A Brief Review and Conclusions of the Discussion on Seed Orchards

By RYOOKITI TODA[1])

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1. Introduction

In early February, 1963, I received a letter from Dr. W. LANGNER, who asked me to act as moderator for a discussion of the relative merits of clonal and seedling seed orchards. One issue of the 1964 Silvae Genetica was to be devoted to such a discussion, because of the current interest and importance of seed orchard establishment. Indeed, somewhat of a controversy had developed and as requested by Dr. ZOBEL, clarification was needed, both from the applied and theoretical point of view. I was chosen as moderator because of my specialty in the field of population and quantitative genetics and because I had not been involved in the diseussion previously. In fact, I was not too well versed on publications dealing with the relative merits of vegetative and seedling orchards and had not even read the widely distributed paper of GODDARD and BROWN (1961). Since it is essential for a moderaior to have a working knowledge of the subject, I have made an attempt to become better acquainted with the problem and accepted Dr. LANGNER's offer. It was especially necessary for me to do this because tree breeders in Japan also have seed orchard programs of rather large scale and must be kept well informed on this subject.

I asked Dr. STERN and Dr. ZOBEL to help obtain information on the problem and to make the necessary contacts to initiate the special issue. This took nearly two months, and it was already April 3rd when letters requesting contribution of papers were sent to the following persons:

Emphasizing clonal seed orchards:
ENAR ANDERSSON,
JONH C. BARBER and KEITH W. DORMAN,
BRUCE ZOBEL.
Emphasizing seedling seed orchards:
E. BAYNE SNYDER,
KLAUS STERN,
JONATHAN W. WRIGHT and ERNST J. SCHREINER.

Papers could not be prepared by SNYDER and ANDERSSON. Luckily, HELGE JOHNSSON was willing to replace ANDERSSON, even though the request came very late and gave him only a short time to prepare the manuscript. Additionally, R. E. GODDARD and W. J. LIBBY consented to prepare papers, so seven papers will compose this special issue. These papers are well prepared and present a variety of opinions that should be of great interest to readers of Silvae Genetica.

The author wishes to express his thanks to Dr. W. LANGNER, who made it possible for him to undertake this interesting assignment, and to Dr. B. ZOBEL and Dr. K. STERN, who helped and informed him very much and also kindly read the manuscript. The author also is thankful to all of the contributors who worked so nicely within such a short period.

2. Seedling seed orchard proposals

Although seedling material had not been rejected entirely as the component of a seed orchard, it was quite natural that most early seed orchards consisted of grafted clones because the principle of establishing orchards was to bring selected genotypes together side by side (LARSEN, 1934). Since the end of the World War II, this approach to tree improvement became very popular, and many clonal seed orchards have been established throughout the world.

The first arguments against clonal orchards were presented by WRIGHT (1959)and others who advocated seedling seed orchards which were to be established first as progeny testing plantations and then converted into seed orchards. The superiority of the seedling orchards were discussed from the standpoints of expected genetic gain and cost considerations..

WRIGHT (1961) stated that the largest increase of fitness can be obtained by selection based upon the performance of full-sibs in two-parent progeny tests. The superiority of full-sib progeny selection upon the rogued clonal seed orchards depends on the relative amount of additive genetic variance, and under some possible assumption it may reach four times the latter gain. He also calculated that progeny selection in open-pollinated one-parent progeny tests may result in about a half of the gain expected from progeny tested and rogued clonal orchards. GODDARD and BROWN (1961) stated similar ideas in plain words without the use of special symbols or formulae. They proposed the use of controlled pollinated seeds from selected trees produced by a pollen mix. They stressed that the cycle of successive selection is faster in the seedling seed orchard approach.

When the seedlings are grown from open-pollinated seeds collected on tho original selected trees, the costs for raising material and time required for establishment of seed orchards will be low in comparison with costs of establishing clonal seed orchards. WRIGHT (1961) emphasized low costs from the seedling approach and stated this would be a preferred approach, even though the expected gain may be inferior to the clonal one. SCHREINER (1963) also advocated such a procedure and proposed parallel establishment of both type seed orchards by using the same plus-tree parents to examine the efficiency-cost relationships from both schemes.

