

## BREEDING POPULATIONS FOR RECURRENT SELECTION: CONFLICTS AND POSSIBLE SOLUTIONS\*

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### ABSTRACT

Requirements for advanced generation breeding populations in forest trees are considered in terms of initial selection of parent genotypes, mating designs, and the nature of progeny plantings.

Large numbers of parent genotypes, 200 or more, are considered desirable, to minimise inbreeding, and to avoid loss of uncommon genes which might eventually prove valuable.

Mating designs should combine immediate efficiency of genetic gain with maintenance of effective population size. Several mating designs, commonly used to test parent genotypes or to estimate genetic parameters, are unsuitable for producing advanced generation breeding populations.

The most promising designs appear to be single-pair matings, and some modifications of the polycross. These are considered in detail, but further study is needed of the effects of non-additive genetic variance on their expected efficiencies. Final choice of mating design, however, may depend on availability of certain information from existing progeny trials, and on the possible need to fulfil other objectives, such as testing parental genotypes.

Progeny plantings could, in some circumstances, be designed entirely for efficient evaluation of individuals in relation to their family means. Clonal replication of seedlings should be explored as a procedure in selecting for traits with "all-or-none" expression.

### INTRODUCTION

Most existing tree breeding programmes were initiated long before any close analysis had been made of the problem of developing advanced generation breeding populations. However, the numbers of trees that are initially selected and involved in progeny tests strongly influence certain contributions to the overall selection differentials, and thus the genetic gains. They also control the effective size of the breeding population in the next generation of a recurrent selection programme, and the future degree of inbreeding. In fact the number of select parents, as well as the way in which these have been mated, may be such that the breeder has little option but to go back to the base population, greatly increase numbers of selections, and make a completely new series

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of matings to provide a proper base for recurrent selection. A case history from our own programme will illustrate this.

#### NEW ZEALAND CASE HISTORY

In New Zealand there has been a gradual realisation of the implications of the requirements for effective roqueing of clonal seed orchards and for developing satisfactory populations for recurrent selection. When the *Pinus radiata* D. Don breeding programme was initiated in 1950, preliminary phenotypic selection of plus trees was highly intensive, averaging about one selected per 400 ha (1,000 acres) of plantation searched. The number of plus trees was further reduced by a second phenotypic screening to 14, and these clones were used in two small initial clonal seed orchards which were planted in 1958. In later extensions of these orchards this number was increased to 25 and then to 36, partly by retaining more trees from the preliminary field selection, and partly by additional field selection. It was subsequently appreciated that the extremely large numbers of trees screened in relation to those saved were giving selection differentials (the absolute differences between the means of populations under selection and means of select populations) that were little higher than could be achieved by screening far fewer trees. At the same time the small numbers of parents that were being selected would allow only very small selection differentials in a reselection of clones on the basis of progeny tests. Within existing orchards, any roqueing of worthwhile intensity would leave very few clones indeed; so these initial 14- to 36-clone orchards will be left as established.

It was therefore decided to make a further phenotypic selection in the field, greatly increasing the number of selections to about 800, and accepting a major reduction in degree of culling to about one tree per 1,000 (about one per 1.2 ha (3 acres)). Provision could thus be made for more intensive reselection of the clones for immediate seed production on the basis of progeny test performance, i.e., from 800 down to about 30. In the long-term breeding population, however, it is anticipated that as many as 200 of these genotypes may be represented as parents.

The large number of selections in turn raised practical problems of evaluating progenies effectively, quickly, and economically. It is convenient with the serotinous cones of *P. radiata* to collect open-pollinated seed from the original parents, and this is now used to establish progeny tests as soon as possible after selection. Since it is unlikely that there is much local differentiation among the base population that was screened, we are assuming that satisfactory rankings of genotypes for general combining ability, or GCA (at least with respect to the base population), will be obtained from the tests. An additional 80ha (200 acres) of seed orchard are now needed in order to meet seed requirements, and these new orchards will be established with the intention of doing a 2/3 to 3/4 roqueing by clones on the basis of results from the open-pollinated tests. In addition, 8 to 10 years hence the first of the clonal orchards will come due for re-establishment as it will be getting too tall for economic seed collection. These orchards will then be progressively replanted with ramets of top-ranked clones as determined by the open-pollinated tests. Quite intensive reselection will be possible if the 800 clones are to be reduced to as few as 20 to 40.

These orchards of the best progeny-tested genotypes should in fact take care of improved seed production to the year 2000 and beyond. Having achieved an acceptable strategy which will take us to this point, the requirements for the second generation selection and the derived orchards came under consideration.

None of the existing progeny tests is really suitable as a new population for selection. Wind-pollinated progenies\* collected from within the first two series of orchards with 14-25 clones will only allow limited selection on the basis of progeny (family) means, if an adequate effective population size is to be maintained, and the best individuals within progenies may well be sired by a restricted number of pollen parents. Selecting within bulked seed collections from these orchards is quite unsuitable because it could result in an even smaller number of effective parents. The few control-pollinated progenies that are available are from a very restricted number of parent trees. The extensive wind-pollinated progeny tests from the recent selections have the major disadvantage of being sired by completely unselected parents. Once the new orchards of much larger numbers of clones become productive it would be possible to collect seed by clones and plant these offspring for future selection. The main disadvantage in this approach stems from the variation in the time that different clones take to start producing abundant pollen, since seed collection must be delayed if there is to be any chance of obtaining a reasonably balanced representation of pollen parents. It thus appears that some form of control-pollinated mating programme will be necessary to produce second-generation material.

#### GENERALISED REQUIREMENTS FOR A BREEDING POPULATION FOR RECURRENT† SELECTION

For a given base population the parameters which directly influence long-term genetic gain are:

1. Efficiency of estimating the genotypic values of trees in the second and subsequent generations, thence in identifying the superior individuals.
2. Selection differential between the base population and phenotypic selections of first generation.
3. Selection differentials in the second generation and subsequent generations.
4. Effective population size and amount of inbreeding.
5. Error effects.

The three operational determinants of a breeding population, namely number of

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\* These are not to be confused with the wind-pollinated progenies discussed elsewhere; in this particular case both seed and pollen parents are select.

† For detailed discussion on tree breeding methods, of strategies, and terms used, see Shelbourne (1969).

parental genotypes, the mating design, and the progeny planting will be considered later, largely in the light of their influence on the above parameters.

