Review of the Swedish tree breeding programme

SKOGFORSK

PHOTO: BO KARLSSON COVER PHOTO: ERIK VIKLUND

PREFACE

The current Swedish tree breeding programme was established towards the end of the 1980's. After about 20 years of application it is an appropriate time to assemble all experiences and knowledge acquired, and to evaluate new methodology and suggest improvements if required.

Some years ago, Skogforsk initiated an investigation with the objective to revise the programme if that turned out to be desirable. The final revision will use this review and the results of computer simulations currently on-going for a number of alternative breeding strategies.
The investigation presented here was carried out by the team of tree breeders at Skogforsk with a considerable support from Dag Lindgren, professor in forest genetics at SLU. Dr Tim Mullin, who at present is a member of the Skogforsk team, is deeply involved in the project in-progress, using computer simulation to develop and evaluate a number of alternative breeding strategies. Tim has also carefully reviewed this report, added important information and improved the language. I compiled the report and its conclusions, based on contributions to the different sections from the breeder working groups. All contributions are gratefully acknowledged.

Uppsala January 2011

Ola Rosvall

REVIEW OF THE SWEDISH
TREE BREEDING
PROGRAMME

www.skogforsk.se

OLA ROSVALL
Editor

PETER BERGMAN
Graphic design

PRINT

GÄVLE OFFSET
Gävle

SKOGFORSK
Uppsala Science Park, 751 83 Uppsala
Tel. 018-18 85 00. Fax. 018-18 86 00
E-post. info@skogforsk.se
www.skogforsk.se

ISBN: 978-91-977649-6-4

CONTENTS

EXECUTIVE SUMMARY

The Swedish breeding programme was developed in the second half of the 1980's. After more than 20 years of effort, much experience and new knowledge has been gained. The purpose of this investigation is to support a revision of the breeding strategy by analysing and developing the range of alternative methodologies now available.

Profitability of tree breeding. Using genetically improved planting stock is like a technology breakthrough. There is a great increase in gain with little additional cost, sometimes even at reduced costs. The predicted 10% realised growth increase of Swedish forests from present seed orchard programmes will increase future annual income by 1.7 billion SEK. From 80 to 600 million SEK can be invested annually in a tree improvement programme, depending on a 2 to 10% real interest rate used for discounting the investment. These are conservative figures, as current harvesting can increase long before planted trees reach rotation age, as a consequence of enhanced land expectation value. Furthermore, vegetative propagation has the potential to reduce the time lag from breeding to stand establishment by 15-20 years, increasing even more the scope for investments in tree improvement.

Breeding objectives under changing conditions. A number of market and environmental changes have occurred since the current Swedish breeding programme was initiated. The breeding objectives were therefore reviewed, with particular consideration to climate change and the widening objectives of forest management. These include serving as a natural resource for new biomaterials, biochemicals and bioenergy, as well as delivering a number of fundamental environmental services. The very general and basic programme objectives of improving tree characteristics and managing genetic diversity were found to address all these issues, but would benefit from enhanced efforts to increase tree adaptation and adaptability to changing conditions, with special emphasis on resistance/tolerance and on plasticity/adaptability. These goals will be achieved by modifying approaches to testing and selection, but there is also a need for more research.

While the existing objective traits continue to be relevant, it is concluded that an increased effort must be put on developing economic weights to improve the balance of effort among objectives.

PHOTO: ERIK VIKLUND

Molecular genetics and other biotechnologies. Molecular genetics, genomics and biotechnology are among the fastest developing areas of science and the possibilities to apply new technologies in the near future were thoroughly reviewed. At present, most of these methods are still for research purposes and far from being applicable to operational tree breeding. In the future, genome-wide selection has perhaps the greatest potential to become a powerful tool in combination with conventional methods for selection. In addition to providing direct observations of DNA variation, current marker technology can help identifying relatives, such as determining paternity of individual trees raised from polycrosses or open pollination, establishing ancestral pedigrees for trees used in pair crosses, estimating contamination rates in orchards, etc. Marker technology for association to phenotype will require further development and greater cost efficiency to be of real interest for operational breeding, but this could be realised in the not-too-distant future. It is suggested to store a sample of DNA from all founders for future use, e.g., to allow for tracking their genetic contributions over generations.

