

Figure 8. — Crossing chart and mean degree of attack of full-sib groups originating from seed orchard L 55 Harastorp, growing in the field trial in Tönnersjö. Highly significant differences between full-sib groups within half-sib groups appeared. Crossings within mother D 7003 and mother L 3007 are such examples. Within other half-sib groups only minor differences between full-sib groups were registered, e.g. mother L 3005.

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Establishing a *Picea glauca* (Moench) Voss Base Breeding Population for the Lake States Region of the United States

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Annotation

Discusses problems and solutions in selecting founders (parents) and in establishing and maintaining base breeding

populations, using *Picea glauca* in Minnesota, Wisconsin, Michigan as an example. Selection from existing breeding collections leads to genetic imbalance followed by loss of genetic diversity in future generations. Equalization of the population is discussed.

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Zusammenfassung

Es werden Probleme und Lösungen zur Selektion von Ausgangsbäumen sowie zur Erreichung, Erhaltung und Weiterführung von Basis-Züchtungspopulationen am Beispiel von *Picea glauca* (MOENCH) in Minnesota, Wisconsin und Michigan diskutiert. Eine Selektion aus bereits existierenden Züchtungs-Sammlungen führt zu einem genetischen Ungleichgewicht und demzufolge zu einem Verlust der genetischen Vielfalt in zukünftigen Generationen. In die Diskussion wird ein Ausgleich der Population einbezogen.

Abstract

Selecting the founders and establishing the base breeding population are crucial first endeavors in long-term tree breeding. Those processes will determine the potential for future breeding efforts. Errors in execution may not manifest themselves until several breeding cycles have been completed, and correction then may be costly in terms of the genetic gains achieved. Selecting founders from breeding materials in existing short-term tree improvement programs may be particularly difficult. Yet in many instances it would be the preferred approach because resampling from natural populations would be costly and would eliminate the genetic gains achieved through the short-term breeding. This paper illustrates the problems of selecting founders, procuring the seed for the base breeding population, and structuring the population, using *Picea glauca* (MOENCH) Voss in the Minnesota, Wisconsin, Michigan region of the United States as an example. The available breeding materials are described. The sampling of this material will yield founders that: (1) do not represent a systematic allelic sampling effort; (2) represent multiple origins of great complexity i.e. different climates, untested clones or highly effective progeny tests; selection in such material could result in rapid loss of genetic diversity in future generations; and (3) represent a closed population from the beginning; reopening the population would require adjustments in breeding strategies. Details of the selection of the 380 parents are discussed. The scheme is a compromise between long- and short-term breeding goals. The objective was to achieve genetic diversity as well as genetic improvement. The genetic advance was achieved at a cost of some genetic imbalance in the population. Other topics of discussion are: Overcoming the problem of imbalance through the structuring of the first and second breeding population, and the equalizing selection process when the second breeding populations are selected. The need for short-term improvement within the long-term breeding effort is recognized; some strategies for the production of improved seeds are discussed.

Key words: long-term breeding, genetic disparity, genetic equalization, population structure, breeding strategies.

Introduction

Long-term breeding programs are beyond the capabilities of most organizations (WEIR and ZOBEL 1975, KANG 1982, KANG and NIENSTAEDT 1987). Requirements in genetic plant resources, land, financing, and in many cases trained personnel will exceed the capabilities of all but the very largest single agencies. Cooperative breeding programs are the viable alternative. Short-term tree improvement efforts of limited scope have been started in many regions with high priority tree species. Working independently, organizations have initiated programs that differ greatly in sophistication, ranging from simple seed production areas to clonal or progeny test seedling seed orchards. The criteria and intensity of parent tree selection have been different, and the programs often have been started over a

period of many years so that the plant materials have reached different stages of development.

One of the responsibilities of contemporary tree breeders is to select the founders and establish the base breeding populations (KANG and NIENSTAEDT 1987). Ideally such populations should include the maximum amount of genetic diversity originating from regions known to produce genotypes adapted to the breeding environments. In reality, however, selecting founders and establishing a base breeding population are difficult. Concepts such as maximum genetic diversity and adaptive genotypes are hard to quantify. And in practical terms most active tree breeding organizations already have invested in their own short-term breeding stock. Because this easily accessible material represents a degree of improvement, it may be preferred to new selections from natural stands or plantations. Furthermore, potential cooperators with investments in an established program would be reluctant to go back to the wild populations, thereby losing some or all of the genetic gains already achieved.

In an accompanying paper (KANG and NIENSTAEDT 1987), we discuss the conceptual problems associated with founders and breeding populations. In this paper we will discuss the practical problems associated with the selection of the founders and with the establishment and early management of a breeding population of white spruce, *Picea glauca* (MOENCH) Voss in the Lake States Region of the United States, i.e. in Minnesota, Wisconsin and Michigan. Solutions to the problems — most of them intuitive — will be presented as they relate to the goals of multi-generation breeding, the desired characteristics of the founders, and the characteristics of the white spruce breeding system in the region. We will discuss selection of the founders, derivation of seed for the first breeding population, organization of the first and second breeding population, and organization of the first seed production population.

