SEED ORCHARD DESIGN, THEORY AND PRACTICE

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INTRODUCTION

Present seed orchard designs used in the South can be grouped roughly into three major categories--(l) the so-called "free love" orchard, (2) the randomized orchard, and (3) systematically arranged orchards. In the free love orchard, grafts are planted without any particular design and with minimum attention to close proximity of grafts of the same clone. The arrangement is especially prevalent in the older orchards. In the randomized orchard, grafts are randomized either throughout the orchard or within blocks, usually with the restriction that grafts of the same clone cannot be in close proximity to each other. The most common restriction is that two grafts of other clones have to fill the intermediate positions. A number of computer programs are available to accomplish this rather tedious job (Bastide [1967], Feret [1971], van Buijtenen [1971]). In systematically arranged orchards, a number of designs have been developed. One design calls for

blocks of ten clones, which are systematically arranged as shown in Figure 1. The design was developed by Langner and Stern (1955).

IKABCDEFGHThe advantages and disadvantages ofFGHIKABCDEthe various systems can be evaluated bestCDEFGHIKABCDEKABCDEFGHIwarining the objectives of seed-
orchard design.

Figure 1.--Systematic seedorchard lay-out for 10-clone block according to Langner and Stern (1955).

OBJECTIVES OF SEED-ORCHARD DESIGN

In current seed-orchard designs, the following objectives should be satisfied: (1) provision of as high a ratio as possible between pollen from the selected trees in the orchard and contaminating pollen from the outside; (2) provision of an adequate pollen supply throughout the orchard in order to secure a high seed set; (3) maximization of the number of combinations in which trees are crossing with each other, in order to assure maximum genetic variability; (4) minimization of the amount of inbreeding in the seed orchard.

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Objectives one and two are very closely related and so **are objectives** three and four. At first glance it might seem that satisfying one objective would also satisfy the other. This \mathbf{iS} , however, not necessarily the case. For instance, providing a generous isolation zone might **give a very** favorable ratio between improved pollen and contaminating pollen, while at the same time the overall pollen supply might be inadequate. Similarly, randomization in a seed orchard would tend to increase the number of possible crosses that could occur but would not necessarily solve the inbreeding problem.

Objective 1. **Provision** of a Favorable Ratio of Improved to Contaminating Pollen

The accepted method for providing a favorable ratio is the creation of an isolation zone. The standard for seed certification is four hundred feet. As pointed out by Squillace (1967), this still allows a considerable amount of contaminating pollen to reach the orchard, although as shown by McElwee (1970), it is certainly of benefit. In first-generation orchards **there is** not much that can be done about this contamination. In advanced-generation orchards and orchards made up of clones of known characteristics, other techniques are possible. It might be particularly beneficial to designate as pollinators certain clones which are of good quality and produce large amounts of pollen.

To simplify the discussion, the non-pollinator trees will be designated as seed trees. We now have two categories of trees--seed trees, which are known to produce good seed crops but may or may not produce pollen; and pollinators, which are known to produce abundant pollen. Pollinators of low seed-producing capability are designated as Type I. Pollinators which are also good seed producers are designated as Type II. Thus the effectiveness of the isolation zone can be increased by surrounding the orchard with a solid row of pollinators. Type I pollinators could be grown in the isolation zone, while Type II pollinators could be part of the orchard itself. One would expect that the first row of pollinators would have the largest effect, with additional rows contributing less. Further studies would be needed to assess the benefit of various arrangements, but offhand it seems that 1 to 3 rows would cover the range of economically sound possibilities.