Genetic modification of trees (GMO) of interest for Sweden belongs to the far future. The lack of well-characterised gene constructs of commercial value rather than the technology itself makes it far from being applicable. In addition, there is a need for long-term field testing to evaluate all consequences, concerning commercial, environmental as well as social issues.

In general, it is concluded that the traditional tree breeding methodologies will be the basis for improvement in the foreseeable future, but new genetic technology can help traditional breeding.

A promising application of biotechnology comes from somatic embryogenesis (SE) as a method for commercial tree nursery stock production of Norway spruce. Its greatest future potential is to replace seed orchards for mass propagation of superior seed lots, rather than for propagation of superior clones. SE seedlings could thus reduce the time lag from breeding progress to forest plantation by about 15-20 years while maintaining genetic diversity at a high level in operational forest stands. SE technology will also facilitate clonal forestry if used instead of rooted cuttings for field testing in the breeding programme. At present, SE seedlings can be used as donor plants for subsequent propagation on a large scale by rooted cuttings. However, SE technology itself is not yet sufficiently developed to offer a cost-efficient alternative for large-scale deployment under Swedish conditions. In addition, growth and performance of SE seedlings have not yet been verified in comparison with zygotic seedlings.

Updates from research literature on selection and mating strategies. After reviewing recent research and development on breeding strategies, several aspects were identified for further consideration. For example, there is an opportunity for fine tuning founder imbalance in genetic contribution in an individual breeding population, within the current specification of an initial effective population size Ne ≥ 100 and the programme target of Ne = 50. When initiating a breeding population, an increase in variance of founder contributions can be compensated for by using about 10 % more founders without reducing Ne. Imbalance in founder contribution can be dealt with by introducing methods for optimum contribution selection. It is worthwhile to vary test effort among trees according to their breeding values, to increase selection intensity and accuracy for the high-ranking members of the breeding population. For these strategies, there is no trade off with genetic diversity. It is also of interest to explore how a rolling-front strategy can be applied to enhance gain by speeding up development of the breeding frontier. It would also be worthwhile to explore a polymix progeny testing strategy, using genetic markers afterwards for paternal identification. If applied, selected fathers should be used to allow for continuous forward selection.

Experiences from simulations. Based on a number of computer simulation studies over the years, the Swedish programme has been found to be sustainable and robust. For the main species it is a good strategy to keep the original number and size of unrelated breeding populations, but for minor species it is worthwhile to consider keeping two sublines with few breeding populations. It is also a good strategy to primarily practice within-family selection. Under these conditions and by using positive assortative mating (PAM), family variance can be increased and utilised to increase gain when selecting for mass propagation populations. In this way, realised gain is near maximum, while the loss of genetic diversity is the lowest possible. Finally the simulation demonstrates that it is more intuitive in long-term breeding to use proportional gene diversity (GD) as a diversity measure rather than status number (Ns).

Experiences from genetic evaluation and field testing. There has been a continuous accumulation of experience using new methods of genetic field test designs and analysis of collected data. Skogforsk is at present introducing TREEPLAN®, which is an advanced tool for genetic evaluation and for managing very large amounts of data. Using TREEPLAN® will put emphasis on optimising experimental design, spatial analysis, connectedness, site selection, correction for competition, efficient measurement of traits, economic weights, data administration, breeding value reporting, etc.

The suitable stage of tree development for field test measurement and selection for breeding has been found to be at about 3-5 m height, which is typically 20 % of the rotation time. Additional measurements may be required at other stages of development for specific breeding objectives or under special circumstances; for example, resistance/susceptibility to biotic and abiotic factors can best be evaluated during periods of damage.

To improve assessment of climate adaptation and adaptability, the field-test layout should allow evaluation of tree response to climate gradients. Selected trees that tolerate the spatial variation in climate characteristics are also likely to tolerate temporal changes.

A special effort is suggested on large-plot and long-term field testing for assessing unit-area production and group performance of related trees, allowing study of the efficiency of selection at a younger age. These should be developed as a realised performance monitoring system, using a sample of the breeding material.