The Goals of Long-term Tree Breeding

We have defined long-term breeding as: tree breeding efforts designed to provide genetic resources that can be used effectively in short-term breeding at any given time, regardless of future uncertainties (KANG and NIENSTAEDT 1987).

Goal setting in cooperative long-term breeding programs is hindered by difficulties related to the cooperating organizations, space, and time (KANG 1979, 1980; NAMKOONG 1982). Individual members of the cooperative may, because of the product mix of the corporation, have different selection priorities. The paper maker will need superior fiber characteristics, low extractives, and high yields: the saw mill, although interested in high yields, will place a premium on strength properties and have little concern for the content of extractives. Programs must be related to an identified production zone or region of planting — for a discussion of breeding and production zones in long-term breeding see KANG and NIENSTAEDT (1987). Differences in edaphic and climatic conditions and in the distribution of pests and diseases may exist over the zone. This may force nuances in selection to achieve maximum gains. With time goals may change in all areas: product changes may necessitate changes in selection criteria; environments may change, creating problems that will require genetic solutions. The heavy industrial pollution in parts of Europe and North America is an example. Selection for ozone and

SO₂ tolerance is now a serious pursuit in tree improvement.

Faced with different, at times conflicting goals, and with time-related uncertainties, the breeder must make flexibility and versatility primary goals when selecting the founders and organizing breeding populations and breeding systems (KANG 1980).

The White Spruce Breeding System

We have identified the participating organizations, breeding stock, and available information and techniques as the physical components of tree breeding systems (KANG and NIENSTAEDT 1987). A description of the white spruce breeding system in the Lake States follows:

Breeding Organization

The white spruce breeding system has a broad organizational base with a balance of research, public, and industrial agencies. Initially, the program will involve three Universities and the United States Department of Agriculture, Forest Service, in research. The Forest Service and three State forest organizations and several industries will be involved in testing and breeding, and will use the improved material. The region has no funded cooperative with a salaried staff to direct a long-term breeding program. However, the organizations are loosely held together by the Lake States Tree Improvement Coordinating Council (LASTICC), within which species groups attempt to coordinate the efforts of the individual members. In Minnesota and Michigan, the State Forestry Departments, the State Universities and industries are participating as members of State Tree Improvement Cooperatives. Some Wisconsin industries belong to the Minnesota group, but there is no cooperative as such in Wisconsin. The cooperatives and the Forest Service are engaged in short-term breeding programs involving several important species. And all participants in the white spruce breeding system have had some work in progress with that species. They

have not been easily convinced of the necessity and advantages of long-term breeding, which they have seen as diluting the short-term projects. The research capabilities in the group are great, but expertise among the industries and the State Forestry Department ranges from very small to substantial.

The breeding system participants control several million hectares of land concentrated in the northern third of the three States and extending over a range of climatic conditions that become colder towards the North. On this land, 8–10 million white spruce are planted annually. Spruce management objectives are essentially the same for all the participants, i.e. the production of pulpwood. The breeding objectives are therefore the same — yield increase — for all the participants. Management of the species, however, may differ among agencies. Thus the Forest Service generally uses longer rotations.

Available Stock

More than 70 provenances, 850 families, and more than 350 white spruce clones are being tested or have been established in seed orchards in the region (Table 1). Somewhat less than half the material — progenies as well as clones — represent Ontario collections.

The materials in progeny tests are not systematic samples of the Lake States white spruce distribution, yet they are clearly representative. More than 200 scattered collections from the Minnesota range are being tested in Minnesota. Other programs include additional Minnesota collections. Wisconsin and Michigan collections were made on national forests and private land — approximately 100 collections for each area.

Selection intensities and criteria used in establishing the various tests have been quite varied. Some selections were based on intensive phenotypic selections for vigor and form using comparison trees. Others have been less intensive and have in some cases included late bud opening (to avoid spring frost) as a criterion.

Table 1. — Selection of the founders from diverse progeny tests and clonal collections in the Lake States.

Current location	ORIGINS			
	Lake States		Ontario	
	progenies	clones	progenies	clones
Michigan			MICHCOTIP 221 (70) ^{1/}	
Minnesota	Univ. of MN 239 (70)			MTIC 110 + 6 (50)
Wisconsin		USFS, R-9 111 (30)	WI-DNR 150 (30)	USFS, NCFES 38 + 5 ^{2/} (10)
		USFS, NCFES 100 (60)	USFS, NCFES 70 (10) 31 (30)	
Total	450 (160)	220 (30)	402 (130)	159 (60)
	670 (190)		561 (190)	

1/ () Numbers selected for the founder population.

2/ Clones from a Maine provenance.

Older progeny tests of Ontario selections are limited to a single planting of 31 progenies in Wisconsin; progenies from the Lake States are in the same tests. Newer tests involving much larger numbers of progenies have been established in Wisconsin and Michigan. Although these tests have many progenies in common, they are basically different. The test in Wisconsin represents the 80 best families selected in a nursery test of an original 148 families representing 30 white spruce stands scattered over the SE corner of Ontario and adjacent Quebec. This test was field planted in 1982. Seed is available from the majority of the parent trees.

