Forest Tree Breeding by Selection

Clonal Seed Orchards — Seedling Seed Orchards, Progeny Tests

By Helge Johnson, Ekebo

Within a region where a technically valuable tree species is of common occurrence and on average attains a satisfactory development, breeding by selection is a primary task. To accomplish a selective programme, two ways, differing in principle, have been suggested.

Farquhar (1922) proposed the establishment of test plantations with progenies from selected trees after open pollination. At the end of the test period inferior families were to be removed and the plantation would then be used as a seed source. This way of approach can be termed the seedling seed orchard-progeny test method (Wright 1962). The progenies must, of course, not be open-pollinated but might be derived from crosses between the selected trees, the selection in the test plantation being performed in different ways such as individual, family and combined selections.

The other method was suggested by Syrach Larsen (1934), who wrote: "I strongly urge, therefore taking up vegetative propagation and in conjunction with experiments of artificial pollination, the establishment of seed plantations for the supply of seeds for practical use". This demonstrates the fundamental feature of the clonal seed orchard method. Later on a number of authors have contributed to the further development of this method, which is widely applied, not least in the North-European countries.

Recently a discussion has arisen concerning the merits of the two methods, initiated by Wright (1962), who claims that the seedling seed orchard-progeny test method is the most promising one. In this paper some thoughts concerning the problem will be set forth.

Genetical considerations

The relation between plus tree selection and selection in the progenies:

Wright (1962) has performed quantitative genetical calculations of the genetical gain which is to be expected as the result of various selection procedures. As unit he uses the gain, obtainable by individual selection in a plantation, established by progenies from panmictic matings between a number of selected trees (plus trees), this gain being denoted by \( G_i \). In order to emphasize that this unit refers to individual selection in the progenies of the plus trees, it will be written \( A G_i \) here. Consequently the gain of the plus tree selection can be written \( A G = A G_i \). Warrar puts \( A G_p = k \cdot A G_i \) and defines the constant as \( k \) = heritability in wild stand/heritability, determined from a progeny test \( = h^2_f / h^2_p \). According to Warrar \( h^2_f \) should always exceed \( h^2_p \) and thus \( k < 1 \). In his numerical examples Warrar uses \( k = 0.5 \). Thus, the genetical gain of plus tree selection in old stands should always be less than that of individual selection in their progenies. The correctness of this assumption may be doubted for very good reasons. Let us consider the separate factors which determine any \( A G_i \). According to definition \( A G = i \cdot a \cdot h^2_f \) with \( i \) the selection intensity, \( a \) the standard deviation and \( h^2_f \) the heritability. Thus we have:

\[
\begin{align*}
\text{for plus tree selection} & \quad A G_i = i_p \cdot a_p \cdot h^2_{p_f} \\
\text{and for individual selection in the progenies} & \quad A G = i \cdot a \cdot h^2_f \\
\end{align*}
\]

The selection intensity of the plus tree selection can be kept very high with \( i_p \) around and even above 3. If the aim is to use the test plantation as a seed source, the intensity of selection within the progenies must be rather low. For instance, selection of one individual out of ten gives \( i = 1.75 \).

The standard deviation connected with plus tree selection is measured in units other than the same quantity dealt with at the individual selection in the progenies, viz. in measurements for mature trees, whereas \( a_i \) refers to younger ages in a practical application. A priori the correlation between \( a_i \) and \( a_p \) is unknown and \( a_i + a_p \). Thus even \( h^2_f \) really should be greater than \( h^2_{p_f} \). \( A G_p \) may very well be greater than \( A G_i \). Hence Warrar’s estimates of the relations between the genetic gains of the plus tree selection and of the selection in the progenies are without any relevance.

Clonal seed orchards — seedling seed orchards, progeny test:

In his calculations Warrar puts the genetical gain of the seed of a seedling plantation of clones among the plus trees as equal to the gain of a clonal orchard, built up with the same plus trees. This is true according to the Hardy-Weinberg law, provided, of course, that all plus trees enter as parents of the progenies in the same frequency, that the clones are of the same size and that the variation in seed setting and male flowering capacity is negligible. Another condition is that the number of parents of the progenies be so large that the frequency of matings between relatives can be kept out of consideration.

Thus, with these conditions in mind, it is genetical irrelevant whether the genetical gain of the plus tree selection be utilized by means of:

A. clonal seed orchards,

B. seedling seed orchards, established by crosses among the plus trees.

Whichever of these two alternatives is used it represents an initial step only in a rational breeding programme. It is evident that further progress can be made by repeated selection in subsequent generations without guidance of progeny tests, but that progeny testing must be of great value for planning further selection work.

