

perhaps — as evolving entities, they will not develop along identical paths in the future. Even for an individual breeding system, the future organization cannot be predicted at the beginning of the program; adjustment from generation to generation will be essential. Therefore, flexibility and the maintenance of genetic diversity are the most important features of any long-term breeding program.

Literature Cited

CECICH, R. A.: White spruce (*Picea glauca*) flowering in response to spray application of gibberellin A_{4/7}. Can. J. of For. Res. 15, 170—174, (1985). — JEFFERS, R. M.: Parent-progeny growth correlations in white spruce. Proceedings 11th Meeting Committee on Forest Tree Breeding in Canada, MacDonald College, Quebec, Aug. 8—10, 1969, 213—221, (1969). — KANG, H.: Long-term tree breeding. In: Proc. 15th Southern Forest Tree Improvement Conference. Mississippi State University, June 19—21, 1979. Sponsored publication No. 37 of the Southern Forest Tree Improvement Committee. Distributed by Eastern Tree Seed Laboratory, U.S. Forest Service, P.O. Box 819, Macon, Georgia 31202. U.S.A. 66—72, (1979). — KANG, H.: Designing a tree breeding system. In: KHALIL, M. A. K., ed. Proceedings 17th Meeting Canadian Tree Improvement Association. Party 2. Symposium on Tree Improvement in the Boreal Forest: Today and Tomorrow. Gander, Newfoundland, August 27—30, 1979. Environment Canada, Canadian Forestry Service. 51—63, (1980). — KANG, H.: Components of a tree breeding plan. In: Proceedings IUFRO Joint Meeting of Working Parties on Genetics about Breeding Strategies Including Multiclonal Varieties. Sensenstein, September 6—10, 1982. Lower Saxony Forest Research Institute. Dept. Forest Tree Breeding. D-3513 Staufenberg-Escherode. Federal Republic of Germany. 119—135, (1982). — KANG, H. and NIENSTAEDT, H.: Managing Long-Term Tree Breeding Stock. *Silvae Genetica* 36, 30—39, (1987). — MOHN, C. A., RIEMENSCHNEIDER, D. E., CROMELL, W. and PETERSON, L. C.: A white spruce progeny test — seedling seed orchard: 12th Year Progress Report. Proceedings 12th Lake States Forest Tree Improvement Conference, Petawawa Forest Experiment Station, Aug. 18—22, 1975, 98—107. (1976). — MURPHY, J. G. and MILLER, R. G.: Flower production on clonal orchards at Ocon-

to River Seed Orchards. In: Proceedings 13th Lake States Forest Tree Improvement Conference, Aug. 17—18, 1977, Univ. of Minnesota, St. Paul, MN. 26—32, (1979). — NAMKOONG, G.: Challenging tree breeding theory. In: Proceedings, IUFRO Joint Meeting of Working Parties on Genetics about Breeding Strategies Including Multiclonal Varieties. Sensenstein, September 6—10, 1982. Lower Saxony Forest Research Institute, Dept. Forest Tree Breeding. D-3513 Staufenberg-Escherode, Federal Republic of Germany. 155—161, (1982). — NIENSTAEDT, H.: White spruce seed source variation and adaptation to 14 planting sites in northeastern United States and Canada. In: Proceedings 11th Meeting Committee on Forest Tree Breeding in Canada, MacDonald College, Quebec, Aug. 8—10, 1968, 183—194. (1969). — NIENSTAEDT, H. and TEICH, A.: The genetics of white spruce. Forest Service Research Paper WO-15. 24 p. USDA-Forest Service, (1972). — NIENSTAEDT, H.: "Super" spruce seedlings continue superior growth for 18 years. Res. Note NC-265, 4 p. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, (1981). — NIENSTAEDT, H.: Inheritance and correlations of frost injury, growth, flowering and cone characteristics in white spruce, *Picea glauca* (MOENCH) VOSS. Canadian Jour. Forest Research. 15, 498—504, (1985). — NIENSTAEDT, H. and RIEMENSCHNEIDER, D. E.: Changes in heritability estimates with age and site in white spruce, *Picea glauca* (MOENCH) VOSS. *Silvae Genetica* 34 (1), 34—41, (1985). — RUDOLF, P. O.: A basis for forest tree seed collection zones in the Lake States. The Minnesota Academy of Science. In: Proceedings 24, 21—28, (1956). — STELLBRECHT, J. W., MOHN, C. A. and CROMELL, W.: Productivity of white spruce seed sources in a Minnesota Test Planting. Minnesota Forestry Notes, No. 251, 4 p., (1974). — WEIR, R. J. and ZOBEL, B. J.: Managing genetic resources for the future — a plan for the N.C. State Industry Cooperative Tree Improvement Program. In: Proceedings 13th Southern Forest Tree Improvement Conference. Raleigh, North Carolina. June 10—11, 1975. Sponsored publication No. 35 of the Southern Forest Tree Improvement Committee. Distributed by Eastern Tree Seed Laboratory, U.S. Forest Service, P.O. Box 819, Macon, Georgia 31202, U.S.A.: 73—82, (1975). — WRIGHT, J. W., NIENSTAEDT, W., LEMMIEN, W. A., BRIGHT, J. N., DAY, M. W. and SAJDAK, R. L.: Better white spruce for Michigan. Michigan Natural Resources Research Report No. 316, Michigan State University Experiment Station, 8 p., (1977).

Managing Long-Term Tree Breeding Stock

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Abstract

In recent years, many tree breeding organizations around the world completed their first generation tree breeding efforts. These accomplishments made multiple generation breeding a reality. The new development necessitated critical examinations of long-term tree breeding concepts. In this paper, these topics in long-term tree breeding are discussed: (1) The need for classifying long-term breeding into two kinds: systematic breeding and repetition of single generation breeding; (2) Fundamental concepts necessary to develop a systematic breeding; (3) Difficulties involved in determining population size, structure, and breeding zone; (4) Classification of population structure; (5) Distinction between breeding zone and production zone; and (6) Distinction between population closure and breeding stock closure.

Key words: Population size, population structure breeding zone, production zone, population closure, systematic breeding.

Zusammenfassung

In den letzten 40 Jahren haben viele Züchtungsinstitutionen in aller Welt, die Waldbaumzüchtung betreiben, die erste Generation ihrer Züchtungsversuche abgeschlossen. Durch die erreichten Ergebnisse wird eine Züchtung multipler Generationen zur Realität. Diese neue Entwicklung macht es notwendig, langfristige züchterische Konzepte kritisch zu prüfen. Zur langfristigen Waldbaumzüchtung werden deshalb in dieser Arbeit die folgenden Themen diskutiert: 1.) Es ist notwendig, die Forstpflanzenzüchtung in 2 Kategorien aufzugliedern, d. h. in die systematische Züchtung und in die Wiederholung der Einzelgenerationszüchtung. 2.) Es sind fundamentale Konzepte zur Entwicklung einer systematischen Züchtung zu entwickeln. 3.) Zur Festlegung der Populationsgröße, der Struktur und der Züchtungszone, 4.) zur Klassifikation der Populationsstruktur, 5.) zur Unterscheidung zwischen der Züchtungszone und der Produktionszone und 6.) zur Unterscheidung zwischen

einer geschlossenen Population und einer geschlossenen Bestockung.