The test in Michigan is larger and involves progenies from trees in stands that represent a much wider region. Flowering in both the Wisconsin and the Michigan test may be limited for several years to come.

Clonal material from Ontario represents five populations. Most of the clones are from the Ottawa River Valley near Beachburg and Douglas, 100 km west of Ottawa. Beachburg clones were selected for vigor in five provenance tests established in 1962 and located in Minnesota (2), Wisconsin (1), and Michigan (2). The original seed was received as a stand collection. The Douglas clones represent trees selected for vigor in a provenance test planted in 1936 in Wisconsin. Available records do not show the nature of the original seed collection. Additional clones are from Mapleleaf, Denbigh, and Carnarvon, Ontario, and a few are from Maine. They were all selected in provenance tests in the Lake States. Some of the clones are included in newer progeny tests of Lake States populations.

Available Information and Techniques

A number of findings from white spruce genetic research and information on climate have a direct bearing on the development of a white spruce breeding system for the Lake States.

The climate over the region is severely continental, characterized by extremely cold winters and short hot summers. Springs are short and the warm-up abrupt. Based on climatic data and some tree growth information, RUDOLF (1956) divided Minnesota, Wisconsin, and Michigan into 26 seed collection zones. Ten of these fall in the primary white spruce regeneration area; seven are on the margins. In the coldest zones, mean January temperature is -18°C , in the mildest approximately -4.5°C . Accumulated degree days range from 8,000 (50°F (10°C)base) in the coldest zone to 11,000 in the mildest. Precipitation decreases from approximately 800 mm in the east to 600 mm in the western parts of the region.

White spruce research has shown:

1. Throughout the region, southeastern Ontario provenances have been repeatedly shown to be superior to local Lake States sources. The oldest test was planted in 1936 and was followed by newer tests in the fifties and early sixties (NIENSTAEDT 1969; STELLBRECHT *et al.* 1974; WRIGHT *et al.* 1977).

2. Detailed seed source information is not available for Lake States white spruce. However, the species may show clinal variation in the region related to latitude (JEFFERS 1969). A limestone-adapted ecotype may exist on the limestone soils in eastern parts of the Upper Peninsula of Michigan (data on file, FSL, Rhinelander). White spruce from the extreme northeastern regions in Minnesota is inferior and should not be planted in other parts of Minnesota or elsewhere (MOHN *et al.* 1976).

The seed collection zones for the Lake States developed by RUDOLF (1956) are not species specific and are as mentioned primarily based on climatic information. Similarly, breeding zones (MURPHY and MILLER 1979) have been developed on the basis of climate and administrative considerations.

3. White spruce family variance is high but progeny \times environment interaction, although statistically significant, shows no clear trends; thus, family performance is inconsistent. On the other hand, if families are grouped on the basis of climates at the points of origin, the groups are very stable (NIENSTAEDT and RIEMENSCHNEIDER 1985).

4. The species is highly variable (MOHN *et al.* 1976; NIENSTAEDT 1985; NIENSTAEDT and RIEMENSCHNEIDER 1985), and this variation is expressed at an early age. Seedlings selected for superior growth at age 4 in the nursery maintain growth superiority at least until age 22 from seed (NIENSTAEDT 1981). Furthermore, white spruce is one species in which phenotypic selection in older stands may be possible under certain circumstances (JEFFERS 1969).

5. Treatment with $\text{GA}_{4/7}$ can increase both male and female flowering in white spruce. Trees 12 years old from seed have responded to the treatments (CECICH 1985).

Much other information is available on white spruce biology and genetics (NIENSTAEDT and TEICH 1972), but this is the information pertinent to a breeding program in the Lake States. It shows that:

1. Southeastern Ontario genotypes should be included in a Lake States white spruce breeding program.

2. Testing of the first breeding population must be designed to give information on genotype \times environment interactions. The first phase of the program should provide data that can guide breeders in selecting of the parent material for the multiplication populations and in distributing seed from such populations.

The breeding population and the strategy for future breeding must be flexible so that they can meet any possible future needs for restructuring of the breeding population.

3. The program should take advantage of juvenile selection where the test trees have developed under uniform test conditions without the interference of competition.

Combining the Selection of Founders and the Establishment of a Base Breeding Population with Short-Term Breeding Needs

In the past, potential participants in a cooperative regional white spruce breeding program have not considered a strong regional breeding organization to be financially viable. They have invested only limited funds in short-term state breeding programs and are not expected to be able to invest much additional money in the development of a long-term multigeneration breeding effort. The limited funds rule out selecting founders and establishing the base breeding population by a systematic resampling of the natural population to obtain as much diversity as possible. The breeding population must be developed from the available materials that we have described. The strategy adopted must provide for early short-term outputs and immediate genetic gains. Without early improvement from short-term breeding, the long-term program is not likely to find continuous support.