Experience with rooted cuttings for clonally-replicated field testing in a number of Scots pine breeding populations is promising, but requires further improvement and verification when successively introduced in the operational breeding programme. For lodgepole pine, however, the methodology is already applicable to the operational programme.

Experiences with breeding archives and controlled crosses. Based on experience and this investigation, controlled crosses of selected trees need to be carried out in a well-managed breeding orchard or archive, using top grafting to stimulate both male and female flowers. Emphasis should be put on selecting flower-promoting inter-stock clones, as well as the application of gibberellins. To minimise the time for propagating superior trees in seed orchards, special archives for scion production should be established.

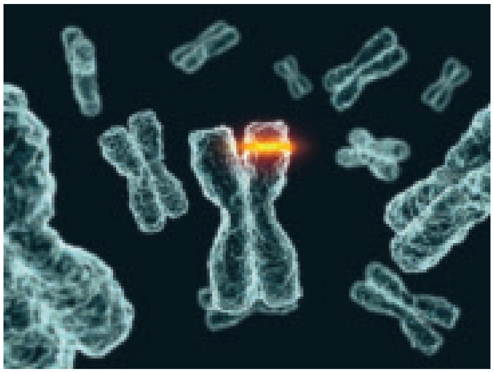
New technology has to be developed to minimise the time required to complete a great number of crosses after trees have been selected. Large areas are needed for keeping field-tested clones ready for crossing. Forest sites close to a breeding station may be the best alternative.

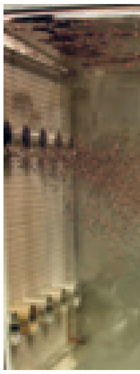
Double-pair mating (DPM) can remain the general mating design for generating the recruitment population, while it is also rather accurate for progeny-testing. Single-pair mating (SPM) is sufficient for cycling the breeding population and can be used in low-input situations or in lower-ranking strata of the breeding population. For polymix (PMX) testing, a pollen-mix with 25 parents and 30 progeny per family will give robust results. The pollen parents should be intensively selected to make possible forward selection aided by paternal analysis following the PMX/WPA strategy.

Experience from the third round of seed orchards. There is a general problem with the time-lag from progress in the breeding programme to deployment of improved nursery stock. New concepts for seed orchards are needed.

PHOTO: ERIK VIKLUND

PHOTO: MIKAEL ANDERSSON PHOTO: ISTOCKPHOTO





Synchronisation between breeding and mass propagation activities should be improved, including scion and cutting propagation archives for producing grafts or rooted cuttings. Decisions for new orchards should be based on profit analysis rather than just seed demand.

An appropriate effective number of clones for seed orchards considering both gain and diversity has been found to be 16 (status number) for the Swedish multiple-use forest situation. This is more than would be necessary for a more industrial plantation situation, e.g., for an introduced species like lodgepole pine. Using linear deployment is preferred and will increase the census number of orchard clones at a given status number.

Alternative mating and selection strategies. While clonal testing has proved efficient for Norway spruce, the time required to produce F1 pine progeny in breeding archives for "dead-end" progeny testing in Scots pine has been excessive. Instead, pine progeny in the supplementary F1 field tests (established in parallel to the breeding archives) are now suitable for forward selection based on their own phenotype. An important question at present is how this should be done, as well as to find the best strategy for future Scots pine breeding.

Based on new knowledge and breeders' experiences, a number of alternative mating and selection systems were specified and evaluated in terms of time and resources to be used, potential genetic gain achieved and genetic diversity maintained. In their basic form, these strategies can be seen as different approaches to within-family selection (among sibs), while among-family variance is maintained in the breeding population and used only for selection to production populations such as seed orchards. In reality, by relaxing selection restrictions, part of the family variance can also be exploited when cycling the breeding population. The following alternatives were investigated:

1. Seedling candidates backward – basic (establish dead-end polycross progeny tests of archived full-sib seedlings when flowering occurs naturally to select backward a breeding population of size 50)

2. Seedling candidates backward – intense (as for strategy 1 but with intensive management and use of flower stimulation to accelerate crossing)

