Forest Tree Breeding by Selection

Clonal Seed Orchards — Seedling Seed Orchards, Progeny Tests

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Within a region where a technically valuable tree species is of common occurrence and on an 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.

FABRICIUS (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 performad 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 af seiected trees (plus trees), this gain being denoted by ΔG. In order to emphasize that this unit refers to individual selection in the progenies of the plus trees, it will be written ΔG_i here. Consequently the gain of the plus tree selection can be written ΔG_p. WRIGHT puts $\Delta G_p = k \cdot \Delta G_i$ and defines the constant as k = heritability in wild stand/heritability, determined from a progeny test $= h^2_p / h^2_i$. According to WRIGHT h^2_i should always exceed h^2_p and thus $k < 1$. In his numerical examples WRIGHT 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 ΔG! According to definition $\Delta G = i \cdot \sigma \cdot h^2$ with i = the selection intensity, σ = the standard deviation and h^2 = the heritability. Thus we have:

for plus tree selection $\Delta G_p = i_p \cdot \sigma_p \cdot h^2_p$,

and for individual selection in the progenies

$$\Delta G_i = i_i \cdot \sigma_i \cdot h^2_i.$$

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 $i_i = 1.75$.

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 σ_i refers to younger ages in a practical application. A priori the correlation between σ_i and σ_p is unknown and $\sigma_i \neq \sigma_p$.

Thus even h^2_i really should be greater than h^2_p, ΔG_p may very well be greater tban ΔG_i. Hence WRIGHT'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 tests:

In his calculations WRIGHT puts the genetical gain of the seed of a seedling plantation of crosses 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 negligeable. 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 genetically 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 WRIGHT 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:

Type of Planting	Thinned to	Genetic Superiority of Seed Produced	
		Before thinning	After thinning
FAMILY SELECTION METHODS - SEEDLING SEED ORCHARDS, PROGENY TESTS			
IV. Selected $\times$ wind	Best families	$\frac{1}{2}\, k\, \Delta G$	$\frac{1}{2}\, k\, \Delta G + \Delta G_{hs}$
CLONAL SEED ORCHARDS - ACCOMPANIED BY SEEDLING PROGENY TESTS			
VIII. Selected clones	Clones with best general combining ability	$k\, \Delta G$	ΔG_{hs}

In this writing $\Delta G = \Delta G_i$ = the gain of individual selection in the progenies, and ΔG_{hs} 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 follow:

$$\frac{ABC}{aBC},\ \frac{ABC}{AbC},\ \frac{ABC}{Abc},\ \frac{ABC}{abC},\ \frac{ABC}{aBc},\ \frac{ABC}{abc}.$$

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:

ABC : ABc : AbC : aBC : abC : aBc : Abc : abc.

The progenies of the first two plus trees ($\frac{1}{3}$ of the families) are selected in a seedling seed orchard – progeny test. These two progenies have the following composition:

$$1\frac{ABC}{ABC} : 1\frac{ABC}{ABc} : 1\frac{ABC}{AbC} : 2\frac{ABC}{aBC} : 1\frac{ABC}{Abc} : 2\frac{ABC}{aBc} : 2\frac{ABC}{abC} :$$

$$1\frac{ABC}{abc} : 1\frac{aBC}{aBC} : 1\frac{abC}{aBC} : 1\frac{aBc}{aBC} : 1\frac{Abc}{aBC} : 1\frac{aBC}{abc}.$$

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 4 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 ($\frac{1}{3}$ of the clones), the progeny will be:

$$1\frac{ABC}{ABC} : 1\frac{ABC}{aBC} : 1\frac{ABC}{AbC} : 1\frac{AbC}{aBC}$$

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 WRIGHT to produce seed with a genetical superiority = ΔG_{fs}, 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 biclonal 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 (ΔG_i) 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.

