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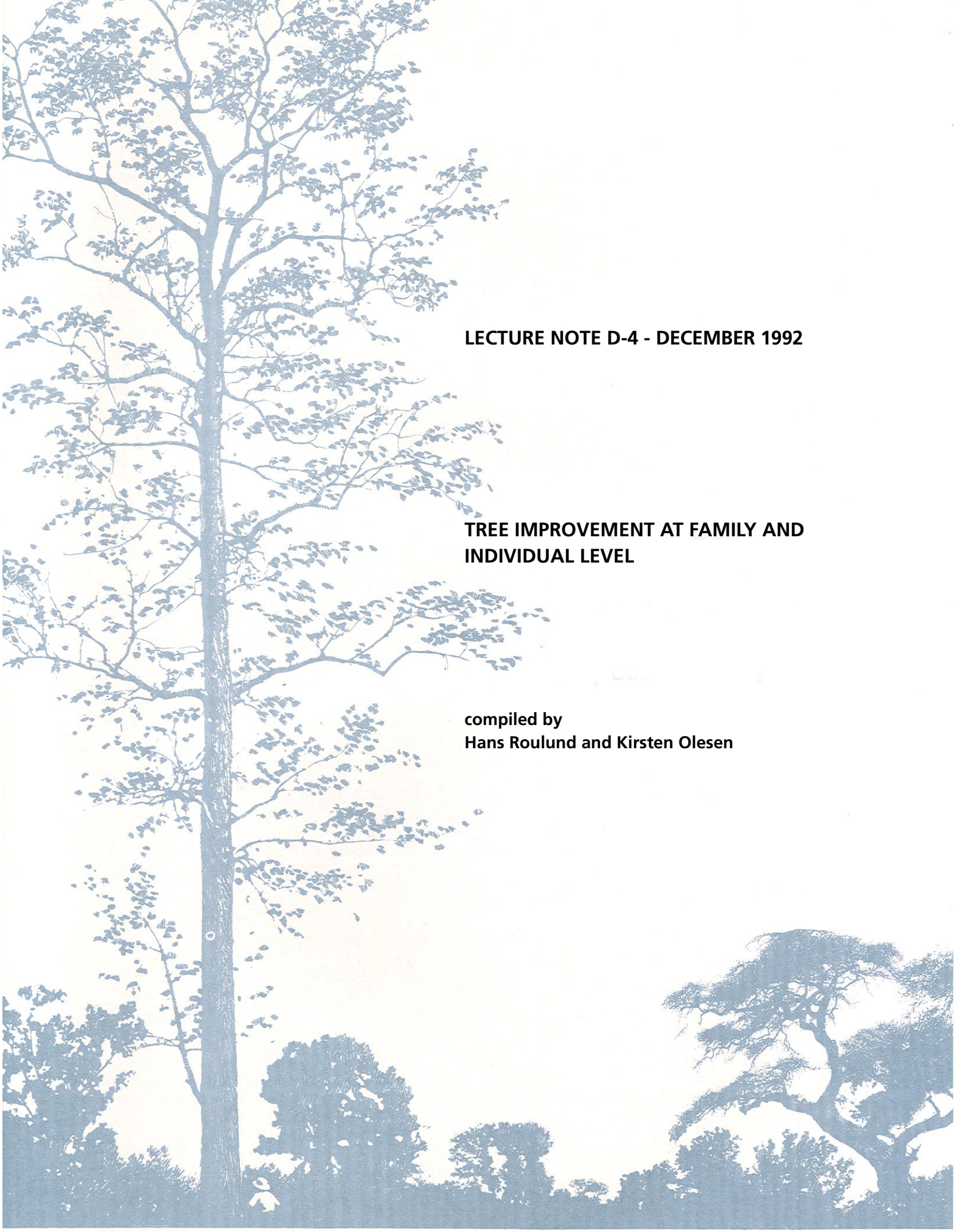

LECTURE NOTE D-4 - DECEMBER 1992

# TREE IMPROVEMENT AT FAMILY AND INDIVIDUAL LEVEL

compiled by
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DANIDA FOREST SEED CENTRE

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# 1. INTRODUCTION

Nearly all countries with managed forestry have started tree breeding not only at provenance level, but also at family and individual level. Such work started in the temperate zone in the 1930's and very soon spread to the sub-tropical and later on to the tropical zone. The breeding work was inspired by the findings in genetic science and by the results already obtained in agriculture and horticulture. Often the possibilities of tree breeding were overestimated and later on it has been very difficult to fulfil the optimistic expectations of the pioneers.

