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Problems Involved in Some Models of Selection in Forest Tree Breeding

By K. STERN and H. H. HATTEMER[1])

In recent decades the breeding of forest trees by selection has been started in several countries. The objects of the breeding programs have been numerous and many species are involved. The breeders chose methods in accord with the biological features of the species and the objectives of their work. Within the last years, however, methods of quantitative genetics have been employed to test and compare the prospects of success from the various selection methods. It is a merit of authors as GODDARD and BROWN (1961), WRIGHT (1960), SCHREINER (1961) and others that all over the world forest tree breeders though being sometimes not too familiar with genetic statistics try to check their breeding programs for efficiency. One should not overemphasize on the other hand, the use of mere calculations because in general little is known about genetic parameters of the populations dealt with, about certain biological features of the species, and about the complexity the breeder is confronted with in a given case. Readers should not think that there is something controversial to older papers on forest tree breeding methods, for example those by the "Scandinavian School" (refer to ANDERSSON, 1943 who for the first time introduced quantitative genetics into forest tree breeding and ANDERSSON, 1960 for more detailed informations). In the opinion of the present writers nothing justifies a controverse between the group of authors named first who strongly advocate the concept of "seedling seed orchards" and those tree breeders who prefer to use "clonal seed orchards". Here must be stressed that such analyses must be confined to those methods which are possible for a particular situation because the conditions may restrict the number of feasible methods. In this paper we shall try to derive the expectations of gain from some standard methods of selection.

1. Selection based on parental merit

Four procedures are possible:

11) Selection of seed stands and thinning of these seed stands to the best trees.
12) Selection of plus trees and collection of seed from these plus trees after free pollination.
13) Selection of plus trees in seed stands thinned to the best trees, and collection of seed from these plus trees after free pollination.
14) Selection of plus trees and establishment of seed orchards using the seedling offspring of the plus trees
    141) after free pollination in a normal stand,
    142) after free pollination in a seed stand thinned to the best trees,
    143) after controlled inter-pollination of the plus trees using a pollen mix derived from all the plus trees.
15) Selection of plus trees and establishment of a clonal seed orchard.

Now the gain from selection of seed stands cannot be estimated without progeny tests (the term "progeny test" is used here to refer to a seedling progeny test); consequently it may be neglected. Moreover, the assumption of an effective selection from the use of the best stands as seed sources involves the assumption of a base population with other than random-mating structure. All our methods of estimation, however, are based on the assumption that we are dealing a random-mating population; consequently they are not applicable to the given situation. Recently GRIFFING (1962) investigated several methods of simultaneous selection using different base populations. His study is very relevant but the use of his methods requires knowledge of population parameters we do not possess. It will later be seen that even in selection using a random-mating population difficulties arise in this context. An earlier paper by the senior author (STERN, 1961) dealt with the assumptions which permit deviations from a random-mating structure if appropriate progeny tests exist.

Let us suppose that the random-mating population from which we select consists of the population of a tree species occurring within the boundaries of "plantagenzoner" (a seed orchard zone as in Sweden) or of a "Wuchsgebiet" (a growth region as in Germany). We will further assume that this area is uniform so that interactions between genotype and environment do not exist. Likewise, interactions between genotype and age, and between genotype, age and environment are also excluded (the selections are to be used within the range of the base population). Finally, this population has the best conditions for selection in the area concerned, that is, the most favourable combination of all characters to be subjected to selection. and in the extreme case a high mean genotypic value of all these characters. This assumption like that of non-existence of interactions can be proved only by progeny tests.

Moreover, in estimating genetic gain it is necessary to know at least the additive genetic variance of the characters, their genetic correlations and heritabilities. Reliable estimates can only be obtained by progeny tests. The results of SAKAI and HATAKEYAMA (1953) indicate new ways and we hope that further studies of the method will help to overcome the obstacles still existing; but it is not yet advanced far enough.

Because of the lack of evidence, the reader may join with some authors in thinking that estimatiors of genetic gain are reasonable only in some simple situations. For example, SQUILLACE and DORMAN (1961) and SQUILLACE and BENGTSON (1961) make calculations of this kind for gum yield in *Pinus elliottii*; this is a simple character.