When the progeny test has been accomplished, new clonal orchards could be established either by using only those clones in the original orchards which have shown themselves to possess the highest general combining abilities or laying out new seedling seed orchards of progenies from these clones.

In the seedling seed orchard — progeny test approach the same plantation is used for progeny testing as for seed production. After the test period the progeny test is transformed into a seed orchard by removing inferior families and individuals. In his efforts to demonstrate the advantages of this method Warrar has made calculations of the genetical gains obtainable in different kinds of seed orchards. According to these calculations a clonal orchard thinned to the clones with the best general combining ability gives less progress than a seedling seed orchard, established with progenies of the plus trees after open pollination and thinned to the best families. Wright says:

41
In this writing \( \Delta G = \Delta G_s \) = the gain of individual selection in the progenies, and \( \Delta G_{bs} \) the gain following selection among open pollinated progenies of the plus trees (approximately half-sibs). The comparison, quoted above, is completely misleading, which can be shown in the following way:

Assume a population with the three pairs of alleles, A-a, B-b, C-c in the same frequencies.

Six plus trees are selected, whose constitution happens to be as follows:

\[
\begin{align*}
\text{ABC} & : \text{AbC} : \text{ABC} : \text{AbC} : \text{ABC} : \text{ABC} \\
\text{abc} & : \text{AbC} : \text{abc} : \text{AbC} : \text{abc} : \text{abc}
\end{align*}
\]

By open pollination all trees are assumed to be pollinated by the total genotype of the population, i.e., in this case by a pollen mixture with the following composition:

\[
\begin{align*}
\text{ABC} : \text{AbC} : \text{aBC} : \text{aBC} : \text{AbC} : \text{AbC} \\
\text{ abc} : \text{AbC} : \text{aBC} : \text{aBC} : \text{AbC} : \text{AbC}
\end{align*}
\]

The progenies of the first two plus trees (5% of the families) are selected in a seedling orchard progeny test. These two progenies have the following composition:

\[
\begin{align*}
\text{ABC} : \text{ABC} : \text{ABC} : \text{ABC} : \text{ABC} : \text{ABC} \\
\text{abc} : \text{abc} : \text{abc} : \text{abc} : \text{abc} : \text{abc}
\end{align*}
\]

By a random mating the seed of the orchard will have the same genetic constitution as the parent families. With respect to recessive genes the following frequencies occur:

Number of recessives: \( 0 \ 1 \ 2 \ 3 \ 4 \)

Frequencies: \( 1 \ 2 \ 6 \ 4 \ 1 \)

The mean number of recessives per individual is 2.

If, on the other hand, a new clonal orchard is constructed with the clones of the same two plus trees (5% of the clones), the progeny will be:

\[
\begin{align*}
\text{ABC} : \text{ABC} : \text{ABC} : \text{ABC} : \text{ABC} : \text{ABC} \\
\text{abc} : \text{abc} : \text{abc} : \text{abc} : \text{abc} : \text{abc}
\end{align*}
\]

with the mean number of recessives = 1. Thus, the clone selection must give a better result than the family selection under the indicated conditions, or expressed in other words: half of the gene pole of the selected half-sib family orchard comes from the mother plus trees and half from the unselected population. But the whole of the gene pole of the selected clonal orchards is derived from the plus trees.

A clonal orchard constructed of the two clones which have the best specific combining ability is said by Warbur to produce seed with a genetical superiority \( \Delta G_{cl} \), i.e., = the superiority obtained in a seedling orchard after selection among full-sib families. This statement is equally false. Specific combining effects are completely uncorrelated with additive variance and cannot be predicted. Utilization of specific combining effects in bionic seed orchards can give result far above what is obtainable by any kind of selection, founded on general combining ability.

**A breeding value model:**

It might be possible to express the genetic gain to be expected by clone selection, based on the general combining ability of the clones, estimated in a progeny test, by the gain of individual selection in the test plantation \( \Delta G \) as unit. However, the pertinent selection relations can be illustrated in another and more concrete way. Let us start with a clonal seed orchard, comprising 30 clones. For progeny testing these clones are crossed in a partial diallel system.

**Table 1. — Calculated family means for 105 progenies after crosses among 30 plus trees with assumed breeding values in a partial, diallel system.**

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according to Kempthorne and Curnow (1961) with \( s = 7 \), i.e. each clone is one of the parents of 7 families. The number of test families is \( n = 2 \) \( (n = \text{the number of clones}) \), i.e. in our case 105. The total for any characteristic, observed in the progeny test, is \( p = 100 \). We assume that general combining ability strongly preponderates in comparison with specific combining ability. The family mean for a progeny, \( M_p \), is then additively made up by \( a_i + a_j = \text{the sum of the parents' breeding value} \). The mean of the breeding values for all clones is 50 and the breeding values of each clone can be calculated from the family means. We assume that the progeny test has given clonal breeding values ranging from 44 to 57. Breeding values and family means for this constructed case are given in Table 1.