Objective 2. Provision of Ade.uate Pollen Throu.hout the Orchard

In first generation orchards not much can be done to help the situation. In orchards constituted of known clones, however, pollinators-preferably Type II--can be planted throughout the orchards in a number of different arrangements. They can be distributed randomly, they can be planted in rows, or they can be interspersed throughout the orchard in a grid-like arrangement. This last type of arrangement would insure the best distribution of pollen throughout the orchard, with the minimum number of pollinators needed. In order to keep the genetic base from becoming too narrow, it is recommended that a minimum of three pollinator clones be used and preferably more. The design can be varied according to the number of clones available. Following are some designs that will fit a number of common situations. (1) If, out of a total of 10 clones, five pollinators are available, Langner's design could be modified by assigning a pollinator clone to alternate positions. This would result in a complete checkerboard distribution of pollinators, as shown in Figure 2. (2) If a smaller number of pollinators is available, every other tree in alternate rows could be

K G D A H E B T H E B H F C K G D A F C K G D A H E F C K G D A H E F C K G D A H E $\frac{A}{H}$ BCD $\begin{array}{cccc} \underline{I} & \overline{K} & \underline{A} \\ \overline{F} & G & \overline{H} \end{array}$ EB HF CK G HEBHFCKC G H I D E F H I E F GD B C A F E G L H K A B C

Figure 2.--Modification of previous design by designating alternate clones as pollinators. Underlined letters are pollinators (Type II). Others are seed trees.

assigned as a pollinator. Including the pollinator row at the outside of the orchard and assuming an arrangement of 31 x 31 trees, there would be 645 seed trees, 196 pollinators (preferably Type II) in the orchard and 120 pollinators (Type I or Type II) around the orchard for a total of 961 trees (Figure 3). (3) If a lesser proportion of pollinators is desired, they could be planted every third row and every third tree within the row (Figure 4). The arrangement described would result in 760 seed trees, 81 pollinators (preferably Type II) in the orchard, and 120 pollinators (Type I or Type II) around the orchard.

Objective 3. Maximization of Cross Pollination

The most effective way to assure that the greatest number of possible crosses occurs is by complete randomization within the orchard. The picture **is**, however, confused by several factors. (1) Some clones produce a disproportionately large amount of seed. This effectively reduces the number of crosses that actually occur. (2) Some clones produce an excessively large amount of pollen. This further reduces the number of possible combinations that do occur. (3) Normally, at any time only a small portion of the clones are fully receptive and a small portion are shedding pollen. The flowering dates of the different clones vary, with a few clones starting early, the bulk of them being intermediate, and finally a few flowering considerably later than the majority. This, again, serves to further restrict the number of crosses among clones. These factors have a much more profound influence on the mixture of crosses produced than the physical arrangement of the clones in the orchard.

In a first-generation orchard, we have no control over these factors. In second-generation orchards we do. Every effort should be made to help the situation by balancing both seed production and pollen production among clones. Also to be examined in evaluating the effectiveness of randomized versus systematic designs are the benefits derived from a maximum number of crosses. We might approach this problem as follows. In looking at the table of all possible crosses, the ideal that we might strive for is to have all squares filled with an equal number of seeds except for the selfs, which should be completely absent. Now let us see how we are affected if part of these crosses are missing. First of all, one half is simply the 0 . . . 0 0 . 2 3 . 4 2 · 3 · 4 · 1 · 2 · 3 · 4 · 1 · 2 0 1 1 0 4 . 0 . 0 . 3 2 3 2 3 . . 1 . 4 1 4 1 . 4 2 * 3 * 4 0 0 0 0 1 2 3 4 1 ÷ 2 3 . 4 . 1 . 2 · 3 · 4 · 1 2 0 0 0 . 2 3 . 1 • 2 • 3 • 4 • 3 4 1 4 . 1 . 2 . 3 . 0 . 4 4 0 0 . . 0 2 3 4 1 2 3 . 4 1 2 . 3 . 4 0 1 8 ÷ . ٠ * . . 1 . 2 0 0 0 2 3.4 .1.2.3.4.1.2.3.4 0 . 1 . . 3 4 . 0 . . 0 0 3 . 4 . 1 . 2 . 3 . 4 . 1 . 1 2 3 4 1 2 0 . . . 2 . 0 0 0 1 • 2 • 3 • 4 • 1 • 2 • 2 3 . 4 . 3 . 0 . 3 . 4 1 . . . 4 . 0 ٠ ٠ 0 . 0 2 · 3 · 4 · 1 · 2 · 3 · 4 · 0.1 2 3 . 4 . 1 . 1 2 0 0 . 0 3 2 3 4 1 2 . . 4 1 4 2 . 3 0 . 3 4 1 4 0 0 0 2 3 . 4 . 1 2 . . 3 • 4 • 1 • 2 . 3 . 4 0 * 1 . . 1 2 0 . . ٠ . ٠ . . 0 0 0 . 3 . 4 1 . 2 . 3 . 4 • 1 • 2 • 3 • 4 • 1 . 2 . 3 . 4 ٠ 0 0 0 . . . 1 2 3 4 1 . 2 3 ٠ 4 . 1 + 2 . 3 . 4 . 1 2 0 0 * 0 0 2 • 3 • 4 • 1 • 2 • 3 • 0 • 3 • 4 • 1 • 2 . 3 . 4 .1. 4 . 0 0 * * * * . 0