Clone No.		13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
	Breeding values	45	45	50	53	53	50	48	57	46	43	51	47	49	48	56	51	50	52
1	52	97	97	102	105	105	102	100											
2	54		99	104	107	107	104	102	111										
3	55			105	108	108	105	103	112	101									
4	44				97	97	94	92	101	90	87								
5	49					102	99	97	106	95	92	100							
6	49						99	97	106	95	92	100	96						
7	50							98	107	96	93	101	97	99					
8	55								112	101	98	106	102	104	103				
9	54									100	97	105	101	103	102	110			
10	51										94	102	98	100	99	107	102		
11	46											97	93	95	94	102	97	96	
12	47												94	96	95	103	98	97	99
13	45													94	93	101	96	95	97
14	45														93	101	96	95	97
15	50															106	101	100	102
16	53																104	103	105
17	50																	100	102
18	48																		100

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.s/2 (n = the number of clones), i. e. in our case 105. The total for any characteristic, observed in the progeny test, is put = 100. We assume that general combining ability strongly preponderates in comparison with specific combining ability. The family mean for a progeny, M_F, is then additively made up by $a_i + a_j$ = 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 th best 35 families (family selection),

C. The test plantation is transformed to a seed orchard by selection of the best third of the best 35 famlies (combined selection).

D. A new clonal orchard is established with the best tree in each of the 35 best families.

A l t e r n a t i v e 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 108 2.

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.

Clone No		2	3	8	9	16	17	20	27	30
	Breeding value	54	55	55	54	53	53	57	56	52
1	52	106	107	107	106	105	105	109	108	104
2	54		109	109	108	107	107	111	110	106
3	55			110	109	108	108	112	111	107
8	55				109	108	108	112	111	107
9	54					107	107	111	110	106
16	53						106	110	109	105
17	53							110	109	105
20	57								113	109
27	56									108

A l t e r n a t i v e 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:	*98*	*99*	*100*	*101*	*102*	*103*	*104*	*105*	*106*
Percentage of all families:	0.2	0.6	1.6	3.4	6.1	9.3	12.1	13.9	13.9
Families with mean:	*107*	*108*	*109*	*110*	*111*	*112*	*113*	*114*	*115*
Percentage of all families:	12.3	9.8	7.0	4.6	2.7	1.4	0.7	0.3	0.1

The total for all families is 105.8.

A l t e r n a t i v e 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	860	694	313	254	98	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*
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

Percentage of all families: (second row above)

The total for all families is 108.8.

A l t e r n a t i v e 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:

110	*111*	*112*	*113*	*114*	*115*	*116*	*117*	*118*	*119*	*120*
2.9	8.8	16.4	20.6	18.0	14.2	9.0	5.9	3.0	0.5	0.7

Percentage of all families: (second row above)

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%

Table 3. — Frequencies of individual breeding values in the 35 best progenies.

Family means	Number of families	Individual breeding values of the progenies													
		47	48	49	50	51	52	53	54	55	56	57	58	59	60
102	6	6	48	168	336	420	336	168	48	6					
103	5		5	40	140	280	350	280	140	40	5				
104	4		4	32	112	224	280	224	112	32	4				
105	6			6	48	168	336	420	336	168	48	6			
106	4			4	32	112	224	280	224	112	32	4			
107	4				4	32	112	224	280	224	112	32	4		
108	2				2	16	56	112	140	112	56	16	2		
110	1					1	8	28	56	70	56	28	8	1	
111	1						1	8	28	56	70	56	28	8	1
112	2						2	16	56	112	140	112	56	16	2
Total	35	6	57	250	674	1253	1705	1760	1420	932	523	254	98	25	3

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 $\Delta G = i \cdot \sigma \cdot h^2$ the stronger selection in D will always give better response than the weaker one in C. We have:

$$C = 105.8 + 1.7\,\sigma \cdot h^2$$
$$D = 105.8 + 2.9\,\sigma \cdot h^2.$$

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:

Frequencies of matings		
between full sibs	between half sibs	between unrelated
2.9%	14.0%	83.1%

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.

