REALIZING GENETIC GAINS THROUGH SECOND-GENERATION SEED ORCHARDS

Robert J. Weir[1/]

Abstract.--Second-generation forest tree seed orchards are being established with early selections from first-generation progeny tests. Although much has been learned from first-generation orchard experience, there are new challenges encountered and new methods used to achieve maximum effectiveness in this second improvement cycle.

Effective procedures for selecting trees with outstanding general combining ability, the best trees of the best families, are being developed. Precautions are necessary to avoid detrimental inbreeding effects by using only individuals with known pedigrees in the new orchards.

Second-generation orchards are established at close spacing to allow for further selection through roguing following more complete testing. In addition, several outstanding first-generation clones are grafted to provide an early pollen source for second-generation grafts.

Based upon our knowledge of heritability and selection differentials, genetic gains of 20% in growth over and above first-generation orchards can be predicted. Although major emphasis has been placed on growth rate and disease resistance, a threshold value for foini and quality traits will be maintained.

Additional keywords: Selection methods, orchard establishment, inbreeding depression.

INTRODUCTION

In an applied forest tree improvement program, even small genetic gains can bring enormous returns when distributed over thousands of acres annually. For this reason it is imperative that the improved material resulting from recurrent selection efforts be introduced into the production phase at the first practical point in time. Such activities are underway with the N. C. State University-Industry Cooperative Tree Improvement Program[2/] which has begun establishment of second-generation production seed orchards. Through the spring of 1973, eight cooperators have started establishment of 10 orchards. Currently totaling 40 acres, these orchards will consist of over 400 acres of commercial forest tree seed orchards when completed.

1/ Liaison Geneticist, N. C. State University, School of Forest Resources, Raleigh, N. C.

2/ The Cooperative membership is composed of 25 industrial and three State Forest Service members in 13 southeastern states having combined regeneration programs of over 300 million trees annually.

While many of the techniques are similar and there is much to be gained from the first-generation orchard experience, new and improved technology is being utilized with the second applied improvement cycle. This paper describes the second-generation orchard program being implemented by members of the N. C. State University Cooperative. Where appropriate, suitable alternatives which may find application under a differing set of conditions are examined.

Selection Base

Over 1400 acres of control-pollinated progeny test plantings have been established in conjunction with the N. C. State University-Industry Cooperative Tree Improvement Program. These tests, which include over 6000 control cross seed lots, have the dual objectives of (1) assessing breeding values of seed orchard parents, and (2) providing a base population from which individuals are selected to serve as parents in second-generation production seed orchards.

Use of control cross progeny with complete pedigrees is mandatory if the potentially damaging effects of inbreeding are to be avoided. Nearly every orchard in the Cooperative progeny test program has been shown to contain several clones (5 to 20 percent of the clones tested) which are excellent general combiners (Weir and Zobel, 1972; Zobel, et al., 1972). If mass selection is practiced, i. e., selecting the best individuals with no regard to family performance, progeny from the outstanding clones are chosen at much higher frequencies than would be expected from the frequency with which the clones occurred in test plantings. This is evidenced by the second-generation selections from loblolly pine under test by International Paper Company, Georgetown, S. C. (Figure 1). If selections were made from tests identifying only one parent (open-pollinated, top-cross or pollen-mix matings where only the mother is identifiable) the chances are very high that many selections would have one common male parent. Use of such selections in production seed orchards could result in disastrous genetic gain reduction resulting from inbreeding depression. Volume growth depression of 20 percent has resulted from matings among half-sibs (Gansel, 1971). Discretion then dictates that related matings be avoided and this can only be assured when the complete pedigree of second-generation seed orchard parents is known.

It is of additional concern that the population serving as a base for selection of second-generation orchard parents be derived from a mating scheme which provides a sufficient number of unrelated families so as to allow inbreeding avoidance. Nearly all the Cooperative progeny tests have employed a tester design wherein four to six clones designated as testers are mated to all other clones. For any single breeding program this is a severe restriction on the number of unrelated families created; there can be no more unrelated crosses than the four to six testers used in the breeding program, no matter how many clones are under test. The tester system does have application in a cooperative where member organizations within a region pool their resources to obtain the 20 to 40 unrelated selections required to establish a second-generation production seed orchard. However, breeding programs which must stand alone and have a single closed system would find the tester design

