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A model for tree breeding

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Abstract

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The breeding strategy for Norway spruce and Scots pine for southern Sweden was discussed in a series of workshops organized by the Swedish University of Agricultural Sciences, Department of Forest Genetics, Uppsala, Sweden. Tree breeding was defined as a continuing process in which the development of improved genetic stock is balanced against the need to conserve genetic variability, while at the same time the properties of the trees being bred and multiplied are learned.

A model of tree breeding, consisting of the functions long-term breeding, short-term activity and supportive research, was presented. It was stated that this kind of effort cannot be fitted into a short-term economic perspective, but it is justified as long as the nation is committed to managing biological resources. The components of a tree breeding system were given as breeding stock information/techniques and organization. The breeding strategy was viewed as an operating mechanism that makes the evolution of this system possible when the environment and human needs are changing.

Key words: Tree breeding model, long-term breeding population. ODC 165.3.

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Introduction

During October 1983, to February 1984, the Swedish University of Agricultural Sciences, Department of Forest Genetics, Uppsala, organized a series of workshops to discuss strategies for breeding Norway spruce and Scots pine in southern Sweden. All types of organizations related to Swedish tree breeding were represented in the workshop. Tree breeders

from the other Nordic countries as well as breeders of agricultural crops also participated, altogether 58 participants. In this report we shall present the model that constituted the conceptual framework of the workshop series. In a separate report (Gullberg & Kang, 1985) we present our conclusions regarding tree breeding in southern Sweden.

What is tree breeding?

Tree breeding functions in an environment where, in comparison with most other large scale ventures, it is difficult to give precise operational goals. Both the long rotation times in forestry and the low intensity of forest management contribute to this situation, since they make the problems in a changing environment so unpredictable. From the breeders' point of view this means that we cannot concentrate all efforts on one single solution but have to diversify in order to lower the risks of total failure. It is also in the breeders interest to improve the predictability by improving the knowledge about breeding material.

Breeding is frequently viewed as an activity that enables man to utilize the genetic variability existing in an organic population(s) by artificial selection and associated techniques. From this idea two schools of thought have evolved, one emphasizing the selection, and the other emphasizing the conservation of genetic variability. In recent treatments of the subject this dichotomy is evident (Namkoong et al., 1980; Zobel & Talbert, 1984).

In the past the selection school dominated tree breeding. A common perception shared by many tree breeders was that they could obtain genetic gain and transfer the gain to the production forests by selection and seed (or propagule) orchards. One has consequently defined fairly precise operational goals, such as 10% value increment over 50 years, and geared the programs to fulfill these goals. The major task of forest geneticists has been to find and analyze variance components of different populations, because the presence of genetic variability is a prerequisite for selection.

More recently, genetic resource conservation has become popular. The conservationists took the opposite position to the selectionists' premise. They assumed that the selection would produce genetic gain

by consuming genetic variability, and that the product of the selection would have a small genetic variability.

Although both schools have their own merits, their conclusions would not be compatible if they assumed instant results. Selectionists could argue that if plus trees were selected and seed orchards were established, improved seeds would be produced and they yield increase in the entire production land would surely come in good time. Conservationists could think that the use of propagules from an orchard of small size or a small number of clones would automatically narrow the genetic basis of production lands and invite disaster, and the selection would exhaust all the genetic variability of the breeding populations.

Under such extreme views there is no room for developing breeding strategies. Tree breeding will be either an instant success or a disaster no matter what tree breeders do. To establish tree breeding as a valid form of biological resource management, proper time and space factors should be introduced to the concepts of selection and genetic variability conservation. The area between the two extreme conclusions will then be recognized. Tree breeding represents efforts do develop improved stocks while maintaining genetic variability. Balance is a key word in this context (Kang, 1982; Namkoong et al., 1980, pp. 42–44.)

The extreme views also leave an impression that breeding is a single, isolated action. Tree breeding is a continuing process where the multigeneration developments will create values that never could be obtained in a few generations (Kang, 1982).

Tree breeding is also a learning process to generate necessary information for managing biological resources. Selecting and multiplying superior trees from testings increase the expected yield of the pro-

duction lands. To improve the predictability of these activities breeders must be well informed about the biological and ecological behavior of the trees that are being planted. The knowledge will help them to prescribe the proper distribution of the trees and the cultural scheme. As more lands become artificially regenerated, knowledge of the trees planted will become increasingly important to manage forest resources.

We define tree breeding as a continuing process of balancing improved genetic stock development and genetic variability conservation, and of learning the properties of the trees that are being bred and multiplied.