But arguments of this kind do not concern us here because we are dealing only with general ideas and their discussion. The breeder must himself decide on their use in a

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given situation and this will become even more evident from the considerations which follow.

Suppose that heritability $h^2_{(s)}$ refers to the narrow-sense heritability of a character to be subjected to selection in stands, and σ_{Ps} refers to the phenotypic standard deviation of the character; then, additional assumptions must be made. The most important is that the ratio between additive genetic and phenotypic variance must be constant to result in equal heritability in all stands. Also the phenotypic variance of the trait must be equal in all stands. We overcome this difficulty by assuming average conditions and refer to the paper of Toda (1963) which presents a way of obtaining realistic estimations of h^2 even if the variances in single stands differ from each other.

Let R be the response to selection and i the selection differential. If the conditions mentioned above are fulfilled we obtain for the procedures mentioned at the beginning of this section:

$R_{11} = h^2_{(s)} \sigma_{Ps} i_t$

$R_{12} = \frac{1}{2} h^2_{(s)} \sigma_{Ps} i_p$[3]

$R_{13} = h^2_{(s)} \sigma_{Ps} \frac{i_t + i_p}{2}$

$R_{141} = \frac{1}{2} h^2_{(s)} \sigma_{Ps} i_p$[3]

$R_{142} = \frac{1}{2} h^2_{(s)} \sigma_{Ps} \frac{i_t + i_p}{2}$[3]

$R_{143} = h^2_{(s)} \sigma_{Ps} i_p$

$R_{15} = h^2_{(s)} \sigma_{Ps} i_p.$

(i_t is the selection differential in thinning, i_p is the selection differential in plus tree selection)[2].

Most of these procedures have been suggested in the literature on tree breeding or put into practice. The exceptions are 142 and 143, although the expectaticn of gain of 143 is equal to that of a clonal seed orchard with plus trees. We shall now discuss the reasons.

The advantage of plus tree selection when compared with the seed stand consists of the difference between i_p and i_t. Naturally, i_p is very much greater but the stands selected as seed stands and thinned in an appropriate manner do produce seed at once; they save time and the expenditure of seed orchard establishment with seedlings or clones[4].

One advantage of the seedling seed orchard is lower establishment cost because no grafts have to be produced. This advantage is not the same for all species and all countries. It can be estimated by taking into account the local climate, cost of labor, the success obtained in grafting and the flowering of the grafted plants.

An eventual benefit from the clonal orchard is that it usually flowers earlier and more abundantly but also this varies with species.. This benefit is important for the spruces, for instance, but is probably not important in some early-flowering pine species..

The genetic gain from all procedures without progeny testing is, however, greatly influenced by $h^2_{(s)}$. If the narrow-sense heritability in stands is high we may expect great genetic gain from selection of phenotypes. If it is low, none of the foregoing procedures will suffice.

There is good reason to suppose that little is known about the heritabilities of important traits.. Also the methods for estimating heritabilities must still be considered inadequate if we consider the difficulties involved in studying some important characters, particularly those influenced by competition as growth characters and others. The procedure of Toda (1963) is certainly a most remarkable step forward and investigations made by other authors into the elimination of the effects of competition by means of regression techniques may also be mentioned in this context. But there is still much room for basic research. It is still impossible to predict how selections will develop under the new conditions of competition which they will meet from other orchard offspring. Hence volume production per unit area is the most uncertain character from the breeder's point of view. Unfortunately volume production is usually the most important character for the practicing forester.

Under the circumstances sketched out above it seems most reasonable when selecting plus trees to emphasize those characters with known or supposedly high heritability. Tests take time, and often they do not provide results before selection of plus trees in the base population is finished. But tree breeders will hardly give up after one stage of selection, and in the second stage — of whatever kind it is — they can profit from information on the effectiveness of what they do.

