THE USE OF BREEDING GROUPS IN ADVANCED GENERATION BREEDING

J. P. van Buijtenen[1] and W. J. Lowe[2]

Abstract.--In a continuing tree breeding program inbreeding will occur after a fairly limited number of generations regardless of the mating design that is used. The available evidence strongly suggests that in many forest trees inbreeding is associated with a high degree of inbreeding depression. By dividing the breeding population into breeding groups and only crossing individuals contained within a breeding group, it is possible to confine inbreeding within a breeding group. The different breeding groups are and will remain unrelated to each other.

Seed produced commercially can then be outcrossed, by assigning one individual of each of nine or more breeding groups to a given seed orchard block.

It appears advantageous to use a complementary mating design, when making crosses within a breeding group. One set of crosses will be made to estimate GCA by means of a polycross using unrelated pollen. This will circumvent the problem of having to compare individuals with different degrees of inbreeding. The other set of crosses provides the trees for the next generation of selection.

The system used by the WGFTIP Cooperative is described to show how these ideas can be implemented.

Additional keywords: inbreeding, mating design, polycross

In order to evaluate different advanced generation breeding systems it is necessary to make a number of assumptions, that may not be entirely realistic, but that are essential for making comparisons. Let us examine these first.

1) The same breeding system is maintained over an extended number of generations. In other words, the same number of individuals is selected each generation; the same mating scheme is employed, regenerating the same number of families each time; and the intensity of selection is the same each generation. Although in practice this will never happen, one has to make this assumption to make valid comparisons and to avoid designing a system that will eventually self destruct.

2) No new material is brought in after the first generation selections have been made. Again this assumption is not realistic, but was adopted to

---

[1] Principal Geneticist, Texas Forest Service and Professor, Texas Agricultural Experiment Station; College Station, Texas.

[2] Associate Geneticist, Texas Forest Service and Assistant Professor, Texas Agricultural Experiment Station; College Station, Texas.

facilitate comparisons, to evaluate the systems on their own merit, and because in advanced generations it will become increasingly difficult to bring in new material without losing much of the previously obtained genetic improvement.

Under these assumptions inbreeding starts to build up after a few generations in a small population. Let us take a hypothetical orchard with 50 clones as an example. Using the WGFTIP partial diallel mating scheme to produce the progeny tests, 100 families will be generated (Figure 1). Assumption 1 says we need to make 50 new selections for the second generation orchard. There are many ways of doing this, e.g., selecting 50 trees in the single best family, 25 trees in the two best families, etc. Let us assume we select the five best trees from the ten best families. The rate of inbreeding depends on the way in which the families are selected and is, therefore, somewhat unpredictable. A computer simulation indicates we can expect the results given in Table 1.

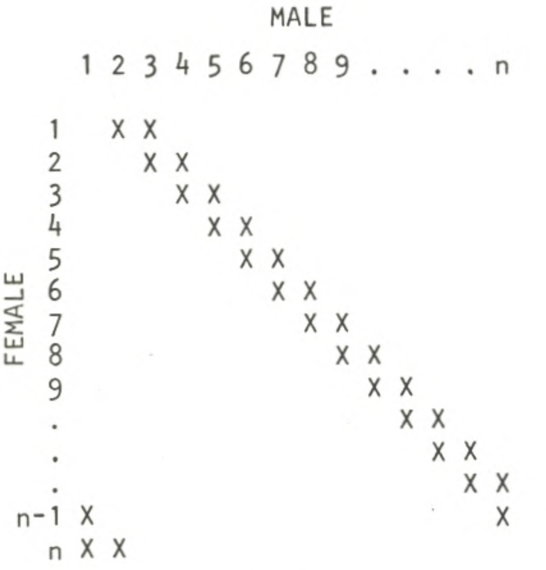

Figure 1. WGFTIP partial diallel mating scheme.

Inbreeding takes place at an average rate of slightly over three percent per generation. Although inbreeding obviously will not be a problem in our lifetime, as long as it takes about 20 years to produce a new generation, it does not take very many generations to reach significant inbreeding levels. If accelerated breeding procedures are developed allowing the production of a generation in less than 10 years, the problem could become serious more quickly.

Regardless of the time-frame the problem will force itself on us eventually and it would be much better if the researcher could establish positive control of the rate of inbreeding.

Table 1.--Results of computer simulation of inbreeding within a breeding population of 50 clones, assuming selection of the 5 best individuals of the 10 best families in each generation.