3. Field forward (establish full-sib family tests to select forward a breeding population of size 50)

4. Field candidates backward (establish full-sib family tests to preselect candidates for OP progeny testing to select backward a breeding population of size 50)

5. Field candidates pair-wise forward (establish full-sib family tests to select forward candidate trees for pair crosses in a breeding population of increased size to allow both among- and within-family selection)

6. Field candidates poly-mix forward (establish polycross family tests with selected fathers to select forward candidate trees in a breeding population of increased size to allow both among- and within-family selection, guided by paternal analysis)

7a. Seedling candidates clonal forward without breeding archive (establish clonally replicated full-sib family tests to select forward a breeding population of size 50)

7b. Seedling candidates clonal forward with breeding archive (as for strategy 7a, but with a breeding archive established in parallel to the field tests)

Strategies 1 and 2 are variants of the current Scots pine programme, while Strategy 3 is the present Scots pine alternative programme. Strategy 7b is the current Norway spruce programme. All current programmes start with seedlings selected within the nursery, while alternatives 4, 5 and 6 all start with selecting an excess number of candidate trees in field tests.

Scots pine. Strategies 1 and 2 start with planting a Scots pine breeding archive with 10-20 full-sib seedlings to make them flower, in order to produce polymix progeny for what is effectively a "dead-end" progeny test. The sole purpose of the progeny test is to evaluate which of the original full-sibs should be bred to generate the next cycle. While this is very accurate methodology, it has been found to be too time-

PHOTO: ERIK VIKLUND

consuming, taking up to 36 years for a full breeding cycle. It also provides less gain per unit time if compared to the less accurate but faster strategy 3 that relies on forward selection in field tests and takes only 21 years.

Alternatives 4, 5 and 6, like number 3, all use forward selection in field tests as a starting point, but select a number of candidate trees and use different approaches to mating and testing to determine to what degree these candidates should contribute to the next generation. The cycle length for strategy 5 and 6 is 21 years, as they use forward selection, without a second, progeny-testing step.

The final resource allocation to these strategies and a fair comparison among them still has to be optimised through computer simulation, but some basic conclusions can be drawn:

Generally, for the best use of resources, any alternative to the present Scots pine breeding strategy should be a flexible combination of alternative strategies rather than just one single approach. This includes adaptation to operational constraints as well as applying more intense methods to the best part of a population The strategies chosen can vary among populations as well as among parts of a population, however, in order to effectively synchronise sequential activities such as testing, selection and mating, time schedules for field tests, breeding and propagation archives need to be carefully planned and prepared in advance.

From the short-term perspective, three stages of development of the present Swedish Scots pine breeding populations can be distinguished where different strategies are suitable:

Generally in the long run, but also for those populations of Scots and lodgepole pine that are about to be crossed in the near future, clonal testing is of greatest interest, as used in strategy 7b. The operational experiences so far are sufficiently good to continue gathering experience on an operational level.

For most of the pine breeding populations, the next activity is to select and breed F1 trees growing in field experiments. For these situations there is a choice between simple forward selection of 50 trees, as in strategy 3, or to select a number of candidates (100-300) for further progeny testing as in strategy 4, or breeding as in strategy 5 and 6.

For breeding populations already following the current main strategy 1 (Seedling candidates backward with an established archive), and in those cases with no F1 field experiment available for forward selection, it would be preferable to either make pair crosses, like in strategy 5, or to use a polymix composed of selected pollen parents for PMX crossing like in strategy 6. In both cases, this allows for both forward and backward selection.

To gain experience, it is worthwhile to carry out all these options as large-scale experiments at the size of a whole population, even if the simulation studies may prefer one over others.

For all strategies, a carefully planned breeding archive for top-grafting needs to be established in advance. There is no time to lose for developing these breeding archives. Research resources should be directed in parallel to support these activities and to improve the technology to carry out controlled crosses.

In line with directing efforts towards clonal testing, more resources should be spent on improving this technology to support operational activities. This supportive research should include managing clonally replicated breeding archives on forest sites close to breeding stations.