Three characteristics of the founders will result from the sampling of existent improved material. They have important consequences for future breeding strategies and should be emphasized from the beginning:

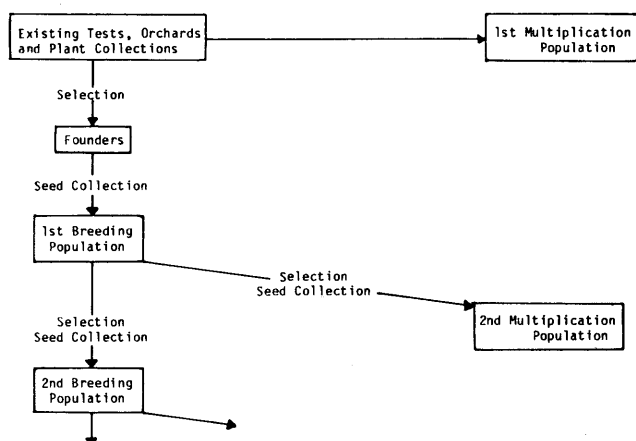
(1) The founders will not represent a systematic allelic sampling effort.

(2) The founders will represent multiple complex origins. Several climatic origins will be involved, the original breeding stock may be untested clones or progenies in highly effective progeny tests, or different selection intensities may have been used in the original selection of ortets or parents. These types of differences may result in the "origin" related problems described by KANG and NIENSTAEDET (1987). In the highly variable white spruce, selection in future generations could result in rapid loss of genetic diversity. An example of this has been described by NIENSTAEDET and RIEMENSCHNEIDER (1985).

(3) The overall population will essentially be closed from the beginning, but may be reopened in the future. If it is, breeding strategies would have to be adjusted.

In the following we will propose a scheme for selecting the founders and for generating and organizing of the first and second breeding populations and multiplication populations. Minimum actions have been described; they will provide a flexible system and a strategy that can be modified at any time if white spruce gains in importance in the managed forest of the region and/or if funding improves.

The diagram below shows the overall derivation of the founders and populations that will be discussed. Note that the founders are not at the beginning of the flow chart.



Selecting the Founders

The "right" size of the long-term breeding population cannot be definitely determined (KANG and NIENSTAEDET 1987), but between 300 and 400 parent selections is adequate (KANG 1979).

The existing breeding collections and the make-up of the founders derived from these collections are shown in Table 1. The numbers throughout the Table are approximations.

The approach taken is a compromise between long- and short-term breeding goals. The objective was to achieve genetic diversity as well as genetic improvement. The genetic advance undoubtedly has been achieved, but at a cost of some imbalance in the population. This imbalance can become a problem with advancing generations (KANG and NIENSTAEDET 1987; NIENSTAEDET and RIEMENSCHNEIDER 1985).

As shown in Table 1, the 380 founder selections are made up of equal numbers of Lake States and Ontario selections. Sixteen percent of the Lake States selections are untested phenotypic selections now established in clonal archives or in seed orchards. For the Ontario material, 32 percent of the selections will be of a similar background. In total, about 24 percent of the selections will come from cloned, but untested phenotypic selections.

Several factors justify the selection scheme:

1. White spruce is a species in which phenotypic selection is likely to be advantageous (JEFFERS 1969).

2. The Ontario selections were all made in provenance tests in which the Ontario source was of proven superiority, and under uniform test conditions that are likely to improve the efficiency of phenotypic selection.

3. More than 350 of the ca. 400 Ontario progenies being tested are in recent tests in which it may be difficult to obtain seed without special treatments.

4. It is desirable to include the older phenotypic selections to increase the genetic diversity of the base population.

The scheme shown in the table includes some intuitive adjustments aimed at equalizing improvement through differential selection:

1. Selections from progeny tests make up 76 percent of the founders because selection in progeny tests is more reliable than selection among clones.

2. Selections are concentrated in the older progeny tests, in which the risk of selection errors is smaller.

3. Selections favor tests in which heritability and the potential for gains are high.

Generating Seed for the First Breeding Population

Generating seed for the first breeding populations also necessitates compromise. As already described, the origins and methods of selecting and testing the collections from which the founders will be selected were very diverse. Even with the described adjustments in the selection, it would be impossible to generate progenies that will represent the same approximate magnitude of improvement. That could only be achieved by restricting the population from which the founders were selected to materials that are similar, such as clones of phenotypic selections or selections in progeny tests of the same age. It would result in substantial reduction in the genetic base.

Seed for establishing the new breeding population can be derived from control pollination or from open pollinated seed. And, in the case of open pollinations, it could come from either rogued or unrogued tests. The difference in gain from the three approaches is relatively minor, with the least gain realized from seed from unrogued progeny tests, clonal collections, and from untested clonal seed orchards. However, because equal levels of improvement cannot be achieved in the selection process, it will not be worthwhile to be restrictive in the way the seed is generated for the new base population. It should also be considered that open-pollinated seed collected in progeny tests of families of diverse origin will sample more alleles than control-pollinated seed from crosses among a limited number of superior selections. Therefore, with regards to the long-term aspects of the program, including open-pollinated seed may be a distinct advantage.

There are several young progeny tests in Minnesota, Wisconsin, and Michigan of both Lake States and Ontario origins. They are a special problem because they may not flower until much older. For these, three types of seed can be used:

- Seed stored or recollected from the original selected superior trees.
- For progenies representing clones in seed orchards — open-pollinated seed stored or recollected from seed orchard clones.
- Controlled-pollinated (top cross) seed from artificially induced flowers.

