

étape après les vergers de clones. La conversion d'un test de descendance en un verger de semis a été illustrée par une plantation comparative de *Pinus elliottii* comportant 15 lots de graines. En prenant comme critère de sélection la hauteur des arbres à l'âge de 8 ans, on a éliminé tous les arbres des familles dont la croissance en hauteur moyenne était faible et 75% des arbres des meilleures familles. En procédant de cette manière, on réduirait le nombre primitif d'arbres à l'acre de 1210 à 189, soit 15% du peuplement primitif. La hauteur moyenne des arbres conservés était de 20,05 pieds (env. 6 m) pour 15,64 pieds (env. 4,75 m) dans un lot témoin. Certains arbres ont déjà produit quelques cônes. Si l'on dégage bien les arbres de cette manière, leur production de cônes doit augmenter très rapidement après application d'engrais et autres traitements culturaux.

Zusammenfassung

Titel der Arbeit: Baumverteilung in einer Sämlings-Samenplantage nach Auslese *zwischen* und in Familien.

Die Sämlings-Samenplantage stellt eine Methode der Massenerzeugung züchterisch verbesserten Saatguts dar, deren Züchtungsfortschritt dem einer Klonamenplantage vom gleichen Elternmaterial zumindest gleich sein sollte. Sämlings-Samenplantagen aus Nachkommenschaftsprüfungen eignen sich besonders zur Erweiterung früher angelegter Klonamenplantagen. Die Überführung einer Nachkommenschaftsprüfung in eine Sämlings-Samenplantage wird an einer Versuchsfläche mit 15 Sorten von *Pinus elliottii* erläutert. Als Auslese Kriterium diente die Baumhöhe im Alter von 8 Jahren. In Sorten mit geringem middle-

rem Höhenwachstum wurden alle Bäume, in den besseren Sorten 75% der Bäume verworfen. Durch diese Maßnahme wäre die ursprüngliche Bestockung von 1210 Bäumen pro acre (2990 Bäumen pro ha) verringert auf 189 Bäume pro acre (465 Bäume pro ha) oder etwa 15% des ursprünglichen Bestandes. Die Mittelhöhe der beibehaltenen Bäume war 20,05 Fuß (etwa 6 m) im Vergleich zu 15,64 Fuß (4,75 m) für eine Kontrollsorte. Einige Bäume haben schon einige Zapfen getragen. Nachdem die Bäume auf diese Weise völlig freigestellt sind, sollten sie bei Anwendung von Düngung und anderen Kulturmaßnahmen sehr schnell ihre Zapfenproduktion erhöhen.

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Flowering Age of Clonal and Seedling Trees as a Factor in Choice of Breeding System

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A scion collected from an old tree and grafted on a young seedling often continues to behave as if it were still a part of the old tree. This phenomenon, known as "topophysis" has been studied intensively by MUCKADELL (1959) in Denmark. It includes such things as continued prostrate growth habit on the part of cuttings taken from the lower branches of some trees, continued thornlessness of grafts made from thornless branches of a thorny tree, early or late leaf fall according to whether scion wood is taken from leaf-dropping or leaf-retaining portions of a tree crown, and persistent growth-rate differences of rooted cuttings taken from various portions of a tree crown.

Topophysis also includes the ability of a scion taken from the upper, fruiting portion of a tree crown to continue flowering after being grafted on a young rootstock. This precociousness on the part of grafted trees is a very useful property to tree breeders because it permits the assemblage of flowering material of many scattered clones in a compact breeding arboretum where control-pollination is convenient. It also hastens the time at which seed orchards can be brought into commercial seed-bearing.

The amount by which grafting hastens flower production varies considerably. Seedlings of some northern species do not flower much before their 40th year whereas grafts may bear commercial quantities of seed by the 10th to 15th

year. At the other extreme are forest trees which reach sexual maturity before their 5th year and in which recourse to grafting might slow down seed production. Also, there are trees in which flower production seems to be controlled by general vigor and in which grafting has the same effect as would cultivation or fertilization.