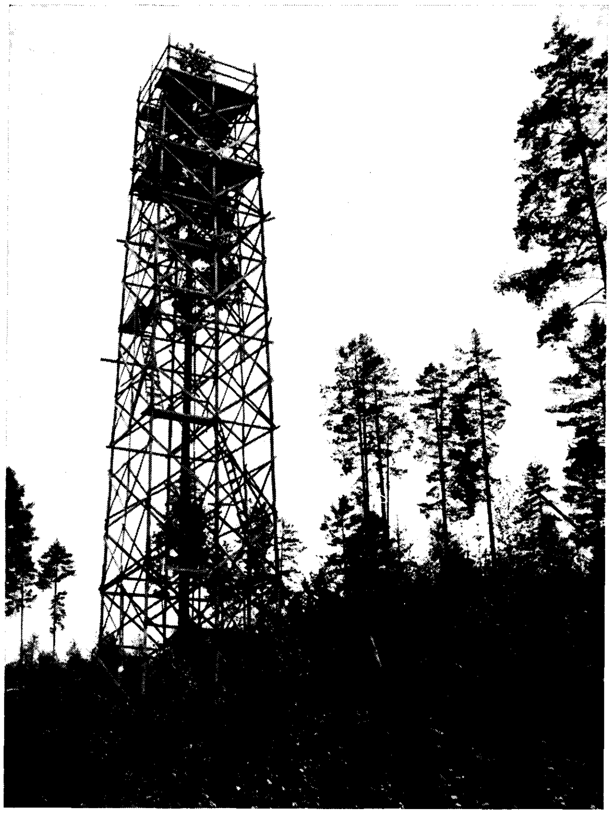

Fig. 1. — Scaffolding for making possible crosses on old plus trees

Fig. 2. — Scaffolding and plus tree have blown down.

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 scaffoldings. 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 seed-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

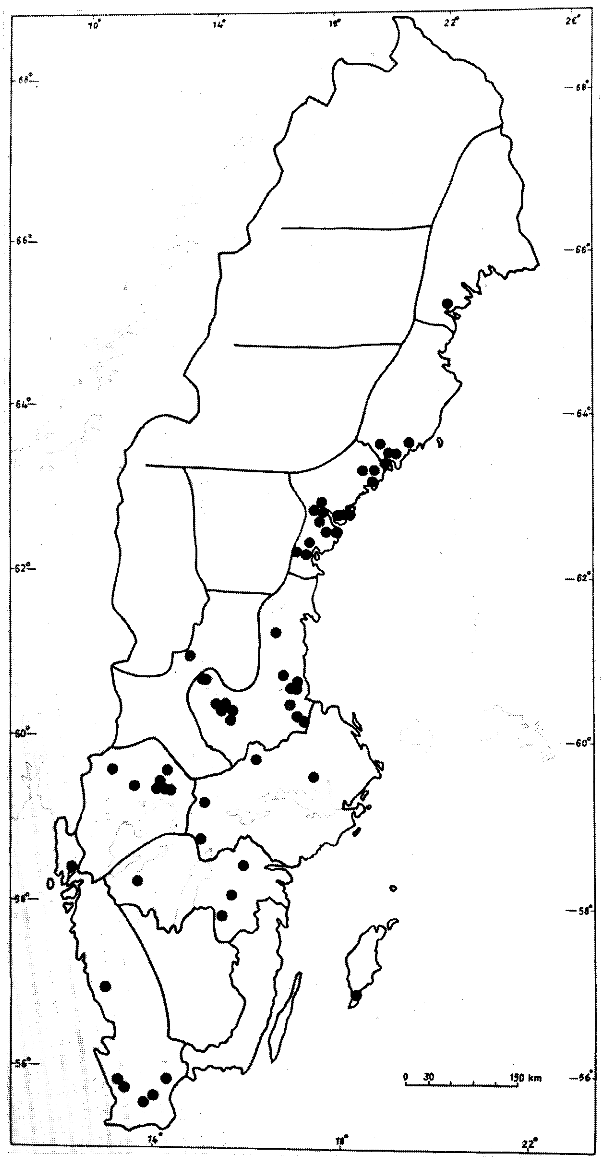

Fig. 3. — Map showing the sub-division of Sweden in 15 orchard zones for *Pinus silvestris* and locations of the seed orchards.

