

Survey of past, current and future Swedish forest tree breeding

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The Swedish tree breeding programme in brief

Tree breeding in Sweden started in an organized form in 1936 by the establishment of an association for the breeding of forest trees (Sylvén 1943). The following years saw enthusiastic activities, to some extent being inspired by the successes already achieved in crop breeding. In 1967, The Institute for Forest Improvement was founded and the activities of the former association and its successors were taken over. Since then the breeding of commercially utilized tree species in Sweden has been carried out by the Institute as a joint activity financed by the forest owners and the state. In addition, limited breeding activities are carried out by various companies and by university departments in connection with research projects.

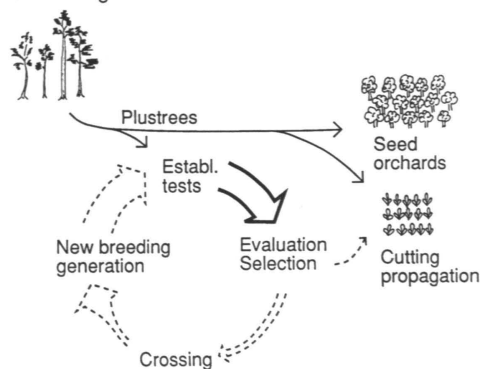
The main species in the Swedish breeding programme are Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and lately lodgepole pine (*Pinus contorta*) and birch (mainly *Betula pendula*). In addition fairly limited breeding activities occur in hybrid aspen (*Populus tremula* × *P. tremuloides*), oak (*Quercus*), larch (*Larix*), black spruce (*Picea mariana*), and a few other native and exotic tree species. Currently, exotic species, other than lodgepole pine, do not seem to have any possibility of becoming important in Swedish forestry, and thus the breeding activities in these species will probably remain small.

Current breeding activities include i) applied tree breeding including research and development to support the breeding, ii) research and development in mass propagation of reforestation material, and iii) consulting activities and extension directed towards small-scale forest owners, companies and the forest industry as a whole.

Fig. 1 gives a general survey of the present state of tree breeding and the direction in which

it is evolving. The dominating initial effort has been to select plustrees in natural stands and use them for production of reforestation material of improved production value and of known origin. The basic approach was to establish seed orchards which were intended to guarantee sufficient amounts of good seed crops. In parallel with this, a considerable body of tests was built

A) Present stage



B) Future programme

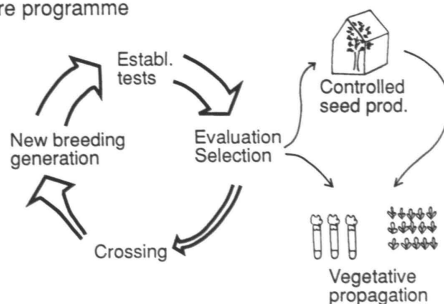


Fig. 1. Illustration of a) the present stage in Swedish forest tree breeding, which is evolving towards a sustainable long-term breeding programme, and b) the probable functional components in the future breeding programme.

up, today including around 1000 different test sites all over the country. Ideas on how future genetic improvement of the material should be performed was certainly discussed already in the early days but resulted in few actual measures. More recent activities are trying to integrate the immediate needs to secure propagation of reforestation material with measures aiming to support long-term breeding programmes.

In the main species the collection of plustrees and establishment of plustree tests is almost completed. Evaluations of the previously established tests are culminating and will dominate the breeding work for the coming decade, together with a gradual transition to long-term breeding programmes based on recurrent selection in breeding populations over many generations. The improvement generated in these breeding populations will probably be utilized in many different types of propagation activities. However, a proper utilization of the higher genetic superiority of the future material will require more efficient propagation methods than those used today.

The Institute's research and other activities in connection with breeding aims to support this development. Important areas are i) application of new techniques (REML, BLUP) for estimation of genetic variation and parameters and for genetic evaluation of clones for selection purposes, ii) design and strategy of future long term breeding programmes, iii) development of new techniques for seed production, and iv) development of vegetative propagation methods for large-scale utilization.

Status of materials in breeding — providing forestry with genetically defined material

The material available for breeding originates to some extent from several decades of plustree selections. The approximate size of the base material for the four most important species is given in Table 1. A brief account of the current situation in the breeding of them is given below.

First and second batches of Scots pine and Norway spruce plustrees

The Scots pine and Norway spruce material originates mainly from two batches of plustree collections. The first started in the late 1940's and lasted till 1960's. The plustrees were se-

Table 1. Summary of available base material for establishing breeding populations.