However, through careful and persistent work, considerable gains have been achieved for some species in a number of countries. Besides, a lot of information and knowledge have been gathered. This makes up a very important and necessary prerequisite for future breeding.

**A family** in the sense of tree breeding is a group of individuals deriving from the same tree. If a tree has been pollinated by a large number of other trees we call it an open pollinated family and call the offspring half-sibs. If a tree has been pollinated only with pollen from another single tree under controlled conditions, we call the progeny a controlled pollinated family or a full-sib family.

**An individual** is a genotype deriving from sexual reproduction. An individual can be cloned to genetically identical trees. The original tree is called an ortet and the propagules are called ramets.

The objective of tree improvement at family and individual level is to improve a number of characters, more than is possible at the provenance level.

It is well known that there is variation between populations. This is reflected in a large number of provenance tests, and it is experienced through practical use of specific seed sources. But there is also variation within the populations or provenances, and this variation is quite often considerable. Therefore, the chances of an additional gain, to that obtained by using the best provenances, are good if the right trees are selected for further breeding.

One of the reasons for aiming at individuals instead of populations is that the selection can be more specific. We can make greater progress and have smaller variation in a specific character. However, breeding at the family and the individual level is usually more costly than finding the best provenances and establishing adequate seed sources of them. There are numerous costs: selection of the right trees; propagation of these trees; establishment of clone banks, pollen facilities, field tests, etc. These costs should be justified by the superiority of the plants produced by the breeding programme. This will usually only be possible in major species grown over large areas.

# 2. ELEMENTS AND TECHNIQUES OF TREE IMPROVEMENT

**Breeding plan**. It is important to formulate long-term plans through several generations. The plans should be flexible and robust enough to incorporate changes in forest policy, silvicultural methods, and innovations in genetics and propagation methods (see further in Lecture Note D-10).

**Selection**. Natural selection favours the trees best fitted for a local environment. Artificial selection for tree improvement favours those in possession of desirable characteristics suited for specific planting purposes and end uses. In phenotypic selection (also called mass selection or plus-tree selection), trees are selected according to their appearance; genetic selection can be made when trees have been tested in replicated trials (see further in section 3).

**Progeny and clone tests**. After phenotypic selection, the performance of both sexually and vegetatively propagated offspring must be compared under uniform conditions to test their genetic value. This is done in progeny and clone trials, respectively (see further in section 4).

**Vegetative propagation**. By propagating selected material vegetatively (either by grafting or cutting) the genetic constitution of the parent is maintained in the offspring. This means that selected material may be moved to suitable breeding areas to be included in further improvement programmes, e.g. in clone banks or for pollination with other selected material. It also means that desirable individuals may be propagated in large numbers (see further in Lecture Note D-7).

**Open pollination**. Progress in individual characters can be achieved by pollination of selected individuals. In stands or seed-orchards, seeds from selected trees are supposed to have a higher genetic value for the traits in question. The magnitude of this may be found through testing of their progenies.

**Controlled pollination**. Progress in individual characters as well as combination of characters can be achieved by controlled pollination of selected trees. For controlled pollination special techniques are necessary. These include isolation of female flowers, pollen extraction, pollen storage, and transfer of pollen to the female flower.

# 3. SELECTION

An important matter in a breeding strategy is to formulate the right criteria for selection. The characters we want to improve may vary from species to species, but they may also vary from time to time and depend on different end uses. That makes the whole procedure complicated.

## 3.1 Selection Criteria

**List of criteria**. Most lists of criteria will comprise some of the following:

Volume
Stem straightness
Branching characteristics
Wood density
Drought resistance
Resistance to specific insects
Resistance to specific fungi.

For some species, a particular product is essential such as rubber, resin, fruit or foliage for fodder.

When a number of criteria have been listed and discussed with foresters, silviculturists, wood technologists, sawmillers, pulp manufacturers, and maybe other consumers, the breeder should try to get as good an idea as possible about their relative importance and value, and rank them accordingly.

**Limitation of criteria**. Very often one will have a list of ten or more criteria, which have been mentioned by growers and consumers. Some of these characters may be independent of each other and some may be positively correlated. A positive correlation between characters means that an improvement in one character will also give an improvement in the other character. In such situations improvement through breeding is not so difficult. Other characters may be negatively correlated, which means that a progress in one character will cause a decrease in the other. This is often the case with volume production and quality characters, and this makes breeding much more difficult.

