DESIGN AND LAYOUT OF ADVANCED GENERATION SEED ORCHARDS

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Abstract.--A set of criteria for establishment of advanced generation seed orchards has been developed for The North Carolina State University-Industry Cooperative Tree Improvement Program, based on experiences with first generation seed orchards and a few early blocks of advanced generation orchards. Basic considerations in developing these criteria were to maximize the flexibility for orchard improvement through roguing and to minimize the potential for inbreeding. To achieve these goals, the criteria for orchard layout are: (1) initial stocking of at least 135 trees per acre, (2) the inclusion of thirty to forty clones in each orchard block, (3) a minimum distance of 90' between related ramets, (4) relatively equal clonal frequencies, and (5) avoidance of repetitive neighborhoods.

Additonal keywords: Orchard configuration, clonal composition, inbreeding, panmixis, roguing.

The N. C. State Cooperative Tree Improvement Program has been actively involved in the establishment of clonal seed orchards since the early 1960's. Through the sixties and early seventies, efforts were directed primarily toward the establishment of first generation orchards. In the mid-seventies, attention turned toward establishment of advanced generation seed orchards. As we contemplated this new phase of orchard development and reflected upon our experience with first generation orchards, it became apparent that the choice of orchard configuration and design required re-evaluation. In the first generation a broad range of criteria were used in design selection. The most important criteria were ease of orchard management, the usefulness of a given design for experimental purposes, minimizing selfing, the compatibility of the design with anticipated thinning and maximizing panmixis. The considerations thought to be most important were minimizing selfing and maximizing panmixis (Giertych 1975). All of these criteria were considered for advanced generation orchards. Additionally, several considerations specific to the advanced generation program required evaluation. These included the use of related selections (full-sibs and half-sibs) in the same unit area, and the initiation of orchard development with very young selections. Each of these considerations, old and new, were examined to determine their potential impact on the primary objective of seed orchard establishment--to maximize the genetic quality of seed produced at all times.

ORCHARD ESTABLISHMENT CRITERIA

The primary objective of orchard development is to produce seed of maximum genetic quality for regeneration programs. In this regard, two of the

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considerations previously used for design selection i.e., the suitability of a design for experimental purposes, and the ease of orchard management were concluded not to contribute to the primary objective and were discarded from further consideration in orchard design. The orchard management criterion eliminated concerned the placement of clones in some repeatable and predictable pattern that made it easy to work in the orchard and to locate a specific clone with ease. However, certain mechanical aspects of orchard operation and management provided significant input to decisions relative to the orchard configuration (tree spacing and arrangement).

With the elimination of these considerations, basically only four factors remained for consideration in establishing orchard criteria.

1. Minimizing inbreeding.
2. The compatability of orchard design with anticipated thinning requirements.
3. Maximizing panmixis.
4. Minimizing the impact of selection errors.

The effects of selfing have long been a concern in orchard establishment. As stated earlier, Giertych (1975) reported that minimizing selfing was one of the most frequently mentioned criteria in design selection. With the inclusion of related selections (full-sib and half-sib selections) in the same unit area in advanced generation orchards, the potential for reduced genetic gain as a consequence of inbreeding is substantial. One inbreeding study reported a reduction of 20% in volume alone as a result of half-sib matings (Gansel 1971). Reductions of this magnitude in the genetic quality of seed would negate the expected response to selection. it was concluded, therefore, that minimizing inbreeding is an important criteria in the selection of orchard design and configuration.

The desire to quickly capitalize on the potential gain of advanced generation improvement has resulted in the initiation of orchard development with extremely young selections, often as young as five years of age. As a result of imperfect juvenile-mature correlations, selection at this age is subject to errors (La Farge 1972, Wakeley 1971). Therefore, if the potential gain from advanced generation orchards is to be realized in a timely fashion, consideration must be given to minimizing the impact of the errors likely to occur from the use of young selections. A solution to minimizing the impact of selections subsequently judged unsuitable is to maximize the flexibility to upgrade the orchard through roguing. This can be accomplished by establishing more trees per acre and by using more selections than might otherwise be desired.

The advantages and disadvantages of maximizing panmixis were heavily debated during establishment of first generation orchards. The advantage mentioned most frequently was the desire to maintain maximum genetic variability in the crosses produced. Others believed that maximizing panmixis should be avoided since it eliminated the potential to capitalize on specific combining abilities and thus achieve even greater gain. The latter proposal would he a realistic consideration if information on specific combining abilities was available at the time of orchard establishment. This, however, is rarely the case in advanced generation orchard establishment. The desire to capitalize on potential genetic gain quickly will generally result in the establishment of production orchards prior to the availability of information from progeny tests of the selection used. Therefore, maximizing panmixis was considered to be a valid concern.