Species	Approx. size of breeding material
<i>Pinus sylvestris</i>	6800 plustrees
<i>Picea abies</i>	5600 plustrees + ~13000 clones in clonal forestry programmes
<i>Pinus contorta</i>	200 plustrees + 1200 o.p. families
<i>Betula</i> spp.	1450 plustrees

lected in mature stands and a very thorough documentation was done for each individual tree. The original strategy was largely to first establish the plustree orchards, await the start of their flowering, make crosses in order to get full sib families from them and then progeny test the plustrees. The immediate purpose was to verify the original plustree selection and to make a renewed selection among the collected plustrees in order to establish seed orchards based on a superior fraction of the plustrees (1.5 generation orchards). With the climatic conditions we have in Scandinavia, this became a slow procedure. Most progeny tests from the first plustree batch became planted in the 1970's and evaluations of them started on a larger scale from the mid-1980's. There are now 68 seed orchards of Scots pine and Norway spruce in production, originating from the first set of plustrees. The seed orchard owners are recommended to use the information from the progeny tests to make selective harvesting in the orchards, since regular genetic thinning was not planned to occur when the orchards were designed.

Selection of the second batch of plus trees, comprising 4–5 times as many trees as in the first batch, was initiated in around 1980 and almost completed at the end of the decade. In this batch the selections were made in 20–40 year old plantations in order to facilitate comparisons with neighbouring trees. The main objectives of the selection were growth, wood density and various quality characteristics. Again the immediate purpose was to secure material for seed production, but collection of base material for a subsequent long-term breeding programme was another aim. The country was divided into seed orchard zones (20 zones for Scots pine and 9 for Norway spruce) and the seed orchards were compiled for each of them considering certain rules for transferring material over climatic gradients (Scots pine southwards and/or lower

altitude, and Norway spruce northwards and/or higher altitude). In the second batch, open-pollinated seed was collected directly on the plus trees and progeny tests were established before the seed orchards were built. The new orchards, which sometimes also include good proven clones from the first plustree batch, are designed to enable a subsequent genetic thinning when results from progeny tests have become available. The establishment of the new set of orchards is not yet fully completed.

Clonal forestry with Norway spruce

Clonal forestry programmes were initiated during the 1970's for Southern Sweden and in 1989/90 for Central Sweden in cooperation with forest companies. Almost 10000 clones have been tested in field trials in the southern programme and around 3000 are in the course of being tested in the new programme. The aim is to test and select a sufficient number of well-performing clones for commercial clonal mixtures. The material includes parts of the previously-mentioned spruce material as well as new selections in natural stands in Sweden and elsewhere. Although a large proportion of the materials are specially selected for the clonal forestry programme, the intention is to use them also in the basis for the long-term breeding of Norway spruce.

Lodgepole pine material

The breeding material includes more than 200 plustree clones available as grafts in seed orchards, and about 1200 open-pollinated families of plustrees in Canada available in seedling seed orchards and progeny tests for six orchard zones intended for use north of lat. 59.5–60° N. The grafted seed orchards were established largely during the 1970's and the seedling seed orchards during the 1980's. The first evaluations of progeny tests have been made for the four southernmost orchard zones. Based on these, the corresponding orchards have been subjected to genetic thinning, and selection of breeding material for potential use in southern Sweden has started.

Birch breeding material

Little birch material for breeding was available before 1988. At that time a plustree selection programme started in order to provide selected material for propagation purposes and to initiate long term breeding of birch. The programme now includes about 1400 selected clones of *Betula pendula* and small number of *B. pubescens*. The material is currently being tested in progeny and clonal tests and the first evaluations will be made in a few years.

Future work — establishing breeding populations and long-term breeding programmes

The major forthcoming task is to turn from the plustree selection and retrospective testing phase to a sustainable breeding programme for each species. Plans are currently under development and have to be put in practice within a few years. Formal decisions have not yet been taken on these matters by the funding and participating organisations, however. The following is a survey of some of the major points in the current thoughts and planning.

Three levels of breeding activities are distinguished, having different purposes, time perspectives, and most likely also different funding and participation from interested parties: i) long-term breeding in closed nucleus breeding populations having different adaptation profiles and possibly somewhat different selection objectives, ii) medium- and short-term breeding activities starting from contemporary breeding populations and aiming to create suitable materials for mass propagation, and iii) mass propagation of genetically improved material.

Long-term programmes

The purpose of the long-term breeding populations is to secure material and options for genetic improvement during at least some centuries of breeding for all parts of the country. It is aimed that the breeding populations will function as dynamically developing reservoirs of material and genetic variation for the other levels of breeding activities. The long-term breeding is likely to be a concern on at least the national level, where immediate commercial interests are less pronounced. It is desirable, or even neces-

sary, to base it on long-lasting agreements and decisions about the size as well as the financing of the programmes.