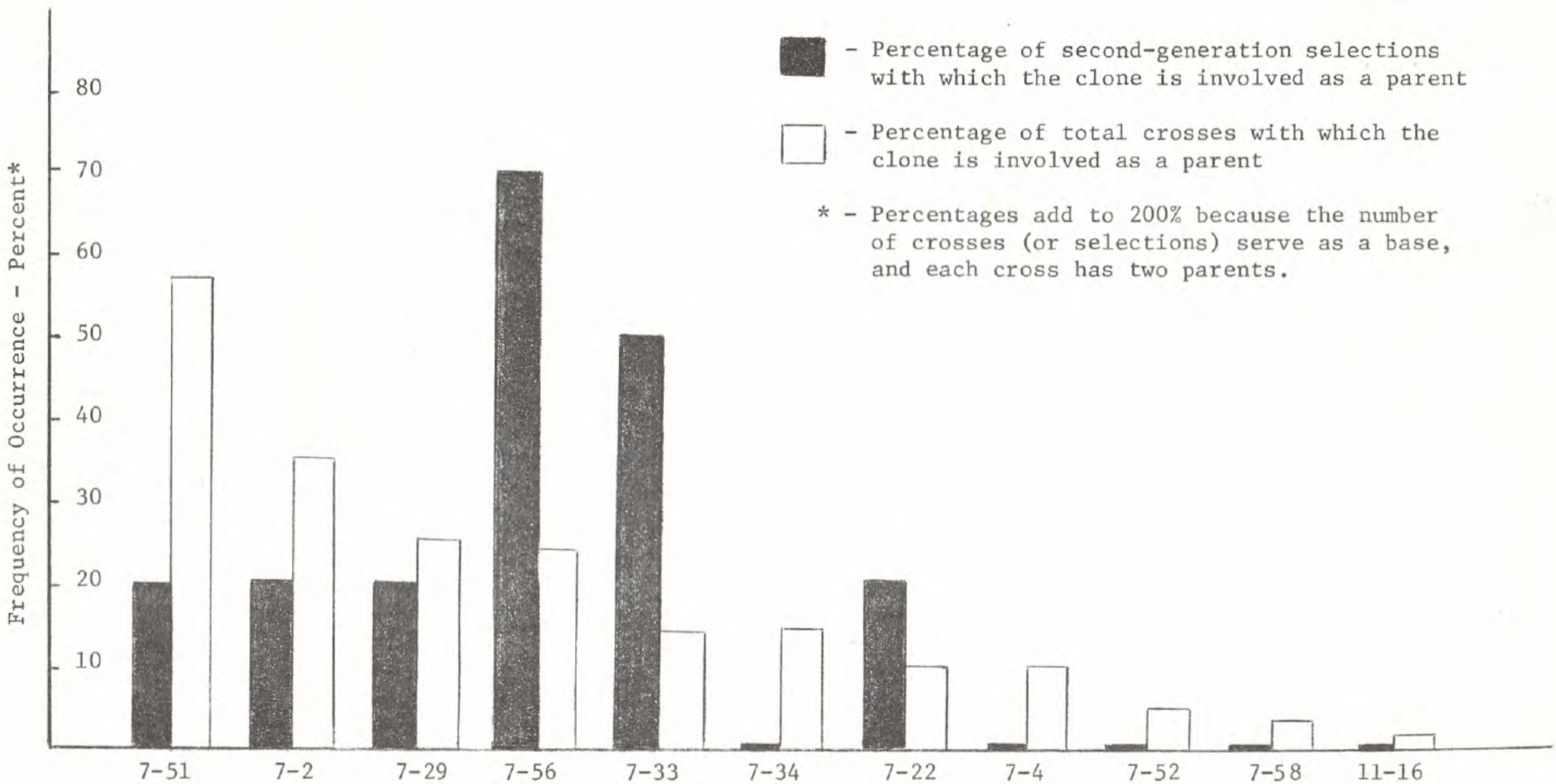

Figure 1. Comparison of the percentage of second-generation selections with chich a clone is a parent, related to the percentage of all crosses using that clone as a parent

inadequate. They should resort to one of several alternative breeding schemes described which would properly serve their needs, e. Zobel, et al., 1972; van Buijtenen, 1972; Franklin, E. C. and Squillace, A., 1973.