### *Identification of Desired Genotypes*

The estimates of the genotypic value of an individual can be improved by using information concerning its relatives as well as itself. Most commonly the relatives include its progeny (half-sibs and full-sibs) and its own sibs (half and full), but they can also include the parent ortets\*, ramets from the parents, and of course ramets from the individual itself. The information can be combined by means of a selection index (not to be confused with the multiple-trait index) which will depend on the heritability, the degree of relatedness with the individual, and the number of relatives within each class. The wider the range of relatives for which information is available the better the estimate of the genotypic value of the individual (Osborne, 1957; Namkoong, 1966). We, however, must be concerned with whether the features of mating designs and progeny plantings which provide additional information are worth the cost in terms of the effort involved or its effect on selection differential and effective population size. This must be considered in relation to the biological constraints involved in tree breeding (cf. Libby, 1969). Two circumstances which contrast with the situation in animal breeding, for instance, are the monoecy of parents (i.e., the ability to produce both pollen and seed) and the feasibility of obtaining half-sib progenies from a single cross.

All further discussion is based on the assumption that selection is to be made on the basis of combined information for both the individuals in question and their relatives.

### *Selection Differentials*

Genetic gain from selection is normally directly proportional to the selection differential for that stage of selection, which in turn is controlled by the proportion of the selection units, be they trees or families, that is saved. It follows, then, that for a given investment in the programme, selection differentials must be maximised in order to maximise genetic gain. However, in an advanced generation breeding population there are various conflicts in requirements. Selection differentials will normally be increased at the expense of effective population size, at least for a finite resources model. When a selection index is being used to combine information concerning both the individual and its relatives, the concept of the selection differential becomes less simple; we can no longer talk of between-family and within-family selection differentials. Nevertheless, we can say that when the number of families is increased, family differences will make a greater contribution to the overall selection differential. However, under a finite resources model the increase in number of families would decrease the contribution made by the differences between individuals within families to this differential. The net effect on selection differential of the allocation of a finite number of individuals between and within families is notably small over a wide range of alternative family sizes and thus the numbers of families possible.

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\* Ortet = original plant from which the ramets of a clone are derived.

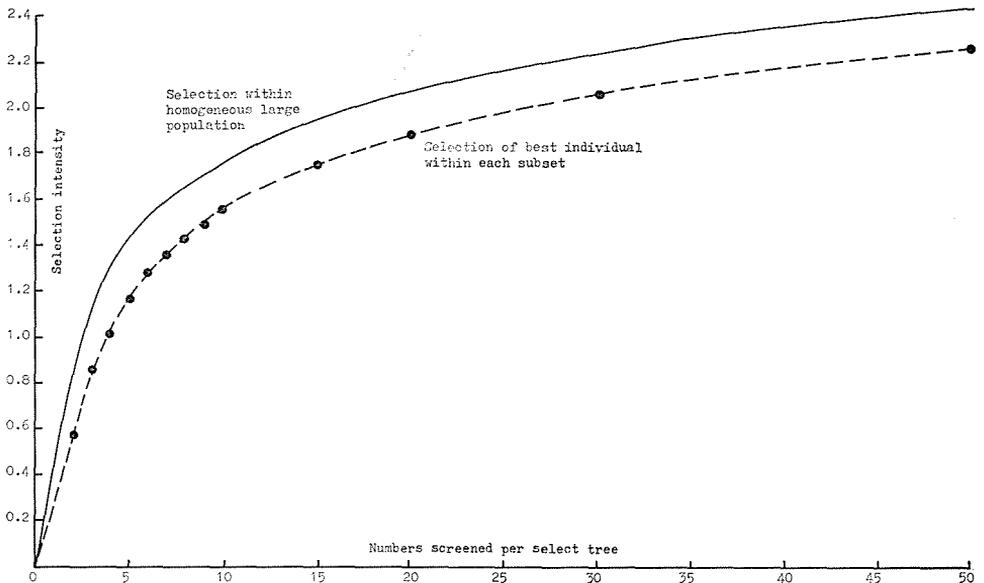


FIG. 1.—Relationship between selection intensity (standardised selection differential) and number of trees screened per select tree.

From Fig. 1 it can be seen that the selection differential increases curvilinearly with the number of individuals screened for each one selected. Thus the increase in selection differential drops off rapidly in relation to additional effort with increasing number of trees screened for each one selected. The lower curve (dashed line) shows that when the best individuals are selected within finite groups or subsets the selection differentials are lower than when the same proportion of individuals is saved from a homogenous infinite population. The relative drop in selection differential becomes greater as the groups become smaller.

The general nature of the relationship would argue, when it is desired to maintain effective population size and when it is impossible to rank the parents effectively prior to crossing, for a spreading of contributions to the overall selection differential between progenies and within progenies, and between seed parents and pollen parents among progenies. In practice, however, this will often be achieved only with an excessive effort in relation to the number of parent genotypes involved.

These few considerations illustrate the point that selection differentials at different levels are subject to numerous countervailing effects, so that comparisons between certain breeding strategies can only be made on the basis of detailed calculations of gain expectations for varying proportions of the population selected and for traits with varying heritabilities.

#### *Effective Population Size*

Our contention is that the effective size of the breeding population should be large. Provided large numbers of first generation selections are mated to produce large numbers of families and of individuals within families, selection differentials can be kept

high, and yet the frequency of related matings kept low and inbreeding minimised. We do not insist on strict preclusion of mating among related individuals but rather that the probability of related matings be kept low, if not negligible, over successive generations; many mating designs which with finite populations ensure complete outcrossing in early generations may accentuate inbreeding later on.

A large effective population size should also insure the breeder against having to meet new criteria for selection when the programme is already under way, such as having to breed for resistance to a freshly introduced pathogen. This reasoning is intuitively attractive and in general terms has been advanced in the past, e.g., by Zobel and McElwee (1964), with the concept of the tree bank.

However, some recent theoretical work by Libby (1969b) indicates that, starting from only a few parent genotypes, it is possible by correspondingly increasing family sizes, to achieve overall selection differentials which give large if not almost maximal expectation of genetic gain. But there is a catch in the classical genetic models\*: they have been formulated on the simplifying assumption that there are only two possible alleles, or alternative genes, per locus, each present at virtually equal frequencies within the population. We must insure against the possibility of losing valuable genes which are present in the base populations at low frequencies. To be sure of recovering such genes when and if required, it would be necessary to maintain a large breeding population.