Introduction

During the last four decades, breeders have successfully demonstrated short-term economic benefits of tree breeding. Initially, a few breeding techniques were used, such as provenance testing, and progeny testing of trees selected in natural stands or plantations. The techniques, were combined with seed production methods such as the development of seed production areas and seed orchards, were broadly applied to many different species.

Subsequently a wide range of biological, biochemical, ecological, and silvicultural techniques have been introduced into tree breeding. Tree breeders and forest geneticists have discussed concepts such as advanced generation breeding, long-term breeding, and genetic resource conservation.

When compared to the original breeding concepts and techniques, the new ones tend to have a less direct relationship with short-term economic gain. We view the new trend as an indication that tree improvement has reached a juncture where its future outlook needs to be reevaluated. This need has become increasingly serious because of a growing awareness by tree breeders that whatever they do today will influence future tree breeding for a long time; what is good for today may not necessarily be good for tomorrow. Decisions made or not made now will limit future options.

In this paper, we take the view that tree breeding is maturing as an important discipline in forest resource management, and is no longer a collection of simple tools necessary to add genetic gains to artificially regenerated trees. With this premise we will attempt to construct some founding concepts for future tree breeding. We will deal with ideas at three different conceptual levels: 1) tree breeding system and strategy, 2) long-term breeding as a functional component of the tree breeding system, and 3) breeding stock management techniques under long-term breeding. We are primarily interested in discussing the third subject, long-term management techniques of breeding stock. We will, however, review the first two subjects because they establish the long-term perspective necessary for subsequent discussion. More detailed discussion of the concepts is found elsewhere (GULLBERG and KANG 1985).

Tree Breeding System and Strategy

A system represents a collective entity composed of interdependent parts. The tree breeding system may, therefore, be defined as the collection of all available resources including the institutional organizations — their staffs, financial capabilities, and landbase; the breeding stock¹⁾; and the available knowledge and techniques. Tree breeding strategies represent the operating mechanisms that make evolution of the system possible under changing environments and objectives (GULLBERG and KANG 1985). The above strategy concept is different from an action plan, which assumes the presence of a specific institution to perform the breeding and describes actions to be taken to accomplish a fixed set of objectives.

Obviously, a strategy cannot exist without a corresponding system, and a system cannot be directed without a

strategy. Any evolving system must have long-term evolutionary strategies as well as short-term plans for maximizing values under the given environment. Past breeding efforts have concentrated on the highly profitable short-term end of the breeding system, and much is known about developing short-term plans and executing them. Little is known about long-term strategies.

Currently many organizations have reached a point where breeders have to consider their basic strategies for advanced generation breeding. The first strategic dichotomy deals with the concept of long-term breeding. One could consider repetitions of single generation breeding as long-term breeding. Under this concept, continuous refinement of single generation breeding techniques will be sufficient for long-term breeding because they will be iterated over generations. Alternately, a new conceptual frame called long-term breeding can be created in addition to the ongoing short-term activities (KANG 1982). This approach, which will be referred to as systematic breeding (Fig. 1) requires a new breeding philosophy and a new set of long-term techniques.

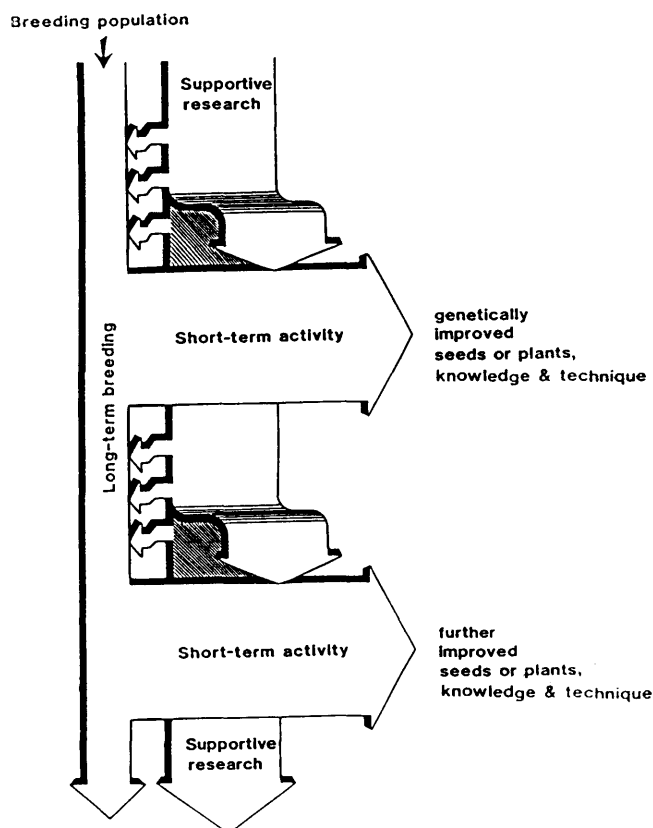


Figure 1. — Functional components of a systematic breeding (From GULLBERG and KANG 1985).

The definition of breeding system as it appears in the text deals with physical components of tree breeding. The above figure represents functional components of tree breeding. The long-term breeding is aimed at maintaining an optimum balance between continuous genetic improvement and diversity conservation by manipulating the long-term breeding population in a structured manner. The short-term activity is further divided into short-term breeding and multiplication. The short-term breeding manipulates long-term breeding populations through intensive testing, selection, and mating efforts to maximize the possible genetic gain with respect to the economically important traits of the time. The products of such short-term efforts are subsequently multiplied, research supports both long- and short-term breeding. Long-term supportive research tends to emphasize solving inherent problems in tree breeding. Short-term supportive research tries to develop means of maximizing the short-term economic gain.

¹⁾ The term „stock“ is used to represent the entire collection of populations and individual trees a breeder (or a breeding organization) uses in breeding.

Long-Term Breeding

Recently, many long-term philosophies have been discussed (NAMKOONG 1978, 1984, KANG 1979, 1980, 1982, NAMKOONG *et al.* 1980, GULLBERG and KANG 1985). For the present purpose it is enough to note that long-term breeding is a functional component of tree breeding systems, designed to provide genetic resources that can be used in short-term breeding under changing environments and societal demands. Its relation with short-term activities and supportive research is described in *Figure 1*. Some salient features of the long-term (both breeding and supportive research) concept under systematic breeding are summarized as follows.

1) many long-term breeding activities cannot be justified based on short-term economic merits.

2) the goal of long-term breeding is to make future short-term breeding continuously successful under changing environments and societal demands.

3) long-term activities tend to focus on inherent structural problems of tree breeding, such as the diversity in breeding population, the generation turn-over period, and the purging of deleterious alleles. In many long-term activities, economic traits are not involved. Under systematic breeding, short-term activities deal with economic traits.

4) long-term breeding as described in this paper does not imply long time. Frequently long-term activities will take less time than short-term ones, because many of them can be completed at a juvenile stage of tree growth.

5) population management concepts and technical recommendations for long-term breeding will frequently contradict those short-term, or repetition of single-generation techniques (KANG 1982).