If the characters we want to improve are not positively correlated, an increasing number af characters will result in a decreasing gain in each character. Therefore it is recommended to restrict the number of characters to five or six or less. Another possibility is to split the breeding programme in two or more directions. This may be the best solution, but will most often be more costly.

**Criteria suited for early or late selection**. Selection will not always take place for all characters at the same time. Some characters are clearly expressed in the juvenile period and some are only possible to assess in the mature stage. It is important to start with a large enough number of trees to secure that there are sufficient trees to select from for the characters which must be judged in the mature stage.

A character of drought resistance is very important in the juvenile stage. High mortality may occur during the establishment of the stand. Some diseases are bound to the juvenile stage too. Resistance to fungi and insects may be related to either the juvenile or the mature stage. Characters like stem form, volume, and wood density are best assessed when trees are not too young.

**Criteria suited for phenotypic and/or genotypic selection**. All characters are a sum of their genetic value and the environmental influence. What we measure is called the phenotypic value. If we want to extrapolate our results to other situations, we must know the genotypic value. Characters that are controlled to a high degree by the genes have a genetic value close to the phenotypic value. Geneticists use the expression that the character has a high herit-ability. Such characters can with good result be subjected to phenotypic selection. Other characters, such as volume, are highly influenced by the environment. Their genetic value can only be estimated through progeny or clonal tests.

Phenotypic selection can be used for characters with high heritability. For characters with low heritability, genotypic selection by means of progeny or clonal testing is necessary.

## 3.2 Phenotypic Selection

In forest tree breeding, selection is carried out both as phenotypic selection and as genotypic selection. Phenotypic selection is nearly always used in the first stage of a breeding programme.

Phenotypic selection is also often called mass selection or plus-tree selection. A number of trees are selected in stands according to a total impression of their phenotype, an impression which combines the characters listed in the breeding programme. It is important to choose the right base populations for plus-tree selection. For indigenous species, natural popula-tions will form a good material. One problem with natural stands is, however, that the trees are often of uneven age. This makes it difficult to compare one tree with another. For exotics, the situation is different. Exotic tree species ought to be grown in one generation in the country or to be tested in reliable progeny tests for the same time before tree breeding starts at the individual level. Sometimes breeding starts before provenance tests have been carried through, particularly if there is good information from practical use of the species or information from other countries with similar climate. This will save time, but includes a risk. For exotic tree species it will often be possible to select in even aged plantations, which makes the selection procedure a lot easier.

**Plus tree selection**. Knowing the criteria for which we are going to select, and knowing that the response will be greater for the characters with high heritability, we have to consider how many trees that we should select. This depends on the importance of the species, the intensity of the breeding programme, and the capacity of the organization that will carry out the actual breeding work, and it also depends on the necessity of propagating all the selected trees. No exact number can be given, but many breeding programmes start with about 200 plus trees in the first generation. They should be selected with not more than 10 per hectare.

If propagation material cannot be harvested at the time of selection, it is very important to mark the tree clearly. It is common practice to paint a ring around the tree and a number above the ring. This will last for some years and can then be repainted.

Proper records are necessary, including map of the area, description of ownership, and geographical information.

### 3.3 Genotypic Selection

Genotypic selection is selection according to the genetic value of a family or an individual. To estimate the genetic value of a family or an individual, either progeny trials or clonal trials are needed. The results of these form the basis for calculation of heritability. The heritability multiplied with the phenotypic value is an estimate of the genetic value (see further in Lecture Note D-2).

The genetic value of the clones can be estimated in clonal trials. The genetic value of the progeny can be estimated in progeny trials.

Also the breeding value of the parent trees can be estimated through progeny trials. Genotypic selection can be performed for all characters, but as earlier mentioned it is particularly useful for characters with low heritability.

## 4. TESTING

### 4.1 Progeny and Clone Testing

Progeny testing is done to

(1) estimate the breeding value and general combining ability (GCA) of the parent trees
(2) estimate heritability of certain traits
(3) calculate specific combining ability (SCA)
(4) estimate genetic value of the progenies
(5) create new generation of breeding populations.

Clone testing is done to

(1) estimate the genetic value of the clone
(2) estimate broad sense heritability of certain traits (see further in Lecture Note D-2).

As to the practical aspects of field trials see Lecture Note D-5.

As to the design of trials and the assessment of these see Lecture Note D-6.