Total preclusion of mating among relatives may involve costly and inconvenient constraints on the mating design, and yet there is no certainty that the theoretical occurrence of inbreeding will eventuate. There is reason to believe that when pollination is made by a mixture of related and unrelated pollen, preferential outcrossing will occur even when self-fertility is quite high (Barnes *et al.*, 1962; Sarvas, 1962).

#### *Error Effects*

These include items of variance which are confounded with the genetic variance that can be utilised in the breeding programme. Their presence will naturally reduce genetic gain. The classic case is special environmental variance among individual seedlings within families, but specific combining ability (SCA) if present will be an error item both among full-sib families and among individuals within families.

### NUMBERS OF PARENTS SELECTED

The desirability of initially selecting a large number of clones has already been discussed, but even so the precise number is still very arbitrary. However, we would think in terms of 200 or more, and certainly not the 20-30 which have formed the base of some programmes.

### MATING DESIGNS

#### *Objectives*

Most mating designs in forest tree breeding are used for one or more of several possible objectives:

1. *Screening or ranking* of genotypes and families, genotypes for GCA, families for

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\* This has occurred to Dr W. J. Libby (pers. comm.) independently.

mean GCA and in certain situations for the SCA of their parents when crossed together.

2. *Estimation of components of variation*, which include additive genetic variance (which determines GCA), non-additive genetic variance (which determines SCA), environmental variance and genotype-environment interactions, as well as phenotypic and genotypic correlations between traits. From these statistics can be calculated heritabilities, optimum weighting of different characters, and expectations of genetic gain.
3. *Producing the population for the second generation of selection* from the offspring of initially selected parents.
4. *Direct estimation of realised genetic gains*, for purposes of evaluating the progress to date.

Thus, when we are considering the merits of a mating design for producing the base for an advanced generation of selection we should take some account of the need for fulfilling other objectives. We will consider several current mating designs, and then two designs or groups of designs which do not appear to be in common use.

Before going any further, however, we must state that our immediate concern will be entirely with utilising GCA. Screening for SCA, except perhaps at the level of interpopulation crosses, is laborious, and can only be done satisfactorily in experiments designed essentially for that purpose. Even if high SCA is recognised for several combinations of clones its advantages have to be weighed against the costs of a method of propagation which will recover this form of genetic gain. For present purposes, therefore, SCA is of concern mainly as a potential source of bias in screening for GCA.

#### *Currently Used Mating Designs*

WIND-POLLINATED PROGENIES, if they approximate closely to half-sib families, provide a quick and economical method of estimating GCAs of individual genotypes and GCA variance among the sample of parents from which the seed was collected. The estimates of GCAs of the selected clones will, of course, only apply with respect to the base population and not necessarily with respect to a selected population of clones. The GCAs (and to a lesser extent GCA variance) with respect to the select population could, in certain situations, be substantially different, but in the balance we consider this possibility unlikely. It is also possible, under certain circumstances, to predict genetic gains from a clonal seed orchard from tests of such progenies. The progenies, however, are not attractive as a base for second-generation selection because the pollen parents are normally unselected, and the half-sib relationship is not as efficient as higher levels (e.g., full-sib).

POLYCROSS mating designs normally utilise a standard pollen mix from a number of parents, which is mated to all parents under test. This can be expected to provide good estimates of GCAs and GCA variance, particularly if the pollen is from the genotypes under test, with only one cross per clone being needed. These designs can also provide good estimates of the genetic gains which will be achieved with a particular seed orchard. However, a simple polycross with a limited number of parents cannot be recommended as a base for second generation selection; most of the trees

selected within each progeny are likely to come from the same few pollen parents, which would seriously reduce the effective population size. Again, the half-sib level of relationship is less efficient than higher levels of relationship in index selection.

NORTH CAROLINA (NC) DESIGN II is an example of a *Factorial Design*\*. It usually involves about four genotypes used as males (or females) each mated to all of the remaining genotypes. GCA of each female is estimated from the half-sib family average of four full-sib families (with the four testers). In relation to the parent genotypes under test the design allows estimates of GCA and SCA variances. As in all factorial designs each parent genotype is involved in full-sib matings with several others. The successful completion of all the specified crosses is difficult and time-consuming, and yet missing crosses involve the loss of considerable information. For purposes of selecting among offspring, efficiencies due to the availability of both full-sib and half-sib information are normally vitiated by one or more of three effects: (1) reduction in the number of genotypes that can be used as parents in the mating design, (2) reduction in the number of individuals per family, or (3) increase in the size and cost of the experiment.

In connection with (1) the effective population size under the NC II design is much reduced by the fact that four parents contribute at least half the germ plasm of the progenies, and it will be further reduced if any discrimination is to be made against the progenies of the poorer testers. Unless phenotypic selection is highly reliable or there is prior confirmation of the GCAs of the testers there is always the risk that through random sampling error the testers could have been appreciably poorer than the average for the phenotypically selected clones. Even where several NC II designs are pooled they still involve all the operational inefficiencies which are inherent in the unequal contributions made by the parents, unless the tester parents have been proven to be outstanding.

The NC DESIGN I is an example of an *Hierarchical Design*, involving the mating of different groups of females (common sex) to each male (rare sex), or vice versa. It is normally used for the estimation of GCA and SCA variance components, but is not satisfactory for estimating GCA for individual genotypes, and selection on the basis of sib-family performance will be biased by SCA effects, unlike the polycross. As with the NC II the preponderance of germ plasm contributed by the limited number of trees of the rare sex reduces effective population size, particularly if discrimination is to be made against the poorer rare-sex parents. The use of parents which are known to be the best clones as the rare sex will give the best overall selection differential, and thence a high gain expectation. However, it is only for these rare-sex parents that the design affords estimates of GCA which are not fully confounded with SCA, and with these parents already proven such estimates of GCA would be superfluous. In the context of forest tree breeding it is not always possible to rank the select trees on phenotypic performance, for example, when the best trees are selected

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\* A factorial design involves the mating of each of **a** parents to each of **b** parents to give (**a** × **b**) crosses. A select population can be subdivided into a number of such cells.

from very different sites. Even if ranking is possible, biological constraints, such as the "best" trees producing only enough pollen to be used as common sex parents, are likely to reduce actual gains.