The value of using orchard design restrictions to achieve panmixis has been questioned. For example, van Buijtenen (1971) argued that the design constraints imposed to restrict the occurrence of repetitive neighborhoods were so confounded with factors such as the flowering phenology of clones that the imposed restrictions were likely to have little effect on the genetic variability or the average genetic quality of the seed produced. We agree with van Buijtenen on this point, yet strongly support the argument for the elimination of repetitive neighborhood patterns for other reasons. One of the major frustrations encountered in first generation orchards resulted from the occurrence of repetitive neighborhoods. The negative effect of repeating neighborhoods was recognized when the first genetic thinnings were attempted. Invariably, clusters of good or poor clones occurred. When clusters of good clones were encountered, only two options existed. A clone of good genetic quality could be removed to provide the necessary crown release, or the need for crown release could be ignored and the clone retained with a susbsequent decline in cone production resulting from overcrowding. The second option was obviously incompatible with the objectives of a seed orchard program. A cluster of poor clones required either a "patch clearcut" resulting in a nonproductive area within the orchard, or the continued existence in the orchard of genetically inferior clones. Regardless of the cluster type, a no win situation existed. When such clusters occur in orchards with repetitive neighborhoods, the impact on the genetic quality of the seed produced, as well as the quantity of seed produced, is significant. To minimize the effect of such clusters, nonrepetitive neighborhoods were established as a primary criteria in orchard design selection.

In summarizing the above considerations it became evident that two basic criteria were essential to achieving the primary objective of production seed orchards.

1. Flexibility for the improvement of the genetic quality of the orchard must be maximized.
2. The potential for inbreeding must be minimized.

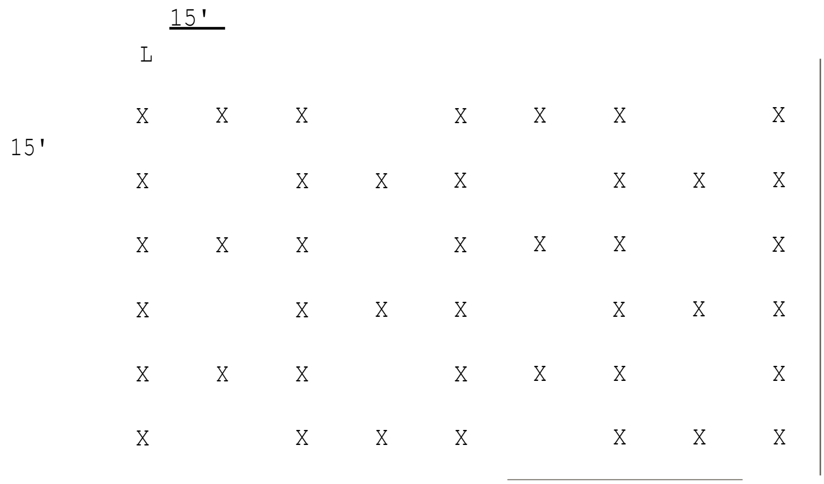
ORCHARD CONFIGURATION

Maximizing roguing flexibility was the primary objective in determining the orchard configuration, initial ramet spacing and arrangement. Each configuration meeting the primary objective was further evaluated for orchard management and operation.

The first orchard configuration component evaluated was the initial spacing of ramets. To determine the effect of various spacings on the primary objective, some basic assumptions were required relative to the roguing schedule and intensity. Under the prevalent spacing in first generation orchards (15' x 30'), the first thinning required for crown release generally occurred 8-10 years after establishment. By the time of this first thinning, orchards were already producing a significant quantity of seed. Yet at the time of the first thinning, information on the genetic quality of the clones was generally still insufficient for genetic roguing purposes. Therefore, initial roguings were primarily based on silvicultural and sanitation requirements. Under these circumstances an initial spacing of 15' x 30' was more than adequate to maximize the genetic quality of the orchard through roguing. In advanced generation orchards, information on the genetic quality of selections is available much earlier as a result of analysis of individual and sibling performance in tests from which selections were made. Therefore, the potential to upgrade the genetic quality of the orchard occurs much earlier. Our experience indicates that by the time progeny tests are about age 10 selection errors are minimal, therefore the errors resulting from the use of very young selections could be identified within five years following initial orchard establishment. Since it was considered advantageous to eliminate selection errors as early in the life of the orchard as possible, it was concluded that the initial spacing should provide for a genetic roguing as early as age five. This initial roguing should not, however, decrease the potential for genetic improvement or seed production in the future.