The importance to be placed on early fruiting also varies. Breeders working with very late-blooming species may set early seed harvest as their primary goal. They are justified in ignoring cost and genetic gain considerations. On the other hand, a breeder may wish to achieve the greatest possible genetic improvement over a period of time such as 50 years. In doing so he may consider age of fruiting as less important than heritability or cost.

The present paper is a brief summary of available knowledge on the flowering ages of clones and seedlings, and of the use of such data when choosing a breeding system.

Experimental Evidence on Age of Flowering

Pine (*Pinus*)

RICHTER (1939) compiled a list of minimum flowering ages for 57 pine species or varieties propagated by seed at the Institute of Forest Genetics in California. The minimum

ages varied from 1 to 13 years, most falling within the range 3 to 7. For the production of male strobili the average minimum age was 4.4 years; for female strobili 5.2 years. In a third of the species the two sexes appeared at the same age; in most cases the difference was less than 4 years. In many of the species the meager first flowering was followed by abundant flowering in a year or two.

One species, Chinese pine (*Pinus sinensis* or *P. tabulaeformis* CARR.) was reported by RIGHTER as having male flowers at age 1. There are later reports of pollen production on year-old seedlings of mugo pine (*P. mugo* TURRA) (MERGEN and CUTTING, 1957) and Scotch pine (*P. sylvestris* L.). All three belong to the series *Lariciones* (*Sylvestres*). In each case the seedlings were grown outdoors and the flowers were borne by a small percentage of the total number of trees.

The minimum flowering ages show what may be expected under exceptional conditions. Such data need to be supplemented by average performance records.

Cone production on grafted Scotch pine has been studied intensively in Scandinavia, where there are several hundred acres of clonal orchards. The fruiting records of a few of the Swedish orchards were summarized by JOHNSON (1961). These orchards were established from 1948 to 1952 and evaluated in the winter of 1959-60. For different clones the number of cones per tree varied from 58 to 582 at Maltesholm, 1 to 224 at Trollebo, 22 to 488 at Skullebo, and 1 to 277 at Ekebo. Those cone yields correspond to seed yields of 1 to 22, 1 to 27, 2 to 36, and 0 to 16 kilograms per hectare at the four locations respectively. In general the clonal orchards are expected to yield commercial quantities of seed by the 15th year after grafting (ANDERSSON and ANDERSSON, 1962). Thus they have an approximate 25-year time-advantage over seedlings, which may bear a few female flowers by age 10 or 15 but do not normally produce commercial cone crops until age 40.

Fruiting occurs much earlier on Scotch pine seedlings in the southern part of the Lake States and in some other places where the species is commonly planted. In Michigan, seedlings of central European provenance produce a few cones by the fifth year when cultivated and widely spaced, and large numbers of cones can be observed on unsheared Christmas trees which are less than 7 feet tall. Comparable American data on grafted trees are scanty although the late FRED U. KLAHN obtained moderate numbers of cones in the fifth year after grafting.

Red pine (*P. resinosa* AIT.) is another northern species belonging to the series *Lariciones*. It is noted as being a late fruiter because cone production is usually slight on plantations less than 20 feet tall. Observations in southern Michigan indicate that quantity cone production can be expected earlier if more than the normal 6 × 6-foot spacing is used. One plantation was established in 1952 and by 1958 there were 25 or more conelets on the majority of trees. In subsequent years heavy flowering was maintained on the trees along the border but not on those in the interior of the stand.

Data on the flowering of red pine grafts were supplied by DONALD T. LESTER (personal communication of data to be published separately) of the University of Wisconsin. Of many 6- to 8-year-old grafts planted in various parts of the state some have been flowering for at least 4 years. In northern Minnesota AHLGREN (1962) found that a few 5-year-old grafts produced pollen but that none bore conelets.

The Japanese red pine (*P. densiflora* SIEB. and ZUCC.) and Japanese black pine (*P. thunbergii* PARL.) are noted as being very precocious. Most seedlings grown under good nursery conditions will bear small crops of female and male strobili by their fourth or fifth year. Under field conditions good seed crops can be expected by the sixth or seventh year and it is not unusual to find natural reproduction around trees less than 10 feet tall.