Selection Methods

Before any advanced-generation selection is done, one must determine when to select with respect to progeny age. Early selection will allow a more rapid turnover of generations but would tend to result in more selection errors as a result of lower juvenile-mature correlations (LaFarge, 1972; Sluder, 1972; and Wakely, 1971). However, delaying second-generation parent selection until selection errors are eliminated would also delay the commercial utilization of available improved material. Compromises are needed to optimize the total cumulative improvement as measured over time. Published accounts of such efforts have recommended selection at surprisingly early ages (Nanson, 1970; Squillace, 1972). It is apparent that the greatest long-term improvement is achieved by effecting a rapid turnover of generations rather than waiting to assure that the transition from one generation to the next is made, with only proven winner selections.

The Cooperative's initial second-generation selection work provided for early establishment of records on outstanding trees in each progeny test. Initial selections were identified by a two-stage process which included screening four-year field measurement data in the office and field assessment during or after the fifth growing seasons. At this time three or four ramets of each selected tree were grafted into a research clone bank to allow evaluation of graftability and eventually flower production and phenology. The tentative selections continue to develop in the progeny tests and are scheduled for reassessment at age 9 and again at approximately age 12.

Many trees having the desired combination of growth, form, and disease resistance characteristics were identified in the above manner. The procedure is best described as mass selection whereby outstanding trees were chosen solely on their own phenotypic superiority. Such a selection system is analagous to wild stand selection used with the initial improvement cycle except that it has been more effective as a result of greater environmental control including uniform sites, spacing, competition and identical aged trees. However, the theoretical limitations to this approach were realized as evidenced by the too frequent selection of outstanding individual trees which came from below average parents, i. e., too many good trees from poor families were picked. Although some of these trees have been retained for testing, it is recognized that selection of such trees will theoretically not yield as much genetic gain as combined family and within-family selection.

As second-generation selection work progressed and the need to establish production orchards with the most improved material available became evident, selection techniques were refined to include both family and within-family performance. An independent culling level system was introduced which included:

1. Selection of individuals from only those full-sib families which rank in the top 50% for a given test in growth traits.

2. The individual tree height is arbitrarily required to exceed the sum of the test average plus twice the square root of error variance (replication by family interaction).

3. The tree must be disease-free.

4. The tree must score above average in both crown conformation and stem straightness ratings.

5. Culling levels have been introduced at the 8-year assessment to reflect selection for wood specific gravity and volume. Requirements for volume superiority are determined as for height.

The independent culling level approach is applied in two stages. First the measurement data are screened and then an on-site assessment of each candidate tree is made prior to final acceptance. The independent culling level system has led to marked improvement in selection; most trees chosen are derived from progenies of the very best general combiners from the initial seed orchard. However, such an approach has shortcomings and continual improvements are being developed.

When only full-sib family performance is used as a basis for family selection, a bias is introduced. Intended selection for high general combining ability may in fact reflect outstanding positive dominance deviations or specific combining ability which is of little utility using current production seed orchard methodology. Future evaluation work is to be revised to include half-sib family selection (general combining ability) as well as full-sib family selection. Simultaneously methods are being devised to make use of sibling information from other tests in other years and locations.

The ultimate refinement in second-generation selection would be development of indices which optimize the weighting of half-sib, full-sib and individual tree values. However, if index selection is to be applied, accurate variance estimates or heritability estimates are needed to determine the appropriate weights. Good estimates are not usually obtainable from most progeny tests, since such tests are not designed for variance estimation but rather to evaluate first-generation clonal performance. An alternative is to use published heritability estimates or variance component estimates but this introduces the inherent dangers of extrapolation from data which apply to only one population in one single location or set of locations. Results using index selection can be no better than the data used to construct the index.

The full- and half-sib family information base will increase simultaneously with development of improved selection methods. The results of these advances are already apparent and indicate that, increasingly, selected trees come from matings among only the very best and strongest general combiners of the first-generation breeding population. While breeders strive arduously for such gratifying results which are prerequisite to maximizing genetic improvement, a subsequent dilemma results in the applied or production phase of the program. One is constantly confronted with the decision of whether it is best to use several outstanding but related selections or to use moderately good clones with no common ancestors. Certainly some related selections can be used with restrictions (see next section) but the extent of such use will depend on the magnitude of inbreeding depression resulting from related matings.