The DIALLEL CROSS is the most elaborate full-sib mating design. In its complete form  $n$  parents are crossed in all possible combinations, which include selfings and reciprocal crosses, to give  $n^2$  crosses. When the selfings and reciprocals are omitted the design is known as the half-diallel. It provides the most comprehensive genetic information for the material employed, since it furnishes both half-sib and full-sib information concerning progenies of all the parent clones. It is possible to select on the basis of GCA information for both seed- and pollen-parents, but unless the mating design involves a very large number of crosses the number of parents that can be used will not allow a large effective population size.

The large number of crosses and thus the work load involved in relation to the information available on GCA is such that the diallel cannot be recommended as a means of establishing an advanced breeding population in which further gains are sought on the basis of recovering GCA. The work load increases roughly according to the square of the number of parents used, which rules this design out when we want to ensure a large effective population size.

Partial and disconnected diallels permit the employment of larger numbers of parent clones, but in common with factorial mating designs, they are inherently inefficient by depending on several full-sib crosses in order to obtain half-sib information (which may be very imprecise) for each parent.

In practice the diallel cross and its modifications are mainly useful in providing efficient estimates of SCA variance and in screening for SCA among crosses. Improved estimates of GCA variance can be obtained by using partial diallels and disconnected diallels, which allow larger numbers of parents to be used, but this will be at the price of inferior GCA estimates for individual clones. Missing crosses (families), however, have a serious effect on the recovery of information.

#### *Disconnected Single-Pair Mating Design and Modifications of the Polycross*

We will now consider some mating designs which do not appear to have been in regular use, but which we feel have the greatest promise for the current purpose. Firstly, there is the SINGLE-PAIR mating design, proposed by Libby (1968, 1969b), which involves the mating of disconnected pairs of genotypes, so that each genotype is only mated to one other in the entire series. Then there are three alternative forms of the NESTED POLY-CROSS, and finally the TESTER POLY-CROSS.

The advantages and disadvantages of the single-pair mating design compared with the simple polycross will be reviewed, with some reference to other mating designs. The problem of comparative expectations of genetic gain for these two designs when non-additive gene effects are present will then be discussed. Lastly we will consider how the modifications of the polycross may mitigate certain disadvantages of the simple polycross.

Table 1 lists the main advantages and disadvantages of single-pair mating when compared with the polycross.

Under an additive genetic model at least, the expected efficiency of single-pair mating in identifying the best genotypes is maximum for most, and near maximal for all heritabilities and population structures, compared with other mating designs. This is in spite of the risk of wasting outstanding parents through chance mating with inferior ones. Unlike single-pair mating, the polycross is subject to the constraint of each parent receiving pollen in which the mean breeding value is that of the select population in general, and the family information which the polycross affords is inferior. The operational simplicity of single-pair mating is very attractive, although the polycross still compares well in this respect with some other designs. Another attractive feature of single-pair mating is the efficiency with which it maintains effective population size. However, our proposals for modifications of the polycross should partially offset its disadvantage in this respect. The inability of single-pair mating to provide estimates of GCA is an important disadvantage, the implications of which will be considered later.

TABLE 1—Advantages and disadvantages of the single-pair mating design compared with the polycross

Single-Pair Mating	Polycross
Advantages	Disadvantages
1. High expectation of genetic gain, under additive genetic model	Somewhat lower expectation of genetic gain
2. Maintains effective population size with maximum efficiency	Risk of appreciable loss of effective population size
3. Only one cross per two parents	One cross per parent
4. Direction of crosses immaterial—only seed or only pollen needed from any one parent	Seed and pollen needed from each parent
5. Pedigreed breeding method—both parents identified	Pollen parent not identified
Disadvantages	Advantages
1. No estimates of GCA available for individual parents	Estimates of GCA available for all parents
2. Bias in selection on basis of family means due to non-additive gene effects	Very little corresponding bias due to non-additive gene effects
3. Risk of wasting outstanding parents through chance mating with inferior ones	Assured utilisation of outstanding parents

The net effects of SCA or non-additive gene effects on the comparative expectations of genetic gain have not been explored, but we will review the expected genetic

parameters for single-pair mating and polycross families respectively (c.f. Kempthorne, 1959, p. 423), in order to illustrate the nature of the problem.

Firstly, consider the expected variance *between* family means. For single-pair mating the expectation (assuming random mating) is:

$$\frac{1}{2} \sigma_A^2 + K_{s-p} \sigma_{NA}^2 + m \sigma_{W(s-p)}^2$$

where  $\sigma_A^2$  = additive genetic variance

$\sigma_{NA}^2$  = non-additive genetic variance

$K_{s-p}$  = at most  $\frac{1}{4}$ , and can be appreciably less (s-p = single-pair)

$\sigma_{W(s-p)}^2$  = variance within full-sib families = error

m = reciprocal of the number of individuals per family or a somewhat greater value, depending on the field design

Alternatively this expectation can be written,

$$2 \sigma_{GCA}^2 + \sigma_{SCA}^2 + m \text{ Error}$$

For polycross families (assuming a half-sib model) the corresponding expectation of variance *between* family means is:

$$\frac{1}{4} \sigma_A^2 + K_p \sigma_{NA}^2 + m \sigma_{W(p)}^2$$

where  $K_p$  = at most 1/16, and can be considerably less

(p = polycross)

$\sigma_{W(p)}^2$  = variance within half-sib families = error

Alternatively this expectation can be written,

$$\sigma_{GCA}^{*2} + m \text{ Error}$$

For any design, when the crosses are made between select parents, the  $\sigma_A^2$  component of between-family variance will be reduced to  $\sigma_{A'}^2$ , according to the relationship,

$$\sigma_{A'}^2 = \sigma_A^2 (1 - \beta v')$$

where  $\beta = (\sigma_A^2) / \sigma_P^2 =$  (narrow-sense) heritability

$\sigma_P^2 =$  phenotypic variance

and  $v'$  is a parameter depending on the proportion of the population saved (Finney, 1956). For example, for heritability = 0.6, proportion saved = 1 : 1,000,  $\sigma_{A'}^2 = 44\%$  of  $\sigma_A^2$