Sexual maturity also occurs early in the series *Insignes*, which includes Monterey pine (*P. radiata* D. DON) and its California relatives jack pine (*P. banksiana* LAMB.), lodgepole pine (*P. contorta* DOUGL.), maritime pine (*P. pinaster* AIT.) and others.

Female flowers were produced in the 7th year on 194/502 (= 38 percent) of the trees in seedling plantations of Monterey pine established on an 8 × 8-foot spacing near Canberra, Australia (J. M. FIELDING, personal communication). There was a tendency for medium and large trees (differences between these classes not significant) to cone earlier than small trees. The percentages of coning trees by size classes were as follows.

Diameter class	Trees with conelets in 7th year
<i>Inches</i>	<i>Percent</i>
0-3.0	28
3.1-5.0	50
5.1-8.0	38

Over 80 percent of the trees produced conelets by the 11th year.

Grafted Monterey pine clonal orchards established on a slightly more favorable site with a 22 × 22-foot spacing provide the most nearly comparable data for grafted trees. Fifty percent of the clones produced conelets in the 4th year; 90 percent in the 6th year. Pollen production was slight through the 6th year.

Jack pine seedlings grown on a wide spacing in a well-watered nursery can be expected to produce flowers by age 3, the maximum number of conelets per tree recorded at that age being 27. This early fruiting is continued and small amounts of commercial seed can be expected from 5-year-old trees given intense care. Under field conditions fruiting is less heavy but relatively early. In a Lake States provenance test 25 percent of the 5-year-old trees of all origins bore cones.

In a 7-year-old provenance trial of maritime pine in New Zealand SWEET and THULIN (1963) reported appreciable differences in cone setting due to origin and site. Fruiting was heaviest in the central portion of the test, presumably due to greater pollen availability. The proportion of trees with cones varied from very low in the slow-growing Moroccan and Corsican origins to 63 percent in some fast-growing types.

Flowering data are available from an extensive series of clonal orchards of loblolly pine (*P. taeda* L.) in southeastern United States (B. J. ZOBEL, personal communication). In most orchards a few female flowers appear in the third year; more female flowers and a little pollen appear in the fourth year; seed in commercial quantities is available by the sixth year. There are a few occasional exceptions to this general trend. For example, some clones are abnormally late, and 3 of 56 orchards are still not producing many flowers.

Over the same region as covered by these orchards there is little flowering on seedling plantations until the 10th

to 15th year, and then only if the trees are planted at a very wide spacing.

GREENE and PORTERFIELD (1962) and others have located a few loblolly pine parents whose seedling progenies bear cones at the age of 3 or 4. Those authors believe it possible to breed for an early flowering type.

Nearly comparable data on flowering of 7-year-old loblolly pine seedlings and grafts can be obtained from two experiments conducted by R. E. GODDARD and J. B. VAN BUIJTENEN in Texas (ANON., 1961). The check plots (no fertilizer or pruning) produced about 34 pollen clusters and 8 female strobili per tree in the seedling plantation; 51 pollen clusters and 5 female strobili per tree in the grafted orchard.

Seedlings of shortleaf pine (*P. echinata* MILL.) and of hybrids between shortleaf and other species grown at Gulfport, Miss. began flowering appreciably in their sixth year. That season there were 25 conelets per tree but the next season there were only 20 conelets per tree (E. B. SNYDER, personal communication).

Virginia pine (*P. virginiana* MILL.) is another southern species which starts appreciable female flower production at a very early age. Small quantities of male and female flowers can be expected on most 3- or 4-year-old seedlings grown under nursery conditions, and large numbers of cones may be found on some 5- or 6-year-old trees (B. J. ZOBEL and E. B. SNYDER, personal communication). Little grafting work has been done.

