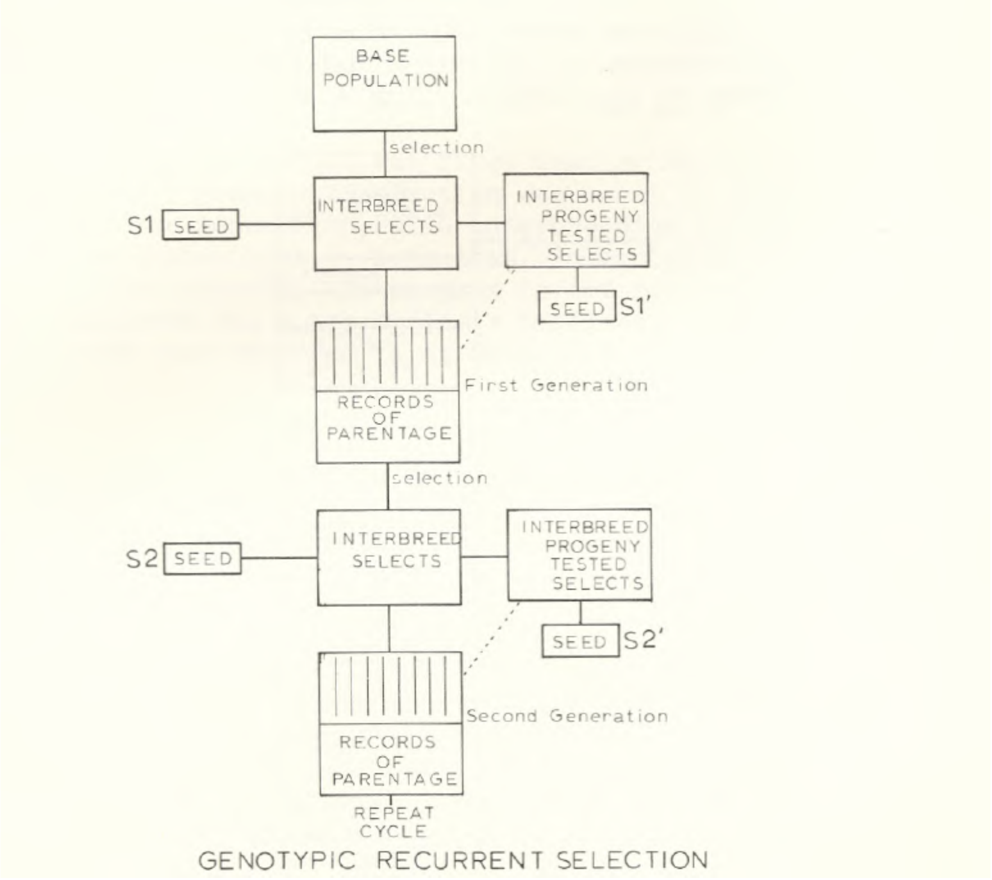


Figure 2. Diagraramatic representation of genotypic recurrent selection. Records of parentage are required and selections can be based on performance of relatives.

RESULTS OF RECURRENT SELECTION STUDIES

As indicated earlier, recurrent selection procedures were initially developed in an attempt to produce superior inbred lines for the production of hybrid maize. Of more general interest to tree breeders at present, however, are the results from crop studies which can be applied to the goal of developing superior populations for commercial production.

In Crop Plants

One of the earliest studies on the effectiveness of phenotypic recurrent selection was that of Sprague and Brimhall (1950) for increased oil percentage in maize. The mean oil percentage *was* shifted rapidly upward through the second-cycle of the series. A similar result was obtained by Jenkins et al. (1954) in selection for resistance to a leaf blight of maize. It should be emphasized, however, that phenotypic recurrent selection has generally not been effective in breeding for improved yield in crops (Allard, 1960).

Of the types of genotypic recurrent selection, data from studies involving recurrent selection for general combining ability are more numerous. Lonnquist and McGill (1956) concluded that improvement in yield and general economic worth was achieved in two cycles of recurrent selection for general combining ability in three synthetic varieties of corn. A synthetic variety is defined by Allard (1960) as a variety produced by crossing inter se a number of genotypes selected for good combining ability in all possible combinations with subsequent maintenance by open-pollination. In alfalfa, Tysdal and Crandall (1948) concluded that clones selected for high general combining ability produced a synthetic variety having a higher yield than standard varieties.