It can be seen that the differences between families contain twice as much additive genetic variance with the single-pair mating design as with the polycross. The larger fraction of the total additive genetic variance makes for a more efficient contribution of family information towards estimating the genotypic value of an individual. However, the estimates of mean parental GCA are biased by SCA in the single-pair mating design, unlike the polycross. The family information, therefore will be contaminated by a much smaller fraction of the non-additive genetic variation with the latter design. This bias will be intensified when select parents are used, because the reduction of  $\sigma_A^2$  to  $\sigma_{A'}^2$  will cause a relative increase in the non-additive components. The difference between  $\sigma_A^2$  and  $\sigma_{A'}^2$  is minimal when heritability is low,

\* It must be noted that GCA is not entirely equivalent to additive gene effects, since it is contaminated with small proportions of certain non-additive variance components. In theory at least, prediction of response to selection by means of GCA estimates is therefore subject to slight bias.

but under such conditions an appreciable proportion of the genetic variance may be non-additive. This sort of situation is a real possibility when we are considering a highly composite trait such as overall desirability. When heritability is high non-additive genetic variance would be small in relation to the additive component, but it would show a greater relative increase on account of the greater difference between  $\sigma^2_A$  and  $\sigma^2_{A'}$ .

We will now consider variance *within* progenies. For single-pair mating the expectation is:

$$\frac{1}{2} \sigma^2_A + K \sigma^2_{NA} + n \sigma^2_E (= \sigma^2_{W(s-p)})$$

where  $K =$  at least  $\frac{3}{4}$ , but less than 1.  
 $\sigma^2_E =$  environmental variance  
 $n =$  reciprocal of the number of ramets per seedling clone (where cloning of seedlings within families is carried out), or a somewhat greater value, depending on the experimental design

For polycrossing the corresponding expectation of variance *within* families is:

$$\frac{3}{4} \sigma^2_A + K \sigma^2_{NA} + n \sigma^2_E (= \sigma^2_{W(p)})$$

where  $K =$  at least  $15/16$ , but less than 1.

In the case of polycrossing with select parents  $\frac{3}{4} \sigma^2_A$  should be rewritten,

$$\frac{1}{2} \sigma^2_A + \frac{1}{4} \sigma^2_{A'}$$

where the first term represents recombinational variance, which is assumed to remain unchanged by selection, and the second term represents variance deriving from the different pollen parents.

Within families the position concerning expectations of variance is largely reversed compared with that between families. There is more additive genetic variance within polycross families than within single-pair families,  $\frac{3}{4} \sigma^2_A$ , compared with  $\frac{1}{2} \sigma^2_A$ . Against this, the estimates of genotypic values of individuals are biased by more non-additive genetic variance within polycross families than within single-pair families, roughly  $\sigma^2_{NA}$  compared with  $\frac{3}{4} \sigma^2_{NA}$ . Nevertheless, within polycross families the non-additive genetic variance is less in relation to the additive genetic variance present than within single-pair families, except when the additive genetic variance between parents has been much reduced by initial selection.

To conclude the consideration of non-additive gene effects, it is far from clear, without extensive theoretical work, what the net results of such effects are on the comparative expectations of gain from polycross and single-pair designs. Greatest efficiency in achieving genetic gain will only be obtained with an appropriate between- and within-family selection index, but we must seek a strategy for which the expected efficiency is robust not only with respect to deviations from the assumed heritability, but also with respect to deviations from a purely additive genetic model.

Let us now consider possible modifications of the polycross. In the NESTED POLY-CROSS, the select parents are grouped into a series of nests, perhaps 20-30 clones each. The nesting should help maintain large effective population size because it should reduce the possible preponderance of the contribution of occasional really outstanding pollen parents to the selected offspring. In any case the selections from different nests should be completely unrelated. Subsequent crosses between nests should

therefore involve no inbreeding at all. If the nests are of reasonable size the sampling error variance between nests should be small and the assumption that nests are all of equivalent average genotypic value should be reasonably reliable. Conversely, very small nests will be subject to appreciable genetic sampling error, so that selection within them on the basis of family means will tend to be inefficient. The nest is a highly convenient operational subdivision of the programme, and a series of nests could be crossed and planted out one after another over a period of years. Minor imperfections in the mating design should be acceptable; it would not be important, for instance, if pollen was unavailable or only in short supply from one or two parents in a nest.

There are three types of polycross nest to consider; the complete nest, the incomplete nest, and the overlapping nest. Within the COMPLETE POLY-CROSS NEST all parents are used both as seed parents and in the pollen mix. This allows estimation of GCA for all parents. Theoretically, some self-fertilisation could occur, but in practice this may be negligible. Of the selfings that do occur, very few if any would be included in the selected offspring. This probable condition of ineffective self-fertilisation will tend to maintain effective population size and reduce inbreeding. In the OVER-LAPPING POLY-CROSS NEST design the parents from one nest are pollinated by the mix from another nest, while the parents from the latter nest would be pollinated by the mix from a third nest, and so on. Self-fertilisation is completely precluded, but this would appear to be of no real advantage, reducing the assurance of outcrossing at a later date.

INCOMPLETE POLY-CROSS NESTS involve the use of part, say half, or the genotypes within each nest as seed parents, and the remainder for the pollen mix. This will reduce the number of crosses required. Against this, estimates of GCA will not be obtained for the pollen parents, and it will be impossible to select their offspring deliberately.

Similar in concept to the incomplete polycross nest is the TESTER POLY-CROSS, which may or may not be subdivided into nests, according to operational convenience. Here the pollen mix is derived from parents all of proven GCA, and it is mated with newly selected or "candidate" trees. These new selections will all be screened for GCA with respect to the main breeding population and at the same time they will have been mated to the best available parents. The proven GCA of all pollen parents should ensure that they are represented in a satisfactory balance among the selected offspring. The use of parents from a well-established clonal archive should avoid all problems with availability of pollen. After the second generation is reached the tester polycross can be made at any time, so that later generations need no longer be discrete.

On the basis of these considerations it is clear that a serious investigation should be made of expected genetic gains and effective population sizes under these types of polycross.

#### PROGENY PLANTINGS

In planting out a breeding population from a completed mating programme in a field design, and therefore a given number of families, we are faced with several objectives. These may be listed as:

1. Estimating mean value of each family, which automatically furnishes genetic information concerning parents.
2. Providing satisfactory within-family contributions to selection differentials.
3. Providing genetic information concerning the individual trees with respect to their family means.