Generation	Average inbreeding coefficient	Inbreeding in least inbred family	Inbreeding in most inbred family
1	0	0	0
2	.0375	0	.125
3	.0594	0	.125
4	.113	.078	.188
5	.137	.102	.234
6	.168	.103	.264
7	.161	.123	.264
8	.208	.168	.288
9	.284	.226	.318
10	.307	.233	.358
11	.377	.335	.405

THEORETICAL FRAMEWORK

Theoretically one can distinguish several separate groups of trees in a breeding program: the trees grown for commercial wood production, the seed orchard, the progeny tests and the trees used for breeding. Each of these can have a different inbreeding level. For reasons of economy some are often combined, but they do not need to be. This is the key concept in devising a system to prevent inbreeding in the trees grown for commerical wood production.

Subdividing the Breeding Population

The seed produced from a seed orchard should be outcrossed, but the parents themselves may be inbred. To achieve outcrossing in the seed orchard even though parents may be inbred one only has to make sure that the parents are unrelated to each other. This can be accomplished easily by subdividing the selected trees in groups and not allowing crosses among trees belonging to different groups. This way the groups will remain unrelated forever. To establish an orchard only one selection of a given breeding group is represented in each orchard block. It is still possible to utilize several selections from a single breeding group by putting them in different blocks in the same orchard.

All controlled crosses for the purpose of producing advanced generation selections need to be confined to the breeding groups. As a result the breeding groups themselves will become inbred. One has the option of inbreeding rapidly or rather slowly. At the moment we are choosing to limit inbreeding to low levels. Inbreeding could be a useful tool, however, and some experimental work is needed to determine how well higher levels of inbreeding would work.

Use of Overlapping Generations

Once inbreeding is allowed a considerable degree of flexibility is added in choosing mating designs. Although it appeals to one's sense of order to keep each generation separate, this is not at all necessary. It might, for instance, be advantageous to use an exceptionally good first generation parent in crosses with second generation selections. This would lead to more rapid inbreeding, but could also generate more rapid genetic gain.

The Problem of Testing for General Combining Ability with Different Degrees of Inbreeding

If, as seems desirable, family selection is practiced, it is almost unavoidable that some families have different degrees of inbreeding than others. This would make the present partial diallel and tester schemes inappropriate for testing general combining ability, since general combining ability and inbreeding depression would become confounded. The problem could be circumvented, however, by using a polymix for testing general combining ability. Various kinds of polymixes would be possible, as long as they meet two requirements: 1) the pollen parents should be unrelated to the trees being tested. 2) The pollen should be as similar as possible to that expected in the orchard in which the selections are to be placed.

A Complete System

A complete system would, therefore, need to have the following elements:

1) A seed orchard in which each block contains one representative of each of nine or more breeding groups. A minimum of nine groups are needed if one wishes to maintain the present system of having two members of the same clone separated by at least two intervening positions.

2) A breeding population separated in unrelated breeding groups. The number of individuals in a breeding group is dictated by practical limitations. The lowest theoretical limit is one tree per breeding group. If we accept the need for a minimum of nine breeding groups a practical upper limit would appear to be around 100 trees per breeding group.

3) A complementary mating design (van Buijtenen, et. al., 1976) consisting of two separate sets of crosses each fulfilling a specific purpose: a) a set of polymix crosses to determine general combining ability, b) a set of specific crosses within the breeding group to produce a number of families from which to make selections for the next generation.

THE CURRENT IMPLEMENTATION IN WGFTIP

Because many of the clones in the WGFTIP are widely distributed, many members were using them in a large variety of crosses. Second generation selections obtained from these crosses would have had a high amount of relatedness. This relatedness would increase in future generations and make it difficult, if not impossible, to produce outcrossed seed in our production orchards.

First Generation Breeding Groups

To avoid this problem, the first generation breeding population has been divided into breeding groups. A clone belongs to only one breeding group irrespective of the number of orchards that contain that clone. Each breeding group contains approximately 25 selections, and it is anticipated that each cooperator will maintain four or five breeding groups for each of their orchards. When the base population is obtained, there will be approximately 32 breeding groups for slash and 96 for loblolly pine in our operating area.

The WGFTIP partial diallel crossing scheme will be utilized within each breeding group to complete the first generation breeding program (Figure 1). There will not be any control-pollination efforts across breeding group lines. Approximately 50 control-pollinated families will be generated within each breeding group. These controlled crosses will be field planted in three separate tests by the cooperator that is responsible for the breeding group.