Several additional examples of the effectiveness of recurrent selection for general combining ability are available. In general, this procedure has been successful in producing improved types, particularly in forage crops.

Data from studies using recurrent selection for specific combining ability and reciprocal recurrent selection are scanty (See Sprague, 1967). In general, studies of these two types of recurrent selection are being carried out for evaluations of their efficiency in hybridization programs.

In Forest Trees

Data from specific recurrent selection studies in forest trees are not presently available. There are, however, data available from various sources which can be used to estimate the degree of improvement from use of recurrent selection.

Indication of improvement from first generation selections in tree improvement programs are beginning, to accumulate. Marler (1963) presented a summary of estimates of gains which have been obtained by various workers. Reports to date have indicated that gains of 10 to 15 percent more volume than commercial checks have been attained in southern pine programs.

Estimates of realized gains from second generation selection unfortunately are not available. Estimates of genetic variances have been obtained for tree populations, however, and these estimates can be used to predict gains expected in the second cycle of selection. An example of the use of such estimates is presented below.

AN EXAMPLE OF RECURRENT SELECTION IN FOREST TREE BREEDING

The data for this example were taken from three year total heights of a pollen mix test of 22 slash pine clones (*Pinus elliottii* Engelm) and 2 commercial checks of International Paper Company's Gateswood Seed Orchard in the Gulf Woodlands Region. The test involved 12 tree row plots planted in h replications on each of 2 locations.

Realized gain in total height of the select progenies was nine percent of the mean of the commercial source. This difference between the selects and commercial check was significant at the five percent level.

In order to predict gains expected from second cycle selection in this population, genetic and environmental variances were estimated from an analysis of the progeny of the selected clones only.

Gains in three year total height were estimated using the formulae developed by Namkoong et al. (1966) and are presented in Figure 3 as percent of the means of the selects and in Figure 4 as hundredths of feet.

Two selection methods were compared in Figures 3 and 24. In the combined selection procedure the best half-sib families are chosen and the best individual, or individuals within these families is selected. Such a procedure would lead to the production of the S2 seed of Figure 2. Progeny test selection involves the selection of desirable parents based on the performance of their offspring. The first cycle of this system would lead to the production of the S1' seed of Figure 2.

Figure 3 compares these two selection procedures in terms of predicted gain in percent of the mean of all the select progenies. As can be seen from Figure 3, the predicted gain using the combined selection procedure is over double the gain of the progeny test procedure when the number saved is 1c or over. It, would appear that, because of practical considerations related to seed production, the number of clones saved in a progeny tested orchard would be at least half of the original selections.

The comparisons of the selection procedures of Figure 3 should not be construed as an argument against progeny testing per se. What these graphs do point out is the importance of considering the progenies themselves as the basis for the next cycle of selection.

In Figure 4, comparisons of the methods are based on gain per unit time. In constructing this graph, the gain was divided by the estimated time in years to produce seed from each of the methods. It was assumed that the progeny would be evaluated at 10 years of age at which time the seed orchard would be rogued and the benefits of this roguing would occur two years later in the 81' seed of Figure 2. The combined selection gain figures were estimated by assuming the progenies would, produce seed in commercial quantities at 10 and 20 years after initial assessment at age 10.

The comparisons in Figure 4 clearly show the importance of considering the progenies as a base for the next cycle of selection. Note that even in the case where 30 years for seed production was assumed for the combined. selection procedure the gain per unit time gain estimates closely approached progeny test gains at a number saved of 14, and exceeded progeny test gain at numbers saved of 16 and over.

The example developed above is related to a testing procedure using a pollen mix, i.e. only one parent is known. Recurrent selection based on such a mating design with the limited number of clones (22) used in this example would lead to excessive inbreeding. Such inbreeding can be minimized by including more clones in the program and/or by using mating designs in which both parents are known.