As stated earlier the between-family and within-family information can be combined by means of an index in order to make the actual selection.

The first two of the three objectives are both achieved by planting a large number of individual genotypes from each progeny. However, an increase in selection differential will be vitiated if environmental variance is increased at the same time, because the phenotypic value of the individual will become a less reliable guide to its genotypic value. It is axiomatic, therefore, that within the framework of a satisfactory experimental design, tree-to-tree environmental variation be minimised by good establishment techniques.

Maximum genetic information for individuals within progenies can be achieved by clonal replication of seedlings (cf. Libby, 1964, 1969a, 1969b), and the relative gain in efficiency will be greatest when heritabilities are low. However, for a given size of experiment this can only be done by reducing both the within-family contribution to the overall selection differential, and to a lesser extent, the precision of estimating family means. Libby (1969b) found that these latter factors offset the greater precision in identifying good genotypes, and clonal replication could not be justified in comparison with selecting less efficiently among more genotypes. However, the models did not incorporate the case of significant genotype-site interactions, a factor which would favour the use of seedling clones.

The previous theoretical work has been based on the assumption that the conceptual character under selection is a continuously varying metric trait. This is often not so. Malformation, which is a major problem in our tree crops, commonly shows an "all-or-nothing" expression; presumably it is partly governed by a threshold effect and partly by factors of chance. Replication of seedling clones may be essential to reasonably effective selection of individual genotypes for freedom from malformation. Much, of course, depends on the feasibility of cheap and rapid replication of seedling ortets, but this possibility does warrant further study.

It is evident that where seedlings can be replicated clonally there may be conflicts between obtaining progeny information on one hand, and individual genotype information on the other. In extreme cases there may be situations in which the two objectives can best be achieved with separate field plantings from the same mating design. Sometimes, however, such as when wind-pollinated progenies approximate to half-sib families we can already obtain a separate progeny test which will provide genetic information concerning parents and any resulting progenies. The overriding concern will then be to obtain information concerning individuals within progenies. To obtain more precise information at this level each family could be a self-contained trial, without further regard to comparisons among families. Although self-contained, these single-family trials could each embrace several sites.

## TOWARDS A STRATEGY

Although the expectations of genetic gain require much further investigation, the final choice of a mating design and a progeny test design for producing an advanced generation breeding population may hinge on the suitability and availability of wind-pollinated progenies for estimating parental GCAs. We are basing our case on the proposition that in any event, estimates should be obtained of GCA for all phenotypically selected parents. Let us consider the reasons for this assumption.

If it is desired to reselect among the initial selection of clones in order to rogue or re-establish first-generation clonal seed orchards, then the need for estimates of GCA for clones is self-evident, and the sooner they are obtained the better. This consideration aside, a knowledge of GCAs provides insurance in case a change in criteria for selection is required. If in this event we have to utilise genes which are present at low frequencies within the base population, we cannot be assured of a normal distribution of breeding values among the initially selected parents for the newly desired traits. This, in turn, would mean that existing mating combinations could be much less efficient than conventional models suggest they are in utilising those genotypes which are valuable under the new circumstances. A selective remating of parent genotypes in new combinations would then be highly desirable. At the same time it would be desirable to introduce freshly selected clones from the base population in order to maintain the effective size of the breeding population, and it would be necessary to be able to identify and use the best genotypes within the initial selection to mate with the newcomers. The availability of GCA estimates for all the original select genotypes will enable the best to be identified. Those genotypes of highest GCA could be used in a pollen mix to mate with the new selections; this is an example of a tester polycross and it should be highly efficient. Furthermore, this provision for efficient incorporation of new selections into the breeding population should be made regardless of any major changes in selection criteria.

If wind-pollinated progenies do give good estimates of parent GCAs *and are already established in a trial*, then the single-pair mating design would probably be preferred on grounds of its operational convenience and the efficiency with which it can maintain effective population size. The bias caused by SCA in the between-families component of selection can be eliminated by the external availability of GCA estimates. As indicated earlier, the field design in which the pair-crosses are planted need only be concerned with selection within families. If reliable progeny test information can be obtained within a few years, it would be possible to rogue the clones before control-crossing is done. However, our dependence on the assumption of a half-sib model does highlight a need for a good knowledge of pollination behaviour in the field. If a wind-pollinated progeny trial has not yet been established, and is not required for providing early information whereby a clonal seed orchard may be efficiently rogued or re-established, the case is not so clear-cut. The cost of planting two field trials must then be weighed against the advantage of being able to specialise the two functions of evaluating families and individuals within families respectively.

Where wind-pollinated progenies are difficult to obtain and/or do not give reliable estimates of GCAs we would look to a mating design which will achieve this objective

and at the same time be nearly optimal for advanced generation selection. In this case some modification of the polycross could be very suitable. It is possible, though, that separate plantings might be desirable to meet these different objectives.

Figs. 2 to 5 illustrate alternative flow charts, depending on the reliability of wind-pollinated progeny tests and on how quickly they provide information. All charts are