Further, we assume that the individuals within a family have breeding values with mean equal to half the family mean and a variation of 9 units in binomial frequencies. Thus, for instance, a progeny with 104 in family mean should show the following variation in breeding values:

Breeding values: 48 49 50 51 52 53 54 55 56
Individual frequencies: 1 8 28 56 70 56 28 8 1

Let us then investigate the results of the selection procedures, indicated below:

A. A new clonal orchard is established with the 10 best clones.
B. The test plantation is transformed to a seed orchard by selection of the best 35 families (family selection).
C. The test plantation is transformed to a seed orchard by selection of the best third of the 35 best families (combined selection).
D. A new clonal orchard is established with the best trees in each of the 35 best families.

**Alternative A:**

The family means of the progenies in a seed orchard composed of the 10 best clones in Table 1 are computed in Table 2. The total of the 45 combinations is 1082.

**Table 2.** Family means of the progenies in a seed orchard, composed by the 10 clones with the highest general combining ability according to the progeny test.

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<th>Clone No</th>
<th>Breeding value</th>
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**Alternative B:**

The frequencies for individual breeding values in the 35 best families in Table 1 are calculated in Table 3. From these frequencies it is easy to calculate those for progenies with different family means in the next generations. The frequencies are:

**Families with mean:**

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<td>0.2</td>
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**Percentage of all families:**

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**Families with mean:**

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The total for all families is 105.8.

**Alternative C:**

For the sake of simplicity the four plus classes for each family mean in Table 3 are taken as the best third of the families. In fact this fraction amounts to 36.3% of the individuals. The frequencies of individuals with different breeding values can be taken from Table 3 and are as follows:

Breeding values: 52 53 54 55 56 57 58 59 60
Frequencies: 336 672 800 948 313 254 96 25 3

The frequencies of progenies with different family means in the next generation are:

**Families with mean:**

| 104 | 105 | 106 | 107 | 108 | 109 | 110 | 111 | 112 | 113 | 114 | 115 | 116 | 117 | 118 | 119 | 120 |
|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 1.1 | 4.3 | 9.7 | 15.3 | 17.7 | 16.8 | 13.5 | 9.6 | 6.2 | 3.2 | 1.6 | 0.7 | 0.2 | 0.1 | 0.1 | 0.1 | 0.1|

The total for all families is 108.8.

**Alternative D:**

By selection of the best of 256 trees in each of the 35 best families the following frequencies for different breeding values are obtained:

Breeding values: 55 56 57 58 59 60
Frequencies: 6 9 10 6 1 3

The frequencies of progenies with different family means in the next generation are:

**Families with mean:**

<table>
<thead>
<tr>
<th>110</th>
<th>111</th>
<th>112</th>
<th>113</th>
<th>114</th>
<th>115</th>
<th>116</th>
<th>117</th>
<th>118</th>
<th>119</th>
<th>120</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.9</td>
<td>8.8</td>
<td>16.4</td>
<td>20.6</td>
<td>18.0</td>
<td>14.2</td>
<td>9.0</td>
<td>5.9</td>
<td>3.0</td>
<td>0.5</td>
<td>0.7</td>
</tr>
</tbody>
</table>

The total of all families is 113.8.

The results of these calculations, related to a set pattern, can be summarized as follows:

A. New clonal orchard of the best 10 clones — gain = 8.2%
B. Selection of the 35 best families in the progeny test
   - gain = 5.8%
C. Selection of the best third of the 35 best families
   - gain = 8.8%
D. New clonal orchard of the best tree out of 256 in the best 35 families
   - gain = 13.8%

However, some other circumstances must also be considered: firstly, the efficiency with which the different procedures of selection can be accomplished. The 10 best clones can be selected with great accuracy as each breeding value has been derived from a number of plots seven times as great as the number of replicates in the test. The 35 best families can also be designated with comparative certainty if the test has good significance. The individual selection, involved in C and D, is much more precarious on account of the disturbing influences of the environment — the individual heritability in the progeny test is < 1. Consequently, the theoretical progress cannot be fully obtained. However, according to \( \Delta G = \alpha \cdot h^2 \) the stronger selection in D will always give better response than the weaker one in C. We have:

\[
C = 105.8 + 1.7 \cdot h^2 \\
D = 105.8 + 2.9 \cdot h^2.
\]