Many features of long-term breeding as described above coincide with those of the control concept of gene conservation (NAMKOONG 1984). Long-term breeding attempts to maintain an optimum balance between continuous genetic improvement and diversity conservation. Therefore, conservation is an essential component of sound long-term breeding.

Long-term breeding definitely deviates from the familiar short-term concepts of tree breeding. The fifth distinction is a natural consequence of introducing different subjects of concern into tree breeding. Because of the distinction, tree breeders need to determine the conceptual foundation of long-term management of breeding stock and techniques in addition to their present tree breeding philosophy. In this paper, we will classify and discuss various concepts of breeding stock management, with emphasis on long-term breeding. An elementary distinction between long- and short-term views with respect to techniques has been made elsewhere (KANG 1982).

Breeding Stock

Breeding stock is a physical component of a tree breeding system, needed for both long- and short-term breeding. The breeding stocks available to breeders today represent either base populations for long-term breeding or short-term breeding populations, or both.

The organization of the population for long-term breeding will be different from that for short-term breeding. In short-term breeding, the measure of the genetic resource is performance of individuals with respect to some known traits, and co-ancestry control and avoidance (especially early avoidance) of inbreeding will be emphasized. The selection strategy will favor maximizing the genetic

gain. Statistical estimation of population parameters and gain prediction will dominate the research. In long-term breeding, one measure of interest is the presence or absence and frequency of various alleles. The strategy will employ multiple options. Inbreeding will be used freely. Different selection schemes will be adopted, but they will not necessarily lead to immediate maximum gains in known traits. For example, with respect to long-term breeding, 50% selection might generate the best results (DEMPSTER 1955, ROBERTSON 1960). Understanding of the breeding population dynamics will be emphasized in the research (KANG 1979, 1980). For most known breeding techniques, opposing approaches tend to be favored by the two different breeding emphases (KANG 1982).

Short-term breeding emphasizes the property of the populations at a given time (static); long-term breeding emphasizes the dynamic properties over time. At any given time, it is conceptually possible to translate the dynamic property of the population into its static property. The reverse is not true, and tree breeders must avoid organizing long-term breeding stocks based on the static property of the population or on criteria that would primarily facilitate short-term breeding. On the other hand, the organization of long-term breeding stock should consider the mechanisms involved in transforming long-term stock into short-term stock. Therefore, when organizing breeding stock in systematic breeding, tree breeders must have a strategy for maintaining the balance of different emphases while directing the system.

Of the technical issues differentiating long- and short-term breeding stock management, we will discuss population size, structure, breeding zone, sampling and origin of base populations, and population closure. Our primary goal is to facilitate the organization of long-term breeding stock. The short-term aspect of breeding stock will be discussed as needed.

Population Size

Population size and structure have been recognized as essential factors to consider in developing breeding strategies (NAMKOONG 1978). Most contemporary tree breeders are creating base breeding populations. To do so, the breeder must determine the overall base breeding population size. Determining the size, however, is a complex matter, and there is no fixed way of determining the size. To a breeder who has to work with limited resources, an intuitive answer might be: The breeding population should be as large as practically possible. Determining the "practically possible" size, however, is not as simple as it appears. Even for a given breeding organization, the practically possible size will vary. If the organization is primarily interested in collecting open-pollinated seeds and in planting the progenies in a test (or breeding) plot, 2000 selections may not be too large. Incorporating more complex techniques in the scheme will reduce the size; and elaborate schemes that will generate in-depth knowledge about the population will limit the size even further. Future uncertainties make size estimates of the breeding population even more difficult.

Alternatively, the ideal breeding population might be as large as the natural population. This answer is based on the assumption that the current natural populations are the right size for further evolution within the natural system. Excepting natural catastrophes — chestnut blight or Dutch Elm disease — they can survive and thrive in the face of impacts from diseases, insects, or a changing environment.

However, this answer is also of little help in deducing the desired population size. The assumption itself can be criticized, and the natural population size and the mechanisms involved in determining the natural population size vary.

Despite the difficulties associated with assigning actual numbers, the above answers introduce two important limiting conditions to consider in determining the population size — the amount and distribution of available human resources and the need to maintain genetic diversity to encounter potential catastrophes.

A third estimate is derived from theoretical numbers generated on the basis of various breeding assumptions and gene action models. Although the estimates are derived by mathematical means, the assumptions and models are not any more realistic than what might be used for finding approximate numbers for the first two answers. The approach, however, helps in understanding the dynamics of tree breeding populations. Therefore, both the process and the numbers are important sources of intuition necessary for making management decisions.

In each investigation the researcher must define the properties (parameters) that will dictate the population size in the model. The probability of fixing a favorable allele in the population has often been used as a parameter (ROBERTSON 1960), and based on ROBERTSON'S work some suggestions on the population size have been made (RAWLINGS 1970, KANG 1979, NAMKOONG *et al.* 1980). Another parameter that has been used is the loss probability of neutral alleles at a locus linked to a selected locus (NAMKOONG and ROBERTS 1982). The effects of small founder population sizes under different population parameters have been discussed DENNISTON 1978, JAMES 1971, NEI *et al.* 1975, SIRKKOMAA, 1983). In general, the conclusions suggest that the theoretically acceptable population size ranges between 500 and 2000.

The above models do not consider the impact on population size of deleterious alleles, especially lethal alleles at homozygosity. Tree breeding is new, and deleterious alleles have not been purged from breeding populations. Therefore, the theoretical population size could increase further when models incorporating purging of deleterious alleles are evaluated.

The population size also depends on other factors such as the structure of the natural population from which samples are drawn, the structure of the breeding population to be created, and the nature of population closure. These factors will be discussed in subsequent sections. Note, however, that the purpose of discussing the factors is to point out subjects to consider in developing tree breeding systems and strategies; it is not to recommend a specific population size.

Population Structure: Classification

The need to differentiate population types in tree improvement has been recognized for some time (NAMKOONG *et al.* 1966, 1980, NAMKOONG 1976, 1978, VAN BUIJTENEN 1975, LINDGREN and GREGORIOUS 1976, KANG 1980, 1982). Broad functional categories such as breeding, multiplication, and (wood) production populations have been used to classify the populations, and it has been pointed out that the functional populations do not have to coincide with physical populations (KANG 1982). Each of the functional populations can be classified further according to subfunctions. For example, multiplication populations can be subdivided into seed orchards, hedged clones for cuttings, and cultured tissues. Production populations may be classified according

Table 1. — Classification of Breeding Populations*)

NBP	NSP		Single		Multiple	
	B-B	ENV	Single	Multiple (m-)	Single	Multiple
Single			Single	m-Single	Sublines	Subgroups
Multiple	distributed (d-)		d-Single	dm-Single	d-Sublines	d-Subgroups
	confounded (c-)		-	-	c-Sublines	c-Subgroups

*) NSP Breeding subpopulations.

ENV Environment.

B-B Arrangement of origins in breeding populations.

NBP Number of origins of base populations.

to the management intensity, and similarly, breeding populations can be classified further.

Although terms such as multiple populations and sublines have been discussed before (BURDON and NAMKOONG 1983), explicit classification of breeding populations has not been made in the past. An explicit classification is useful because it helps in 1) communicating, 2) developing breeding strategies, and 3) determining the particular types of breeding populations whose merits need to be evaluated.