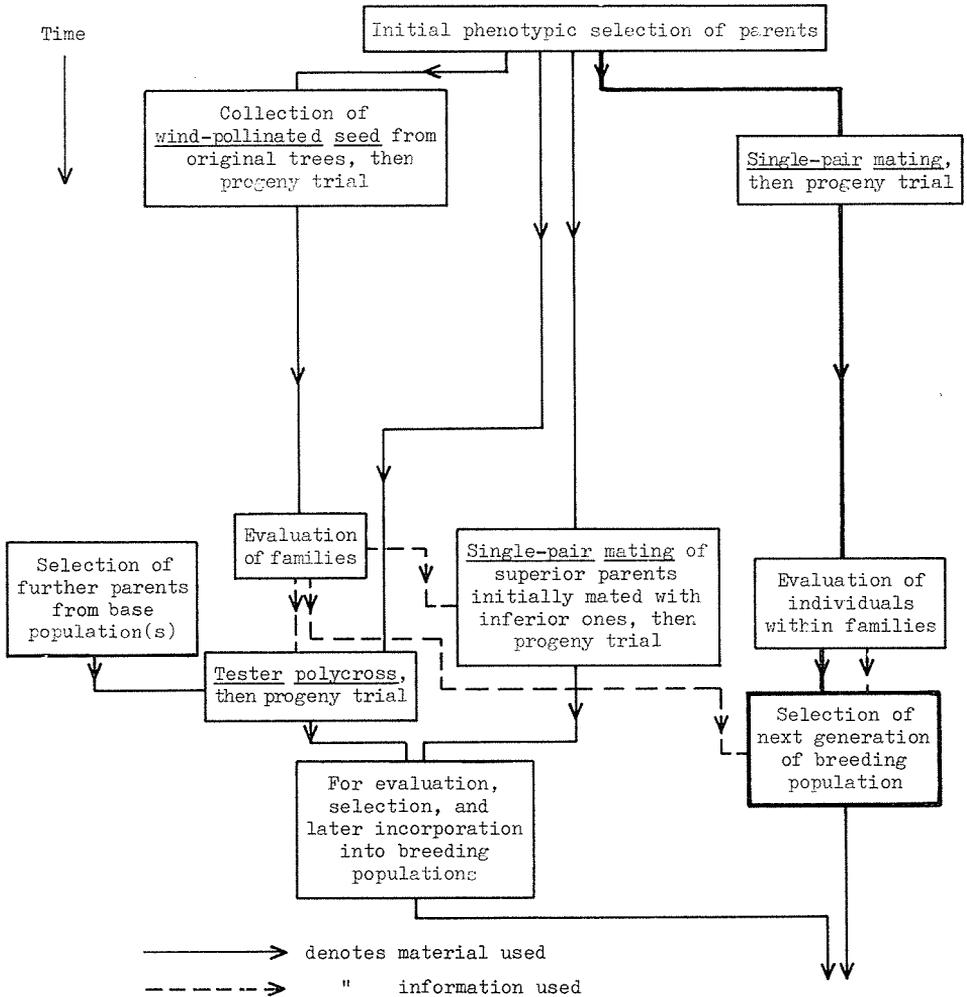


FIG. 2—Flow Chart 1. Suggested deployment of material in mating designs and use of information to produce advanced generation breeding populations

Conditions: (1) Wind-pollinated progenies equivalent to half-sib families.

(2) Early estimates of GCA not available from the wind-pollinated progeny trial.

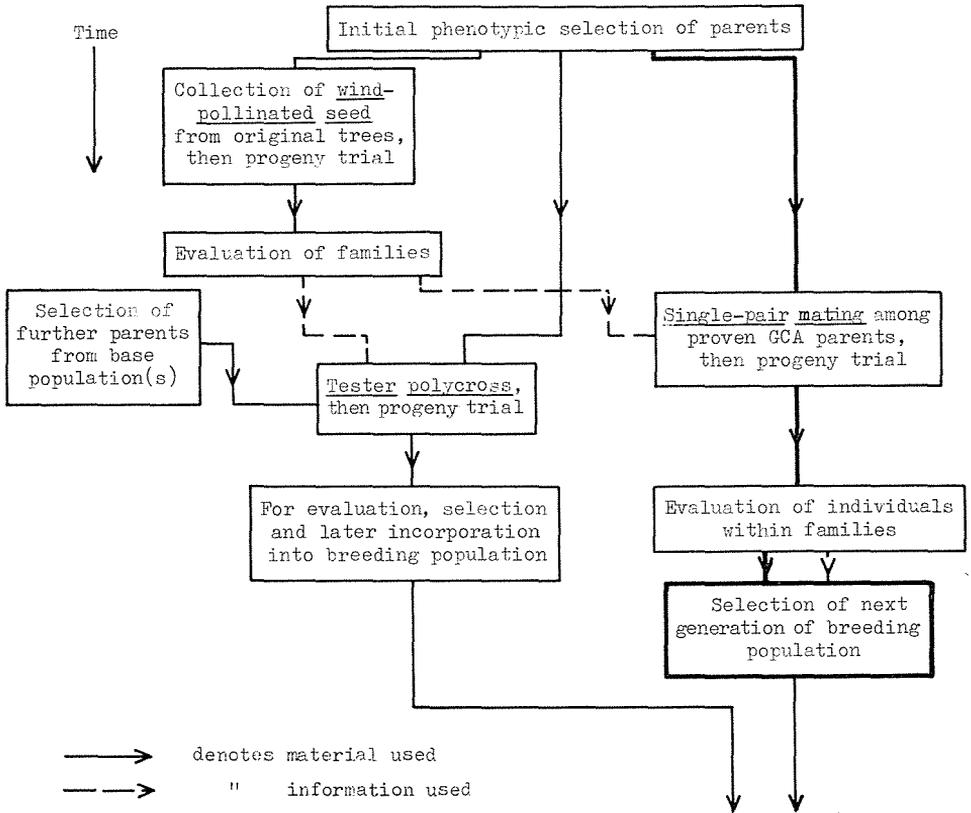


FIG. 3—Flow Chart 2. Suggested deployment of material in mating designs and use of information to produce advanced generation breeding populations

- Conditions: (1) Wind-pollinated progenies equivalent to half-sib families.  
 (2) Early estimates of GCA available from progeny trial.

drawn to the same arbitrary time scale. For simplicity of argument it is assumed that ramets from selected genotypes cannot contribute worthwhile genetic information. Fig. 2 covers the case of wind-pollinated progeny trials providing reliable information, but only with a considerable delay. For Fig. 3 the situation differs in that the relevant information can be obtained with little delay. Fig. 4 applies where wind-pollinated progenies cannot provide reliable information and where any progeny trial can only be evaluated after considerable delay. For Fig. 5 the situation differs from that in Fig. 4 in that progeny-test evaluations can be made with only little delay. Here the second generation can be produced by two main pathways, the relative importance of which may be determined by the particular circumstances.