Further, we have to pay attention to the possible frequencies of matings between relatives in the four cases. In case A no matings between relatives occur, provided that the plus trees have been selected in sub-populations well isolated from each other. In the other three selection procedures a certain amount of matings between relatives must occur, the fewer the plus trees used, the higher the frequencies. In our case the mating frequencies are:

<table>
<thead>
<tr>
<th>Frequencies of matings</th>
<th>between full sibs</th>
<th>between half sibs</th>
<th>between unrelated</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2.9%</td>
<td>14.0%</td>
<td>83.1%</td>
</tr>
</tbody>
</table>

This amount of related matings might be tolerable but represents nevertheless an influence in a negative direction.

**Non-genetical considerations**

In planning a selection programme not only genetical facts are to be considered but the breeder also has to face a number of problems of non-genetical nature, which are more or less important, depending on tree species, climatic region and silvicultural conditions. The most fundamental of these questions will be treated below.

**Performance of artificial crosses.**

Evidently a selected tree can be propagated by grafting immediately after the selection has been made, or anyway in the following spring, but on account of the flowering periodicity in some species and climates it is far from certain that crosses can be performed in the spring. For instance, in South Sweden *Picea Abies* has not flowered at all since 1956. Thus crosses between a number of plus trees, selected in the summer of 1956, could not have been made even at this very moment of 1963, seven years later. In high altitudes in North Sweden the intervals between the seed years are not infrequently ten years or longer.

It can even be questioned whether on the whole it is possible to accomplish a systematic crossing programme of some extent directly on the plus trees. Even if boreal trees are small, Swedish plus trees have a height of 20—35 meters, an absolutely clean bole, 12—15 meters long, and thin branches. Establishment of a seedling seed orchard of 10 hectares (medium size of Sweden) requires about 50,000 seedlings, which means that each cross in the scheme, presented above, must be large enough to give 500 seedlings.
For *Pinus silvestris* it is equal to pollination of 100 "flowers" for each cross and up to 700 on the same mother tree, of which several grow 100–200 kms from each other. Personally, I consider it out of the question to accomplish such a programme by climbing. Earlier we have made serious attempts to perform crosses on trees in the stands by help of scaffolding. Such constructions with a height, comparable to buildings 8–10 stories high, (fig. 1) are expensive and furthermore they run a great risk of being blown down together with the plus tree (fig. 2). Generally speaking, the hazard of damage is high; in stormy weather the isolations are ruined, and the seeds are destroyed by insects, birds and squirrels, etc. In short our many years of endeavour gave very discouraging results and we concluded that the only way to proceed was to graft the plus trees, let the grafts grow out for some years and perform the crosses at a height from the ground of one or two meters. This means that a serious crossing programme cannot be accomplished until 8–10 years after the selection of the plus trees. Thus, if grafting on a broad scale was performed immediately after the plus tree selection was made and a clonal orchard established, seeds would be produced in considerable quantities years before it was even possible to establish a progeny test plantation.

**The experimental period:**

We have a very scanty knowledge of the correlations between juvenile behaviour and performance in higher ages. In Sweden the working hypothesis has been adopted that the test period must cover one third of the rotation period, i.e. most often 25–40 years under our conditions. Consequently the seedling progeny test orchard could not come into existence until 35–50 years after the plus tree selection. During this period the clonal orchard has produced large quantities of seed and most probably this type of orchard will not be kept much longer, firstly because it will be possible to establish better seed orchards when the progeny tests have been accomplished, and secondly, because the seed orchard will be more and more difficult to harvest and manage with age.

However, it has been stated above that the unselected progeny test plantation with full-sib families gives seed of the same genetical quality as the clonal orchard. This is of course true but the seed production in young stands of pine, spruce, oak and beech up to an age of 30–40 years is practically speaking non-existent.

**Flowering behaviour of grafts from old trees and seedlings:**

It is a well known phenomenon that grafts from old individuals more or less retain the senile characteristics of their origin, a phenomenon which is often referred to as topophysis but should rather be called cyclophysis. The cyclophysis phenomenon manifests itself strongly in the flowering of grafts from old trees, which is much more abundant than in young trees from seed. For instance, in a clonal plantation with *Pinus silvestris* grafts from 1949 the cone harvest in 1959 was on an average for 32 clones 70.7 cones per tree with a clonal variation from 1 to 277 cones per tree. In a progeny test plantation of the same species, sown in 1937, the cone production was recorded in 1953, when the trees were 16 years old. It averaged only 1.43 cones per tree for 7,190 trees of 34 families with a highest family mean of 1.94 cones per tree. The comparison is perhaps biased to some extent. However, the fact that the Northern tree species flowers very sparsely in young, dense stands is proved by every day observations. Also when growing solitarily young trees have almost no inclination to flower. For instance, in a rather extensive material of 25-year old, solitary *Picea Abies* at Ekebo almost no cone has appeared up to now. Male flowering on young trees is still more infrequent than female flowering. Thus, the cone production in a seedling orchard-progeny test during the experimental period is completely insignificant.