Figure 3. Alternate trees in alternate rows are designated as pollinators. A minimum of 4 clones is needed, arranged systematically. Seed trees could be arranged either randomly or systematically. 0 = Pollinator (Type I or Type II). 1, 2, 3, 4 = Pollinator (Type II). • = Seed trees. 0 0 0 0 . . · 4 · · 1 · · 2 · · 3 · · 4 · · 1 · · 0 0 . 3 . 1 2 0 0 0 · 0 0 . . 2 . . 3 • • 4 • • 1 • • 2 • • 3 • • 0 3 . 4 . . 1 . . 0 0 0 0 0 . • 1 • • 2 • • 3 . · 4 · · 1 · · 2 · · 3 · · 4 · · 1 · · 0 0 0 0 • • 3 • • 4 . . 1 * . 2 . . 3 * * 4 * * 1 • • 2 • • 3 • • 0 0 0 * * * * * * * * * 0 * * * * 0 0 • • 1 • • 2 4 . . 1 • • 2 • • 3 • • 4 • • 1 • • 0 . . . 3 . 0 • • • • • • • • • • 0 0 * * 3 * * 4 * * 1 * * 2 * * 3 * * 4 * * 1 * * 2 * * 3 * * 0 0 0 * * * * * * * * * * * * * * 0 • • 1 • • 2 • • 3 • • 4 • • 1 • • 2 • • 3 • • 4 • • 1 • • 0 0 0 • • • 0 • • • . • 0 • • 3 • • 4 • • 1 • • 2 • • 3 • • 4 • • 1 • • 2 • • 3 • • 0 0 . 0 0 • • • • 0 * * 1 * * · · 1 · · 2 · · 3 · · 4 · · 1 · · 0 2 3 4 0 * * * * * 0 . . ٠ . . . 0 • • • • • • • • . 0 .

Figure 4. Every third tree in every third row is designated as a pollinator. The design itself puts no limit on the number of pollinators. It is sound practice, however, to use as many pollinators as feasible, certainly not less than 4. Seed trees can be arranged either randomly or systematically. 0 = Pollinator (Type I or Type II). 1, 2, 3, 4 = Pollinator (Type II). • = Seed trees.

reciprocal of the other. Since so far no one has shown the existence of maternal effects in forest trees, one of these halves can be completely eliminated without any loss. A further reduction in number of families, but without loss of entire clones from the pool of crosses, would result in a reduction of the between-family genetic variation, but with little loss of genes from the gene pool. In other words, several combinations of genes would not be represented, but the genes would be preserved and new combinations could be created in future generations. If the reduction in the effective number of crosses were so severe that some clones for all practical purposes were not represented at all, a serious loss of genes from the gene pool would result, and remedial steps should be taken. The controlled crosses made for the purpose of progeny testing serve an essential function here. Except for random sampling variation, the average quality of the progeny would not be affected by the reduction in the number of crosses represented. In other words, one can look at the occurring crosses as a sample of all possible crosses. By chance, each sample could be above or below the average, but over a large number of orchards the fluctuations should-even out. In this light we can evaluate the implications of a systematic design versus a random design. In a systematic design one would expect fewer crosses to occur, but the clones should be equally well represented in the progeny as in a random design, since the representation is determined by the relative abundance of seed and pollen. Because the flowering behavior of the trees is more important in determining which crosses do occur than the physical arrangement, the effect is expected to be slight. It will tend to result in a somewhat decreased variability but without loss of genetic material or average quality of the seed.