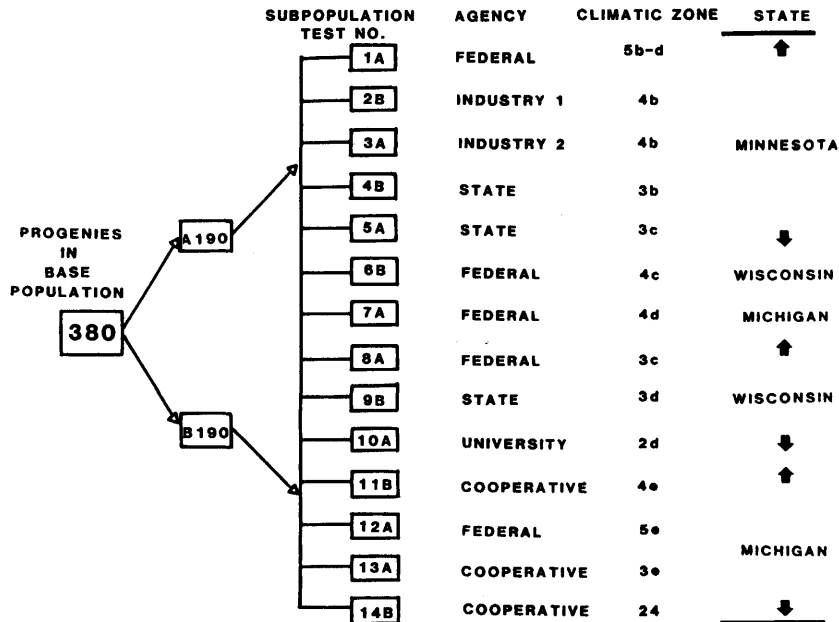


Fig. 1. — Organization of the first breeding population progeny test. (See Fig. 2 for regional distribution.)

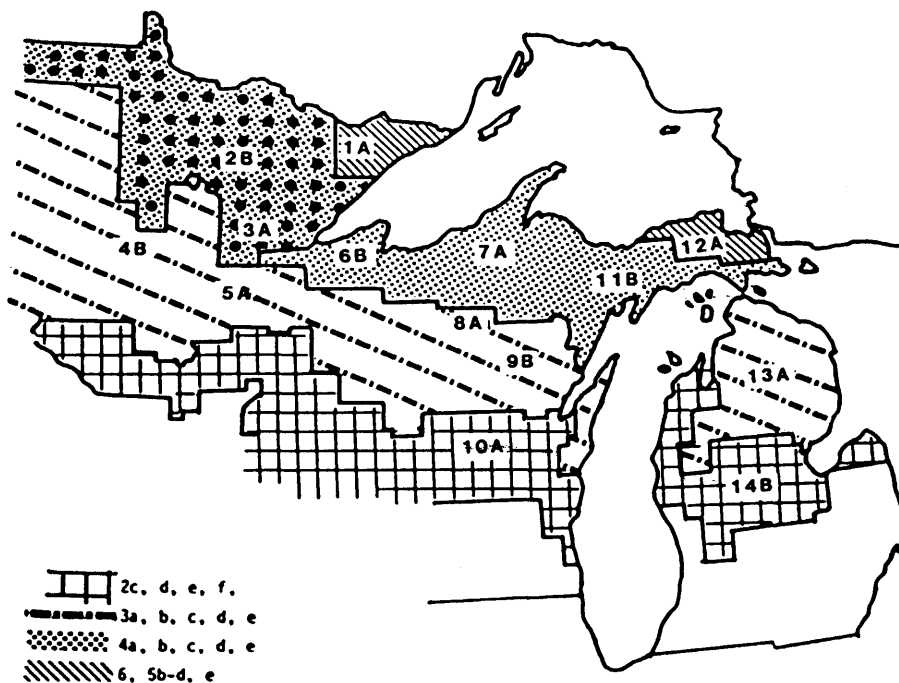


Fig. 2. — First breeding population test site distribution in the Lake States. Distribution based on a simplified version of RUDOLF'S (1956) seed collection zones. For details see original reference. Classes "a-e" signify average January temperature. They follow in order from NW to SE.

Using induced flowers should be a practical approach. A concentrated spray of $GA_{4/7}$ in an Aromox/ethanol solution is effective. Weekly treatment of elongating shoots during the second half of May and the first half of June resulted in large increases in female strobili production the following year (CECICH 1985). Thirty to forty cones are enough to produce the seedlings needed for extensive testing of the progeny. Only a few branches will need to be treated to produce that many cones.

Structure and Distribution of the Tests of the First Breeding Population

The structure and distribution of the first generation breeding population are shown in Figs. 1 and 2. To reduce the size of individual test plantings and to increase statistical precision, the 380 progenies will be assigned to two populations — A and B — of 190 families. Further subdividing them into three or four populations would be possible, but developing the structure of smaller subpopulations for the long-term breeding should not be done until the second generation breeding population, when the need for equalization has been determined and progress has been made in the process. The division of the families to the two

populations will be done at random, but with the provision that the original populations will be represented in the proportions shown in *Table 1*. Thus "A" population represents 45 families of founders selected in Wisconsin progeny tests, 15 from clones in Wisconsin, and 35 founder families from progeny tests in Minnesota — all of Lake States origin. Ontario provenances would include 30 founder progenies from Wisconsin progeny tests and 5 from clones as well as the material from Minnesota and Michigan. Without this provision, future equalization will not be possible.