Norway spruce. In general, the current breeding strategy for Norway spruce is the best strategy from all perspectives, genetic as well as economic. This was clearly demonstrated by both current and previous computer simulations. Experiences from practical breeding also favour the approach. Operational problems are caused by delayed flowering, making it difficult to complete the stipulated DPM crossing scheme. Improving nursery practices for growing of seedlings and replicating them by cuttings in a way that avoids C-effects is a long-standing research task.

There is no reason at this point to change the Norway spruce breeding strategy. This investigation does, however, suggest increasing flexibility by relaxing the DPM mating system and the number of ramets planted per clone, in favour of increasing the number of clones to be tested. It is important to make a detailed operational plan for all breeding activities including the timing of field measurements, planting the breeding archive, top-grafting selected clones, flower stimulation, etc. The cost functions could be extended and used to show the value of investing in methodology that shortens the time from measurement/selection to planting the new generation trees.

Lodgepole pine. Guided by experiences of the original lodgepole pine improvement programme in Sweden, a new breeding plan has evolved. Flowering is early and abundant in lodgepole pine and its seedlings can easily be propagated by rooted cuttings, which greatly facilitates efficient tree breeding. The plan begins with pair-crosses among a great number of selected F1-candidate trees from the Swedish OP-tests of Canadian plus trees. F2-seedlings from these crosses are clonally replicated as rooted cuttings and planted in field experiments, allowing for both backward selection among F1-candidates and forward among F2-clones. After the initial phase, the plan follows the principles of the Norway spruce plan and includes 13 breeding populations

Broadleaved species. The argument for breeding broadleaved species is more for keeping options for future action in response to climate and market changes, than to satisfy the small current demand for reforestation material. Increased interest in biomass production has recently prompted a shift from breeding birch to selection and testing of hybrid aspen and poplars. Nevertheless, the total effort to be expended on breeding broadleaved species, as well as the priority among species, needs to be decided so that appropriate breeding plans can be developed. These plans should be based on knowledge and experiences documented in this review.

To put any optimised strategies into practice, new tools have to be implemented to carry out optimum contribution selection, rolling-front procedures, linear deployment, etc., and the consequences of applying these tools need to be investigated.

Finally, the economic loss due to the time lag between progress in the breeding population and availability of improved regeneration material must be acknowledged. It is urgent to use any means to shorten this delay by means of propagation archives for seed orchard trees, rooted cuttings for clonal testing of the new breeding generation and ultimately to develop vegetative propagation methods such as somatic embryogenesis.

PHOTO: THOMAS ADOLFSÉN/SKOGENBILD

INTRODUCTION

The Swedish breeding programme was developed in the second half of the 1980's (Danell et al. 1993). During the 20 years of application much experience has been gained. New knowledge has developed and new methods have been introduced in Sweden and worldwide.

Over the years, new breeding strategies have been developed. Based on the Swedish breeding strategy, a number of PhD students and others have suggested using new concepts based on group coancestry, introduced positive assortative mating (PAM), nucleus breeding, forward selection, optimum genetic contribution algorithms, etc.

Marker technology permits identification of paternity in progeny arising from a pollen mix (polycross). The genetic architecture of the Swedish populations in terms of genetic parameters including genotype by environment interaction (GxE) has been elucidated from analysis of all field tests. The methodology for estimating breeding values has been refined and TREEPLAN® has been introduced.

Experiences have shown that it is operationally difficult to produce test progeny from young pine trees, and that generation turnover is extremely slow when progeny testing is attempted before recruitment population crossing is performed.

The third round of seed orchards with a focus on effective selection has revealed problems as well as opportunities for comparison among breeding populations as well as timing of progress in breeding with that of mass propagation

The central Swedish Norway spruce clonal forestry programme and the associated greenhouse-based seed orchard programme to produce elite crosses for bulk propagation was terminated and replaced by a research programme using SE technology. Protocols for producing rooted cuttings of Scots pine and lodgepole pine have improved.

Improved grafting techniques can now use smaller scions to produce more grafts per selected tree. Much research has been done on biotechnology as an option for tree breeding.

Resources for tree breeding have declined, although there has recently been a modest recovery. Global warming has become an overriding concern.

Tree breeding has recently become trendy in a more production-oriented forest policy for a sustainable society. New tree characteristics are discussed at all times, for example spiral grain and other wood properties, as well as climate

▷

adaptability and pest resistance. Quantitative forest genetics research at SLU has scaled back, although reconstruction is underway.