A group of Maryland seedlings are among the earliest eastern white pines (*P. strobus* L.) to flower. These were the vigorous open-pollinated offspring of an exceptionally fast growing plantation tree. One of the seedlings produced 14 conelets in its fourth year; 19 trees produced 92 conelets in the fifth year; and 28 trees produced 257 conelets in the sixth year (BUCKINGHAM, 1963). The flowering trees were 4 to 10 feet tall. MERGEN (1963) reported successful stimulation of flowering on very young hybrids between eastern white pine and Himalayan white pine (*P. griffithii* McCLELL.). Two-year-old potted seedlings were brought indoors in midwinter and watered with a strong complete fertilizer solution. Ten percent of the trees developed flowers. Similar results were obtained when the treatment was renewed in successive years.

Slower flowering is the rule over most of the range of eastern white pine. Normally, quantity cone production is not expected before the trees are 20 feet tall, even when grown in the open. Trees between 20 and 40 feet may bear several hundred female strobili but little pollen. Thus in most places a seedling seed orchard would have to be interplanted with clonal pollinators or be control-pollinated.

AHLGREN (1962) made a number of field grafts of eastern white pine in northern Minnesota. By the fifth year 23 and 18 percent of all grafts had produced male or female strobili respectively.

Experience with western white pine in northern Idaho indicates that grafted seed orchards will have a slight advantage (BINGHAM *et al.*, 1963). Commercial seed production is expected to started by the 10th year from a recently established clonal orchard. Flowering of seedlings at that age has been relatively sparse and has not been affected greatly mowing, fertilization, or grafting onto older trees (BARNES and BINGHAM, 1963).

Spruce (*Picea*)

White spruce (*Picea glauca* MOENCH) is one of the earliest blooming species in the genus. Moderate numbers of cones can be found on occasional 3- to 4-foot (6- to 10-year-old) specimens and most trees can be brought into quantity cone production by the time they are 8 feet tall (10 to 15 years old). In some parts of the natural range there is considerable year-to-year variation in cone-bearing but if the trees are planted slightly south of their natural range annual fruiting is often the rule. Also, south of the natural range there is a tendency for young trees to bear only female strobili for several years. Recent experimental application of fertilizers and weed control chemicals to young seedlings plantations have not hastened flowering appreciably (HOLST, 1962; D. P. WHITE, personal communication). Data on grafted trees are scanty.

Black spruce (*Picea mariana* [MILL.] B.S.P.) also can flower at a relatively early age, many cones being found on a 4- to 5-foot plantation in southern Michigan.

Norway spruce (*P. abies* [L.] KARST.) seedlings do not flower appreciably until 30 or 40 years old in Scandinavia and 20 to 30 years old in northeastern United States. In grafted Swedish orchards of this species, clonal variability is very pronounced. Some clones produce moderate to large numbers of cones between the fifth and tenth year and others produce none. In these Swedish clonal orchards commercial seed production is expected by the 20th year, giving the clones a 10- to 20-year time advantage over seedlings.

Blue spruce (*P. pungens* ENGELM.) is grown from seed in large numbers. Also, blue clones such as 'Koster' and 'Moorheim' are commonly propagated by grafts or cuttings taken from the lower (pollen-bearing) branches of a large tree. Lacking written records, it is possible to tell the method of propagation of groups of old trees but not of single specimens. Casual observations in several parts of northern United States indicate that flowering age has not been affected greatly by method of propagation although it varies considerably from place to place. In eastern Pennsylvania few male or female strobili were observed on 50- to 60-foot blue (probably clonal) or mixed (seedling) trees over an 11-year period; in eastern Washington heavy cone production was observed on 25- to 40-foot trees of both types in each of three autumns.

Beech (*Fagus*)

European beech (*Fagus sylvatica* L.) seedlings do not bear fruit until many years old and then have sporadic seed crops. In a British grafting experiment, 3 of 11 clones bore female flowers in the third year; 8 of 11 flowered by the 8th year (MATTHEWS, 1960). A tendency toward periodicity in flowering was noted in the clones, flowering being much heavier in 1956 and 1958 than in 1957 and 1959.

Larch (*Larix*)

In both Great Britain and Denmark grafted seed orchards of European (*Larix decidua* MILL.) or Japanese larch (*L. leptolepis* [SIEB. and ZUCC.] PILGER) have fruited adequately in 3 or 4 years to be used in control-pollination experiments (LARSEN, 1956; MATTHEWS *et al.*, 1960).