Many different criteria can be used to classify breeding populations. The most well-known criterion is the number of breeding subpopulations — single vs. multiple. Examples of other classification criteria are as follows:

- Origin of population — single vs. multiple origins.
- Environment — single vs. multiple environments (caused by different selection criteria as well as the geography).
- Base and breeding population combination — when base populations of multiple origin and multiple breeding populations exist, the base populations can be distributed over or confounded with the breeding populations.
- Breeding for different gene action — within subpopulation vs. reciprocal recurrent selection or other interpopulation selection schemes.
- Gene flow — gene flow among breeding subpopulation (artificial migration), or that from source (natural) populations to breeding populations (open vs. closed breeding population).
- Special functions — speciality breeding subpopulation, inbreeding copy, control line for selection, etc.

Because of space, we will limit our classification to four factors: The number of breeding subpopulations (NSP), origin of base populations (NBP), environment (ENV), and base-breeding population combinations (B-B) (Table 1).

Single population breeding, in the most rigorous sense, is unlikely to exist in tree breeding. Regardless of the main emphasis, breeders are likely to have copies of the main breeding population in some way. Therefore, it is necessary to distinguish copies from multiple populations. Any two populations that share the same ancestors will be referred to as copies. We define multiple populations as a collection of populations originating from non-overlapping subsets of the base population. In this case each subset functions as an independent basis of selection, mating, and gene flow. The definition of multiple populations includes both sublines and multiple populations as discussed by BURDON and NAMKOONG (1983). The subgroups in Table 1 are equivalent to their multiple populations.

The m-single population represents the situation where the multiple copies are complete and are subjected to different environments. The completeness means that all the entries of the copies share exactly the same ancestors. Therefore, except for the lack of the original subdividing procedures, m-single population is identical to multiple populations. Because of the heavy replication needs, breeding by using m-single population will tend to be costly. In most practical situations, breeders will either use single populations with partial copies to perform specialized functions, or they will use multiple populations. Therefore, we will not consider m-single populations here.

Treating breeding populations with multiple origin as if they came from one origin will, as selection and breeding progresses, reduce the population diversity and, consequently, the population size. We will discuss this further in a later section. When multiple origins exist, breeders have the choice of assigning them in separate populations (confounding: c-population), or distributing them in many different populations (d-population). Most currently available breeding populations are of multiple origin. If multiple populations are chosen, breeders will have to make two step decisions; single vs. multiple populations, and distributed vs. confounded population.

Population Structure: Single VS. Multiple Population

The single population approach will breed the entire population without any subdivision. Although difficult, the associated testing at different locations may included all the

members of the population. Even if completely replicated testing is not possible, selection will be performed on the entire population basis. The emphasis of selection will be broadly adapted individuals regardless of the trait of interest. For multiple trait selection, a form of indexing will be used. The single population approach is production oriented and lends itself well to short-term breeding.

The multiple population approach frequently assumes the presence of a transition phase between the subdivided breeding population and the multiplication population. During this phase, trees from various subpopulations undergo short-term breeding designed to determine or recombine individuals to be included in multiplication populations (Fig. 2). Selection criteria and breeding objectives will be, as in the case of the single breeding population strategy, i.e., broad adaptability, and well-balanced performance in different traits, etc. Additional testing designed to verify the selections will take place during this phase. It is, of course, possible to bypass this transition phase, especially in low budget breeding operations such as recurrent maintenance of seed production areas (NIENSTAEDT and KANG 1982), or multiplication populations converted directly from breeding populations (progeny test seedling seed orchards). Because the transition phase is an extra breeding step, the use of the multiple population strategy is not attractive if the overall breeding principle is guided by short-term economics. Only in systematic breeding as discussed in previous sections, does the use of multiple populations become attractive. It provides the foundation for

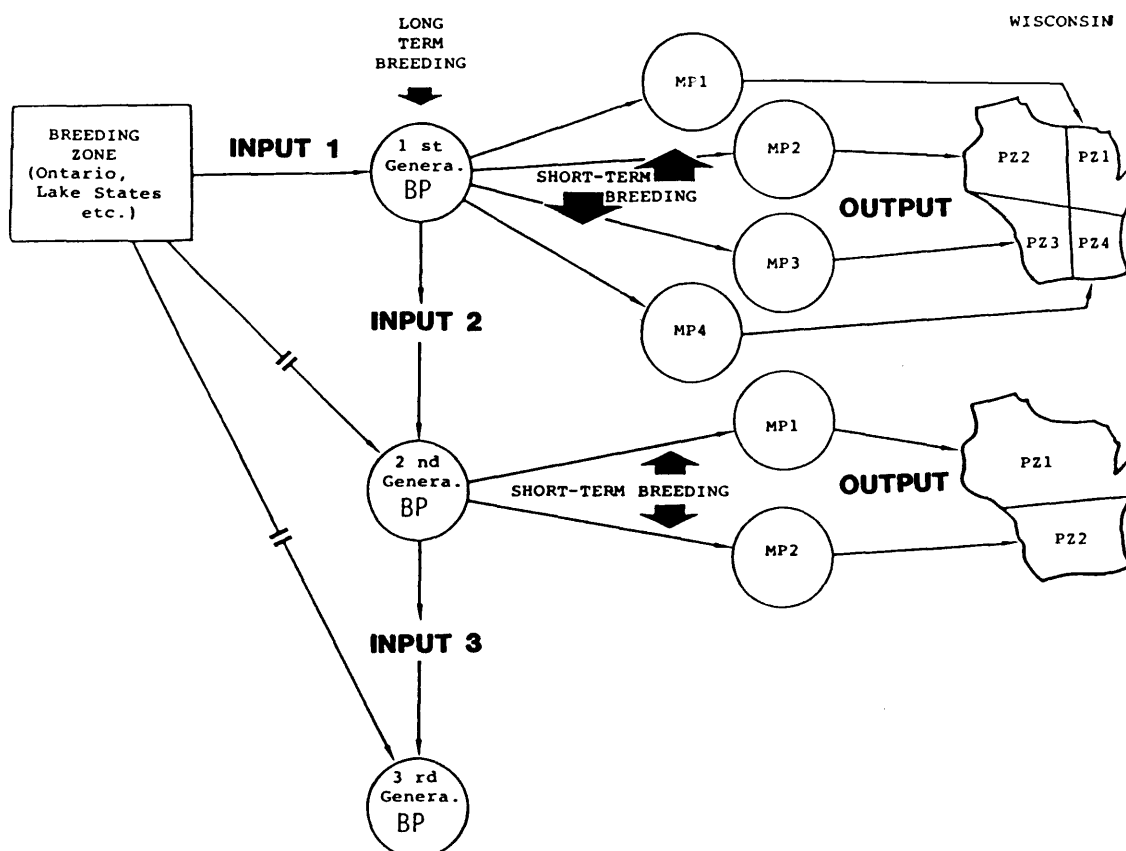


Figure 2. — An interpretation of breeding zone and production zone.

If breeding zone is defined as the region from which the breeding population is sampled, Input 1 corresponds to areas such as provenances, or seed sources. It is, however, more useful to represent Input 2 and Input 3 by the names of the previous generation breeding populations. The outputs, such as improved trees, of breeding efforts must have a geographic area(s) in which they perform well (Production Zone).