With the prevalent spacing used in first generation orchards (15' x 30'), 97 trees per acre were initially established. This stocking level was sufficient for satisfactory seed yields through the early years of orchard production (up to age 10). To enhance early production, it was determined that the initial spacing should provide for a stocking level of approximately 100 trees per acre following the first roguing at age five. Assuming reasonably equal clonal frequencies within a unit area and a selection error rate of 35% at age 5, an initial stocking level of 135 trees per acre was deemed reasonable to insure adequate production levels in the early years of the orchard. It was anticipated that subsequent roguings would occur at five year intervals with the final roguing occurring at approximately age twenty. In first generation orchards the stocking level following the final roguing is approximately 20 to 30 trees/acre. Assuming the same stocking level in mature advanced generation orchards, an initial stocking level of 135 trees/per acre would provide for the removal of 35% of the ramets at each subsequent roguing. Thus, an initial stocking level of approximately 135 trees/per acre was considered sufficiently flexible to achieve the primary seed orchard objective.

Any number of initial spacings and ramet arrangements exist which result in initial stocking levels of approximately 135 trees/acre. A square arrangement with 18 feet between planting positions would yield 134 trees/acre. A rectangular arrangement of 15' x 20' would yield 145 trees/ acre. The modified 15' x 15' configuration proposed by Weir (1973) and illustrated in figure 1 would also yield 145 trees/acre. From the standpoint of initial stocking and orchard management considerations, either of the three configurations were satisfactory. However, the configuration advocated by Weir provided an advantage in crown space since each ramet was surrounded by only three immediate neighbors. For this reason, the modified 15' x 15' is the recommended configuration for use in the establishment of advanced generation seed orchards.



X PLANTED POSITION

FIGURE 1. MODIFIED 15' X 15' CONFIGURATION.
FROM WEIR (1973),

ORCHARD CLONAL COMPOSITION

Both of the primary criteria developed for orchard establishment, maximizing roguing flexibility and minimizing inbreeding, were of significant impact in determining orchard composition. From the standpoint of maximizing roguing flexibility to upgrade the genetic quality of the orchard, it was believed that a sufficient number of clones should be included to allow the lowest 50% of the clones to be rogued. In order to minimize inbreeding, it was determined on the basis of McElwee's (1970) research findings, that the number of clones established must be sufficient to maintain a minimum distance of 90' between ramets of the same or related trees.

Assuming a 35% error rate in selection, an orchard established with 30 to 40 clones would yield 20 to 26 clones following initial roguing for correction of the selection errors. Based on first generation experiences, the orchard would be comprised of the best 10-12 clones following the final roguing. Therefore, an orchard initially established with 30 to 40 clones would allow the removal of the lower 40 to 60 percent of the clones. Thirty to forty clones occurring with relatively equal frequencies would result in three to five ramets of each clone per acre. Roguing down to the best ten to twelve clones would result in a stocking level of 36 to 60 trees per acre. Assuming a final stocking level of 25 trees per acre, the 36 to 60 ramets remaining would provide additional flexibility for selection of specific ramets to achieve a final stand of healthy, vigorous trees appropriately spaced within the orchard with no large gaps or tight spots.

Using the orchard configuration recommended, a minimum of 24 selections is required to maintain the minimum distance of 90' between ramets of the same selection or related selections (full-sibs and half-sibs). Therefore in the total number of selections recommended, there must exist for each selection, a subset of 24 unrelated selections. This means that full-sibs/half-sibs can only be included in the same unit area if the total number of selections recommended exceeds 24. If thirty to forty clones are recommended for an orchard, the recommendations could therefore contain 6 to 16 selections that may be related to each other or to the original set of 24 in some manner. This was considered sufficient flexibility for the inclusion of related selections in the orchard.

Since an orchard composed of less than thirty clones would limit the roguing flexibility and either increase the potential for inbreeding or severely limit the number of full-sibs/half-sibs included, a lower number of clones was not considered. A much larger number of clones within a given unit area was not considered practical from an orchard management standpoint. Exceedingly large numbers of clones will have a negative impact on the genetic gain that can be achieved through the life of the orchard as a result of reduced selection intensity. It was, therefore, concluded that the orchard composition should consist of a minimum of thirty clones and a maximum of forty clones each occurring with approximately equal frequencies.