Controlled pollination on selected trees in wild stands requires labor and costs, but still WRIGHT (1961)and GODDARD and BROWN (1961) state that this is not too expensive in comparison with the grafting costs. In this author's opinion, the statements may be true when the grafting is very diffioult resulting in very high grafting costs, or when the parent trees or their grafts are collected and growing not far from each other, controlled pollination becoming much easier. But the statement of GODDARD and BROWN (1961) which says that controlled pollination on original selected trees will not be too expensive, seems to be of doubtful validity. They mentioned that even in the case of clonal seed orchards progeny tests are also needed and thus emphasized that the conversion of test plantations into seedling seed orchards is more reasonable than establishing special clonal orchards.

Preference for seedling orchards was expressed (Texas Forest Service, 1960) because the performance of clonal

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seed orchards was not as favorable as had been expected. Graft success was reported as being irregular, and many originally successful grafts, after growing vigorously in the field for one or more years, had weakened and died.

3. Genetic gain

In this special issue, the genetic gains expected in various tree improvement schemes are thoroughly discussed by STERN and HATTEMER and also by LIBBY. STERN and HATTEMER point out that the gains expected both from the clonal seed orchards of selected parents and from the seedling seed orchards raised by controlled pollination of pollen mix from the same parents are equal to each other and they are twice the gain expected from open-pollinated seedling seed orchards. They also point out that the gain expected from progeny selection in seedling seed orchards without individual treee selection within the progenies is less than that expected through the clonal selection in clonal seed orchards, but they did not show the comparative gains when selection is made also within the progeny of a seedling orchard.

Relative efficiencies of various types of selection are also discussed in detail by LIBBY. He deals with family selections and family-plus-mass selections which are characterized by the absence or presence of individual tree selection within each family. In Table 8 he shows that clonal selection is always more effective than any of the other schemes, that full-sib and half-sib family selections are less effective than mass selection when the heritability is high, and that the family-plus-mass selections are all more effective than mass selection. But the superiority of half-sib family-plus-mass selection over simple mass selection is not very large especially when the heritability is sufficiently high.

Clonal seed orchards using untested selected clones is mass selection, even when the very superior individual trees are chosen. However, in the above discussion, mass selection refers to the selection of individuals from an unpedigreed bulk population of offsprings of the originally selected trees. These newly selected trees will be utilized in the secondary clonal seed orchards. When the selection intensity is the same, the gain of the secondary clonal orchards will be less than that of family-plus-mass selected seedling seed orchards established with half-sib progenies of the same parents pollinated by a pollen mix of themselves. However, from the practical point of view, the former may exceed the latter, because the selection intensity will not be very high when a progeny test plantation is converted into a seed orchard as mentioned by BARBER and DORMAN and also by LIBBY. The comparative gains when the original clonal seed orchards are rogued, compared with the secondary clonal orchards, will depend mainly on the value of heritability. When heritability is low, rogueing of a clonal orchard is favored, but when that is high the secondary orchard will be better. In either way it is possible to increase the gain in the original orchard by rogueing the inferior clones based on clonal or progeny tests, but the selection intensity in such cases will be lower than in seedling seed orchards because the arrangement of the ramets are carefully balanced and do not usually allow too drastic removal of many clones. Therefore, the expected gain will be higher in seedling seed orchards if the heritability is low and if the juvenile-adult correlation is sufficiently high. Of course, clonal seed orchards may be planned to utilize high clonal selection intensity as LIBBY proposes, and in this case, additional genetic gain will be large enough in comparison with any type of seedling seed orchards.