The distribution of the test plantings on the map, *Figure 2*, is an approximation. Site locations have been guided by the zoning developed by RUDOLF (1956) and by MURPHY and MILLER (1979). RUDOLF's zoning, developed for seed collection, is clearly too detailed for the organization of breeding programs. In *Figure 2* we have, therefore, only shown the major zones, which are based on accumulated degree days. The objective of the distribution of the tests as shown in *Figure 2* is to place at least one test of each subpopulation in each of the major climatic zones. The actual site selection will be left to the individual cooperators with the proviso that the sites must be representative of sites on which spruce will be grown in the future.

Except for the division of the multiple origin founder population into two subpopulations this scheme follows the dm-single classification of KANG and NIENSTAEDT (1987), i.e. founder families of multiple origins are distributed and populations are being tested at many locations.

As mentioned the scheme is a compromise necessitated by our limited knowledge and by the need to accommodate both short- and long-term objectives. Distributing all families widely over the three States will assure the information on genotype \times environment interaction needed to organize multiplication populations and outline production zones as required. In terms of long-term breeding, the scheme should give great flexibility: (1) The second breeding population can be derived from the entire first population even if it becomes necessary to subdivide the major zones shown in *Fig. 2*. (An example will be discussed later). (2) Selection for broad as well as narrow adaptation to the environment can be done using all the breeding stock as the base. (3) If desired, different selection criteria can be applied to the two different subpopulation, again using the entire breeding population as the base. (4) The different replications of the two subpopulations can be used to develop inbreeding and/or selection copies (KANG and NIENSTAEDT 1987) for future breeding. (5) Finally, the wide distribution of the founder population progeny would give the greatest flexibility in subsequent substructuring of the population and the development of index populations (KANG and NIENSTAEDT 1987) for research.

Equalizing and Structuring of the Second Breeding Population

1) Equalization

The problems with selecting founders and with generating seed for the first breeding population necessitate accepting of progenies representing unequal degrees of improvement. If not corrected at the next generation turnover, this disparity could result in drastically reduced genetic diversity during the selection process (NIENSTAEDT and RIEMENSCHNEIDER 1985; KANG and NIENSTAEDT 1987). Equalization is one way to solve the problem. Final decisions on equalization cannot be made until the genetic parameters

of the population have been determined; we will present an elementary solution.

Equalization will require estimates of the population mean, phenotypic variance, and heritability for all the subpopulations²⁾ involved. It is also necessary to determine the number of generations over which one wishes to apply the equalization and the selection intensity to be applied to a standard population (the one with highest mean). Then the selection intensities (i_y) necessary for other populations are determined by

$$i_y = \left(\frac{d_0}{t} + i_x h_x^2 \sigma_{p_x} \right) / h_y^2 \sigma_{p_y}, \quad (1)$$

where

x indices of the standard population,

y indices of the alternate population,

d_0 the difference between the means of the standard population and the alternate population, and

t the number of generations involved in equalization.

If we let $h_x^2 = h_y^2 = h^2$, $\sigma_{p_x}^2 = \sigma_{p_y}^2 = 1$, then (1) becomes $i_y = \frac{d_0}{th^2}$

Table 2 shows values of i_y necessary for 10% selection ($i_x = 1.755$) in the standard population.

Once the selection intensity is determined, an equal number of individuals must be sampled from the selected populations.

If one generation is used for equalization ($t = 1$), the final samples of selected individuals from the subpopulations may be mixed to form the new breeding population. If more than one generation is used ($t > 1$), the identity of the subpopulations must be maintained until equalization is complete. With this strategy, the sample size does not have to be identical until the last step in the process, but it is critical that the number of individuals from each subpopulation not be too small, i.e. — not less than about 30.

Note that the equalization is performed with respect to the trait of selection. The different subpopulations will continue to have disparity with respect to other unrelated traits. This problem may be solved if the trait subjected to selection does not change for a few generations after the populations are pooled.

2) Structuring

Subdividing breeding populations into smaller breeding groups is an accepted approach to maintaining genetic diversity in long-term breeding programs (KANG 1980; KANG and NIENSTAEDT 1987).

In the Lake States example, the region will be divided into production zones on the basis of genotype \times environment interaction and other information from the tests of the first breeding population (*Fig. 2*). For administrative reasons, it will be desirable to keep the number of zones at the minimum dictated by biological consideration. Only by doing so can the workload of the individual agencies be kept at an acceptable low level.

Figure 3 shows the structuring of a second generation breeding population in a hypothetical production zone that includes the Minnesota portions of zone 4 in *Figure 2* (the region with large dots on a background of small dots). Notice that the new breeding population is made up of selections from tests of the entire first breeding population (2B and 3A) growing in the production zone environment.