For each species, a number of breeding populations are founded to cover different climatic conditions and breeding objectives. Since resources devoted to long-term breeding are always likely to be scanty, the dimension of the population sizes vs. number of populations will need to be a compromise. Small populations will limit conservation and improvement prospects within each population in the very long run, but will increase the possibilities to maintain more populations for specialized purposes and also to test and select more intensively at each generation turnover.

The provisional suggestion is to keep each breeding population at an effective population size (N_e) of 50 or somewhat more in certain cases. At this level of N_e very few alleles, which occur at utilizable frequencies in the population, are lost by sampling at each generation shift (e.g. Gregorius 1980). Theoretically, genetic gain will be possible in quantitative traits for 50 to 100 or more generations of breeding in a closed population of that size (e.g. Robertson 1960, 1970, Harris 1982, Dudley 1977, Bulmer 1980, Falconer 1981). This probably exceeds the time we, as humans, will breed trees with conventional methods. The maximum rate of inbreeding, 1 % per generation, is also still very low at that population size. Inbreeding effects like incompatibility problems, segregation of lethals and inbreeding depression, can therefore be counteracted by the ongoing selection without any substantial loss of selection space.

Each of the populations should have a specified profile as concerns light and temperature adaptation. For long-term breeding it seems advantageous to define the adaptation with objective measures rather than by relating them to certain regions, where climate may change with time. The adaptation profile could be defined in several ways. For the populations, light and temperature targets are defined by a target latitude and heat sum, length of growing season and frost occurrence. For testing purposes, the adaptation to the temperature climate is specified further by e.g. heat sum until sprouting (defined stage), heat sum and critical night length for growth cessation (defined stage and temperature regime), and hardiness (susceptibility to climatic injuries at a later age interval under defined climatic conditions), respectively. Suitable sites for use of material from breeding populations

are identified by latitudes, heat sums, growing seasons and frost patterns. As knowledge accumulates, the reactions of each breeding population to different site conditions could be described in order to guide the users, e.g. with regard to expected sprouting date, expected growth cessation date, expected growing period, expected incidence of climate (frost) injuries, etc.

The specified adaptation profile refers to the population mean. Due to the inevitable genetic variation within populations, each of them will cover a range of conditions around the adaptation target. Ideally, the number of populations founded should be sufficient to enable their distributions concerning adaptation variables to become overlapping. Optimally adapted material would then always be possible to find for medium- and short-term breeding and mass propagation. A more sparse distribution of populations over prevailing light and temperature gradients would require either acceptance of sub-optimal adaptations in some mass-propagated materials or adjustment of the adaptation profile to the optimum via short-term breeding programmes prior to the mass propagation.

The current planning indicates that about 60 breeding populations are needed for the four most important tree species (Table 2). This number includes only a few duplicate (multiple) populations with specialized objectives, e.g. extreme phenology to resist frost. These should preferably be assigned light and temperature targets in between other populations in order to cover adaptation gradients more efficiently. With this number of Scots pine and Norway spruce populations the light climate is covered by steps of 1.5–2 latitude degrees and the temperature climate by steps of around 20 days of growing season or 100–200 units (d.d., +5 °C) of heat sum.

The objectives of the long-term breeding populations are suggested to be as general as possible. They should include traits, which both are "safe" to breed for and presumably difficult to achieve or adjust via the processing of the products also in the future. More specialized, or "hazardous", objectives could preferably be satisfied in short-term breeding programmes starting from selections in suitable breeding populations. In broad terms, the breeding objectives may include further adjustments of adaptation to climate targets when necessary, and improvement of general resistance against parasites and diseases, robustness to environmental

Table 2. Probable numbers of long-term breeding populations and medium- and short-term lines in the four most important species if the currently discussed programme becomes fully established.

Species	Long-term breeding populations	Medium- and short-term breeding	
		Elite lines	Other specialized lines
<i>Pinus sylvestris</i>	~ 23	10–40	~ 5
<i>Picea abies</i>	~ 20	20–40	~ 5
<i>Pinus contorta</i>	~11	10–20	few
<i>Betula</i> spp.	~7	~7	none or few

variation, growth (e.g. dry matter production before closure and in closed stands) and fundamental stem and wood quality traits (e.g. straightness, branching, fiber angle/straight-grainedness, fiber length, wood density).

Possibilities of (co-)adaptation to regional environments are kept open by regional testing and keeping populations closed. However, it seems dubious whether this will be effective with the time horizons considered realistic even in long-term breeding.