Simply stated, the situation could be explained as follows: The groups of seedlings produced by diallel crosses among selected individuals or by control-pollination of pollen mix are nearly equivalent to the filial population of seedlings from the clonal seed orchards established with the grafts from the same selected individuals. Genetic nature of a population is determined by the nature of the whole assembly of gametes produced by the parental population, and the filial population reproduces the gametes of the same nature if the population does not undergo any selection. Therefore the seeds, collected in the seedling population show nearly the same genetic nature as the seeds collected in the clonal seed orchards. Additional selection in the seedling population must be effective as far as the original selection has been effective, so the seedling seed orchard must give more gain than unrogued clonal orchard, because the former goes through a secondary selection. The efficiency of secondary selection varies very much by the scheme of selection and the heritability of the trait. Even the most simple secondary mass selection in the bulk filial population produced by the original clonal seed orchards may show not very low effectiveness in comparison with the theoretically most superior scheme when the heritability is sufficiently high. This simple method may be the most adequate one in some cases because the simplicity allows the highest selection intensity. JOHNSSON's study on the breeding value model is also on the same line and is very impressive.

ZOBEL and MCELWEE, also BARBER and DORMAN, point out that the risk of inbreeding depression is larger in seedling seed orchards. The former authors stress the danger of having a strong general combiner or two, resulting in selection of half-sibs and some full-sibs in the seedling seed orchards, especially when a pollen mix with limited number of pollens is used. The same risk is present in the case of mass selection in a bulk filial population. Therefore, as LIBBY mentions, it is necessary to select sufficient number (at least fifty) of trees in these approaches and to have a number of pollens represented in the pollen mix.

4. Cost considerations

There is no doubt that the cheapest way of establishing seed orchards is the use of open-pollinated seedlings from originally selected individuals. Although the gain of this type of seed orchard is not large because the pollen is of average genetic value, still it can give considerable gain through between- and within-family selection. This scheme may be the best one when both vegetative propagation and controlled-pollination are very difficult. For example, in south-western Japan we are now engaged with the selection program of *Acacia mollissima* which cannot be readily propagated by grafting nor by cuttings, and the controlled-pollination on scattered selected trees is very expensive. Under these conditions, the above-mentioned method is recommended for this species.

In making comparisons of costs between grafting and controlled-pollination, each method has its own advocates. Evidently the relative costs depend on the nature of the species, facilities available and the skill of the operators. Costs of grafting are not so expensive as was in early days, and controlled-pollination on scattered original trees is no doubt more expensive than grafting (GODDARD, BARBER and DORMAN).

GODDARD and BROWN (1961) stated that it is necessary to consider the fact clonal seed orchards require additional costs for progeny testing while seedling seed orchards can be converted from test plantations themselves. This does not necessarily favor seedling seed orchards, because the site requirements for testing and establishing seed orchards are usually quite different as was pointed out by ZOBEL and MCELWEE, BARBER and DORMAN, and LIBBY. JOHNSSON also stresses this. Therefore, under most conditions the seedling seed orchard must also have additional progeny test plantations as well as the clonal seed orchards.

5. Juvenile-adult correlation

The present author believes that by a properly designed seedling seed orchard, more or less increased gain can be obtained than from a clonal seed orchard, when the evaluation and rogueing are made properly. But there is the question of evaluation in young test plantations. BARBER and DORMAN, LIBBY, JOHNSSON, and STERN and HATTEMER all mention this question, juvenile-adult correlation, but the present author puts more importance than they do on this problem; in reality, this author cannot as yet put too much reliance upon the evaluation in young ages.

In Kyusyu, the southwesternmost island of Japan, we have a mature clone of *Cryptomeria* which is very fast-growing in its younger ages. This clone became very famous in Japan and many forest owners bought its rooted cuttings and planted them in their commercial forest lands. They really grow very vigorously up to twenty years or more, but after that growth rate decreases. The oldest plantation of this clone is about 35 years old and does not look very healthy. It is not good policy to keep this clone over 30 years, and so short a rotation period is not good for the conservation of soil especially on steep slopes of Japanese forest lands, though the trees do reach a fairly marketable size.