Under normal field conditions fruiting of seedlings would be delayed for 10 to 15 years although an occasional tree might bear a cone in the fourth year. HOLST (1962) recently reported that 10 percent of a group of 2-year-old seedlings sprayed with uracil flowered. MATTHEWS has suc-

cessfully hastened flowering by training the leading shoots horizontally.

Douglas fir (Pseudotsuga)

In coastal British Columbia clone banks of Douglas fir (*Pseudotsuga menziesii* [MIRB.] FRANCO) were established with plus trees selected from 1957 to 1961. By 1962 the grafts had produced male and female flowers in approximately equal amounts if the scions were taken from the tops of sexually mature trees. Experiments with seedlings resulted in abundant cone production but little pollen in trees as young as 7 years (ORR-EWING, 1962).

Poplar (Populus)

A planting of non-aspen hybrid poplars (*Populus* spp.) involved 90+ combinations between 25+ species. The trees were planted on a fertile soil, using a 6 × 6-foot spacing. Growth was rapid and crowding occurred relatively early. Some progenies flowered in their 6th year, others not until the 12th year (E. J. SCHREINER, personal communication).

If flowering branches are taken from old trees in mid-winter and either rooted or grafted, they can easily be made to bear good seed indoors. The amount of seed produced per branch is such that a moderate-sized greenhouse can function as a seed orchard. However, flowering is not hastened appreciably on field plantings established with rooted cuttings taken from old trees. In SCHREINER's hybrid poplar tests, clonal plantings required about as many years to fruit as did the original ortets.

Fruit Trees

The following fruit tree data applicable to southern Michigan were kindly supplied by R. F. CARLSON.

Species	Age at which commercial quantities of fruit can be expected	
	Grafted or budded trees	Seedlings
	Years	Years
Peach (<i>Prunus persica</i> L.)	3-4	4-8
Sour cherry (<i>P. cerasus</i> L.)	5	6-7
Sweet cherry (<i>P. avium</i> L.)	5	6-7
Apple (<i>Malus pumila</i> L.)		
Dwarf rootstock	4	—
Normal rootstock		
Precocious varieties	5-6	6-7
Not precocious varieties	10-12	15-20

In these crops grafted or budded trees have an advantage of 1 to a few years over seedling trees. This advantage is due in part to the headstart provided by grafting and in part to the fact that existing commercial clones were selected for earliness as well as for fruit quality.

Use of Age-Of-Flowering Data in Choosing a Seed Orchard

Age of flowering is one of several factors governing choice of a seed orchard. Others are amount of genetic improvement, reliability of early test results, and cost of propagation. It is the purpose of the present section to show the relative weight to be placed upon flowering precocity and these other factors when planning a breeding program.

For the present discussion four main types of seed orchard are recognized. The main features of each are as follows.

1. A "seed production area" is an existing stand thinned to the best phenotypes. The orchard is of parental

generation and produces F_1 seed. Lowered seed production cost rather than genetic gain is usually the objective.

2 and 2a. A "clonal seed orchard" and "clonal test-seed orchard" are established in the same manner, using grafted ramets from carefully selected phenotypes ('plus' trees). Both are of parental generation and produce F_1 seed. The two differ according to whether or not the clones are unthinned (clonal orchard) or are thinned on basis of clonal performance (clonal test-seed orchard).

In the case of the ordinary clonal orchard, genetic gain results from mass selection and may be high for traits in which there is a strong parent-progeny correlation. If clonal selection can be practiced, the genetic gain will be increased because of the greater reliability of clone means than of individual-tree measurements. Mathematically the two types may be treated in the same manner if clone means are used in place of individual-tree values.

3. A "progeny test plus clonal orchard" consists of grafted clones of 'elite' trees which have previously been progeny tested. The orchard is of the parental generation and produces F_1 seed. The genetic gain per generation is high because it is based upon the proven ability of certain parents to produce desirable offspring.