The functional components of tree breeding as defined above are long-term breeding, short-term activity, and supportive research (Figure 1). The long-term breeding generates gradual genetic gain while maintaining genetic diversity by manipulating the breeding populations in a structured manner as will be discussed below. (For a thorough treatment of this subject see Kang & Nienstedt, 1985.) Short-term activities materialize the maximum possible genetic gain and multiply the selected stocks. The supportive research generates information necessary to perform various management activities.

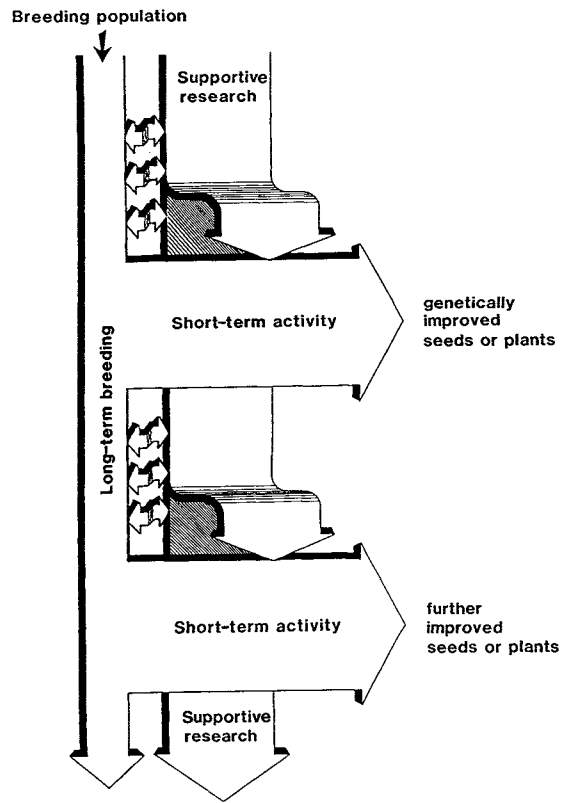


Fig. 1. Functions of tree breeding.

Justification of tree breeding

Tree breeding has been frequently justified by comparing the genetic gain with prevailing compound interest rates. The compound interest rate, however, is a one dimensional measure, and it is critical to learn when and how the measure should be used. To determine the validity of using the short-term economic justification one has to define the organization that is performing the activity and the nature of the activity. Furthermore, the organization and the activity must match properly.

The overall tree breeding as described in Figure 1 cannot be fitted into the framework of a short-term economic justification. It has to be justified at a national or regional (international) level. National defense is an example of such noneconomic justification. Tree breeding is justified as long as the nation is committed to managing biological resources.

At the other extreme, the short-term efforts, especially multiplication, are economically attractive, and private companies can take on such tasks, provided

that long-term breeding stocks are available.

It is self-evident that no industry can expect to generate profits by initiating long-term breeding. Once the products of long-term breeding begin to become available, however, the economic environment will change. The value of the long-term breeding output will exceed that of the input at any given time. Therefore, the critical question is how the initial phase of the long-term breeding should be justified. It cannot be justified by using compound interest rates. It is, of course, possible to argue that the potential economic gain at 30+ years in the future can be multiplied by a large factor assuming that the breeding will be combined with an extremely large multiplication scheme. Such an argument will justify any small net gain, and is a trivial point. Long-term breeding should be justified as a central activity through which future tree breeders and researchers can add on improvements and gain knowledge to manage the biological resources. Because long-term

breeding cannot be replaced by repetition of short-term efforts, it has to have its own starting point (Kang, 1982). The sooner the decision is made to embark on the long-term breeding the sooner the program will become economically justifiable. The government and the industrial cooperatives are re-

sponsible for the initial stage of long-term breeding.

Justifications for different supportive research will depend on the type of management they are associated with. Researches must be carried out by all types of organizations in a coordinated manner so that technique transfer can be made smoothly.

Breeding system

At a national or regional level, a tree breeding system represents a set of operational components that, at a given period of time, are available for breeding. In a system corresponding to the tree breeding model described above (Figure 1) the three major types of physical component are:

1. Breeding stock,
2. Informations and techniques,
3. Breeding organisations.

Physical components and dynamics of a tree breeding system are illustrated in Figure 2. The strategy represents an operating mechanism that makes the evolution of the system in the changing environment and objectives possible. All the entries in the figure keep changing with time. The goal of the system at a given time is to generate products that satisfy the objectives.