Objective 4. Minimization of Inbreeding

The situation here becomes complicated in a hurry. The following few simple models, however, can give us some insight into what may happen and can provide a means for experimentally determining the degree of inbreeding taking place.

A simple way to determine the degree of inbreeding in the seed from an orchard is as follows: $F = P_1 \times .5 + P_2 \times .25 + P_2 \times A_{25}$ in which

F = the degree of inbreeding expected P = the probability of obtaining seed from selfing P₂ = the probability of obtaining seed from full sib crosses P₃² = the probability of obtaining seed from half sib crosses

The assumption is made that the trees used to establish the orchard are not inbred, although this could be readily taken into account if necessary.

Stern (1958) worked out the expected inbreeding in the case of several generations of selection for random mating orchards and for certain conditions of restricted mating.

<u>Inbreeding in clonal orchards.--In</u> a clonal orchard consisting of unrelated clones--as is normally the case in first-generation orchards-the only factor influencing the degree of inbreeding is the probability P of obtaining seed from selfing.

The following factors contribute to P : (1) the pollen contribution from the ramet itself (A_i), (2) the pollen¹contribution from other members of the same clone (BO, t3) the seed set from selfs (C1) , (4) the proportion of sound seed from selfs (D).

The following relation now holds:

 $P = (A_1 + B_1) \ x \ C \ x \ D$. It is easy to see this way wat the relative contribution of the various factors is. A can be expected to be very large compared to B_1 . C_1 can be expected to be somewhat smaller than one. In other words, selfed pollen might not be as effective in pollinating as crossed pollen. D is known to be much smaller than one and very variable from clone to clone, some clones being completely self sterile, which would make D equal to zero, other clones being almost self fertile, making D close to one.

The frequency of mutants appearing in open pollinated progenies of clones carrying marker genes can give us a good estimate of the actual magnitude of the factor P_1 . Since P equals the proportion of selfed seed, then $P_i = Y / X$ in which Y is the percent markers showing in open pollinated seed and X_i is the percent markers showing in the selfed seed. For example, if in one clone one percent albinos were observed in open pollinated seed and 16% in the selfed seed, the value of P_1 is .0625 and the expected degree of inbreeding would be .03.

Inbreeding in seedling seed orchards.--In seedling seed orchards, for example, an orchard derived from n females crossed with m pollen parents, the situation is much more complicated. Selfing, crosses among full sibs and crosses among half sibs, may all occur as in the general model described earlier.

^P (the probability of selfing) cannot be modified readily by the design¹ of the orchard. P (probability of full sib crosses) and P 3 (probability of half sib crosses), however, can be modified strongly. If separation between half sibs by one position is considered adequate, crosses among four males and four females will satisfy this requirement if single pair-matings are made. In order to make an arrangement including all possible crosses, five males and five females are needed. A planting arrangement is presented in Figure 5. If one wants to separate half sibs by two intervening locations, the minimum number of males and females needed is nine. In the case of a 9 by 9 scheme, only a single pair-mating 50 of the 100 crosses is feasible. To plant all possible crosses, the minimum feasible number is 11 males and 11 females. Designs are presented in Figures 6 to 8.

Aa	Bb	Cc	Dd	Ee	
Dc	Ed	Ae	Ba	СЪ	
Be	Ca	Db	Ec	Ad	
Eb	Ac	Bd	Ce	Da	
Cd	De	Ea	Ab	Bc	

Figure 5.--Planting arrangement for all possible crosses among 5 females (capitals) and 5 males (small letters) leaving at least one intervening position between half sibs.