**Estimation of breeding value**

The breeding value (or general combining ability) of a parent is its ability to cross with (combine with) other parents in general to produce superior offspring. E.g. a parent with high general combining ability for height is one which produces tall offspring when combined with any other individual.

In order to estimate the breeding value both seed from open and controlled pollination can be used. If seed from open pollination is used, we only know the mother-tree for certain. The pollen donors are some of the trees in the stand and a proportion of distant pollen. The more trees that take part in the pollination, the better is the estimate of the breeding value of the mother-tree. Therefore, seed from open pollination of a clonal seed-orchard may give a better estimate of breeding value than seed from plus-trees in the forest, because the seed of one ortet is harvested on several ramets in the seed orchard where they are exposed to pollen from a larger number of other genotypes.

If controlled crosses are used for selection of parents with a high breeding value or large general combining ability, the number of males per female must not be too small. It is cheaper and easier to get seed from open pollination than from controlled pollination, and it will often - in the beginning of a breeding programme - be more efficient to test a larger number of plus-trees with openly pollinated seed than to test a smaller number with seed after controlled pollination.

**Specific combining ability**

Full-sib progeny trials yield information both about general combining ability and about specific combining ability, which is a tree's ability to transmit superiority to its offspring when crossed with a specific tree rather than with trees in general. (General and specific combining abilities result from additive and non-additive genetic variance, respectively).

Selection of trees with high specific combining ability is not much used in tree breeding and there are several reasons for this. Only seed from controlled pollination can be used for that purpose. Many of the important characters are regulated more by additive genes than by genes that act in specific combinations. It is very expensive to make and test a large number of trees in order to find a few good combinations. Specific combinations can only be mass produced by vegetative propagation.

**Estimation of heritability**

Estimation of genetic parameters, such as additive variance ($V_A$), variance due to dominance ($V_D$), and heritability ($h^2 = V_A/V_P$) needs a fairly large number of progenies to be accurate (see further in Lecture Note D-6).

Openly pollinated progenies are often used for estimation of $V_A$ and $h^2$. In such cases it is assumed that the individuals in a progeny are half-sibs. In fact they are an undefined mixture of half-sibs and full-sibs. The estimates of $V_A$ and $h^2$ will therefore be too high.

**Breeding populations**

A progeny trial can also be useful for creation of base material for selection of the next generation of plus-trees. Again it is important that the number of progenies in the trial is not too small. A breeding population must not be genetically too narrow, and the gain from selection will be too small if the number of families and individuals per family is too small. In this connection it can be wise to establish, together with the progeny trial, a plantation with large plots - say 200 individuals per family. Within-family selection can then be carried out in such plots.

Seedling seed-orchards are used in many breeding programmes. They are progeny trials laid out in specific design in such a way that they later - after thinnings - can be used as seed-orchards.

This is a cheap way to establish seed-orchards, but there will often be conflicts with the purpose of progeny testing: it is suitable to place a progeny trial in an area where the species is usually grown, whereas a seed orchard should be placed at a site far from any other occurrence of the species. An optimal design for a seedling seed-orchard will often not be optimal for a progeny trial.

**Demonstration areas**

Properly designed field trials, located at various sites all over the country, is a necessity for breeding progress. However, such trials are not very informative for customers of breeding, silviculturists, nursery-men, forest owners, and granting authorities.

Therefore, it will be useful to have some test plantations and demonstration areas close to the breeding station.

## 4.2 Establishment of Trials

If nothing is known about breeding zones, large forest areas with differences in climate and soil structure can be divided into more homogeneous zones, in which breeding programmes can be set up.

A delineation of breeding zones may be done by means of climatic and edaphic data. Another and more efficient way is delineation by means of provenance and progeny tests (Wellendorf et al. 1987), see also Lecture Note D-3 on provenance trials. For such a purpose a relatively large number of sites are necessary. Dependent on the size of the country and the difference in soil and topography, 10-20 sites are needed.

A delineation of breeding zones should be done based on one of the first series of field trials in a breeding programme. When the country has been divided into breeding zones, it is possible to focus on problems concerning a single breeding zone.

Within a breeding zone a smaller number of sites are necessary. In most cases three to four sites will be sufficient to catch the variation in the environmental conditions. On each site the experiment should be divided into blocks (replications) and the variation within each block should be minimised. In practice it means that the blocks should be rather small. However, the block size depends on the number of progenies and the plot size. Therefore the final lay-out is a compromise.

When there are many progenies, the plot size must be small in order to keep the block size and the variation within blocks small. Few progenies allow bigger plots.