²⁾ A subpopulation here is the families originating from a particular test or orchard. For example, the 70 selections from the original progeny test of 239 families in Minnesota (*Table 1*).

Tab. 2. — Selection intensity in subpopulations ¹⁾ necessary to achieve equalization ²⁾.

		h ²					
		t = 1	.1	.2	.3	.4	.5
d ₀ (s.d.)	.2		3.755 (<.1%)	2.755 (.8%)	2.422 (2.0%)	2.255 (3.1%)	2.155 (4.0%)
	.4		5.755 (-)	3.755 (<.1%)	3.088 (.3%)	2.755 (.75%)	2.555 (1.4%)
	.6		7.755 (-)	4.755 (-)	3.755 (<.1%)	3.255 (.15%)	2.955 (.4%)
	.8		9.755 (-)	5.755 (-)	4.422 (-)	3.755 (<.1%)	3.355 (.1%)
		h ²					
		t = 2	.1	.2	.3	.4	.5
d ₀ (s.d.)	.2		2.755 (.8%)	2.255 (3.1%)	2.088 (4.7%)	2.005 (5.7%)	1.955 (6.4%)
	.4		3.755 (<.1%)	2.755 (.8%)	2.422 (2.0%)	2.255 (3.1%)	2.155 (4.0%)
	.6		4.755 (-)	3.255 (.15%)	2.755 (.8%)	2.505 (1.6%)	2.355 (2.4%)
	.8		5.755 (-)	3.755 (<.1%)	3.088 (.25%)	2.755 (.8%)	2.555 (1.35%)

d₀ = difference in the standardized means between the standard population and the subpopulation being compared.

¹⁾ A subpopulation here is the families originating from a particular test or orchard. For example the 70 selections from the original progeny tests of 239 families in Minnesota.

²⁾ Based of 10% (i = 1.755) selection in the standard population i.e. the population with highest mean.

Compare *Figures 1* and *3* and notice that the population(s) maintained by the individual agencies has been much reduced. Notice also that copies of the nine breeding subpopulations have been established as special research populations.

The example in *Figure 3* is hypothetical; if larger production zones are indicated the second generation can be established with selections from more test plantings. Similarly, the substructuring may change depending on the number of agencies within the zone.

The substructuring may also be postponed to a later generation depending on the number of generations required for equalization. In that event, however, the testing of the second breeding population could be much reduced because the required genotype × environment information would have been obtained in the first generation tests.

Production of Improved Seed

How to Meet Immediate Seed Needs. Until the tests outlined in this plan can be used, improved seed will be available from the orchards now in existence (the first multiplication population in the diagram on p. 10). The quality of that seed will gradually improve as roguing progresses. The improvement, however, will not be as great as that which could be achieved with new orchards established now with the best selections from existing progeny tests.

As an example, a grafted orchard of the 25 best trees in a 15-year-old progeny test near Rhinelander of 60 Lake States and 31 Ontario progenies would result in an estimated 27-percent increase in height growth. The selections would include Lake States and Ontario trees (NIENSTAEDE and RIEMENSCHNEIDER 1985).

At age 20 the best trees are producing large volumes of seed and are old enough to permit reliable selection. Cooperators can establish seedling seed orchards using this seed or they can establish orchards of grafts of the selected parent trees.

How to Meet Future Seed Needs. Future progeny tests could be converted (i.e. the subsets of progenies in *Figs. 1* and *3*), but much greater flexibility and gains can be achieved by establishing special seed producing facilities. *Figure 4* suggests two possible approaches.

In Example 1, several of the best trees (10 in the example) are selected at age 15 (from seed) from one or more progeny tests (three in the example). They are propagated by grafting and established in an orchard at a spacing of approximately 8 × 8 m. This approach differs little from the orchard described above.

In the second example, the number of selections is doubled, and they are made at age 4 from seed while the species can be propagated with rooted cuttings. The orchard is initially planted at approximately 8 × 2.4 m. Based on pro-

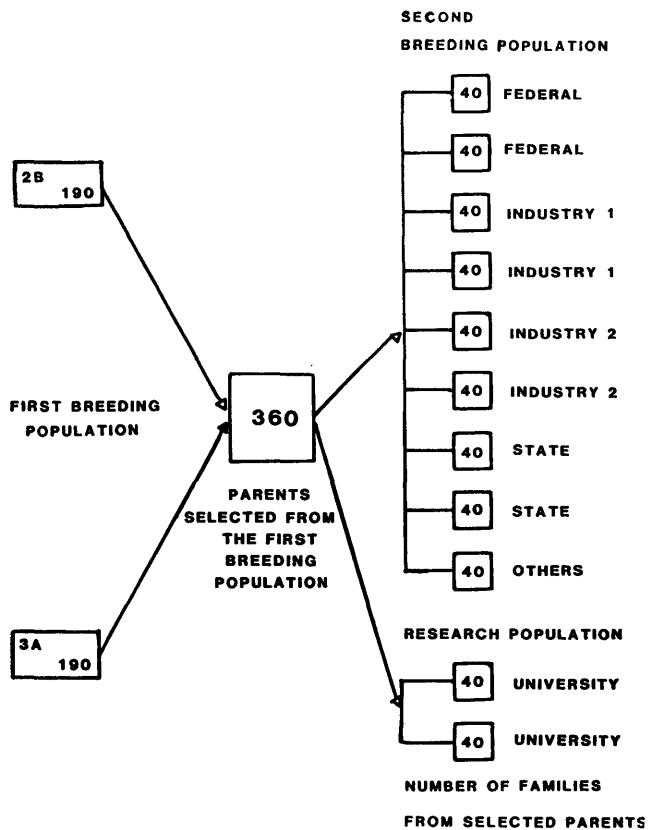


Fig. 3. — Organization of a second generation breeding population for a hypothetical production zone combining climatic zones 4a and 4b in Minnesota. (See Fig. 3 and 4.)