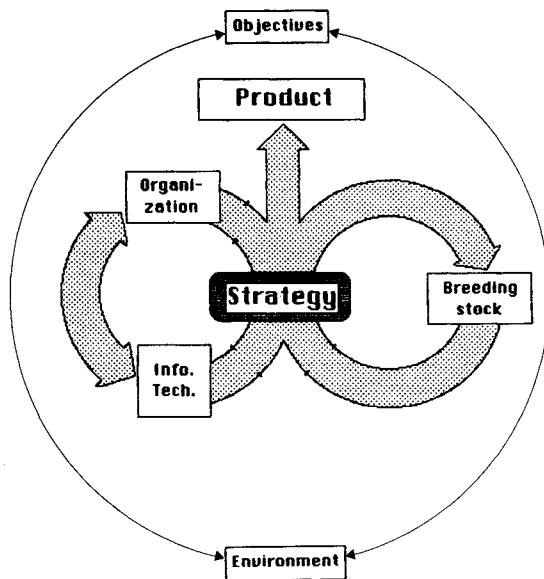


Fig. 2. Physical components and dynamics of a tree breeding system.

Breeding stock

Tree breeding stock represents populations that are utilized to produce improved individuals (or varieties). To coordinate the breeding activities of different organizations it is desirable to classify different functions of the populations that make up the breeding stock as follows:

1. Long-term breeding population,
2. Short-term breeding population,
3. Multiplication stock.

Long-term tree breeding is an open-ended multiple generation breeding with multiple objectives. Here 'open-ended' implies breeding with no generation limit. The long-term breeding population is the basic source from which short-term breeding populations are drawn. It represents the medium of information and technique transfer among different breeding organizations and human generations. The basic research information is integrated around the long-term breeding population.

Maintaining genetic diversity while obtaining gradual genetic gain on a small set of basic characters is of primary importance in long-term breeding. The size of the breeding population would be in the range of hundreds to fulfill the demand for genetic diversity (Kang, 1979). The population would be subdivided into multiple populations (Kang & Nienstaedt, 1985) distributed in different locations in order to utilize the advantages of inbreeding, cope with genotype-environment interaction and create options for future generations by developing land races (Kang, 1980; Namkoong, 1976). A subset of the multiple populations would constitute the index populations (Kang, 1980), that is, populations that will be used to assess the progress of the breeding population. The main genetic principle for managing the population is to increase the frequency of desirable genes in the population, yet not to lose the selectively neutral or even undesirable genes that might be of some value for future breeding. Selection against detrimental alleles through inbreeding or for short generation turn-over

exemplify this principle. It would also seem valuable to develop subpopulations that are adapted to environmental conditions. The management prescription to achieve the goal does not come from empirical experiments of the population itself, but from genetic modelling and results from short-rotation species. The basic unit of management interest is a subpopulation rather than an individual.

The maintenance of genetic diversity in long-term breeding differs from that of gene conservation in two ways. Firstly, long-term breeding maintains genetic diversity and improves economically important characters simultaneously. Secondly, long-term breeding provides genetic diversity necessary to assure the continuous success of yield improvement on production lands only. Gene conservation, however, includes nonbreeding objectives (Anonymous, 1981 and as presented by Peter Krutzsch, the manager of the Swedish gene bank for forest tree, during the workshop) although this has not always been the case (Frankel, 1970).

At any given time tree breeders pick a portion of the long-term population and develop a new population(s) suitable for satisfying the need of the time. Because the long-term population is composed of multiple subpopulations, most development will involve selection of individuals from the best subpopulations followed by hybridization. The products of the selection and hybridization are likely to be broadly adapted and high performing individuals.

Identifying super-individuals of best subpopulations requires many intermediate populations including research populations. Short-term breeding population represents the collection of such intermediate populations. The population size, the number of individuals selected, will be small, and the selection intensity will be high. The breeding techniques are different from those of long-term breeding.

In short-term breeding the basic unit of interest is the individual, and the measure of interest is the performance of an individual and its offspring produced in a systematic way. This is the basis of the well known genetic gain concept in tree breeding. At this stage measures such as frequency of favorable genes and loss of neutral alleles are not as important as they are in long-term breeding.

The multiplication stock is the final product of long-term and short-term breeding. The multiplication method and the quality requirement of the stock greatly determines the type of short-term breeding techniques to be applied. One of the quality requirements is the capability of the copies or progeny of the

stock to grow vigorously in semi-natural conditions throughout the entire rotation period. The capability also depends on wise distribution of the propagules of the multiplication stock. To be able to define the necessary quality of the stock and distribution scheme, breeders must be well informed of population dynamics in production land. This information can be acquired by studying genealogy.

The above classification of functional populations in tree breeding is useful for examining the current breeding emphasis and determining the elements necessary for developing a well coordinated tree breeding system. In the past, worldwide emphasis in tree breeding has been on short-term breeding and multiplication. The short-term breeding populations, however, were not derivatives of long-term breeding populations as described above. Therefore, the short-term breeding concept cannot give satisfactory answers about advanced generation breeding to the breeders who have completed the first round of tree selection and multiplication. Neither is the concept capable of addressing the recent gene conservation issue.