The above examples were presented to emphasize the importance of considering the progenies of selected trees as the base for subsequent cycles of selection. It should be recognized that these examples are simplified in that the breeding system was considered closed. In actual practice this will normally not be the case as new selections at various stages of testing will enter the program This, of course, will further tend to minimize inbreeding.

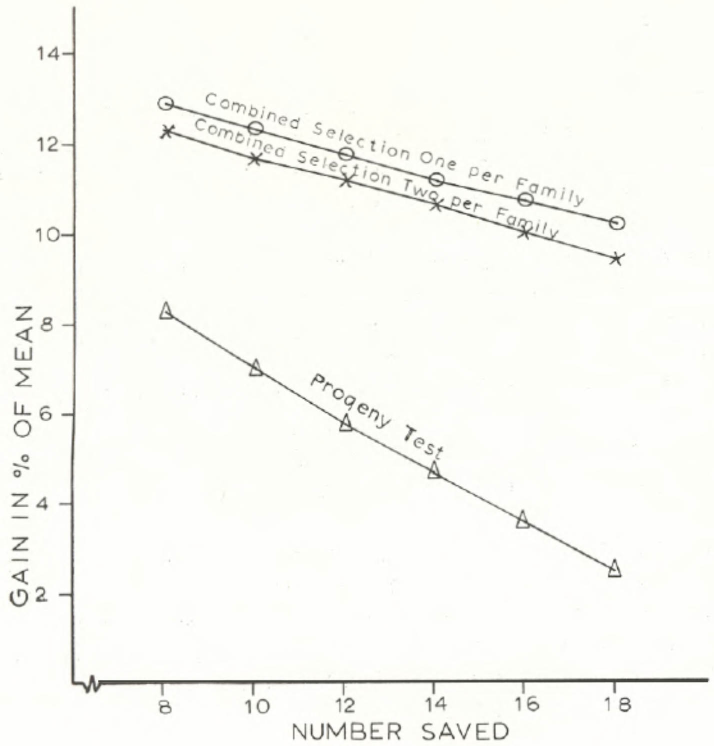


Figure 3. Comparison of two methods of recurrent selection in terms of gain in percent of the mean of the selects. Dumber saved is based on a total of 22 clones and refers to clones saved in the case of progeny testing and families saved in the case of combined selection.

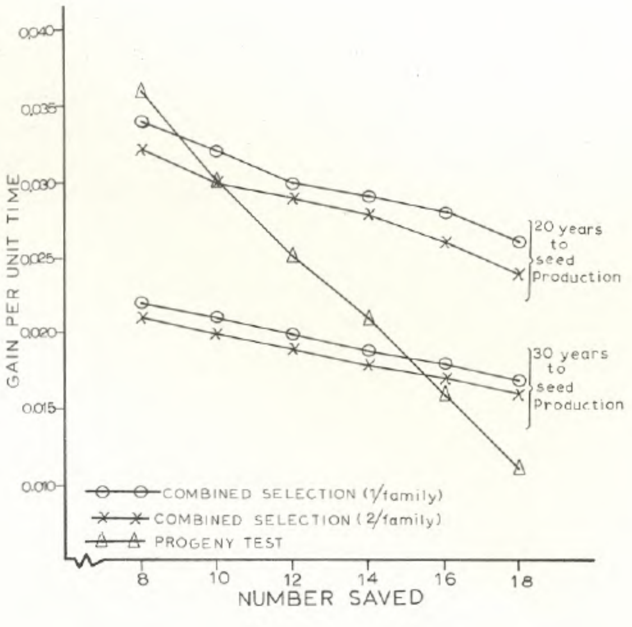


Figure 4. Comparison of two methods of recurren-, selection in terms of gain per unit time. Note where combined selection lines intersect progeny test line.

This paper has attempted a brief discussion of recurrent selection, its use in crop breeding, and its importance to tree breeding.

Recurrent selection implies that the selected material from a given cycle is recombined to serve as the base for the next cycle. Thus, in the example discussed in this paper both the progeny test and combined selection are types of recurrent selection.

The comparisons of the two systems in the example used pointed out the importance of considering the progeny themselves as a base for repeated cycles of selection in an applied tree breeding program.

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