BP: Breeding population, MP: Multiplication population, PZ: Production zone.

multiple strategies. By subdividing populations, breeders can prevent the centralizing tendency of the single large population management, which encourages the reduction in diversity of all kinds. The multiple populations facilitate long-term breeding; the transition phase represents short-term breeding. In the single population approach, one population has to accommodate both long- and short-term breeding functions.

Population Structure: Sublines

In seed orchards, the crossing of sublines not only prevents inbreeding, but if directional dominance genes are involved, seeds resulting from crossing of sublines may show heterosis. Because sublines represent small inbreeding groups, genetic drift will cause the populations to vary in gene frequencies. When populations with different gene frequencies are crossed, the resulting population will have an excess of heterozygotes (ROBERTSON 1965), and they may therefore show heterosis (KANG 1980).

Sublines will also respond to selection more quickly than the large single population (BAKER and CURNOW 1969, MADALENA and HILL 1972, MADALENA and ROBERTSON 1975, MARUYAMA 1970, NAMKOONG *et al.* 1980, ROBERTSON 1960, YOUNG and SKAVARIL 1976). It has also been suggested that the use of sublines resulting from within full-sib family selection may increase the selection limit (DEMPFLE 1975). This is because such a selection system would maintain a larger population size than mass selection (ROBERTSON 1961).

As long as all the sublines combined do not have a lower selection limit than the large single population, the advantage of sublines is their rapid response to selection in early generations. ROBERTSON (1960) estimated the half-life, i.e., the time required to reach halfway to the selection limit, to range between N and $2N$, where N represents the effective population size. For most tree species, in single populations of 100 selections, the actual time required to reach the selection limit will be more than 1,000 years. Therefore, it is unrealistic to begin a long-term breeding program with the idea that some day the single large population will reach its selection limit with respect to the traits of current interest. The selection limit is a conceptual restriction, it is not an operational guide. It is important to know that the alternate strategy will not lower the limit. Within this constraint, however, tree breeders must search for ways of maximizing early progress. In theory, the smaller the sets, the greater the early gains would be. For example, BAKER and CURNOW (1969) showed that the replicate with a size of 1 had the fastest progress from selection for between 1 and 5 generations. A population of size 1 represents a selfing population with within-family selection. As the selected generation progresses, the breeder will always have a chance to modify the population structure. If the selection criteria and breeding environment do not change, but the lines are reaching their limits, they could be combined to create a more productive system.

In single population breeding, breeders frequently sample portions of the population to generate information, which in turn will be used to make inferences about the entire population. By carefully sampling and organizing the individual lines, breeders can facilitate the information gathering and inference making process. The need for information about the entire population can be minimized, and the resources can be redistributed to obtain within-line information. Such redistribution can apply to both mating and testing designs. For example, for a given cross-

ing capability, breeders can choose mating designs that will increase the number of families within subsets, rather than those that are good with respect to estimating overall population parameters. The information from different sets can be combined to determine the average and variance of the subline parameter estimates. This will help the breeders improve their confidence in the parameter estimates of any particular subset. Because selection is performed within the sublines, increasing the number of families within a line will certainly be useful if the selection scheme considers family merits.

Parameter estimates of a small number of traits can be performed on all the sublines or subgroups. This is not possible when many different traits are of interest and/or intensive studies on the basic properties of trees are needed. If the lines represent random samples of a homogeneous base population and have the same subsequent breeding history, the differences among them only represent the initial and subsequent sampling errors. In that situation, breeders can, by choosing a small number of 3 to 4 sets (index populations), generate information on other populations with confidence (KANG 1980). In the single population approach, on the other hand, it is difficult to define a subunit of the entire population suited for integrating information. This is because subunits are not independently reproducing units under breeding. It follows that subunits are not effective means of generating information on the dynamic behavior of the entire population.

Population Structure: Subgroups

Relaxing the assumption that all the subpopulations are subjected to identical breeding environment and the same breeding practices makes subgroups substantially more complex than sublines. Subgroups have different kinds of populations, and the management of such populations become quite cumbersome. Because subgroups are small, they share some of the advantages of sublines. Unlike the case of sublines, subgroups and single large populations cannot be contrasted directly. However, comparing subgroups with m -single populations will yield results similar to comparing sublines and single populations. The properties of the subgroups to be discussed primarily deal with contrasting single vs. multiple environment breeding, which could apply to comparing single vs. m -single population breeding. Our discussion will, however, assume small populations.

In short-term breeding, it is desirable to develop trees that are broadly adapted and perform well with respect to many traits. A multiple-trait index selection can be used in this development. In long-term tree breeding, however, repeated use of the indices is not necessarily the best approach because it will reduce the intensity of selection for a given amount of resources (TURNER and YOUNG 1969, KANG 1982). The strict application of high selection intensity to many locations or traits could reduce the population size dramatically, and the population could become extinct (HALDANE 1957). The response to selection will be fastest when a single selection criterion is applied to a population. Therefore, an alternate strategy in long-term breeding is to assign different functions and use different selection criteria in different populations. From the diverse populations, multiplication populations can then be derived by using inter-population index selection schemes such as discussed in NAMKOONG (1976).

Within each subgroup, selection tends to encourage the fixation of favorable alleles, unless the trait is influenced by a strong non-additive gene action. Therefore, in the absence of such strong non-additive gene action, breeding in a small population will lead to early fixation or loss of alleles. In multiple population breeding, different alleles are likely to be fixed in different subpopulations; in the overall population the impact of fixation or loss of alleles may not be as great as in a single population. In surlines, the differences among populations only stem from genetic drift, and the degree of fixation of alternate alleles in different subpopulations is small if favorable alleles have high initial frequencies, say more than 0.2. In subgroups, on the other hand, both differential selection and genetic drift operate. Therefore, depending on the nature of the selection scheme, the entire population can maintain almost all the alleles existing in the base population for a much extended period; maintaining different alleles in the overall population by wise organization of the subgroups is equivalent to changing the additive gene action to dominance gene action at the entire population level (LEVENE 1953). In practical terms, it enables the breeder to respond to changing economic values of different alleles (NAMKOONG *et al.* 1980). The maintenance of subgroups is therefore an effective means of gene conservation for long-term breeding. An extreme form of within-subgroup organization is selection in opposite directions for the same trait. This approach is considered to be better than maintaining a selected and a control line for statistical evaluation of the progress from selection (HILL 1972). If possible, it would of course be desirable to maintain all three lines; selection upward, control, and selection downward.

The multiple population breeding does not solve the inbreeding problems within the breeding population. Unless the subpopulation is very small, the rate of purging will not be as fast as that of intensive inbreeding such as selfing. Therefore, subpopulations are not effective means of purging. Creating inbreeding copies of the subpopulations is desirable if purging is to be done properly. It is conceptually possible to combine purging and selection in a single subpopulation. Combining the activities, however, will bring a new set of problems. For example, if the selection age and reproductive age are not synchronized, the generation turnover will be dictated by the longer of the two. The breeder may also wish to create extra population to prepare for cases in which the subpopulation may not be continued because of the combined effect of selection and purging. ERIKSSON *et al.* (1984) suggested using both inbreeding-copy and inbreeding-selection copy for *Salix* breeding in Sweden.