It is also of interest to note what has not happened. No elite breeding populations have been initiated as suggested by the breeding plan. No biotechnology breakthroughs of operational significance have occurred. No reduction in pollen contamination in seed orchards despite much research. No improved specialisation of seed lot use in operational forest practice, rather increased simplification

During the 1980's, the Swedish breeding programme was expanded with a large number of new plus-trees selected in planted forest stands and superior seedlings selected in commercial forest nurseries.

These new plus-trees, representing the majority of potential founder trees, have been field tested by open-pollinated progeny or by cloning the seedlings. Based on field test results, groups of about 50 trees were selected and crossed to form about 20 Scots pine and 20 Norway spruce F1 breeding populations, following the breeding plan.

Similar programmes were conducted for birch and for lodgepole pine. The F1-generation field tests intended mainly for within-family selection are deployed differently for different species.

While clonal testing has proved efficient for Norway spruce, the time required to produce F1 pine progeny in breeding archives for "dead-end" progeny testing has been excessive. Instead, pine progeny in the supplementary F1 field tests established in parallel to the breeding archives are now suitable for forward selection based on their own phenotype. An overwhelming question at present is how this should be done as well as to find the best strategy for future Scots pine breeding.

PURPOSES OF THE INVESTIGATION

This introduction gives some background to the decision by Skogforsk and its advisory board to initiate an examination of the Swedish breeding programme in 2005, with the following objectives:

1. The primary goal was to review the breeding strategy as a basis for a revision, if appropriate, to help reach the overall objectives of the Swedish tree breeding and mass propagation programmes. Different methods and techniques were to be evaluated and/or developed, taking into account both theoretical progress and the experience gained so far by Swedish breeders, considering practical and realistic conditions.

2. The examination was also to analyse the genetic, operational and economic consequences of new or alternative methods. These include the costs of breeding activities as well as the economic value of genetic gain to forest owners and society at-large.

3. Finally, the exercise was to identify knowledge gaps and suggest priority areas for research and development to help improve the breeding programme.

It was considered desirable that the report present technical guidelines for those alternative methods found suitable for application.

The purpose is not to revise the general objective of the Swedish breeding programme (i.e., integrated maintenance of genetic diversity, adaptation to present and future climate, and effective improvement of productivity), the main strategies (meta population of unrelated breeding populations, mainly within-family selection, general breeding objectives, possibility for elite breeding and separate selection for mass propagation), or the policy of fairly even distribution of resources over the country.

The investigation was divided into nine subprojects, each carried out by a group of breeders/researchers.

Using genetically improved planting stock is like a technology breakthrough. There is a great increase in income at low additional cost, sometimes at a reduced cost. In this section we evaluate the profitability of running a tree breeding programme and planting genetically superior trees as compared to other investments.

THE ECONOMIC VALUE OF TREE IMPROVEMENT

Ola Rosvall

To assess profitability of tree breeding and to compare alternative strategies, the net present value (NPV) of future incomes from planting genetically improved seedlings and the running expenses of the breeding programme should be calculated. Alternative investments are compared by using an alternative real rate of return considered to be realistic from a variety of perspectives.

Generally, there is a very large leveraging effect from using improved seedlings. For pine, the additional establishment and management costs for the orchard seed add 0.60–0.70 SEK per extra cubic meter produced, resulting in 7% internal rate of return on the orchard investment (Rosvall and Eriksson 2002). This adds 0.03–0.04 SEK to the cost of each improved seedling. The cost is increased somewhat if the investment in the tree improvement programme is also incorporated. According to "Förädlingsutredningen", the cost of a future cubic meter is 0.65 SEK, calculated at a 3% rate of interest (Skogforsk 1995).

The great profitability is because an investment in tree breeding provides a technology breakthrough. A more comprehensive economic analysis can in fact show decreased costs from using genetically improved trees. If the survival of seedlings is improved, fewer seedlings need to be planted, while at the same time producing even more timber. Per-unit logging costs will decrease due to slightly larger tree sizes and higher stocking. Forest operations can be concentrated on fewer hectares if total production is not to be increased. Using improved seedlings will increase land expectation value, shorten rotation time and enhance the immediate allowable cut with a great positive impact on economy (Rosvall et al. 2006). It is therefore known that investments in tree breeding are very profitable.