Fig. 4. — Seed orchard of *Pinus silvestris*, crop trees trimmed by removal of leaders in order to facilitate the seed harvest.

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.

Fig. 5. — Progeny test plantations of *Pinus silvestris*, 20 years old.

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, Fagus silvatica)* 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 σ. 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 σ. 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 WRIGHT (1962), 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 SYRACH LARSEN (1934) and through seedling seed orchards-progeny tests as proposed by FABRICIUS (1922) and later strongly recommended by WRIGHT (1962) 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 WRIGHT, is very doubtful.
3. It is stated that WRIGHT'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 — 5.8%
   - 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 — cyclophysis.
   - 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 Fabricius (1922) et plus tard fortement conseillés par Wright (1962) est étudiée des points de vue génétique et non génétique.
2. On fait remarquer que les rapports établis par Wright 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 Wright 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: 8,8%.
   IV. Sélection du meilleur arbre dans le meilleur tiers des familles. Gain supplémentaire: 13,8%.
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 systèmatique 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 mûrissent tard. Par contre, les greffes prélevées sur de vieux arbres donnent des fruits dès le départ (cyclophysis).
   d. Selon nos connaissances 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 la 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 justifiée.
   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 graines après une sélection combinée qu'à titre exceptionnel, lorsque l'on disposera de conditions particulièrement favorables.

Zusammenfassung

Titel der Arbeit: *Forstpflanzenzüchtung durch Auslese, Klonsamenplantagen, Sämlings-Samenplantagen und Nachkommenschaftsprüfungen.*

1. Auslesezüchtung durch Klonsamenplantagen nach dem Vorschlag von Syrach Larsen (1934) und Sämlings-Samenplantagen, die von Fabricius (1922) vorgeschlagen und später von Wright (1962) sehr empfohlen wurden, wird unter genetischen und nichtgenetischen Gesichtspunkten diskutiert.
2. Es wird darauf hingewiesen, daß der von Wright angenommene Zusammenhang zwischen dem Züchtungsfortschritt bei Plusbaumauslese und bei Individualauslese in Nachkommenschaftsprüfungen sehr zweifelhaft ist.
3. Es wird festgestellt, daß Wright's Berechnungen der genetischen Wirksamkeit der Klonauslese an Hand von Nachkommenschaftsprüfungen falsch sind.
4. Einige Berechnungen der zu erwartenden Züchtungsfortschritte bei verschiedenem Vorgehen der Auslese wurden angestellt. In dem hier untersuchten Modellfall wurden die folgenden Ergebnisse erhalten. Gegenüber einer ursprünglichen Klonsamenplantage gewährleisten:
   I. eine neue Samenplantage 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 Blühperiodizität Kreuzungen erst einige Jahre nach der Plusbaumauslese gemacht werden.

b. Die Durchführung eines systematischen Kreuzungsprogramms mit den Plusbäumen als Mutterbäumen dürfte auf unüberwindliche praktische Schwierigkeiten stoßen. In solchen Fällen müssen die Plusbäume als vorbereitende Maßnahme vegetativ vermehrt werden, wonach Kreuzungen erst einige Jahre nach der Plusbaumauslese gemacht werden können.

c. Viele Baumarten erreichen die Geschlechtsreife spät. Auf der anderen Seite fruchten Pfropflinge von alten Bäumen von Anfang an — Zyklophysis.

d. Soweit wir heute wissen, muß der Versuchszeitraum der Nachkommenschaftsprüfung wenigstens ein Drittel der Umtriebszeit umfassen, d. i. in der borealen Zone 30 bis 40 Jahre.

e. Werden Samenplantagen für Gebiete mit harten Klimabedingungen, wo die Intervalle zwischen Mastjahren 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. Versuchsflächen müssen jedoch in der Region liegen, für die gezüchtet 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 Saatguterzeugung müssen die Bäume so behandelt werden, daß sie diesen Zweck am besten erfüllen; sie müssen m. a. W. beschnitten werden, damit das Höhenwachstum vermindert und die Saatguternte erleichtert wird. Solche Maßnahmen stehen in einer Versuchspflanzung außer Frage.