When the experimental period is finished and the strong, selective thinning to a spacing of about 5 × 5 meters is carried out, the trees have small crowns. During the following years after the thinning, the trees will enter a vegetative phase, characterized by crown development and limited fruiting, on account of which it will take 50–60 years from the plus tree selection before a more considerable seed harvest may be expected.

**The location of the seed orchards:**

A seed orchard should be established at a distance from other occurrences of the same species in order to avoid contaminating pollen. Moreover, orchards for climatically

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*Fig. 3.* Map showing the sub-division of Sweden in 15 orchard zones for *Pinus silvestris* and locations of the seed orchards.
unfavourable regions, where the intervals between the seed years are long and the seed maturity often unsatisfactory, should be located in better climates. In Sweden these rules have been followed logically; this is partly illustrated by the map in fig. 3, which shows the sub-division of the country into 15 orchard zones for Pinus silvestris and the location of the seed orchards of the same species. The possibility of obtaining seed orchards, isolated by distance, is often dependent on choice of a site, detrimental to the vegetative development of the species. Seed orchards of Pinus silvestris are located in areas with clay soil where spruce and broad-leaved forests prevail, and orchards of Picea Abies in areas with sandy soil and pine as the dominating tree.

A plantation for progeny testing must, however, be located in the intended zone of cultivation and on a site where the species belongs in order to have any significance. Under Swedish conditions it means that a plantation for progeny testing can rarely be located on a site, isolated by distance; and as regards the northern part of the country location of the seed orchards to climatically more favourable places in the coastal region further south is of decisive importance. Thus, the locations of a seed orchard and of a progeny test plantation are determined by controversial factors.

Measures for facilitating the seed harvest:

For the seed harvest it is desirable that the crowns of the orchard trees stand directly on the ground without a bole as connecting link. Therefore, in the orchards, established with wide spacing, the trees are trimmed by systematic removal of leaders and thus desirable crop trees are obtained as seen in fig. 4. Such a treatment is, of course, out of the question in a seedling orchard-progeny test during the experimental period. If we keep to a test period of 30 years for Pinus silvestris in Sweden, the plantation has the appearance, shown in fig. 5, at the end of the test period. The mean height is about 12 meters, the stem without living branches 6 meters long and the D.B.H. 10 cms. In this situation there is hardly anything else to do than to permit the trees to grow intact in the future also, which entails greater difficulties in harvesting the seed than in an orchard with trees, trimmed from the start.

Conclusions

The genetical gain which may occur by selection of a certain number of plus trees can be utilized in seed production in two ways.

A. The plus trees are propagated vegetatively and a clonal seed orchard is established. This is planted in wide spacing, on a site, isolated by distance, and in a climate, favourable for seed production, if necessary outside the zone of cultivation. The trees are trimmed in order to reduce the height growth, thus facilitating the seed harvest and in other respects (manuring etc.) treated solely with the aim of promoting seed harvest, quantitatively and qualitatively.

B. The plus trees are crossed among each other. Of the seedlings obtained a seed orchard is established as for A.
If all clones in the alternative A are of the same size and have equal seed and pollen production, and if in the alternative B all plus trees are parents of the orchard trees in the same frequency and the orchard trees have the same fertility, the genetical gain will be equal in both cases (the Hardy-Weinberg law).

If all necessary crosses can be performed in immediate connection to the plus tree selection and if the species in question attains fruiting maturity early, the method B may be preferable, particularly if the vegetative propagation of the species is difficult, otherwise method A is superior. Under Swedish conditions (species such as Pinus silvestris, Picea Abies, Quercus robur, Pagus sylvestris) method A will give a time gain of 20–30 years on account of which this method is the one exclusively used.

Repeated selection can be performed after progeny tests which have been observed over a sufficiently long period. For the progeny testing the plus trees are crossed with each other in suitable combinations, conveniently in a partial diallel system. The test plantations are established with the current silvicultural spacing on a site within the region, which is fit for the species. The test results can be expressed in breeding values for the parents as well as in individual and family heritabilities.