When choosing among breeding strategies, the economic objective is to find those strategies that produce as high a gain as possible, while preserving diversity at a specified level and fulfilling the requirement of profitability, i.e., reaching the threshold alternative rate of return. The criterion for comparison should be the NPV per unit invested. For example, forward selection of the trees for breeding in field experiments without any testing is both the cheapest and most efficient strategy in terms of gain per unit time and cost, but has a limited capacity to produce large genetic gain. Other programmes that are less efficient in terms of gain per unit cost and more expensive to carry out can produce greater gain and higher NPVs. Those strategies are nevertheless highly profitable if compared to alternative investments as long as they have a positive NPV at the specified alternative rate of return.

The potential growth increase of Swedish forests by using genetically improved trees was estimated by Rosvall et al. (2004) using the Hugin system. Recently, Rosvall and Lundström (2010) based a new analysis on the national forest growth-and-yield forecast, updated for the period 2010-2110, SKA-VB 08, carried out by the Swedish Forest Agency (Skogsstyrelsen 2008). They analysed a variety of scenarios with different application of genetically improved trees and

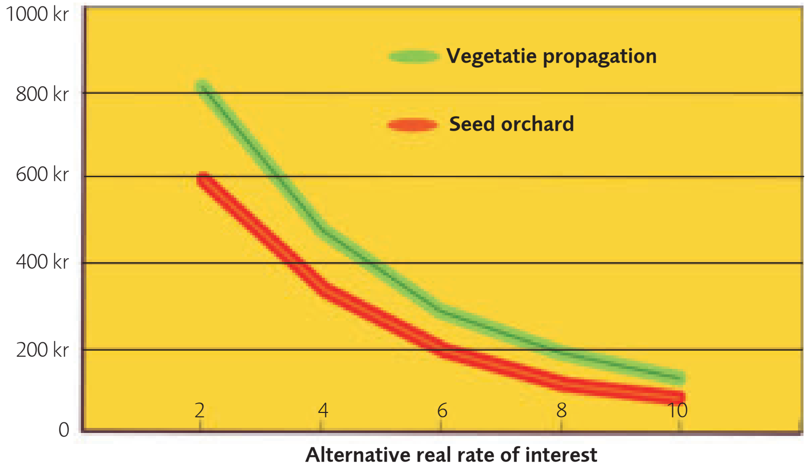


Figure 1. Opportunity for annual investment, million SEK per year for a Swedish tree improvement programme including tree breeding and the investment in establishment and annual management of seed orchards to produce 300 million seedlings as compared to a mass propagation programme using vegetative mass propagation with less time delay between progresses in the breeding programme and use in forest plantations at alternative real rates of return. The annual seed orchard cost is 12 million SEK/year for an interest rate of 6%. The breakeven cost for vegetative mass propagation is the difference between the two lines. Net timber value at roadside is 166 SEK/m3sk.

used the long-term genetic gain forecasts by Rosvall and Wennström (2008). The potential genetic gain for new plantations from now onwards using seed orchard seedlings will increase logging by about 10% by the end of this century.

Here we used the predictions of Rosvall and Lundström (2010) from the scenario assuming no lack of orchard seed to calculate the NPV of the future increase in logging. We did not include the growth increment of plantations already established that are to be logged during the current century, nor did we assume an immediate increase in potential logging in the short term as a result of increased land expectation value (the so-called "allowable cut effect"). We calculated average net timber value at roadside to be 166 SEK/m^{3}sk. The NPV of future increase in logging was transformed to an annual value for the period of 100 years. Given the alternative rate of return, this value is the maximum economic annual investment for a tree improvement programme.

When calculating the maximum justified annual investment, we defined a tree improvement programme as both the breeding programme and the corresponding seed orchard programme. The seed orchard programme includes the cost of seed orchard establishment and annual management, while the costs of harvesting and processing the seed were not included to obtain the true marginal cost of the tree improvement programme. By this definition, the annual seed orchard cost to produce 300 million seedlings is 12 million SEK for an interest rate of 6% (Rosvall and Eriksson 2002).