In practice, many different combinations of surlines and subgroups can be used. The breeder can split the base population into two parts, and convert one part into surlines and the other into subgroups. Similarly, this can be done by making two copies of the base population. It is also possible to nest surlines in subgroups so that each subgroup is composed of smaller surlines.

Although surlines and subgroups are differentiated according to the number of environments involved, they are not necessarily opposing models. Each approach reflects different aspects of tree breeding. Decisions on the organization of the breeding population can only be made when the specific breeding circumstance is known. Only then will it be possible to discuss the advantages and disadvantages of the structure of the breeding stock.

Breeding Zone VS Production Zone

Concepts such as breeding zone and seed zone have been used for many years in tree breeding. They have been considered important tools for organizing breeding stock and for distributing the production populations. In the past, it was frequently assumed that fixed breeding zones could be determined, and many attempts were made to identify geographic regions within which genotype \times environment interaction was negligible. In the first generation breeding or in a strict single generation breeding, the concepts of the breeding zone and production zone may be used interchangeably. In multiple-generation breeding both zones tend to change with time, and could cause communication problems. Therefore, it is desirable to differentiate the two zone concepts, and to define possible alternate meanings of the zones.

Breeding zone

After removing the production aspect, breeding zone may be defined in two ways: 1) The region from which the breeding population is sampled. For example, in provenance testing a provenance can be used to represent a breeding zone to which breeders can return to obtain superior seeds (Fig. 2). 2) The region to which an initial breeding population is distributed. This region could also be the place where the trees are bred in subsequent generations.

Under the first definition, the breeding zone represents the area where the input (selection) for the breeding population was sampled. In multiple population breeding, the source of input for an advanced generation breeding population is the previous generation breeding population. In this situation keeping the breeding zone concept is no longer critical. The zones will reduce to dots on the map. At that time using the cultivar names becomes more convenient than using the breeding zone concept.

Even in a breeding scheme where migrations are allowed among some subpopulations, the breeding zone concept becomes cumbersome. Even if all the subpopulations in an area exchange genes among themselves every generation and the area does not change over generations, a finite cluster of subpopulation does not represent a zone.

Under the second definition, the breeding zone has a historical significance; it does not have subsequent operational significance. Suppose a breeding zone is defined such that tree breeders can interchange the breeding stocks at the first generation. As long as multiple population breeding is applied, the subpopulations will diverge in the subsequent generations. One might choose to determine the area where the products of each subpopulation perform well. This area is better defined as a production zone. Conceivably, it is possible to determine an area where a breeding subpopulation can be transferred in the following generation, and the area might be referred to as a breeding zone. If the determination involves extra testing, this would create much additional work under multiple population breeding. In general, breeders are likely to try to keep the following generation near the parental population sites. Therefore, the breeding zone concept can easily be replaced by the cultivar names.

The same is not true in a single population breeding, in which incomplete replicates of the population are distributed in a zone. If the distribution is random in different generations and the individuals from different replicates can be combined freely to form the following breeding generation, the breeding zone concept is useful.

Production zone

On the output side of *Figure 2* production zones can be defined as the area to which the products of the multiplication populations are distributed. At this stage, breeders will determine the impact of genotype \times environment interaction, using candidates for the multiplication population. Therefore, the production zone can only be delimited with reference to a specific multiplication population. It will change as the breeding population evolves and will depend on the combination of subpopulations in the multiplication population. Because of the hybrid nature of the production population, the production zone in a multipopulation breeding model may become larger than it would be in short-term, single population models in which the breeding population is converted to a multiplication population as, for example, in the progeny test seedling seed orchard approach.

Sampling and Origin of Base Populations and Population Closure

Most currently available tree breeding stocks were sampled with short-term breeding in mind. Provenance tests, for example, were created to identify the best seed sources for production populations. Plus tree selection in natural populations also emphasized the performance of trees. Questions such as maximizing the number of alleles sampled in the base population were not considered. Sampling for allelic diversity, however, is a more important criterion for creating base populations than the performance of individuals. Contemporary breeders are responsible for the decisions that must guide the sampling. Some limited information on allelic sampling is available (MARSHALL and BROWN 1975, GREGORIUS 1980). The size and adequacy of the sampling are some of many questions breeders must consider in establishing base breeding populations. For example, should the breeding populations be left open in case the base population does not have sufficient genetic diversity? If closing the populations is necessary for making progress from selection, when should the populations be closed? At the initiation of a multigeneration breeding effort, most tree breeding organizations have access to large numbers of collections of different origin. Can such materials be used to form a diverse base population? Will the base population thus synthesized be as good as that sampled new from natural populations using different sampling schemes?

Breeding Stock Closure

The two kinds of population closure are; closing (1) the entire breeding stock, or (2) individual subpopulations regardless of the structure, i.e., replicates in single population breeding, sublines, subgroups, and combinations of such units.

The closing of individual subpopulations is not a critical factor in determining the genetic diversity of the entire breeding stock. Unless artificial migration among subpopulations is used, subpopulation closure is desirable to make selection efficient. Should it become desirable to augment the breeding stock with new superior individuals, it is best to create new closed subpopulations using the new introductions or combinations of the new individuals and samples from other closed subpopulations. Subpopulations can be discarded if there are viable alternative in the entire stock. For example, if the inbreeding copy of a closed subpopulation is more desirable, the breeder might discard the original subpopulation.

The openness of the entire breeding stock is a more critical issue, and we may define two kinds of openness: active and passive. Breeders tend to save and use good or rare individuals whenever they encounter them. Very little cost is involved in being passively open for such individuals. Therefore, passive openness always is likely to exist in tree breeding.

Active search occurs either during the initial stage when the base population is sampled, or later when the breeders encounter some limiting conditions that compel them to make more samples. For example, breeders will actively search for new genes if and when the selection limit of the entire breeding stock is reached, or when they need rare genes useful for specialty breeding.

Many tree breeders engaged in short-term breeding currently have available populations that might be converted into base populations. Therefore, active search for allelic diversity for long-term breeding does not have economic incentives (NIENSTÄEDT and KANG 1985). Furthermore, the potential performance disparity between the new samples and available materials makes it difficult to justify resampling. As the generation progresses, this difficulty will be compounded. In active searches in future generations, the disparity will be the primary difficulty. At that time other limiting conditions such as a need for diversity or specific genes will generate sufficient economic incentives.

Tree breeders tend to emphasize the need for the second type of search, but little is said about the first. For example, many advocate the need for gene banks to prepare for the future. The more critical need, however, is to determine the long-term values of currently available breeding stocks. If a good base population is established and the subsequent breeding is organized carefully, the gene bank may never become necessary.

Because of the increasing genetic disparity, shortcomings in the initial search will become more and more difficult to correct with progressing generations. Therefore, breeding stock closure is now occurring in the initial phases of the multigeneration breeding efforts — much sooner than has been generally recognized.

If we are closing our breeding stock already, is our sampling of the genetic diversity adequate? To determine adequacy, we require information on the relation between sampling for alleles and selecting for performance. Little is known about the subject, and each breeding organization will need to investigate the matter separately.