2. Selection based on the performance of relatives

The breeding value of trees is determined best from tests involving the trees and their relatives. The different types of such trials that can be applied to forest trees are summarized below:

21) Clonal tests followed by thinnig to the best clones.
22) Half-sib progeny tests
    221) followed by thinnig to the best families,
    222) followed by the establishment of elite orchards (after Gustafsson, 1949), that is clonal seed orchards containing the parents of the best families.
23) Full-sib progeny tests
    231) followed by thinning to the best families,
    232) followed by the establishment of elite orchards.

It is assumed here that the trees to be tested are drawn at random from a random-mating base population[5] and this assumption reveals the conditions for the superiority of the procedures mentioned above. The selection of plus trees is the cheapest step in the series of steps in a breeding program; moreover, it can be quickly completed. The breeder who believes he can omit this step would seem to hold the view that the selection of plus trees will not yield any gain. This situation may indeed exist if the character subjected to selection does not show considerable heritability and this may be the case with growth characters in uneven-aged forest or as a consequence of competition effects also in even-aged forest. It may be mentioned

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[2] The values of i_p and i_t are variable and depend on the given conditions. i_p in a progeny test is not necessarily comparable with i_p in a seed stand, the same is true for i_t.

[3] Multiplication by ½ is required because the selected trees are randomly pollinated.

[4] The authors are indebted to Dr. J. W. Wright who pointed out in his critical view of the manuscript that also here the contrary is possible. In a stand of *Pinus resinosa* with slender crowns due to heavy competition he found that the trees reacted to thinning with rich seed set later than seedlings of that stand would have flowered.

[5] There exist several experiments consisting of material that cannot be considered to be a random sample drawn from a random-mating population. In those cases the estimates of h^2_e and R_e are something particular. They are parameters of just that experimental population and depend on the layout of the experiment. Informations drawn from this kind of experiments are very interesting and useful. They cannot serve, however, as a basis for estimating best procedures of selection because the experimental procedure is unique and cannot be reproduced.

The authors are indebted to Dr. J. W. Wright who raised this problem.

that some tree species usually or exclusively occur as single specimens or in small groups where no comparisons with other trees of the same species are possible..

Artificial stands produce particular problems which we cannot discuss in detail here. In several countries, however, only artificial stands are available which often are mixtures of different provenances in the zero or a later generation.

Progeny tests can be established in numerous ways. This statement refers both to the crossing designs and the experimental designs used to produce the progenies. The "heritability" of such tests is also affected by the skill and experience of the breeder; it is a parameter of the experiment rather than of the population concerned

In planning these eperiments the upper limit for intensity of selection is predetermined. This limit is set by the number of parent trees and the crossing design, while in selecting plus trees a practically infinite population is dealt with. Hence the number of parents and families to be tested should be as large as possible. On the other hand this fact forces us to divide the progeny tests into several parts because increasing the number of progenies lowers the heritability of experiments[6]).

In all cases the response to selection can be obtained by

$$R = h^2_{(e)}\, \sigma_{P_e}\, i.$$

The index (e) is a reminder that both heritability and phenotypic variance are parameters of an experiment. The genetic variance however is the basis of genetic gain; this amounts to

σ^2_A in 21
$^1/_4\, \sigma^2_A$ in 221
σ^2_A in 222
$^1/_2\, \sigma^2_A$ in 231
σ^2_A in 232.

Suppose a breeder established a half-sib progeny test which he converts to a type-221 seed orchard, and that he also establishes a type-222 elite orchard of clones proved superior in the progeny test. The quality of seed produced by the grafted orchard will considerably exceed that of the seedling seed orchard because in the latter only $\frac{1}{4}\, \sigma_A$ is available.

We have already stated that R is not the only criterion for the choice of the procedure to use in selection. The trees in a progeny test converted to a seedling seed orchard by thinning will flower before the testing was finished, whereas the elite seed orchard in most cases still has to be established.

Sometimes the clonal orchard could however be established either at the same time or before the progeny tests and after the assessment of the progeny tests it has only to be thinned to make full use of the genetic gain. In this case the advantage of the seedling seed orchard disappears and what remains is the disadvantage of the special expense of establishing the clonal seed orchard. Less trees may be left after thinning the experiment or the clonal orchard; this depends on the tree species and the type of the clonal orchard. One should take these things into account in planning the program.