6. Mit Bezug auf die angeführten genetischen und nichtgenetischen Umstände werden diese Schlußfolgerungen gezogen:

a. Es wird zugunsten der Anlage von Klonsamenplantagen entschieden.

b. Wenn verläßliche Ergebnisse von Nachkommenschaftsprüfungen vorliegen — in Schweden nach 40 bis 60 Jahren — so werden sie sehr wahrscheinlich zur Anlage neuer Samenplantagen benutzt, indem von den ursprünglichen Klonen die mit den höchsten Zuchtwerten oder neue Klone von den besten Bäumen in den Nachkommenschaftsprüfungen verwendet werden. Die Benutzung der Versuchsflächen zur Nachkommenschaftsprüfung, selbst als Saatgutbestände nach kombinierter Auslese, wird wahrscheinlich nur in Ausnahmefällen eintreten, wenn besonders günstige Umstände vorliegen.

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Proceedings, Tenth Northeastern Forest Tree Improvement Conference, Durham, N. H., August 1962. Publ. in 1963, p. 88.

Mergen, F., and Stairs, G. R.: *Progeny test from a Pitch Pine — oak forest damaged by low level chronic gamma radiation* (p. 3—8). —

Bei *Pinus rigida* Mill. nahm das Keimprozent deutlich mit der akkumulierten Strahlungsmenge ab, die der Mutterbaum empfangen hatte. Bei *Quercus alba* war eine starke Zunahme der Mortalität in den Nachkommenschaften mit Zunahme der empfangenen Dosis zu beobachten. Auch die Hypokotyllänge war bei *Pinus* mit zunehmender Strahlungsmenge geringer, während bei *Quercus* diese Erscheinung nicht so klar zutage trat. Die größere Empfindlichkeit von *Pinus* wird auf den 5- bis 10mal größeren Durchmesser der Interphase-Kerne zurückgeführt. Polleneinflug von nicht bestrahlten Bäumen konnte die Ergebnisse beeinträchtigt 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 Anbauorten auf. In zwei Versuchen mit fünf bzw. acht Herkünften aus Europa und New York wurden bei mehreren Merkmalen signifikante Unterschiede festgestellt.

Brown, I. R., and Valentine, F. A.: *Natural variation in specific gravity and fiber length in Populus tremuloides clones* (p. 25—39). —

Vier auf verlassenem Farmland natürlich angesiedelte Klone von *Populus tremuloides* Mixch. wurden durch die Einheitlichkeit des Geschlechts und nach Messung von Blattmerkmalen auch als Klone identifiziert. Auf Grund signifikanter Unterschiede zwischen Klonen in den Merkmalen Längen-Breiten-Index der Blattspreite (Länge und Breite waren straff positiv korreliert), Blattspitzenwinkel, Blattbasiswinkel und Blattstiellänge wurde im Verein mit dem Befund der Untersuchung der Blütenknospen geschlossen, daß die Baumgruppen einklonig waren. In einigen Fällen waren jedoch Unterschiede zwischen Bäumen gleicher Klone ebenfalls vorhanden. Unterschiede im spezifischen Gewicht des Holzes zwischen den 4 Klonen sind signifikant, die Variation zwischen Mark und Rinde hängt zusammen mit der Geschwindigkeit des Durchmesserwachstums. Die Regression auf die Jahrringbreite ist entweder positiv oder negativ, jedoch ebenfalls signifikant. Da die vom Effekt der Jahrringbreite und namentlich der Entfernung zum Mark bereinigten Faserlängen signifikant unterschieden sind zwischen acht Bäumen (je zwei pro Klon), und die Unterschiede zwischen diesen beiden Bäumen eines Klons nur in einem Falle signifikant waren, wird auf signifikante Klonunterschiede in diesem Merkmal geschlossen. Die Notwendigkeit wird betont, bei Schätzungen genetischer Parameter die Innerklonvarianz von der Kovarianz des Baumdurchmessers bzw. der Entfernung zum Mark zu bereinigen, die nach dieser Verkleinerung des „Fehlers“ ermittelten Schätzwerte für Heritabilitäten sind realistischer.