OKADA (Unpublished) studied the change of individual growth rate accompanying the increasing age of stands, using several species of larch, pine and spruce. He shows that in most cases studied the correlation between the diameters of final age (35 to 40 years) and of early age do not exceed 0.5 up to 10 years and not 0.7 up to 20 years. Changes of height growth were not studied fully, but one example studied showed more change than that of diameter in the same material; the correlation of height growth did not reach 0.5 up to 20 years of age, while that of diameter reached the level of 0.7 when the stand was ten years. Unfortunately, OKADA has not studied older material, but there is good reason to believe that many early starters will not be a superior in older ages.

Therefore, the author believes that progeny test plantations must not be rogued heavily while young, but should be evaluated continuously until fairly old ages, say two-thirds or half of the rotation period, or at least one-third as JOHNSSON says. As a seed orchard requires special care for promoting flowering, for keeping the vigor of trees under accessible height and so on, and as these procedures evidently disturb the proper evaluation, a progeny test plantation cannot be converted into a seed orchard, in the strict sense of the word. They must be treated as a seed producing plantation area, where very high quality seeds can be obtained. When progeny tests are made in separate sites, the seedling seed orchard can then be managed for seed production, but the value of combined progeny test-seed orchard is lost and still the early selection within families is doubtful.

6. Conclusions

Although the concept of progeny test-seedling seed orchard has already been presented by FABRICIUS (JOHNSSON), it is to the credit of WRIGHT and others that they showed there are other schemes than the clonal seed orchard to produce genetically improved quality seeds in large quantity. The method of seedling seed orchard should be applied in many cases where the nature of the species and other conditions require it. GODDARD's paper shows that a test plantation can be successfully converted into a seed orchard, when the expected period of rotation is not very high or the juvenile-adult correlation is high.

However, seedling orchards will not entirely replace clonal seed orchards. The latter is still the most reliable and safe procedure in a tree improvement program unless grafting costs are very high or the heritability is very low. The author intends to recommend clonal seed orchards in general cases, combined with the mass selection of high intensity in the bulk filial population.

It really is not necessary nor possible to say which is definitely superior to the other. Each scheme has its own advantages and can find their application somehow. The necessary thing is, as ZOBEL and MCELWEE point out, to have some kind of seed orchard for the mass production of genetically improved seeds regardless of the scheme employed.

It is regrettable that I could not discuss the interesting proposal of ZOBEL and MCELWEE for separate production seed orchards and the supplementary longer term tree bank. Certainly tree banks are very necessary and the author wants to add more material to be collected in connection with tree banks; that is the sample of the whole natural gene pool, to prevent the extinction of useful individual genes. This can be accomplished by collecting seeds and establishing new plantations from at least 30 to 50 scattered trees in each stand showing good performances.

7. Summary

This paper was prepared to summarize the discussion about clonal and seedling seed orchards presented in this issue of *Silvae Genetica*. It is not possible nor necessary to say which scheme is entirely better than the other. Relative efficiencies in terms of genetic gain and costs vary largely according to the heritability, easiness of vegetative propagation, controlled pollination, and so on. Detailed discussions are presented in individual papers, but the present author intends to recommend clonal seed orchards as the most reliable method in general cases. The importance of juvenile-adult correlations received more attention in this paper than in any of the contributed papers.

Résumé

Titre de l'article: *Bref exposé et conclusions de la discussion sur les vergers à graines.*

Cet article a pour but de résumer la discussion sur les vergers à graines de clones et de semis présentée dans ce numéro de *Silvae Genetica*. Il n'est ni possible ni nécessaire de dire que l'un de ces systèmes est nettement supérieur à l'autre. L'efficacité relative en termes de gain génétique et de coût varie largement en fonction de l'héritabilité, de la facilité de propagation végétative, de la pollinisation contrôlée, etc... Des études détaillées sont présentées dans des articles séparés, mais l'auteur de ce résumé recommande les vergers à graines de clones comme la méth de la

plus efficace dans les cas généraux. Cet article consacre plus d'attention à l'importance des relations entre individus jeunes et adultes que tous les autres articles présentés.