An essential advantage of the clonal orchard is that a great number of clones can be brought together; this is not possible in progeny tests. So by thinning the clonal seed orchard the genetic gain from several progeny tests can be exploited. In these circumstances the cost of establishing the clonal orchard will be compensated by the higher genetic gain.

The tree breeder can be confronted with many situations all of which demand special procedures and an optimum procedure suitable for all situations cannot be given. Methods similar to linear programming can be employed to advantage in this connection. Like in the solution of complex problems in theoretical genetics modern computer facilities have to be used. Computers can give the optimum answer for particular situations if supplied with data on heritability, cost, time, seed per tree, selection intensity, and breeding procedure.

3. Selection based on both parental phenotype and the performance of relatives

The breeder of farm animals or crop plants knows the properties or characters of the material he intends to use in developing new breeds or varieties. Hence there exist a lot of experiences on the genetic parameters of the populations and the range of variation of these parameters. As a consequence breeders were able to develop standard procedures with the known main points. It is otherwise in forest tree breeding which is still at an early stage of development. Hence we may confine our discussion to some points of view that will probably become important for forest tree breeding in the years ahead. Because fundamentally different situations exist we must restrict the discussion to general considerations. One may keep in mind the possible combinations of the procedures presented in the two previous sections of this paper.

The tree breeder may know:

31) The phenotype of the stand from which the plus tree was selected,
32) the phenotype of the plus tree compared with the mean of the stand,
33) the mean breeding value of a family or the breeding values of one or both of the parents,
34) the phenotype of the individual members of the family compared with the mean of the family.

Two things can be achieved when all this information is brought together into a selection index: the precision of selection and consequently the expectation of genetic gain is improved. The gains from the individual activities in selection are accumulative; hence, the response to selection is increased.

We must note here that selection "between" stands (subpopulations) in a growth region is based on a genetic variance with the expectation $2\,F\,\sigma^2_A$ (where F ist the inbreeding coefficient of the subpopulations; see Stern, 1961 for details). The genetic variance within stands then has the expectation $(1-F)\,\sigma^2_A$ which should be respected for higher inbreeding coefficients. All other consequences were already discussed in the preceding paragraphs.

But we may realize again that the genetic gain from the single stages depends on the amount of genetic variance σ^2_A and on

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[6]) The number of progenies in an experiment depends on many things. If the breeder can afford to make small plots he can include more progenies. If he is backed by a strong organization he can raise several hundreds of progenies a year. Appropriate field designs and careful choice of the experimental site will guarantee him high efficiency as Dr. J. W. Wright pointed out to the authors. Field experiments under way at Schmalenbeck containing more than a hundred "varieties" of Norway Spruce showed a heritability of 85% for height growth, and that if only 4 replications were used. But this really means to spend money if the breeder wants to continue along this line.

F in 31
h^2_s in 32
$h^2_{(e)}$ in 33
h^2_s in 34.

We can expect a gain from the selection within families (34), but with the same justification also from the selection of plus trees in uniform and even-aged stands (32).

When selecting between and within the best families it should be remembered that incomplete diallel crossing designs are often used for progeny tests (Hinkelmann, 1961) or other designs, all of which have in common the fact that the "best" combination is not necessarily produced. To secure production of the "best" combination all possible crosses must be made — and this is an absolutely impossible undertaking.

For this and other reasons a selection design which is modifiable on the basis of new information is recommended. It was Matthews (1958) who emphasized the necessity of flexible selection procedures. This concerns also seed orchards destined to exploit genetic gain. Maximum progress must be achieved and, on the other hand, it must be made available immediately and steadily to practical forestry. How this is attempted by means of a clonal seed orchard in a particular species may be shown without claiming general applicability for this example.

In a breeding program in birch plus tree selection proved unreliable as regards growth rate which is the most important character. But because $h^2_{(e)}$ is high, mass selection based on filial performance has a high expectation of gain. The first experiments were designed to provide information on the breeding values of the plus trees and precise estimates of expected gain from different selection patterns.