When the progeny test has been accomplished the following possibilities for repeated selection are open, provided that the test results show that general combining ability outweighs specific combining ability:

C. A new clonal orchard can be established by repeated vegetative propagation of the clones having the best general combining ability.

D. The test plantations can be transformed into seed orchards by individual, family and combined selection. The highest selection intensity is around 1:10, which equals a selection differential of 1.7 o. By stronger selection the number of trees left per unit area will be all too small.

E. A small number of the best trees in the test plantation are selected, the selection differential being ca. 3 o. These trees are propagated vegetatively and a new clonal seed orchard is established.

If alternative C is applied in such a way that one third of the original clones are used anew and alternative D is practised with combined selection of the best third of the individuals in the best third of the progenies, a genetical gain of the same magnitude will probably be obtained. The calculations, presented by Wacour (1963), are completely wrong. However, it must be kept in mind that the D-method always involves certain frequencies of full-sib and half-sib matings. The applicability of this method is limited also by the fact that the test plantations are rarely isolated by distance or located in a climate, favourable for seed production. Moreover, from the start it has been impossible to give the trees a form suitable for seed harvest. Under Swedish conditions this type of repeated selection will probably play a minor role, and the methods C and E will certainly be preferred.

The seedling seed orchard-progeny test method according to D can substitute the original clonal orchard according to A only if the test crosses can be made on the plus trees in close connection with the plus tree selection, if the test period can be made very short, if the fruiting maturity sets in early, and if the test plantation is isolated by distance and located in a favourable climate. Establishment of clonal orchards of type A is therefore almost well accounted for, particularly under the conditions prevailing in Scandinavia.

Summary

1. Breeding by selection through clonal seed orchards as proposed by Synge (1934) and through seedling seed orchards-progeny tests as proposed by Faber (1925) and later strongly recommended by Wacour (1963) is discussed from genetical and non-genetical points of view.

2. It is pointed out that the relations between the genetical gains of plus tree selection and of individual selection in progeny tests, assumed by Wacour, is very doubtful.

3. It is stated that Wacour's calculations of genetical effects of clone selection, based on progeny tests, are wrong.

4. Some calculations of the genetical gains to be expected by different procedures of selection have been set forth. In the model case, examined here, the following results were obtained.

I. A new clonal orchard, established with the one third best clones. Additional gain in relation to the original clonal orchard 8.2%.

II. Selection of the best one third of the families in the progeny test. Additional gain 3.8%.

III. Selection of the best one third of the individuals in the best one third of the families. Additional gain 8.8%.

IV. Selection of the best tree in the best one third of the families. Additional gain 13.8%.

5. The following non-genetical circumstances must be considered.

a. On account of the periodicity of the flowering, crosses can at first be performed several years after the plus tree selection in boreal regions.

b. Accomplishment of a systematic crossing programme with the plus trees as mothers might be associated with unconquerable, practical obstacles. In such cases the plus trees must be propagated vegetatively as a preparatory measure, the crosses being made at first several years after the plus tree selection.

c. Many tree species attain fruiting maturity late. On the other hand, grafts from old trees fruit from the start—cyclophyll.

d. As far as we know at present the progeny test period must comprise at least one third of the rotation period, i.e. 30–40 years in boreal regions.

e. If seed orchards for regions with hard climates, where the intervals between the seed years are long and the seed development often poor, are located in regions with better climates the seed production is promoted quantitatively and qualitatively as well. Test plantations, however, must be located in the region.

f. Seed orchards should be isolated by distance. For this reason it is often necessary to choose sites which are unnatural for the species in question. Test plantations, on the other hand, must be established on sites where the species belongs.

g. In a plantation with no other aims than seed production the trees can be treated in ways most suitable for seed production, in other words, be trimmed in order to reduce the height growth, thus facilitating the seed harvest. Such measures are out of the question in a test plantation.
6. With reference to the genetical and non-genetical circumstances set forth the following conclusions are drawn:
a. Establishment of clonal seed orchards is well accounted for.
b. When reliable results of progeny tests are obtained — in 40–60 years in Sweden — these will most likely be utilized for the establishment of new seed orchards by using these original clones, which possess the highest breeding values or new clones raised from the best trees in the test plantations. Utilization of the test plantations themselves as seed sources after combined selection will probably be practised only exceptionally, when particularly favourable circumstances are at hand.