4. A "progeny test-seed orchard" consists of a progeny test thinned to the best progenies and then to the best trees within the best families. The orchard is of the F_1 generation and produces seed of the F_2 generation. Either half-sib or full-sib progenies may be used, the half-sibs often giving the most gain per unit of effort and the full-sibs always giving the most gain per parent. Genetic gain from the parental to the F_1 generation results from the proven ability of certain parents to produce desirable offspring and the ability of those F_1 's to transmit the additive variance to their offspring. Gain from using the best trees within the best progenies as parents results from mass selection.

Earliest harvest of genetically improved seed. — This is a legitimate goal with commercially important species in which genetic improvement is urgently needed.

With this goal the number of years required for clones to fruit (Y_c) or for seedlings to fruit (Y_s) is the most decisive factor governing type of orchard. If the Y_c/Y_s ratio is much less than 1, clonal orchards are best. That is true for some important north European species (Y_c/Y_s ratios of 10/40 or 15/30) and for the most important southern pines (ratios of 6/15).

If both Y_c and Y_s are small and their ratio is nearly 1 (as with some of the precocious northeastern conifers) time and cost of grafting must be considered. Suppose that seedlings and grafts fruit at about the same time but that 1, 2 or 3 years are needed to establish an adequate half-sib progeny test, clonal orchard, or full-sib progeny test. Then preference would be given to the half-sib test, the clones, or the full-sib test in that order. Or suppose that the grafted trees fruit a few years earlier but that grafting is so expensive that the initial orchard could supply only a part of a forest's needs. In that case a larger half-sib test might give usable quantities of seed first.

There is a possibility that fruiting age may be lowered considerably by moving trees to a region other than that in which the seed is to be used. The probable lowering is

the only factor to consider in the case of a clonal orchard where genetic gain depends on the original mass selection in the wild forest. In the case of a progeny test-seed orchard, however, such a move may affect genetic gain adversely. Duplicate progeny tests in the region of seed use and the region of early seed production would be necessary to insure that early seed was genetically improved.

Maximum early gain if the Y_c/Y_s ratio is nearly 1. — This model is applicable to species in which differences in fruiting age are so small that attention is focussed on achieving maximum early gain.

Clonal orchards give highest gain for traits with high heritabilities. The amount of improvement is pre-determined by the original mass selection and is independent of the age at which the clones start to flower.

Progeny-test and clonal-test seed orchards give higher gain for traits with low heritabilities. Most of the gain results from selection within the orchard. Presumably the first selection will be practiced at age $Y_s = Y_c$. There will be an imperfect correlation ($r_{Y_s, \text{mature}}$) between performance at that time and at maturity. It is the gain in mature performance which counts, and this will be less than the apparent gain at age Y_s by the amount $1 - r_{Y_s, \text{mature}}^2$.

The critical heritability above which clonal orchards are preferred is usually determined on the basis of mature performance. It can be converted to performance at age Y_s by multiplication with the factor $r_{Y_s, \text{mature}}^2$.

In this model differences in fruiting age of even 5 years may be of little consequence in determining whether to graft or raise seedlings. However, actual fruiting age can be a decisive factor, especially with traits such as branch retention and crown flattening which are impossible to evaluate in young trees.

Maximum economic gain per year from a several-generation breeding project. — A breeder may have to develop several improved lines at the same time. Or he may have a series of clonal orchards which satisfy the immediate needs for improved seed. If so, he will want a breeding system which will give the most return for the money. Generation length, rate of gain per generation, and cost will be the decisive factors. Four possibilities are as follows:

1. A "clonal orchard" or "clonal test-seed orchard" will be established at year 0 and will fruit at age Y_c . At that time seed will be collected to start a seedling plantation which will fruit at age Y_s , at which time a new clonal orchard will be established. It will fruit in year $Y_s + Y_c$. The initial orchard will have a useful life of Y_s years.
2. A parental-generation clonal orchard and a first-generation progeny test will be established in year 0. At age Y_s the progeny test will be evaluated and the clonal orchard will be thinned, leaving only the clones of best proven combining ability. Also at year Y_s a first-generation clonal orchard and a second-generation progeny test will be established, the clones to be thinned at year $2Y_s$. It is assumed that each clonal orchard will replace the previous one and have a useful life of Y_s years.
3. There will be a succession of "progeny test-seed orchards" started at years 0, Y_s , $2Y_s$, etc. Each will have a useful life of Y_s years.
4. There will be a succession of "progeny test-seed orchards" as in case 3. Every tree will be cloned as a seedling. Early fruiting is not expected and the clones

will probably start to produce seed at age Y_s or a little later. The period from seed to seed will still be Y_s years.