The first step of the final program (which, of course, can be changed in some points when additional information on population parameters will be available) comprised the selection of 600 trees chosen for good stem form and other characters known to have high h^2_s. This information was obtained from preliminary field experiments as already mentioned. The great number of 600 trees were chosen to increase the selection coefficient. The next step will be the crossing of the 600 trees with tester clones having high breeding values; the tester clones are seleted on the basis of the results of the first field experiments. Since it is impossible to produce all crosses in one year the number of 600 trees are split into groups comprising 50 trees each. Trees of the same group will be mated with one and the same tester clone in one year. Their progenies will be outplanted in one field experiment or, if the experiments under way will reveal an appreciable amount of genotype by environment interactions they will be planted out in one series of field experiments. In this way only such progenies are produced for further selection that have a high average genetic value because the tester clones used had been selected for high breeding value. Naturally, the breeding values of the trees to be tested were unknown at the beginning of the experiments. The use of another tester clone in each of the 12 groups secures a low degree of inbreeding which can be kept under control in further work.

The genetic gain will be exploited in clonal seed orchards planted at wide spacing. As soon as the results of a progeny test are obtained the best parents of a group of 50 are retained in the orchard while less promising clones are removed. Such an orchard is, of course, uneven-aged due to steadily replacing clones, and so it cannot be used for all tree species for biological reasons. The method makes possible early and continuous use of the results of selection. We mention this to show that the clonal seed orchard concept can also be sufficiently flexible.

4. Simultaneous selection for several traits

Only in few cases the aim of forest tree breeding is the improvement of a single character but the phenotype of a tree or stand depends on many characters all of which can normally be improved. Because intensity of selection for given characters mostly decreases by including another the breeder is forced to choose between the characters under study. He may choose those with the greatest expectation of economic success.

The economic success of selection is determined biologically by the expectation of genetic gain per generation, or in other words by the heritability of the characters and the genetic variation. The genetic gain has then to be weighed against the economic profit involved. At the present stage of forest tree breeding the estimation of genetic gain is possible only in a few particularly simple situations because the genetic parameters of the populations are still unknown. In addition prognoses of relative economic values at the time the results of the breeding become available are most uncertain. The relative economic values are influenced by the market situation and this assumes that it is possible to predict the markets of thirty or even more years ahead.

In spite of this difficulty it is reasonable to consider these things and to make a provisional economic weighting of the characters. The selection program, however, must be flexible enough to be brought into line with new and unpredictable developments. The "genetic weighting" of the characters with respect to the expectation of gain can, of course, not be made until experiments yield the informations required.

Simultaneous selection for several characters involves new problems and demands employment of special methods. There are three main procedures. In index selection each individual or familiy is represented by an index value written in a multiple regression equation. The coefficients of the equation are calculated taking account of the genetic parameters and the relative economic values of the characters. Tandem selection shifts to other characters in successive generations. In the method of independent culling levels least admissible values are fixed for each character. If an individual or family in any character falls below these limits it is rejected.

At present index selection is most popular because theoretically it has the highest expectation of progress. Its applicability, however, is limited by lack of knowledge of the economic importance, heritability and genetic correlations of most tree characters. For the time being procedures are in use which have some features derived from all three methods.

Most forest tree breeders compare their plus trees by rating systems. In constructing such a system a kind of weighting is employed as in index selection. Culling levels are set for susceptibility to diseases as in the method of independent culling levels. Selection for some characters may by be postponed to a later generation due to lack of information. This is typical of tandem selection. Changes in the situation on the market or increase in basic knowledge may lead to alterations in the emphasis put on characters.

5. Selection in field tests not permitting direct assessment of characters under selection

One of the principle aims of selection programs is increased volume production per unit area. For the exact assessment of the increase in volume production experiments had to be designed in which the entries contained are identical to the populations to be released to practical forestry in the future. Besides that, these experiments had to be observed until the end of the rotation period. Neither of these requirements can be met by the experimenter.