In all cases provision is made for the introduction of fresh selections of clones, which can contribute to the breeding population perhaps after the second generation of

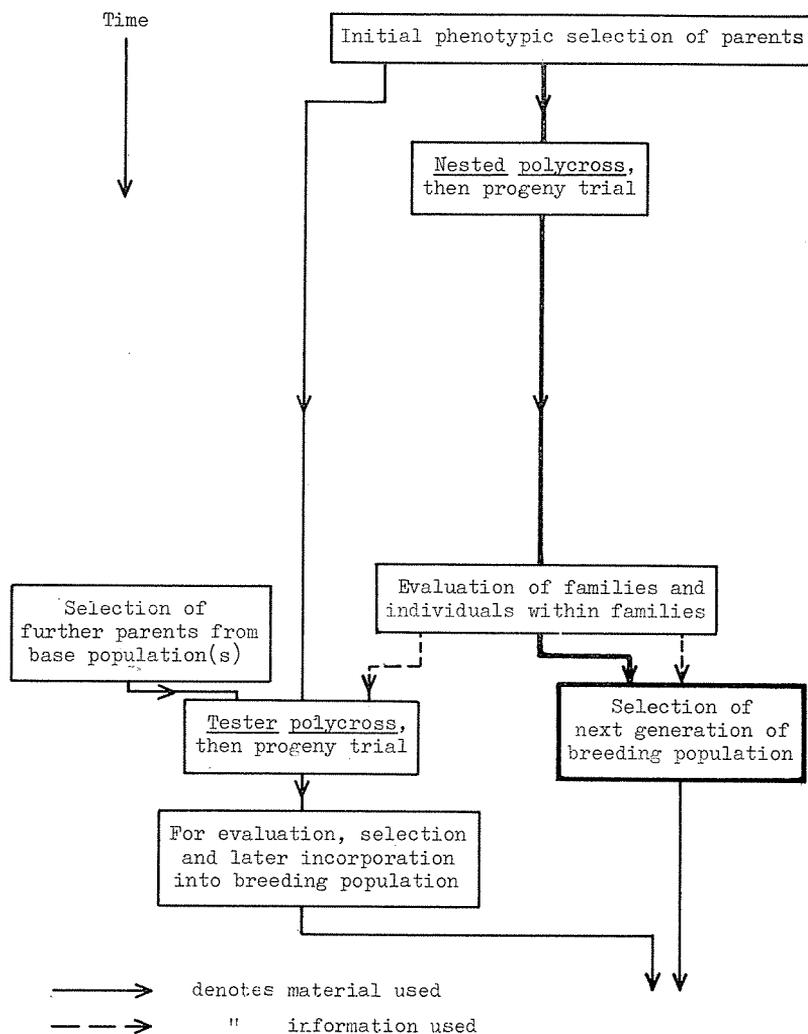


FIG. 4—Flow Chart 3. Suggested deployment of material in mating designs and use of information to produce advanced generation breeding populations

Conditions: (1) Wind-pollinated progenies not equivalent to half-sib families, or not obtainable.

(2) Early estimates of GCA not available from progeny trials.

selection. It must be noted that for actual seed orchards only a small proportion of the breeding population genotypes would be used, and that these orchards are not envisaged as a major source of selections for subsequent generations of the breeding population.

Finally, we can suggest a way in which SCA can be utilised within the general scheme which we have proposed. When new selections are introduced to the breeding

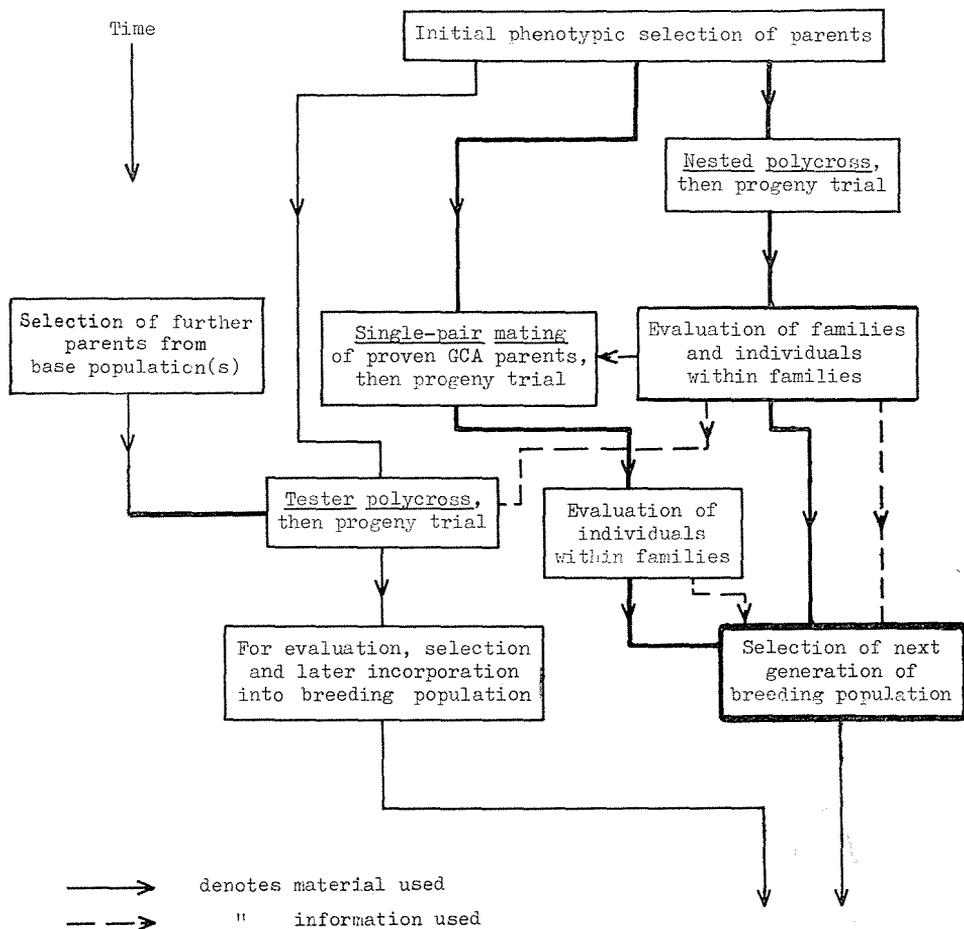


FIG. 5—Flow Chart 4. Suggested deployment of material in mating designs and use of information to produce advanced generation breeding populations

Conditions: (1) Wind-pollinated progenies not equivalent to half-sib families, or not obtainable.

(2) Early estimates of GCA available from progeny trial.

population by crossing with parent clones, the new selections can be derived from a population which combines heterotically with the original base population. Alternatively, the new clones could be selected for particular desired characteristics in the hopes that their less desirable characteristics could be later eliminated through genetic recombination. In one or both of these ways we hope to utilise some of the natural populations of radiata in our own breeding programme.

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