geny performance at about age 15 from seed, the orchard can be rogued to the best 6—7 clones leaving approximately 70 ramets per acre. This approach has the advantage of lower propagation costs. It could also lead to earlier sustained seed production because grafting could not cause rejuvenation at age 15 and accompanying reduced flowering and because the ramets after growing undisturbed for several years will have healthy full crowns and root systems by the time seed production is likely to occur.

Conclusion

NAMKOONG (1982) stressed that it may be risky to accept “first approximation” models of population genetics and for breeders to assume that substantial progress can be made by continuing what they have been doing in the past. He describes the potential problems that may develop from erroneous “first approximation” models. Breeding systems working with limited base breeding populations will be able to show considerable gain by repeating short-term breeding efforts over two or three generations. The gains more than likely will justify the investments in the programs. Sooner or later, however, problems may develop, gains will plateau, and the population may actually deteriorate as the effects of inbreeding accumulate. An alternative is to plan for long-term multigeneration breeding from the start and begin with founders selected with allelic diversity as a major objective. For many commercially important species with which tree improvement has been in progress for some time, this is no longer an acceptable alternative because the driving force of such programs — short-term economic gains — is not easily abandoned. Then a compromise solution must be found that can meet short-term goals while creating the main frame for long-term breeding. In a previous paper, we discussed concepts associated with the selection of founders and organization of breeding populations. (KANG and NIENSTAEDT 1987) Here we developed a system based on an actual case. The proposed system is only one of several solutions to the organization of white spruce breeding in the Lake States.

In describing the development of the system, we have stressed some of the factors to be considered in the design process including: (1) The differences in long-term and short-term breeding objectives; (2) selection objectives; (3) the problems encountered in selecting founders population from existing improved breeding stock, with a discussion of (4) the equalization process required in early generations to avoid early narrowing of the genetic base, and (5) structuring of the first and second breeding populations with emphasis on the need for flexibility.

These factors are unique for every species and every situation. Every breeding system and strategy will have unique features from the outset, and — more important

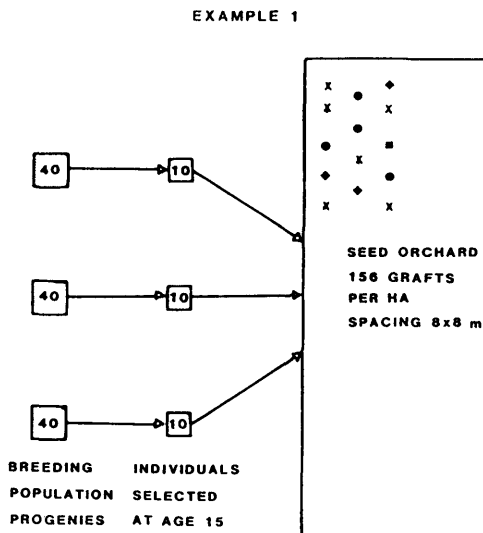


FIGURE 4A

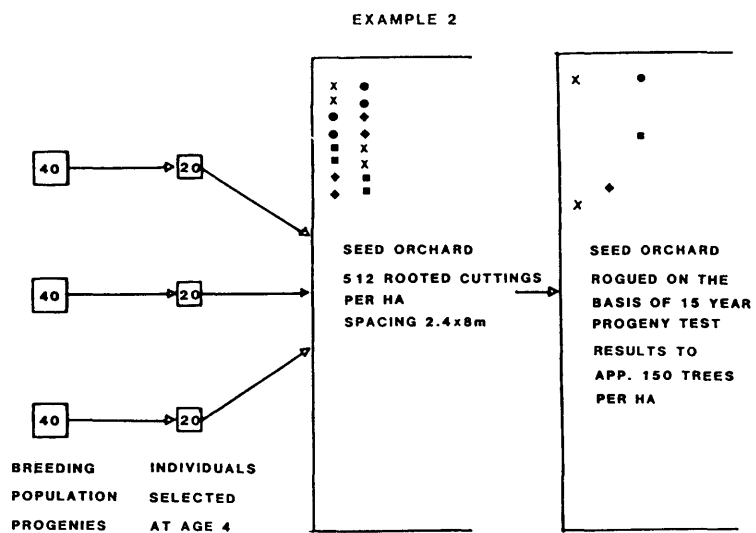


FIGURE 4B

Fig. 4. — Converting the second breeding population to a multiplication population.

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.

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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