Résumé
Titre de l'article: Amélioration des arbres forestiers par sélection, vergers à graines de clones, vergers à graines de semis, tests de descendance.
1. L’amélioration par sélection à l’aide de vergers à graines de clones proposée par Syrach Larsen (1934) et à l’aide de vergers à graines de semis — tests de descendance proposés par Fabricus (1922) et plus tard fortement conseillés par Wschn (1953) est étudiée des points de vue génétique et non génétique.
2. On fait remarquer que les rapports établis par Wschn entre les gains génétiques de la sélection d’arbres plus et de la sélection d’individus dans les tests de descendance sont très douteux.
3. On démontre que les calculs faits par Wschn des effets génétiques de la sélection de clones, basés sur les tests de descendance, sont faux.
4. Des calculs de gains génétiques à attendre des différentes méthodes de sélection ont été exposés. Dans le cas type étudié ici, on a obtenu les résultats suivants:
   I. Un nouveau verger, établi avec le premier tiers des meilleurs clones. Gain supplémentaire par rapport au verger primitif: 8,2%.
   II. Sélection du meilleur tiers des familles dans le test de descendance. Gain supplémentaire : 5,8%.
   III. Sélection du meilleur tiers des individus dans le meilleur tiers des familles. Gain supplémentaire: 6,8%.
   IV. Sélection du meilleur arbre dans le meilleur tiers des familles. Gain supplémentaire: 13,9%.
5. Il faut considérer les conditions non génétiques suivantes:
   a. En raison de la périodicité de la floraison, les croisements peuvent être effectués pour la première fois plusieurs années après la sélection des arbres plus dans les régions boréales.
   b. L’exécution d’un programme de croisement systématique où les arbres plus sont pris comme mères pourrait être entravée par des obstacles pratiques insurmontables. Dans de tels cas, il faut multiplier les arbres plus par voie végétative comme mesure préparatoire et ne commencer les croisements que plusieurs années après la sélection d’arbres plus.
   c. Chez de nombreuses espèces d’arbres, les fruits mûris tard. Par contre, les greffes prélevées sur de vieux arbres donnent des fruits dès le départ (cyclophysis).
   d. Selon nos connaissance actuelles, la durée du test de descendance doit être au moins le tiers de la durée de révolution, c’est-à-dire de 30 à 40 ans dans les régions boréales.
   e. Si les vergers à graines destinés à des régions à climat rigoureux où les intervalles entre années de production sont longs et le développement des graines souvent médiocre, sont situés dans des régions à climat plus favorable, la production de graines est améliorée aussi bien quantitativement que qualitativement. Les plantations comparatives doivent cependant être situées dans la région d’origine.
   f. Les vergers à graines doivent être isolés. C’est pourquoi il est souvent nécessaire de choisir des emplacements en dehors de l’aire naturelle de l’espèce. Par contre, les plantations comparatives doivent être installées dans la zone naturelle de l’espèce.
   g. Dans une plantation destinée uniquement à la production de graines, les arbres peuvent être traités de manière à favoriser la production de graines, en d’autres termes, être élagués de manière à réduire la croissance en hauteur et ainsi favoriser l’production de graines. De telles mesures sont hors de question dans une plantation comparative.
6. En ce qui concerne les conditions génétiques et non génétiques exposées, on peut tirer les conclusions suivantes:
   a. L’établissement de vergers à graines de clones est parfaitement justifié.
   b. Lorsqu’on aura obtenu des résultats valables à partir des tests de descendance (dans 40 à 60 ans en Suède), on pourra très vraisemblablement utiliser ces résultats pour l’établissement de nouveaux vergers à graines à partir des clones primitifs qui possèdent les meilleures qualités d’amélioration ou de nouveaux clones obtenus en prenant les meilleurs arbres des plantations comparatives. Il est probable qu’on n’utilisera les plantations comparatives elles-mêmes comme sources de grains après une sélection combinée à titre exceptionnel, lorsque l’on disposera de conditions particulièrement favorables.

Zusammenfassung
Titel der Arbeit: Forstpfanzenzüchtung durch Auslese, Klonensamplanteagen, Sämlings-Samplanteagen und Nachkommenschaftsprüfungen.
2. Es wird darauf hingewiesen, daß der von Wschn angegebene Zusammenhang zwischen dem Züchtungsfortschritt bei Plusbaumaulese und bei Individualauslese in Nachkommenschaftsprüfungen sehr zweifelhaft ist.
   I. eine neue Samplanteagen mit den 33% besten Klonen einen zusätzlichen Züchtungsfortschritt von 8,2%.
   II. Auslese der 33% besten Familien in der Nachkommenschaftsprüfung 5,8%.
III. Auslese der 33% besten Einzelbäume innerhalb der 33% besten Familien 8,8%.
IV. Auslese der besten Bäume in den 33% besten Familien 13,8%