It may be more satisfactory to state generation length in terms of Y_e , number of years needed to evaluate a test satisfactorily. If so, Y_e will replace Y_s in each case.

Note that the age at which clones or seedlings fruit affects only the time at which seed is expected in the first generation. Once a long-term breeding project is underway, generation length will be the same (Y_s or Y_e if that is larger) for all four schemes. Choice of procedure will be governed by rate of gain per generation and by cost.

Maximum genetic gain by the end of the first generation.

— Maximum genetic gain by the end of the first generation can be achieved by either of two methods. First is the "progeny test plus clonal orchard" approach. A progeny test is established and evaluated at age Y_e . Then the parents with the best proven combining ability are cloned and placed in a clonal orchard which will fruit at age Y_c . The generation length is $Y_e + Y_c$. This approach gives the highest gain if a large portion of the genetic variation is non-additive.

Second is the "progeny test-seed orchard" approach. A progeny test (probably full-sib) is established and evaluated at age Y_e . Then it is thinned to the best trees in the best progenies. The seed produced is F_2 and there are really two generations of selection even though only one generation (of Y_e years length) has elapsed. This promises the greatest genetic gain if most of the genetic variation is additive.

Time is not a factor in answering the question "Which approach gives the most improvement per generation." However, it should be considered in answering the question "Should highest gain per year or per generation be the objective?"

Mass production of a proven species hybrid. — The Danish tree breeder SYRACH LARSEN has established seed orchards for the production of F_1 *Larix decidua* \times *leptolepis* seed. An orchard is composed of a self-incompatible clone of one species to act as seed parent and clones of the other to act as pollen parents. Relative age of flowering did not influence the design of the orchard.

The South Korean tree breeder, S. K. HYUN, has orchards for the production of *Pinus rigida* \times *P. taeda* seeds by mass controlled pollinations. The fact that *P. rigida* flowers very early was a decisive factor governing the decision to use seedlings. If seedlings did not fruit until the 20th year he would have been obliged to use old-tree grafts for the female parent.

Under some conditions *Pinus strobus* and *Picea glauca* produce pistillate strobili for many years before they produce pollen. This opens the possibility that seed orchards can be established without resorting to self-incompatible clones or to controlled pollination. Age of flowering would be a factor when choosing between grafted trees and seedlings.

Storing superior genotypes for future use. — Some superior trees are so outstanding that they must be propagated clonally. In others the superiority is less certain; a selected seedling might be equal or better than the original parent. In the latter case preference will be given to clones if they fruit considerably earlier. Cost and genetic considerations will be most important if there is little difference between Y_c and Y_s .

Determination of total genetic variance (clones) or additive genetic variance (seedlings), breeding for late-generation segregates (seedlings), etc. — With objectives such as these, choice of propagation method is determined solely by genetic factors. Youthful flowering will not determine whether grafts or seedlings are used.

Summary

Grafts or cuttings taken from the tops of old trees often continue to behave as if they were still attached to the tree. They tend to retain the old-tree fruiting potential so that a grafted tree can fruit many years earlier than a seedling.

The difference in fruiting age between grafted and seedling trees is most pronounced (up to 25 years) in some of the north European timber trees. It may be as little as 1 or 2 years in the case of some species which normally reach sexual maturity at a very early age. Experiments with flower stimulation indicate a possibility of reducing the flowering age of seedlings considerably by appropriate fertilizer or cultivation treatments.

The importance to be placed on age of flowering varies with a breeder's objectives. If earliest harvest of genetically improved seed is the goal, preference will be given to clones or seedlings solely on the basis of the time at which flowering is expected. If maximum rate of gain per generation is the goal, age of flowering will determine the time at which the first seed is produced but will not affect choice of propagation method thereafter. Genetic considerations will be much more important than sexual precocity when planning experiments to determine total genetic variance, additive genetic variance, the possibility of breeding for late-generation segregates, etc.