Aa Bb Cc Dd Ee Ff Gg Hh Ii Kk Hd Ie Kf Ag Bh Ci Dk Ea Fb Gc Eg Fh Gi Hk Ia Kb Ac Bd Ce Df Bk Ca Db Ec Fd Ge Hf Ig Kh Ai Ic Kd Ae Bf Cg Dh Ei Fk Ga Hb Ff Gg Hh Ii Kk Aa Bb Cc Dd Ee Ci Dk Ea Fb Gc Hd Ie Kf Ag Bh Kb Ac Bd Ce Df Eg Fh Gi Hk Ia Ge Hf Ig Kh Ai Bk Ca Db Ec Fd Dh Ei Fk Ga Hb Ic Kd Ae Bf Cg

Figure 7.--Arrangement to separate half sibs by two intervening positions. When 10 females (capitals) and 10 different males (small letters) are used, 50 of the 100 possible crosses can be utilized.

Aa	Bb	Cc
Dd	Ee	Ff
Gg	Hh	Ii

Figure 6.--Planting arrangement for single pair-mating scheme among 9 females (capitals) and 9 males (small letters) leaving at least 2 intervening positions between related trees.

Aa Bb Cc Dd Ee Ff Gg Hh Ii Kk Ll Id Ke Lf Ag Bh Ci Dk El Fa Gb Hc Fg Gh Hi Ik Kl La Ab Bc Cd De Ef Ck Dl Ea Fb Gc Hd Ie Kf Lg Ah Bi Lb Ac Bd Ce Df Eg Fh Gi Hk Il Ka He If Kg Lh Ai Bk Cl Da Eb Fc Gd Eh Fi Gk Hl Ia Kb Lc Ad Be Cf Dg Bl Ca Db Ec Fd Ge Hf Ig Kh Li Ak Kc Ld Ae Bf Cg Dh Ei Fk Gl Ha Ib Gf Hg Ih Ki Lk Al Ba Cb Dc Ed Fe Di Ek Fl Ga Hb Ic Kd Le Af Bg Ch

Figure 8.--If 11 females (capitals) and 11 males (small letters) are used, all 121 possible crosses can be used in the above design.

ROGUING AND THINNING OF SEED_ORCHARDS

The systematic designs ordinarily will leave the distribution of clones undisturbed if a systematic thinning is done, for instance, if every other row is removed. In a randomly arranged orchard, thinning may result in an imbalance of the clones. Ordinarily no serious problem would result. There is no practical way in which an orchard can be designed to provide for true roguing, since one does not know ahead of time which clones are to be removed. As a consequence, true roguing tends to result in a somewhat uneven distribution of the trees in the orchard. If the number of clones to be removed is small in comparison to the total number of trees which need to be thinned to provide adequate spacing, the problem is not too serious. Usually, however, some holes and some clumps are unavoidable.

Giertych (1965) developed a design which provides for thinning of the orchard by a well-planned arrangement of the clones in the orchard. There is no opportunity for removal of entire clones, however, without deviating from the design.

The overriding factor in roguing a seed orchard is economics. The potential loss in seed production needs to be balanced against the expected improvement in quality. Whether a loss in seed production may result in turn depends on the spacing in the orchard and the cone production of the clones to be removed. The best solution can readily be obtained by weighting each clone according to its seed production and the percent of superiority of its seed. For example, a clone producing 100 pounds of seed annually, which is 10% better than nursery-run seed, is equal to a clone producing 200 pounds of seed, which is 5% better than nursery-run seed. Both are inferior to a clone producing 75 pounds of seed which is 20% better.

SUMMARY

Most acceptable seed-orchard designs are arranged either according to a modified randomized block design **or a** systematic design. Various designs were discussed according to the following four objectives:

- 1. Creation of a favorable ratio of improved to contaminating pollen.
- 2. Provision of an adequate pollen supply throughout the orchard.
- 3. Maximization of cross pollination.
- 4. Minimization of inbreeding.

Several new designs were presented which may better accomplish some of these objectives.

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