5. Folgende nichtgenetische Umstände sind zu beachten:
   a. In der borealen Zone können auf Grund der Blüh-
      periodizität Kreuzungen erst einige Jahre nach der
      Plusbaumauslese gemacht werden.
   b. Die Durchführung eines systematischen Kreuzungs-
      programms mit den Plusbäumen als Mutterbäumen
      dürfte auf unüberwindliche praktische Schwierigkei-
      ten stoßen. In solchen Fällen müssen die Plusbäume
      als vorbereitende Maßnahme vegetativ vermehrt wer-
      den, wonach Kreuzungen erst einige Jahre nach der
      Plusbaumauslese gemacht werden können.
   c. Viele Baumarten erreichen die Geschlechtsreife spät.
      Auf der anderen Seite fruchten Prorpflinge von alten
      Bäumen von Anfang an — Zyklophysis.
   d. Soweit wir heute wissen, muß der Versuchszzeitraum
      der Nachkommenschaftsprüfung wenigstens ein Drit-
      tel der Umlaufzeit umfassen, z. i. in der borealen
      Zone 30 bis 40 Jahre.
   e. Werden Samenplantagen für Gebiete mit harten Kli-
      mabedingungen, wo die Intervalle zwischen Mastjah-
      ren lang sind und die Samenentwicklung oft mäßig
      gut ist, in Gebiete mit günstigerem Klima verlegt, so
      werden Qualität und Quantität der Saatguterzeugung
      in gleicher Weise förderlich beeinflußt. Versuchsflä-
      chen müssen jedoch in der Region liegen, für die ge-
      züchtet wird.
   f. Samenplantagen sollten durch Distanz isoliert sein.
      Aus diesem Grunde ist es oft erforderlich, Standorte zu
      wählen, die für die betreffende Species unnatürlich
      sind. Auf der anderen Seite müssen Versuchsflächen
      auf Standorten angelegt werden, auf die die Species
      gehört.
   g. In einer Pflanzung zum alleinigen Zweck der Saat-
      guterzeugung müssen die Bäume so behandelt wer-
      den, daß sie diesen Zweck am besten erfüllen; sie
      müssen m. a. W. beseitigt werden, damit das Hö-
      henwachstum verhindert und die Saatguternte er-
      leichtert wird. Solche Maßnahmen stehen in einer
      Versuchsanordnung außer Frage.

6. Mit Bezug auf die angeführten genetischen und nicht-
   genetischen Umstände werden diese Schlußfolgerungen
   gezogen:
   a. Es wird zugunsten der Anlage von Klonsamenplan-
      tagen entschieden.
   b. Wenn verlässliche Ergebnisse von Nachkommens-
      schaftsprüfungen vorliegen — in Schweden nach 40
      bis 60 Jahren — so werden sie sehr wahrhaftig zur
      Anlage neuer Samenplantagen benutzt, indem von
      den ursprünglichen Klonen die mit den höchsten
      Zuchtwerden oder neue Klon von den besten Bäumen
      in den Nachkommenschaftsprüfungen verwendet wer-
      den. Die Benutzung der Versuchsflächen zur Nach-
      kommenschaftsprüfung, selbst als Saatgutbestände
      nach kombinierter Auslese, wird wahrscheinlich nur
      in Ausnahmefällen eintreten, wenn besonders günsti-
      ge Umstände vorliegen.

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radiation (p. 3–8).

Bei Pinus rigida Mill. nahm das Keimprozent deutlich
mit der akkumulierten Strahlungsmenge ab, die der Mut-
terbaum empfangen hatte. Bei Quercus alba war eine star-
ke Zunahme der Mortalität in den Nachkommenschaf-
ten mit Zunahme der empfangenen Dosis zu beobachten. Auch
die Hypokotylängen waren bei Pinus mit zunehmender Strah-
lungsmenge geringer, während bei Quercus diese Erschei-
nung nicht so klar zutage trat. Die größere Empfindlichkeit
von Pinus wird auf den 5–10mal größeren Durch-
messer der Interphase-Kerne zurückgeführt. Polleninflug
von nicht bestrahlten Bäumen konnte die Ergebnisse be-
einträchtigt haben.

HAMILTON, L. S., and FROMMER, C. H.: Some seed source
studies of Scotch Pine in New York (p. 8–25).

Bei Nachkommen zweier Individuen aus dem Staate New York
an drei bzw. fünf Anbauorten traten in einigen Merkmalen signifikante Unterschiede zwischen Anbauor-
ten auf. In zwei Versuchen mit fünf bzw. acht Herkünften
aus Europa und New York wurden bei mehreren Merkma-
len signifikante Unterschiede festgestellt.

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specific gravity and fiber length in Populus tremuloides
clones (p. 25–39).