Résumé

Titre de l'article: *Age de floraison des arbres de clones et de semis comme facteur de choix d'un système d'amélioration.*

Les greffes et boutures prélevées au sommet de vieux arbres continuent souvent à se comporter comme si elles étaient toujours attachées à l'arbre. Elles ont tendance à conserver le potentiel de fructification des vieux arbres, si bien qu'un arbre greffé peut donner des fruits plusieurs années avant un arbre issu de semis.

La différence entre l'âge de fructification d'un arbre issu de greffe et d'un arbre issu de semis est très prononcée (jusqu'à 25 ans) chez certains arbres à bois d'œuvre du nord de l'Europe. Elle peut n'être que d'un ou deux ans dans le cas d'espèces atteignant normalement très tôt leur maturité sexuelle. Des essais de stimulation de la floraison indiquent qu'il est possible de réduire considérablement l'âge de floraison des semis à l'aide d'engrais ou de soins culturaux appropriés.

L'importance accordée à l'âge de floraison dépend de l'objectif de l'améliorateur. Si son but est d'obtenir le plus tôt possible une récolte de graines génétiquement améliorées, il choisira les clones ou les semis uniquement d'après leur période probable de floraison. Si son but est d'obtenir le taux maximum de gain par génération, l'âge de floraison déterminera le moment de production de la première graine, mais ne devra pas influencer sur le choix de la méthode de propagation. On attachera beaucoup plus d'importance aux considérations génétiques qu'à la précocité sexuelle dans l'établissement de plans d'expériences visant à déterminer la variance génétique totale, la variance génétique

additive, les possibilités d'amélioration par ségrégation dans les générations ultérieures etc.

Zusammenfassung

Titel der Arbeit: *Das Blühalter von vegetativ und generativ vermehrten Bäumen als ein Faktor bei der Wahl des Züchtungssystems.*

Pfropflinge oder Stecklinge aus der Spitze von alten Bäumen verhalten sich oft so, als wären sie noch mit dem Baum verbunden. Sie neigen zur Beibehaltung der Blühwilligkeit des alten Baums, so daß ein Pfropfling oft viele Jahre früher als ein Sämling fruchtet.

Der Unterschied im Blühalter zwischen Pfropflingen und Sämlingen ist am ausgeprägtesten (bis zu 25 Jahren) bei einigen der nordeuropäischen Massenbaumarten. Im Fall einiger Species, die normalerweise die Geschlechtsreife in sehr frühem Alter erreichen, mag der Unterschied nur ein oder zwei Jahre betragen. Experimente zur Blühstimulation zeigen eine Möglichkeit der beträchtlichen Herabsetzung des Blühalters eines Sämlings durch Düngung oder Kulturmaßnahmen.

Die Bedeutung, die dem Blühalter zukommt, ist je nach den Zielen des Züchters verschieden. Ist frühestmögliche Ernte züchterisch verbesserten Saatguts das Ziel, wird Klonen oder Sämlingen allein auf Grund des zu erwartenden Zeitpunkts der Blüte der Vorzug gegeben werden. Ist größtmöglicher Züchtungsfortschritt pro Generation das Ziel, so wird das Blühalter den Zeitpunkt bestimmen, an dem das erste Saatgut produziert wird, doch wird es nicht die Wahl der später angewendeten Vermehrungsmethode beeinflussen. Bei der Planung von Experimenten zur Bestimmung der genetischen Gesamtvarianz, der additiven genetischen Varianz, der Möglichkeit der Züchtung auf Spaltungsergebnisse in späteren Generationen usw. werden genetische Betrachtungen weit größere Bedeutung haben als die frühe Erlangung der Geschlechtsreife.

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Problems Involved in Some Models of Selection in Forest Tree Breeding

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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 controversy 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 (1963) 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 estimations of genetic gain are reasonable only in some simple situations. For example, SQUILLACE and DORMAN (1961) and SQUILLACE and BENGTON (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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