ORCHARD ESTABLISHMENT

Although the pressure to establish second-generation orchards has been intense by those who rightfully want to maximize production by using the available improved genetic material, it is necessary to move slowly and not rush immediately into large acreages of second-generation orchards. We have chosen to move deliberately, with each Cooperative member currently establishing only two to four acres of second-generation seed orchards in any one year. This allows an annual reassessment of the second-generation selections and provides for establishment each year of the best available clones, including any new selections which may have been obtained since the previous grafting season.

Initially we are establishing second-generation clonal seed orchards at 15' x 15' spacing, modified by leaving every second position in every second row open. Approximately 145 grafted trees per acre are established The alternate rows having alternate blank spaces are staggered such that each tree is surrounded by no more than three immediately adjacent neighbor (Fig. 2).

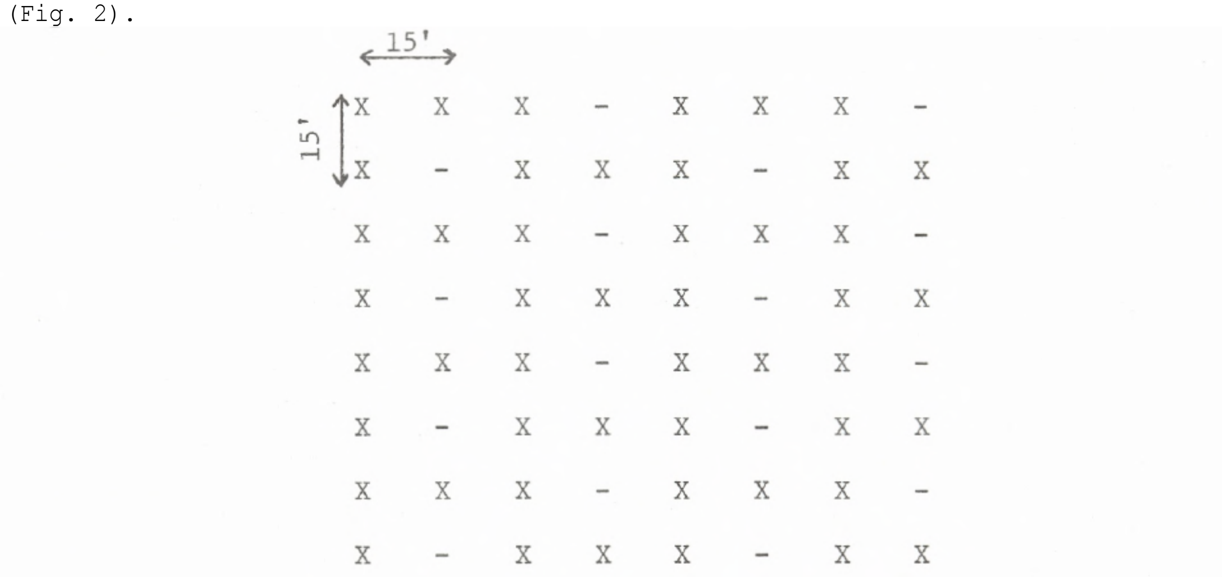

Figure 2. Second-generation orchard layout
X = Grafted Tree
- = Vacant Position

Staggering the alternate, half-filled rows will delay the first orchard thinning one or several years, with no adverse effect on total seed production due to overcrowding.

More trees are established per acre than will be left after roguing, so as to allow for flexibility to remove the poorest individuals. Since the majority of the selections are currently being assessed and grafted after only five growing seasons in the field, some poor individuals will be chosen. We have found that some selections do not maintain the required superiority as time progresses. If we are to begin orchard establishment as early as the fifth year, it is imperative that the system be flexible enough to allow roguing of trees that do not develop as expected. In subsequent years, when the majority of the clones being established are at least eight to ten years old, the number of clones and grafts per acre will be reduced accordingly.