**Statistical considerations and design**

A very important issue in progeny and clonal testing is the statistical considerations and design.

From a statistical point of view, single-tree plots are the most efficient, but they have certain drawbacks. Single-tree plots are more difficult to establish, more sensitive to thinnings, and it is not possible to calculate within-plot variation. As a rule of thumb, trials with more than fifty progenies should use single-tree plots, from twenty to fifty progenies should use four- to eight-tree plots, and below twenty progenies larger plots. Six to ten blocks per site are common practice.

For more on this issue see Lecture Note D-6.

# 5. RECOMBINATION

Recombination of genes takes place when individuals are mated.

Recombination of selected individuals is the only way to increase the value of a certain character. By successive selection and recombination it is possible to increase the number of additive genes for an estimated character in an individual.

## 5.1 Open Pollination

Open pollination takes place in nature. In tree breeding the selected trees are often arranged in seed-orchards, where recombination takes place by open pollination. It is therefore important that seed-orchards are well isolated. Otherwise mating will also take place with surrounding inferior trees. If open pollination is used for large-scale seed production, the genetic quality of the seed may vary

from year to year because of variation in flowering between the different clones. It may also vary because of different background pollination (pollen from outside the seed-orchard). This means that the gains obtained in such seed-orchards will be difficult to predict.

If open pollination is used to produce the next generation of breeding population, one can get into trouble. Firstly, it will result in less gain than can be expected from controlled pollination. Secondly, it is not possible to keep track of the pedigree and, thirdly, inbreeding may take place. Such problems have to be considered when the choice between open and controlled pollination is to be made.

## 5.2 Controlled Pollination

Controlled pollination is a key activity in more intensive breeding programmes.

It is generally easier to be carried out in wind pollinated than in insect pollinated species.

The main points are to have:

- full control of the pedigree
- appropriate number of combinations.

Full control of the pedigree is essential both to ensure maximum gain and to avoid inbreeding in the following generations.

Controlled pollination for commercial production of seed in large quantities is difficult for most species. Controlled pollination combined with mass pro-pagation by rooted cuttings has been recommended for a number of species in the later years. This method combines high gain and precise knowledge of the genetic constitution of the plants.

The other point, the appropriate number of combinations either as basis for next generation of breeding population or to estimate genetic parameters, concerns mating designs.

A mating design is a plan according to which controlled crossings can be made. A large number of mating designs has been described in literature. Mating design depends on the purpose of the crossings and the cost.

4 types of mating design, as described by Ditlevsen (1985), are presented in figures 1 to 4 and in table 1.

**Complete diallel crossing plan**. This crossing plan is the best one, since it includes all crossing possibilities and provides the most complete information on the genetic characters of the clones studied.

| Parents | 1 2 3 4 5 6 7 8 9 10 |
|---|---|
| 1 | x x x x x x x x x x |
| 2 | x x x x x x x x x x |
| 3 | x x x x x x x x x x |
| 4 | x x x x x x x x x x |
| 5 | x x x x x x x x x x |
| 6 | x x x x x x x x x x |
| 7 | x x x x x x x x x x |
| 8 | x x x x x x x x x x |
| 9 | x x x x x x x x x x x x x x x x x x |
| 10 | x x |

*Fig. 1. Complete diallel crossing plan. Self-pollination is indicated in the figure.*

This design can provide information on the general and specific effect of combination and on its variances. The material also constitutes the best starting point for the selection of superior individuals or pairs of clones suitable for two-clone plantations.

Unfortunately, this design is very difficult to use for practical purposes. In the first place, it usually yields clones that produce too small a quantity of male or female flowers. However, the most important disadvantage is the cost. A complete diallel crossing plan with e.g. 20 clones will require 400 controlled crossings or 380 when self-pollinations are excluded. It is usually not realistic to spend so much on each clone and cheaper designs are more common.

**Partial diallel crossing plan**. This design may be distinguished from the complete diallel plan in so far as a clone has not been crossed with all other clones. The design can have a series of different conformations, and 2 types are shown in figure 2.

| Parents | 1 2 3 4 5 6 7 8 9 10 |
|---|---|
| 1 | x x x x x x x x |
| 2 | x x x x |
| 3 | x x x x x x x |
| 4 | x x x x |
| 5 | |
| 6 | |
| 7 | |
| 8 | |
| 9 | |
| 10 | |

Disconnected partial diallel design

| Parents | 1 2 3 4 5 6 7 8 9 10 |
|---|---|
| 1 | x x x x |
| 2 | x x x x |
| 3 | x x x |
| 4 | x |
| 5 | x x |
| 6 | x x |
| 7 | x x |
| 8 | |
| 9 | |
| 10 | |

Brown's diallel design

*Fig. 2. Partial diallel crossing plans.*

As may be expected, these designs are less efficient than the complete design. However, to make up for this, a large number of offspring can be tested at a fairly low cost. Unfortunately, missing values (which cannot be avoided in large-scale crossing plans) will complicate the work of calculation considerably.