Should such an investigation lead to the conclusion that more sampling is necessary, the following questions will become pertinent. Should the resampling be done at once or over many generations? Should the short-term populations that are the sources of the original sampling be discarded after they complete their intended functions? Should the short-term populations be merged with new selections? Should their identity be maintained? The answers to these questions depend on the philosophy and strength of the breeding organization. We can, however, discuss problems associated with managing breeding stock of multiple origins because resampling results in multiple origins.

Managing Breeding Stocks of Multiple Origins

Breeding organizations have several alternatives for managing breeding stocks of multiple origins. If single population breeding is adopted, breeders may consider maintaining two complete replicates of the entire population. One replicate is used in short-term breeding; the other is allowed to repeatedly inter-mate until the breeder feels

that the genes from different sources have recombined extensively. As an alternative, the breeder could pool progenies of different origins immediately and use the pooled population as the basis for the first generation selection. In this case, if the origin differences in the trait of interest are great, the selection will eliminate many inferior sources and reduce the allelic diversity available in the initial sampling. An alternative approach is to keep the identity of the origins separate and make within subpopulation crossings for generation turnover, but apply two sets of selection schemes. For intensive two-stage selection in short-term breeding, within and between populations may be used. For long-term breeding, the selection intensity of the populations may be adjusted over generations until all populations become equalized. After equalization, the populations may be pooled to form a single large breeding base population. Until that time, however, the breeding scheme is c-sublines rather than a single population breeding (Table 1). As a final step, different breeding population types such as single, d-sublines, and subgroups may be developed from the single large breeding base population.

The process of equalization is likely to take at least two generations, and the need for the single large breeding base population can be questioned. There are no biological reasons that would suggest that the use of a confounded population structure would be inferior. Furthermore, a particular source can be distributed over different locations or subdivided to form d-sublines or d-subgroups. Therefore, populations of some origins can be confounded and others can be distributed. The main problem with using confounded sub-populations of multiple origin is the difficulty in managing the populations and information. For a given management capability, the large number of origins will weaken the management intensity. The most extreme form of low intensive breeding management that could result from such confounding is the maintenance of a seed production area network.

Any intensive management of breeding stocks and information will require a certain amount of homogenizing of the breeding stocks. Therefore, the management of distributed populations is easier than that of confounded populations. In view of the difficulty and long time associated in equalizing populations of different origin, one may ask: Why shouldn't breeders discard the short-term populations when their purposes are met and resample trees from a natural population for the long-term multigeneration program? If the breeding organization has the resources, then making an allelic sampling might simplify many management problems in the subsequent generations.

Concluding Remarks

Long-term breeding is a reality, and breeding actions taken by contemporary breeders will have a long-lasting impact. Therefore, breeders must deal with futuristic problems. The uncertainty of the future is itself the guiding principle in dealing with such problems. Breeders must define the broad scope of the tree breeding function rather than only outline specific goals. They have to develop a breeding system and a strategy for the evolution of the system. They should not be only asking which techniques will yield higher genetic gain.

We have discussed the breeding system from a philosophical point of view. We have also discussed a functional component, long-term breeding, and a physical component, the breeding population, of the system. We have made a

conceptual classification, which can be useful for developing an actual breeding system design and strategy.

The extent to which contemporary tree breeders can prepare for long-term breeding is influenced by the amount of available resources. However, the way the limited resources are used will differ significantly after the tree breeding organization has gone through the classification process of defining the actual breeding system and initial strategy.

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Literature Cited

- BAKER, L. H. and CURNOW, R. N.: Choice of population size and use of variation between replicate populations in plant breeding programs. *Crop Sci.* 9: 555-560, (1969). — BURDON, R. D. and NAMKOONG, G.: Short Note: Multiple populations and sublines. *Silvae Genetica* 32: 221-222, (1983). — DEMPFFLE, L.: A note on increasing the limit of selection through selection within families. *Genet. Res. Camb.* 24: 127-222, (1975). — DEMPSTER, E. R.: Genetic models in relation to animal breeding. *Biometrics* 11: 535-536, (1955). — DENNISTON, C.: Small population size and genetic diversity: implications for endangered species. In: S. A. TEMPLE (Ed.). *Endangered birds: Management techniques for preserving threatened species.* Univ. of Wisconsin Press, Madison. Pp. 281-289, (1978). — ERIKSSON, G., GULLBERG, U. and KANG, H.: Breeding strategy for short rotation woody species. In: PERTTU, K. (Ed). *Ecology and Management of Forest Biomass Production Systems.* Dept. Ecol. and Environ. Res., Swed. Univ. Agric. Sci. Rep. 15: 199-216, (1984). — GREGORIOUS, H. R.: The probability of losing an allele when diploid genotypes are samples. *Biometrics* 36: 643-652, (1980). — GULLBERG, U. and KANG, H.: A model for tree breeding. *Studia Forestalia Suecica* No. 169: 8 p, (1985). — HALDANE, J. B. S.: The cost of natural selection. *J. Genet.* 55: 511-524, (1957). — HILL, W. G.: Estimation of realized heritabilities from selection experiments. II. Selection in one direction. *Biometrics* 28: 767-780, (1972). — JAMES, J. W.: The founder effect and response to artificial selection. *Genet. Res.* 16: 241-250, (1971). — KANG, H.: Long-term tree breeding. In: Proc. 15th Southern Forest Tree Improvement Conference. Miss. State Univ., June 19-21, 1979. Pp 66-72, (1979). — KANG, H.: Designing a tree breeding system. In: KHALIL, M. A. K., ed. *Proceedings 17th Meeting Canadian Tree Improvement Asso. Gander, Newfoundland, August 27-30, 1979.* Pp 51-63, (1980). — KANG, H.: Components of a tree breeding plan. In: *Proceedings IUFRO Joint Meeting of Working Parties on Genetics about Breeding Strategies including Multiclinal varieties.* Sensenstein, September 6-10, 1982. Pp 119-135, (1982). — LEVENE, H.: Genetic equilibrium when more than one ecological niche is available. *Amer. Natur.* 87: 331-333, (1953). — LINDGREN, D. and GREGORIOUS, H. R.: Inbreeding and conacestry. *Proceedings of Joint Meeting on Advanced Generation Breeding.* Bordeaux, France. Pp. 49-55, (1976). — MADALENA, F. E. and HILL, W. G.: Population structure in artificial selection programmes: simulation studies. *Genet. Res. Camb.* 20: 75-101, (1972). — MADALENA, F. E. and ROBERTSON, A.: Population structure in artificial selection: studies with *Drosophila melanogaster*. *Genet. Res. Camb.* 24: 113-126, (1975). — MARSHALL, D. R. and BROWN, A. H. D.: Optimum sampling strategies in genetic conservation. In: O. H. FRANKEL and J. G. HAWKES (Eds.). *Crop genetic resources for today and tomorrow.* IBP2, Cambridge University Press, Cambridge. Pp. 53-80, (1975). — MARUYAMA, T.: On the fixation probability of mutant genes in a subdivided population. *Genet. Res. Camb.* 152: 221-225, (1970). — NAMKOONG, G.: A multiple-index selection strategy. *Silvae Genetica* 25: 199-201, (1976). — NAMKOONG, G.: Choosing strategies for the future. *Unasylya* 31: 38-41, (1978). — NAMKOONG, G.: A control concept of gene conservation. *Silvae Genetica* 33: 160-163, (1984). — NAMKOONG, G., BARNES, R. D. and BURLEY, J.: A philosophy of breeding strategy for tropical forest trees. *Tropical Forestry Paper No. 16.* Commonwealth Forestry Institute, Univ. of Oxford. 67 p, (1980). — NAMKOONG, G. and ROBERTS, J.: Short-term loss of neutral alleles. *Silvae Genetica* 31: 1-6, (1982). — NAMKOONG, G., SNYDER, E. B. and STONECYPHER, R. W.: Heritability and gain concepts for evaluating breeding systems such as seedling seed orchards. *Silvae Genetica* 15: 76-84, (1966). — NEI, M., MARUYAMA, T. and CHAKRABORTY, R.: The bottleneck effect and genetic variability in populations. *Evolution* 29: 1-10, (1975). — NIENSTADT, H. and KANG, H.: A budget