For flexibility in roguing it is necessary to establish as many trees per acre as feasible and to graft many different clones into each orchard. This is being done as a result of the stepwise establishment procedure with new selections being added each year. In contrast, however, there is need to use only the best clones so as to maintain a selection intensity sufficient to achieve substantial genetic gains prior to roguing. This constant dilemma must always be faced and the direction chosen for the inevitable compromise will depend largely on the strength of the juvenile-mature correlation among actual and potential second-generation selections. There is, however, a lower limit to the number of clones which must be included in the second-generation orchard if one is to achieve the desired 90- to 100-foot spacing between ramets of the same clone and thus minimize chances for selfing (McElwee, 1970). With the recommended layout described above (Fig. 2), a minimum of 18 unrelated clones are needed to maintain compliance with the 90- to 100-foot rule. If it is necessary to use related (half-sib) selections when developing the clonal arrangement, they must be separated by 90 to 100 feet just as if they were ramets of the same clone. Thus a pair of related clones effectively counts as only one clone in the determination of the total number of clones needed or being used.

Previous experience with grafts of young trees has indicated "female flower" production will commence in a 3- to 5-year period after grafting. Usually pollen production lags several years behind this (personal communication, Bruce Zobel[3/]). In an effort to provide an interim pollen source, we use several of the very best general combiners from first-generation orchards, grafted into the second-generation orchard as "pollen parents." This is sometimes difficult, however, since the most outstanding first-generation parents are nearly always related to the best second-generation selections. Thus, again, a compromise must be reached as to which pollen parents are to be employed if inbreeding is to be avoided. The most common result is that we use the best available unrelated first-generation clones. Such trees provide a satisfactory interim pollen source, but since they will be rogued as soon as the second-generation clones produce pollen they will provide no long-term dilution of genetic gain in the advanced-generation orchard.

[3/]Professor, Forest Genetics, N. C. State University, Raleigh, N. C.

In first-generation seed orchards, a 400- to 500-foot isolation or dilution zone is maintained which is kept clean of any trees that will pollinate the orchard species. Such a zone appears to be an effective means of increasing the ratio of improved to contaminating pollen (McElwee, 1970). Such dilution zones are more critical for second-generation orchards, as the contaminating pollen from wild stands becomes, in relative terms, increasingly inferior to that from the orchard trees. Although of less importance, second-generation orchards should also be isolated from first-generation orchards. If this cannot be fully accomplished, the adjacent portions of the first-generation orchards must be very severely rogued prior to the onset of commercial flower production in the new advanced-generation orchard.

Genetic Gains

The ultimate objective of the Cooperative is to produce enough seed to meet all regeneration requirements for each cooperator. Simultaneously, we strive to maximize the genetic quality of such seed at any given point in time. We look forward to the assessment of realized genetic gains to be obtained through second-generation production seed orchards, but until this is possible we must estimate the benefits of improvement efforts by means of predicted genetic gains.

Results to date show realized gain in growth resulting from first-generation seed orchards ranges from 10 to 20 percent. Although more difficult to quantify, gains in quality traits such as crown conformation and bole straightness have been even more dramatic. Because of the occurrence of escapes and the nature of inheritance, mass selection for rust resistance has resulted in only minimal improvement. However, when combined with progeny testing and subsequent roguing or establishment of improved-first-generation orchards, the percentage of rust infected trees can be reduced by as much as 20 percent (Blair and Zobel, 1971).

The outlook for genetic gains possible from second-generation seed orchards is bright. Based upon the most reliable estimates of heritability available in conjunction with realistic selection differentials, a genetic gain of 25% has been predicted for volume growth, obtained as a consequence of mass selection (Stonecypher, et al., 1973). With family plus within-family selection volume improvement could be even greater. Such improvement is expected over and above that which was achieved in the first generation. Although family plus individual within-family selection for percentage of trees rust free is impossible, family plus within-family selection for number of galls per tree has shown gains from 50 to 90 percent to be possible (Blair and Zobel, 1971). Additional improvement in form characteristics can be achieved, but because of the excellent response to previous selection, merely maintaining the level of improvement realized to date will be satisfactory. The philosophy behind such strategy recognizes that additional improvement in form traits would be obtained at the expense of additional gains in growth or disease resistance. The value for additional upgrading of form would not offset the value of volume or growth improvement which would be sacrificed.

It must be recognized that the predicted gains previously suggested do not reflect the consequences of multiple-trait selection. While major emphasis is being placed on growth, adaptability and disease resistance, and gains in each will be high, they may not equal the single-trait predictions of above when sought simultaneously. It is very apparent, however, that the genetic gains to be obtained from a properly executed second-generation seed orchard program are well in excess of improvements realized to date. Second and subsequent improvement cycles are expected to have an increasingly greater impact on intensive forest management efforts throughout the South.

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