Table 3 shows the assumed sequence of breeding activities in long-term breeding. A critical point is how to generate sufficient

amounts of material for field testing in species which are difficult to propagate vegetatively. To be useful, the propagation method must be successful for nearly 100 % of the clones to be tested. Progeny testing and selection among parents seems to be the only efficient choice in some species. With the current technique for flower induction (nearly 100 % response is required) this will cause a delay of maybe 5–10 years, however. If difficulties are encountered, an alternative would be to produce higher numbers of individuals in the new generation and perform within-family selection solely on the own performance of each tree. This alternative,

Table 3. Assumed sequence of activities in the long-term breeding programmes from the plustree generation (P) until the 2nd breeding generation (F2).

Generation and stage		Pines	Spruce, birch (?)
P	Candidate plustrees in current tests	~600	~600
	Selected after testing, crossed for new generation	50+	50+
F1	New generation, phenotypic screening in early tests	~5000 clones	~5000 clones
	Selected for field testing	~500 clones	~2000 clones
	Material for field testing at 3–4 sites	Polycross: half-sib fam. of 30–40 trees for prog. testing	Cloning: ~10 ramets per F1 clone for clone testing
	Finally selected with all parents (sel. P) represented, crossed for new generation	~50+ clones	~50 clones
F2	New generation, phenotypic screening in early tests	~5000 clones	~5000 clones
	etc.		

however, trades a shorter time lag for the accuracy and diversity of the testing.

Following this schedule, a total body of 60 breeding populations corresponds to about 1 million trees per generation in field testing (totally about 400 ha or 20 ha per year). Additional test material will be needed in nursery and greenhouse tests.

Medium- and short-term programmes

The purpose is to serve specific propagation programmes with improved material. The programmes include intensive initial selection from one or several breeding populations, possibly followed by one or a few generations of intensive breeding in small populations (in terms of N_e) in order to further improve specific traits. The genotypic diversity of the subsequently mass-propagated materials of concern, rather than the conservation of genetic variability in the breeding material, determines the time horizons of this level of breeding. A particular material may recurrently serve as base for mass propagation as it is further improved. The short-term breeding will probably vary in intensity and volume over time and be financed as cooperative activities by different parties from the forest owners and other organizations.

A variety of medium and short-term breeding programmes of limited size are possible, e.g.:

- i) Breeding of elite lines, each of which starts from the most advanced part(s) of one or several contemporary long term breeding populations. The objectives are chosen according to a specific purpose. This is followed by intensive selection over a few generations. New superior or "unrelated" material might subsequently be brought to the elite lines or new elite lines are started repeatedly in an overlapping sequence to overcome inbreeding problems.
- ii) Creation and breeding of elite lines with adaptation profiles not covered by any long-term breeding population. This is an alternative if the long-term breeding populations are too few and sparsely distributed over adaptation gradients.
- iii) Breeding of specialized lines, which combine specific properties of several long-term breeding populations. These are bred further for 0 to several generations in a way similar to the elite lines suggested above.
- iv) "Hybridization" of material from different populations or (sub-)lines in order to create heterosis

- in a subsequently mass-propagated material.
- v) Blending material in order to create a desired genotypic diversity in mass-propagated material.

Mass-propagation activities

The purpose is to produce reforestation material with sufficient genotypic diversity and with the best possible utilization of the genetic improvements obtained in the previous stages of breeding. The time period of concern is one production cycle (rotation). It is likely that mass propagation will continue to be an activity run by different constellations of forest owners and state organisations.

Propagation is expected to be carried out in intensively managed seed production units, by vegetative techniques or by combinations of the two (cf. Fig. 1). The current technique with open-air seed orchards is probably inefficient in advanced generations, where the genetic gain to be utilized is higher than today, i.e. the disadvantages of the time lag until seed production starts and the pollen contamination from the surroundings become more important, the higher the genetic gain. Techniques for medium scale controlled seed production are being developed and will probably be used in producing genetically defined and genotypically diverse material for a subsequent vegetative multiplication.

Expected gains

Calculations based on our current knowledge of genetic parameters indicate that the original plustree selection has produced about 6 % genetic improvement of growth (Danell 1991). Selection of 50 plustrees to be parents of F1 among the assumed 600 candidate plustrees is expected to give an additional 10 % gain in single trait selection. Testing and single-trait selection in the F1 generation is expected to generate another 5–8 % of genetic gain in the long-term breeding populations.

By intensive selection to medium- or short-term breeding the genetic superiority is expected to be raised initially by 5–10 % above the mean of the contemporary long-term breeding populations. Breeding over several generations in elite lines will increase this gain further.

Multi-trait selection will be practised in reality. This will lower the gain in each trait, but the total gain in economic terms will be corre-

spondingly higher than those indicated by the above figures.

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