ORCHARD DESIGN

Based on the primary objective of seed orchards and the resulting criteria, the orchard design selected had to possess three essential elements. First, the design had to he capable of maintaining the minimum distance between ramets of the same or related clones. Second, the design could not create repetitive neighborhood patterns. Third, each clone had to occur with relatively equal frequency.

In first generation orchards the most prevalent design used was a fixed block. To a lesser extent, the shifting-block design (Malac 1962) was used. Neither, however, met the requirements for advanced generation orchards. The fixed block, and the shifting block to a lesser degree, both resulted in repetitive neighborhoods. Both were capable of maintaining minimum distances between ramets of the same clone, but they resulted in extremely unbalanced clonal representations when related selections occurred. Further investigation showed that all systematic designs had similar disadvantages.

Since the use of systematic designs was not desirable, attention turned to random designs. The two considered were randomized complete blocks and the computer-based permutated neighborhood design proposed by La Bastide (1975). The randomized complete block, in its true form, would not provide for separation of ramets of related selections or of the same selection when represented by multiple ramets within an orchard block. For this design to be used in advanced generation orchards, restrictions would be required to provide the minimum separation of related ramets. The permutated neighborhood design of La Bastide's provided for the isolation of ramets of the same clone, the maximization of panmixis and equal clonal frequencies. It did not however provide for the spatial separation of related ramets along the interface of adjacent blocks. Since advanced generation orchards were generally being established through the installation of adjacent annual blocks, the ability to interface blocks and maintain the minimum separation of related ramets was considered important. Additionally, it would be impossible in advanced generation orchards to retain absolutely equal clonal frequencies as required by La Bastide's design. The **degree of** relatedness among selections determines the relative frequency with which each can occur in an orchard block. The provision for ramet isolation would also require expansion to include separation of full-sibs and half-sibs. The basic concepts in La Bastide's computer generated designs were compatible with the design requirements in advanced generation orchards but their implementation was too inflexible to handle the problems specific to advanced generation orchards.

This led to consideration of the computer program, COOL, developed by Bell and Fletcher (1978) which was based on the permutated neighborhood design concept. Many of the restrictions imposed by LaBastide's program were eliminated in COOL. The major drawback to this version of the permutated neighborhood design was its inability to handle related selections, specifically the triangular relationships sometimes encountered when using half-sibs, without severely restricting their frequency of occurrence. For this reason, Bell and Fletcher's version was eliminated from consideration.

It was believed, however, that the permutated neighborhood concept could provide the essential elements for advanced generation orchard design. Thus, a relaxed permutated neighborhood design was developed along with a computer program, AGSOL, for Advanced Generation Seed Orchard Layout. This design does not provide the rigid neighborhood control of the previous versions. No specific restrictions are placed on the frequency with which a particular clone can occur with another. In other words, no attempt is made to maximize panmixis. It does, however, through the sequence of ramet establishment, prevent the occurrence of repetitive neighborhoods. A minimum distance of 90' between ramets of related clones is specified. Additionally, a specification exists that clones are to occur with as equal frequency as possible. When conflicts occur between these two specifications, maintaining the required spatial separation of related ramets takes precedence over maintaining equal clonal frequencies. If a position cannot be filled without violating the 90' rule, the clone which will provide the maximum separation is selected and the violation is noted. Clonal frequencies are equalized to the extent possible given the degree of relatedness among selections. Typically, a selection related to another in the orchard will occur with 60 to 70% of the frequency of a selection which has no relative. A selection related to two others will occur 40% to 50% as frequently as an unrelated selection. AGSOL provides for the generation of layouts for any orchard shape or size. It also provides the capability of expanding orchards without violating ramet separation along the interface.

The design and layouts produced have been used for the past several years for the establishment of advanced generation orchards in the Cooperative. To date, the relaxed permutated neighborhood design has proved suitable for achieving the desired objectives and the layouts produced by AGSOL have proved manageable in orchard establishment and operation.

SUMMARY

Based on the primary objective of seed orchard establishment, the production of seed of maximum genetic quality, two criteria are required for orchard development. The flexibility for improvement of the genetic quality of the orchard through roguing must be maximized. The potential risk for inbreeding must be minimized. To achieve these goals requires a minimum initial stocking level of 135 trees per acre, composed of thirty to forty clones. Each clone should occur with relatively equal frequency provided a minimum distance of 90' is maintained between related ramets. Repetitive neighborhood patterns should be avoided. The requirements necessary to achieve the stated goals can be accomplished through use of a relaxed permutated neighborhood design.

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