Zusammenfassung

Titel der Arbeit: *Ein kurzer Rückblick und Schlußfolgerungen aus der Diskussion über Samenplantagen.*

Dieser Aufsatz sollte die Ergebnisse der Diskussion über Klon- und Sämlings-Samenplantagen in *Silvae Genetica* zusammenfassen. Es ist weder möglich noch notwendig zu sagen, welches der beiden Systeme im großen und ganzen besser ist als das andere. Die relative Wirksamkeit, ausgedrückt in Einheiten des Züchtungsfortschritts und der Kosten, streuen in breitem Rahmen je nach Heritabilitäten, Schwierigkeiten vegetativer Vermehrung und kontrollierter Bestäubung usw. Die einzelnen Beiträge geben eine ausführliche Diskussion. Vf. möchte jedoch Klonsamenplantagen als die im allgemeinen zuverlässigere Methode empfehlen. Die Bedeutung der Merkmalskorrelationen zwischen jungem und späterem Alter erfuhr in diesem Aufsatz mehr Beachtung als in den übrigen.

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Seed Orchards for the Production of Genetically Improved Seed

By Bruce Zobel and R. L. McElwee[1])

Recent emphasis on forest tree breeding has posed the questions, "How can improved seed be economically produced in sufficient quantities for large scale forestry programs?" and, "How can the greatest genetic improvement be achieved?" New varieties of forest trees can be produced but they will not be of significance in improving yields and quality of wood until they can be produced economically on a commercial scale. Foresters and scientists in related fields have considered these problems and all suggest producing quality seeds in seed orchards. The seed orchard concept is being accepted and already widely used in forestry; it is a term frequently heard at technical forestry meetings or referred to in forestry journals. Even though seed orchards are recognized as one of the few workable methods now available to economically mass-produce improved forest tree seeds, many do not understand their objectives. In some forest regions, new varieties can be developed without having immediate use, while in others the problem is one of putting improvements to immediate use through standard forest management operations.

Where forestry practice is intensive there is a wide gap between the silvicultural improvements that have been made and the development of better trees to take advantage of the improved cultural methods. Forestry has not developed along agricultural patterns where cultural practices and genetic improvement proceed together and complement each other; instead, the plant improvement part in forestry is well behind. Because of the long-term nature of all forest management research, progress to bring culture and plant improvement to the same level will be slow and "crash programs" will not be too effective to bring about rapid narrowing of the gap between the two. Therefore, we need to take immediate action which may involve considerable dependence on ideas that have not as yet been proven.

Production seed orchards are a good example of activities involving some unproven ideas. Large sums of money are being spent in establishing such orchards, and it is necessary to critically analyze the objectives and philosophies involved. Such a situation is present in the Southeastern United States, an area of rapid tree growth, large forest industries and intensive forest management practices. This region is ideal for applying genetics in forestry practices; the current large regeneration programs have produced an urgent need for mass-producing genetically improved seed.

This paper deals with the philosophy, not the techniques, of seed orchard management and will be based upon experience and ideas gained in the N. C. State-Industry Cooperative Tree Improvement Program. This Cooperative Program is supported by 18 organizations located in ten southeastern states, mostly members of the pulp and paper industry. Rather than cover this program in detail, *Figs. 1 and 2* and *Tables 1 and 2* have been prepared to describe the scope of the Cooperative Tree Improvement Program. All cooperating organizations have one thing in common — they all have great and urgent need for improved seed.

The General Seed Orchard Concept

The forest manager is faced *each year* with the problem "Where shall I get seed?" One way to satisfy this need is to establish seed orchards. Data on inherent differences on a racial or individual basis is simply too impressive to ignore, and it is obvious that progeny will be better when both parents are good than if only one or neither of the parents is good. A seed orchard is used to take advantage of both known and suspected areas of inheritance and gain. Despite the present sketchy knowledge of techniques as well as the degree of improvement possible to achieve, there is as yet no satisfactory alternative to a seed orchard program; it is simply this or continuation of use of unimproved seed.

Seed orchards are established to produce seed for trees having specially desired characteristics. They are but one step in the succession of practices necessary to improve seed; they can be established to multiply seed from special provenances, from certain desirable trees within a given provenance or for hybrids. Seed orchards usually contain

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