The introduction of the long-term population will take care of these questions. At the same time it will give opportunities to cautiously introduce new multiplication techniques, e.g. from biotechnology, since they could gradually be incorporated in the program through the long-term breeding population.

Information and techniques

A small number of techniques have dominated tree breeding. Examples are provenance testing with collection of seeds from the best source, progeny testing of plus trees with seed orchard establishment, and vegetative propagation for clonal forestry. More basic researches were characterized by the wide utilization of the analysis (or classification) of variance. Most of the techniques are closely related with short-term breeding and multiplication.

The techniques have been applied to most species that are of commercial interest. The repeated implementation of the small set of techniques was necessary because tree breeding has been in the introductory (or seed source surveying) stage with respect to breeding stock. The repeated implementation, however, did not contribute greatly to technical advance. To attack the breeding problems systematically, long-term techniques, such as described in Kang (1982), and new or advanced short-term techniques that are tailor-made for the system should be developed. In-

roduction of more basic biological techniques, designed to explain the causes of variance in an organized fashion, is necessary. The traditional breeding techniques allow tree breeders to achieve gradual genetic improvement of trees. By learning the causes of the variances, however, breeders can take advantage of biological factors with high impact on tree breeding. Through the study of causes, therefore, tree breeders can generate technical breakthroughs. Justifying basic biological research according to the short-term view, however, is difficult because of the wide distance between knowledge and reality. The combined long- and short-term view makes it possible to justify such basic research as a part of a program creating multiple options.

Breeding organization

Balanced technical systems can have different depths. A technical system could be supported by a group of specialists while another system is supported by a group of generalists whose members have diverse but similar knowledge. Depending on the type of techni-

Breeding strategy

The description of a system alone is not sufficient to make it function and evolve. A strategy is necessary to make the system work.

The strategy is different from an action plan, which describes actions to be taken to accomplish a fixed set of objectives while assuming the presence of a fixed system to perform breeding. As earlier pointed out, the low intensity of investments in tree breeding and the long time periods involved cause a situation where this approach can easily lead to a dead end. Rather than assume fixed predetermined solutions to the breeding problems we therefore acknowledge, like Zobel & Talbert (1984), the importance of intuition in making decisions relating to problems that occur in tree breeding. We call it collective intuition to underline the importance of decisions based on all existing knowledge in the breeding system.

With the collective intuition approach, research is not created to solve an acute applied problem. A general long-term tree improvement strategy is used to identify the areas where continuous improvement in knowledge is necessary. The research areas identified in that fashion may be viewed as research sublines, which are analogous to multiple subpopula-

cal system, the kinds of supporting personnel would be different.

With the short-term breeding concept, frequently used so far, it is desirable to have a breeding organization with generalists to perform the work because their major tasks involve establishing tree breeding and forest genetics as valid forms of biological resource management. The coordination of efforts is relatively easy because both breeders and scientists share a large portion of the knowledge for breeding trees. It is not uncommon to find breeders and researchers working on many species and technical fields simultaneously.

With a long term-term breeding approach it is more difficult to support the system with a group of generalists only. The system must have a proper mix of generalists and specialists. The management of the system becomes substantially more complicated. Communication among specialists of different disciplines is extremely difficult, and the system can easily lose its coherence and sense of direction. The managers of the system, therefore, must be well informed of the dynamics of the system.

tions of breeding populations. The research areas will vary widely in kind and in the level of application. The research then has two functions; to improve the knowledge related to tree improvement, and to help managers, as a group, to make decisions on practical problems.

The development of a breeding strategy takes two iterative steps. First, the breeding system and its silvicultural system are described. Secondly, the options that can be generated from the system are defined and evaluated. The results of the evaluation should be reflected back to the system structure, and from the system new options will be generated and evaluated. The iterative process is open-ended, and the rate of iteration should be adjusted such that the balance between short-term gain and long-term flexibility can be maintained. The systematic iteration accompanied by strategic research is important because it can help prevent the system from changing at random.

The evolution of the technical system takes place slowly. Although it is desirable to have an instant ideal system, one with a proper mix of both specialists and generalists at right places and rapid information flow among the members, the technical develop-

ment depends on other components of the breeding system such as breeding stock and available information and technique. The development also depends on the availability of specialists and of general knowledge in fields other than tree breeding.

Although the current organization and management is responsible for developing a sound tree breeding system, the technocrats are responsible for preparing information necessary for future organiza-

tions and for educating the future generations of managers. The time scale involved and the justification of tree breeding are different from those of commercial enterprises. The strategic information on the organization and management of tree breeding system is therefore absent. To make the future evolution of tree breeding possible, the strategic research must be carried out by contemporary researchers.

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