In progeny tests containing half-sib and full-sib families half-sibs and full-sibs compete within the plots. Much of the competition between plots takes place between non-relatives and this becomes fairly unimportant with increasing plot size. But in the forest stands established with seed orchard offspring there is only competition between non-relatives (provided the number of clones is sufficiently high). Moreover, the structure of seed orchard offspring is different.

Such considerations are helped by making two assumptions:

1) The differences in the situations of competition in families and seed orchard offpring do not play a role.

2) Mean heights, mean diameters and mean stem volume or yield per unit area assessed at an early date on small plots are closely correlated with the yield of mature stands.

Under these premises expected gain by selection for such characters is

$$R_y = i\, h_x\, h_y\, r_A\, \sigma_{P_y}$$

where h is the square root of narrow sense heritability; r_A is the genetic correlation (based on the breeding values as items) between character Y of the mature stand and character X of the young field experiment.

Consistent estimates of R_y can be obtained only if a sufficient number of comparisons between X and Y are possible. To carry out these comparisons the maturity of the stands had to be waited for.

6. Conclusions

Are the procedures and results of quantitative genetics of value for camparisons of selection procedures even though their application to practical tree breeding is limited at present time? We answer this question as follows:

1) The definitions given by quantitative genetics can serve as a basis when planning selection programs. The older literature on selection in forest trees is full of discussions that have little value because they lacked distinct concepts now given in terms of quantitative genetics.

2) Quantitative genetics presents starting points for promising basic research. This could furnish the tree breeder with methods that are both easy to handle and more efficient.

3) From information obtained from the first experimental series of a breeding program we can employ the methods of quantitative genetics to choose the procedure giving probably maximum progress. These procedures would be best in the light of available biological and economic information.

4) The forest tree breeder should set out experiments that both give him practical results and permit estimation of the various parameters needed to plan further work. Owing to remarkable cost of experiments in forest tree breeding the field tests should be usable in both ways.

5) Quantitative genetics and the methods deducted from its results are recommended for application. It may be emphasized that the reservations and doubts expressed here do not cast doubt on quantitative genetics. These methods help to spare time, money and labor. We are however advising against the over-simplifying and over-determining of the premises required for valid conclusions. The breeder should be aware of some fallacies which can easiliy result from choice of inadequate models.

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Summary

A critical survey of some methods of forest tree breeding leads to the conclusion that reliable estimation of genetic gain is possible only in some plain situations. When comparing different methods of selection the biological features of the tree species must be taken into account. These conditions may lead to entirely different opinions on a particular selection method. There is no "best" procedure in general.

Estimations of genetic variances and heritabilities of the most important characters have so far been insufficient. Hence it is in most cases too early to compare expectations of gain from possible procedures.

At present the value of methods of quantitative genetics is seen in that they present a good basis for planning future experiments. These experiments should result in both progress in breeding and the theoretical informations required for extensive application of the methods of quantitative genetics.

Because it is not yet possible to be certain about the best method of tree improvement, breeding programs should be flexible so that alterations are possible in the future.

Résumé

Titre de l'article: *Problèmes posés par certaines méthodes de sélection dans l'amélioration des arbres forestiers.*

Une étude critique de différentes méthodes d'amélioration des arbres forestiers mène à la conclusion qu'il n'est possible d'obtenir une estimation valable du gain génétique que dans certains cas simples. Lorsque l'on compare les différentes méthodes de sélection, il faut tenir compte des caractéristiques biologiques des espèces. Ces conditions peuvent donner naissance à des avis entièrement différents sur une méthode de sélection particulière. Il n'y a pas de méthode «optimum» en général.

Les estimations de la variance et de l'héritabilité génétique des caractères les plus importants sont pour l'instant insuffisantes. Il est donc prématuré dans la plupart des cas de vouloir comparer les gains probables des méthodes possibles.

A l'heure actuelle, l'intérêt des méthodes de génétique quantitative réside dans le fait qu'elles constituent une bonne base pour l'établissement des plans d'expériences futures. Ces expériences devraient à la fois permettre de réaliser des progrès dans l'amélioration et d'obtenir les renseignements théoriques nécessaires à une large application des méthodes de génétique quantitative.