**Factorial crossing plan**. In this design a number of mother clones are crossed with a number of common father clones. Often there is a small number of fathers, also called common testers. This design can also be considered a sort of complete diallel design including all combinations of one group of mothers with another group of fathers, fig. 3.

| Parents | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| 5 | x | x | x | x |
| 6 | x | x | x | x |
| 7 | x | x | x | x |
| 8 | x | x | x | x |
| 9 | x | x | x | x |
| 10 | x | x | x | x |

*Fig. 3. Factorial crossing plan.*

This design is widely used in the United States under the name of North Carolina II. Usually four different fathers are used for the crossing plan, but as a general rule the number of fathers must depend on the magnitude of the specific combining effects. If major specific combining effects are likely, the estimation of the general combining ability of the mothers may turn out to be highly erroneous when too few fathers are used.

Since the design often includes very few fathers and since the same clone does not appear as mother and father, it is difficult to compare the general combining abilities of each parent.

It is also difficult to make a progeny selection for the next generation of seed orchards, since selected individuals (especially when very few fathers are used) very often already are related to each other.

One advantage of this design is that its implementation is simple and therefore relatively cheap. At the same time it makes analysis of the results easier.

**Single pair pairings**. In this system, each clone is involved only once as mother or father.

The system works particularly well if the objective is to produce a population for selection of individuals for new seed orchards or for use in continuous breeding work.

As it is normally very expensive to produce offspring on the basis of controlled crossing, it is another advantage of the single pair pairing that a large number of clones may be tested under the same plan.

On the other hand, the possibilities of estimating the general combining ability and the variance of the general and specific combining abilities are normally not very good. If the specific combining effects are not very important, a quick estimate of general combining ability may, however, be made in order to set aside the worst of the clones tested. If, on the other hand, the specific combining effects are very important, this design may be used to select the best combinations of clones for use in two-clone plantations.

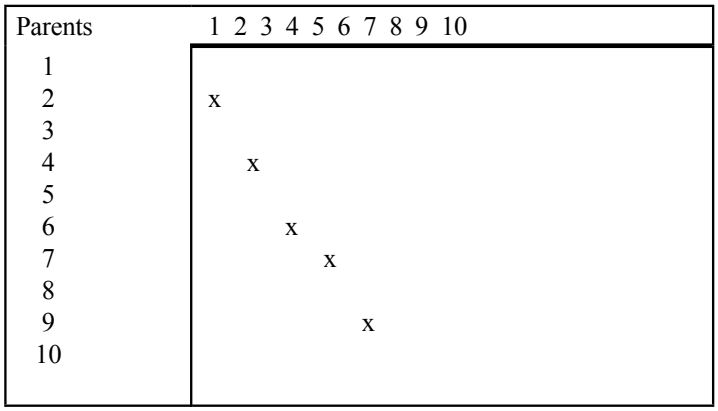


*Fig. 4. Single pair pairings.*

Table 1. Comparison of crossing plans.

| Crossing system | Determination of GCA | Selection of plus trees | Costs | Determination of variance of GCA and SCA |
|---|---|---|---|---|
| Complete diallel | Excellent | Excellent | Very high (unrealistic for large numbers of clones) | Excellent |
| Partial diallel | Good | Very good | Fair | Good for GCA. The variance of SCA can be determined, but it is difficult from the point of view of data processing |
| Factorial | Good | Only in a few cases and where intra-crossing depression is low | Fair | Good |
| Single pair pairings | Bad | Good | Very low | Bad |

GCA = General Combining Ability; SCA = Specific Combining Ability

# 6. MASS PRODUCTION OF IMPROVED MATERIAL

One thing is to breed forest trees and to document genetic gain over one or more generation. Another thing, and just as important, is to produce the bred material on a large enough scale for practical use in the forest. These actions can be two independent activities, but in forest tree breeding they are often combined.

Mass production by vegetative propagation is described in Lecture Note D-7, and Lecture Note D-8 deals with mass production in seed orchards.

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