Second Generation Breeding Groups

Second generation selections will remain in the same breeding group as their parents. To maintain a constant breeding population size, four or five trees from the best six families of the original 25 families will reconstitute the second generation breeding group. Because of our first generation crossing scheme, this will result in different degrees of relatedness among the second generation selections within a breeding group. Pedigree records will be maintained for each second generation selection.

Second Generation Mating Schemes

To evaluate the second generation selections, a complementary mating design will be utilized. A polymix cross will be used to evaluate the general combining ability of the selections. A separate pollen mix will be created for each breeding region. This pollen mix will remain constant over time and will be used for all of the second generation selections from the respective breeding region. A circular mating scheme will be used to produce material for the advanced generation selections that will form the breeding population for the third generation. Operationally, the circular mating design will be applied to a single breeding group which will contain approximately 25 selections. The general combining ability information obtained from the polymix progeny tests will determine which of the circular crosses will be used for the third generation selection activities.

The rate of inbreeding that occurs within a breeding group can be partially controlled by the arrangement of the clones in the circular mating design. Currently, our plans are to initially limit inbreeding during the early generations.

Field Layout of Progeny Tests

A different progeny test layout will be used for the different crossing schemes in the second generation breeding program. The polymix progeny tests will utilize a field planting design which will favor family evaluation for inclusion into production orchards. These progeny tests will be planted at a minimum of six locations, and they will be coordinated on a cooperative basis. The polymix progeny tests will sample the seed zone[1] that the breeding group originated from and all of the seed zones where the selections may be utilized in production orchards. Individual cooperators will be responsible for progeny testing the circular mating tests for their breeding groups. These field tests will be designed to maximize the gains from within family selection efforts. An example would be to plant each cross in 100 tree block plots on three different sites.

Breeding Groups and Seed Orchard Designs

Production seed orchards will be designed in the WGFTIP standard ten clone block (Figure 2). Only one selection from a breeding group will be used in a given block within an orchard. Because there will not be any relatedness between breeding groups, the resulting seed will be outcrossed. Different blocks within a seed orchard can contain different selections from the same breeding group. By assigning selections from the same breeding groups to the same relative positions in two different orchard blocks, at least two intervening positions will be maintained between relatives in the production orchard. Because of the number of breeding groups per orchard type, selection intensity in developing an operational orchard can be applied at both the breeding group level and within the breeding group.

A	B	C	D	E	F	G	H	I	K
H	I	K	A	B	C	D	E	F	G
E	F	G	H	I	K	A	B	C	D
B	C	D	E	F	G	H	I	K	A
I	K	A	B	C	D	E	F	G	H
F	G	H	I	K	A	B	C	D	E
C	D	E	F	G	H	I	K	A	B
K	A	B	C	D	E	F	G	H	I
G	H	I	K	A	B	C	D	E	F
D	E	F	G	H	I	K	A	B	C

Figure 2.--WGFTIP - seed orchard block design. Each letter is assigned a different clone. All ramets of the same clone are separated by two intervening positions. A number of different blocks can be contained in any orchard (Langner and Stern 1955).

---

[1] The WGFTIP operating area is divided into eight seed zones as follows: 1) northeast Texas, 2) southeast Texas, 3) north Arkansas, 4) south Arkansas, 5) north Louisiana, 6) south Louisiana, 7) north Mississippi and 8) south Mississippi.

CONCLUSIONS

1) The division of a breeding population into breeding groups insures that an operational tree improvement program will be able to produce outcrossed seed in advanced generation seed orchards.

2) A special mating design is needed in conjunction with the breeding groups. We chose to use a polymix cross combined with circular matings. Many other schemes would be possible.

3) Only one selection of each of ten breeding groups will be included in a given seed orchard block. Different blocks may include different selections of the same group.

4) The main advantages of this procedure are:

   a) Inbreeding due to relatedness among clones can be avoided in the seed orchard.
   b) The tree breeder assumes positive control of inbreeding, making it a tool rather than a liability.

LITERATURE CITED

Langner, W. and K. Stern. 1955. Versuchstechnische Probleme bei der Anlage von Klonplantagen. Z. Forstgenet. Forstpfzücht 4:81-88.

van Buijtenen, J. P., J. Burley, A. C. Matheson, R. Stonecypher and E. Thor. 1976. Report of Session I, Mating Designs. Proceedings of the IUFRO Joint Meeting of Genetic Working Parties on Advanced Generation Breeding. Bordeaux, pp. 28-29.