Etant donné qu'il n'est pas encore possible de dire quelle est la meilleure méthode d'amélioration des arbres, les pro-

grammes d'amélioration devraient être suffisamment souples afin de pouvoir être modifiés dans l'avenir.

Zusammenfassung

Titel der Arbeit: *Probleme einiger Auslesemodelle in der Forstpflanzenzüchtung.*

Ein kritischer Überblick über einige Methoden der Forstpflanzenzüchtung führt zu dem Schluß, daß die verläßliche Einschätzung des Züchtungsfortschritts nur in wenigen einfach gelagerten Situationen möglich ist. Beim Vergleich verschiedener Selektionsverfahren müssen die biologischen Eigenschaften der Baumart berücksichtigt werden. Diese Verhältnisse können zu einer völlig anderen Beurteilung einer bestimmten Auslesemethode führen. Ein allgemein „bestes" Verfahren gibt es nicht.

Schätzungen genetischer Varianzen und Heritabilitäten der wichtigsten Merkmale waren seither ungenügend. Daher ist es in den meisten Fällen zu früh, Erwartungswerte für den Züchtungsfortschritt denkbarer Verfahren zu vergleichen.

Der Wert quantitativ-genetischer Methoden wird gegenwärtig darin gesehen, daß diese Methoden eine rationelle Grundlage für die Planung zukünftiger Experimente bieten. Diese Experimente sollten sowohl Fortschritt bei der Züchtung als auch Informationen theoretischer Art liefern, wie sie für eine erweiterte Anwendung von Methoden der quantitativen Genetik benötigt werden.

Da noch keine Gewißheit über die beste Züchtungsmethode besteht, sollten Züchtungsprogramme flexibel sein und künftige Änderungen erlauben.

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Clonal Selection, and An Alternative Seed Orchard Scheme

By W. J. Libby1)

I. Introduction

It seems reasonable that the answer to the question: "What kind of seed orchard shall we have?", will depend in large part on the characteristics of the species in question.

It is the purpose of this paper to discuss mass selection, family selection, family-plus-mass selection, and clonal selection in terms of "clonal seed orchards," "seedling seed orchards," and a third alternative seed orchard scheme. This scheme involves evaluation of candidate trees, clones or families at a site or sites other than the seed orchard site, and combines some of the best features of each of the other two seed orchard systems.

The effects of such species characteristics as: (1) ease and expense of control-pollination; (2) ease and expense of vegetative propagation; (3) sexual precocity of grafts and seedlings; (4) genotype-environment interaction; (5) heritability of the characteristic or index being selected; (6) juvenile-adult correlation of this characteristic or index; (7) demand for seed; (8) inbreeding depression; and (9) cost and value; are discussed in terms of the selection and seed orchard schemes. In addition, factors associated with these schemes which determine variability, selection efficiency, and selection intensity are discussed in general.

Since the term "clonal selection" has been used to mean different things, including selection within a clone for sports or disease-free individuals (Babcock and Clausen, 1927), and since clonal selection has not been given a general theoretical treatment in the literature, this treatment is presented below. The treatment is general, and the experiments utilize herbaceous material. The principles apply, however, to forest trees as well as to other organisms which can be vegetatively propagated (Larsen 1956, Chap. 7). It will be shown that clonal selection is useful not only for species which are normally vegetatively propagated, but also for species where the progeny of the selected individuals will be produced sexually. To use clonal selection with species which normally reproduce by seed: (1) vegetative propagation must be inexpensive and reliable; and (2) the vegetative propagules must rapidly take on characteristics which are realistic for, and comparable to, seedlings.

II. Clonal Selection2)

In selection or breeding studies, where a genotype is poorly defined on the basis of the performance of a single organism, it is frequently possible to use supplementary information from relatives of the organism to more accurately identify its genotype. The more genes shared, or closer the relative, the more applicable is the relative's performance to the genotype of the organism in question

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2) This section is based on a dissertation submitted to the Graduate Division of the University of California in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Genetics.