tree improvement program: An example. Research Note NC-294, (1982). — NIENSTADT, H. and KANG, H.: Establishing a *Picea glauca* (MOENCH) Voss base breeding population for the Lake States region of United States. (In preparation), (1985). — RAWLINGS, J. O.: Present status of research on long- and short-term recurrent selection in finite populations — choice of population size, 1—15. In: G. NAMKOONG and K. STERN (Eds.). Proc. of the 2nd Meeting of Working Group on Quant. Gen. Sec. 22, IUFRO; Southern Forest Experiment Station, New Orleans, (1970). — ROBERTSON, A.: A theory of limits in artificial selection. Proc. Roy. Soc. B. 153: 234—249, 1960). — ROBERTSON, A.: Inbreeding in artificial selection

programmes. Genet. Res. Camb. 2: 189—194, (1961). — ROBERTSON, A.: The interpretation of genotypic ratios in domestic animal populations. Anim. Prod. 7: 319—324, (1965). — SIRKKOMAA, S.: Calculations on the decrease of genetic variation due to the founder effect. Hereditas 99: 11—20, (1983). — TURNER, H. N. and YOUNG, S. V.: Quantitative genetics in sheep breeding. McMillan, Melbourne, Australia, (1969). — VAN BUIJTENEN, J. P.: Advanced generation breeding. Proc. of 13th Southern Forest Tree Improvement Conference; Raleigh, NC. Pp. 63—72, (1975). — YOUNG, S. S. Y. and SKAVARIL, R. V.: Computer simulation of within family selection in finite populations. Theor. Appl. Genet. 48: 45—51, (1976).

Genetic change between life stages in *Pinus sylvestris*: allozyme variation in seeds and planted seedlings

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Summary

Genetic changes during artificial regeneration of pine were studied in northern Sweden. Open pollinated seeds were collected from ten maternal trees. Samples of these seeds were germinated and grown in a nursery from January 1980 to April or September 1981. Thereafter the seedlings were planted at their original site in a 2 × 2 m planting design. The genetic structure of the original seed population and that of the surviving population in the field at age three were compared. The genotypic frequencies at four polymorphic enzyme loci were obtained by electrophoresis of the embryos in seeds and buds from the surviving plants (*Got-B*, *F-Est*, *Gdh*, and *Mdh-B*). There had been no statistically significant changes in allelic frequencies. The original seed population had positive fixation indices at all loci (average 0.12), presumably due to some inbred progeny among the seeds. In the surviving population, the fixation index was 0.006, which indicates that the more inbred individuals had been virtually eliminated between the seed stage and the three year old plant stage. There was no detectable relationship between the change in heterozygosity for individual families and survival in the field.

Key words: artificial regeneration, Scots pine, allozyme variation, inbreeding, selection.

Zusammenfassung

In Nord-Schweden wurden Kiefernulturen aus künstlicher Verjüngung auf genetische Veränderungen hin untersucht. Hierzu wurden 1980 Samen von 10 Mutterbäumen in einer autochthonen Population gesammelt, ausgesät, in einer Baumschule angezogen sowie dann wieder auf dem Ursprungsstandort in 2 × 2 m Abstand ausgepflanzt. Nach drei Jahren wurde die genetische Struktur der künstlich eingebrachten überlebenden Kiefern mit der ursprünglichen Samenpopulation verglichen. Hierzu wurden die Embryos in Samen und die Knospen der überlebenden Sämlingspflanzen auf 4 polymorphe Enzym-Loci (*Got-B*, *F-Est*, *Gdh* und *Mdh-B*) elektrophoretisch untersucht. Es gab keine signifikanten Veränderungen in den Allelfrequenzen. Die ursprüngliche Samenpopulation hatte einen positiven Inzuchtkoeffizienten für alle Loci (Mittelwert 0,12), wahrscheinlich wegen teilweiser Inzucht. Bei den Pflanzen, die überlebt haben, war der Mittelwert des Inzuchtkoeffi-

zienten 0,006. Der Anteil an Homozygoten hatte also abgenommen, weil die durch Selbstbestäubung entstandenen Pflanzen eliminiert worden waren.

Es wurde versucht, auch den Umfang der genetischen Veränderung in einzelnen Familien und die Mortalität nach der Pflanzung zu schätzen. In fast allen Familien wurde der Heterozygotiegrad höher. Zwischen der genetischen Veränderung und der Mortalität gab es keine Beziehung. Für solche Zwecke sind genauere Untersuchungen nötig.

Introduction

The reproductive system of Scots pine (*Pinus sylvestris* L.) is characterized by a very large number of seeds. Estimates of early seed production in southern Finland range from 100 and 200 seeds per m² (KOSKI and TALLQVIST, 1978). Among these seeds, severe mortality takes place. Much of this mortality is probably random, but some could be selective resulting in genetic change between different life stages of the population. Unfit plants, e.g. those suffering from inbreeding depression, may be removed from the population at an early stage.

It is well known that some Scots pine zygotes result from self-fertilization (SARVAS, 1962). Some of these selfed embryos are eliminated at a very early stage due to embryonic lethals (see KOSKI, 1973), so that the proportion of selfed embryos is lower in mature seed than in early embryogeny. Estimates of the proportion of selfed seed vary. SARVAS (1962) gave an estimate of 7%, KOSKI has suggested that only 1% of mature seed are due to selfing. Work with marker alleles has resulted in higher estimates, e.g. about 10% by MÜLLER-STARCK (1977). RUDIN *et al.* (1977) found even higher values in a seed tree stand, up to 24%. Mating between relatives may also occur, but this has not been studied in Scots pine. Inbreeding has been found to be reflected in a higher proportion of homozygotes among the seed than expected on the basis of the HARDY-WEINBERG theorem (SHAW and ALLARD, 1982, in Douglas-fir; YAZDANI *et al.*, 1985, in Scots pine). At the adult stage such excess homozygosity has disappeared, and in fact, in some cases excess heterozygosity has been found (SHAW and ALLARD, 1982; YAZDANI, *et al.* 1985). We (YAZDANI *et al.*, 1985) found earlier that in natural regeneration, excess homozygosity was eliminated in a stand aged 10—20 years. Thus adult stands of Scots pine do not seem to suffer from the presence of inbred individuals.

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