The increased timber value at roadside due to increased growth from improved seedlings was 1.7 billion SEK per year for the second half of the coming 100 years. This could be compared to 12.3 billion SEK for the total harvest in 2006. The NPV from 100 years increased logging was 26 billion or 8 billion SEK, at 2 and 4% real rate of interest, respectively. The added value to the processing industry is 10 times this value.

The justified annual investment in tree breeding and seed orchard programmes is as high as 600 or 340 million SEK for 2 and 4% interest, respectively (Figure 1). Even at a real rate of return as high as 10%, it is attractive to invest as much as 80 million SEK per year in a tree improvement programme. In all these cases, the annual seed orchard cost is 12 million SEK at 6% interest rate.

Using seed orchards for mass propagation of improved seed will delay the impact of improvement in the breeding population on actual forest growth by some 15 to 20 years, as this time is required to establish and bring new orchards into significant levels of production. There is much to gain if this time lag could be shortened through vegetative propagation for deployment (Figure 1). Growth over the coming 100-year period would be enhanced by an additional 2% using vegetative propagation, increasing the NPV to 35 billion and 12 billion SEK at 2 and 4%, respectively. At 4% interest, 300 million forest plants can be produced using vegetative propagation at an additional unit cost of up to 1 SEK over that for conventional seed orchard zygotic seedlings, and there would remain at least 180 million SEK for annual investment in tree breeding. The profitability illustrated by these calculations confirms that tree breeding constitutes a technology breakthrough and generates an attractive investment opportunity.

PHOTO: ERIK VIKLUND

Relevant breeding objectives are fundamental to ensuring forest health and providing for key values of Swedish forest owners and society. In this section we analyse the robustness of current breeding objectives in connection to recent uncertainty about changing trends in market and climate conditions.

BREEDING OBJECTIVES UNDER CHANGING ENVIRONMENTAL AND MARKET CONDITIONS

Bengt Andersson
Bo Karlsson
Per Ståhl
Dag Lindgren

GENERAL OBJECTIVES FOR TREE BREEDING

The general objectives of the Swedish breeding programmes are to:
Efficiently improve traits of high economic value; conserve adequate genetic variation; and prepare for possible climatic and other changes.

It remains as overall objectives of the programmes to improve forest production and forest value for the entire country and for a variety of end products. The objectives will be met by continuation of a multiple breeding population strategy covering all Sweden. It will guarantee sustainable progress of gain over generations, providing well-adapted and vigorous regeneration material with adequate genetic variation, under prevailing and future conditions.

Forest trees, especially in northern latitudes, have long rotations and the time interval between selection and industrial use of the improved trees is even longer. Industrial processes and human utilisation of trees will change during this time. Breeding goals thus need to remain very general and relevant over the long term. This is in contrast to short-rotation species where breeding goals can be tailored for a highly specific application with much greater certainty.

Consequently, to meet these general objectives it is of primary importance to improve the long-term performance and robustness of the species in prevailing and future environments. That is, not to direct breeding towards specific industrial demands of today, but towards the fitness and performance of the species *per se* in their quasi-natural environments.

In line with this general approach, breeding must identify and improve the traits and characters that are general and long-term from an industrial point of view. These include aspects broadly important over the entire silviculture and wood supply system, e.g., resource-use efficiency for high unit-area biomass production, biomass allocation (stem production preferred over branches), stem straightness, etc. These traits are also important for efficient harvest and transportation.

Specific traits such as fibre properties will be exploited through new end products and refined by industrial processing technology, rather than modified by breeding. They should be nevertheless considered in the breeding programme from a correlated-response point of view, so that traits are not changed in an unfavourable direction or otherwise jeopardise tolerance to environmental stress. Further, specific aims and end uses can be targeted through particular sub-populations (production populations or short-term elite breeding populations). Vegetative propagation of selected clones or selective harvest in seed orchards for more specific purposes are examples of efficient ways to derive production populations for specific end uses from a breeding programme with general improvement objectives.

PHOTO: ISTOCKPHOTO.COM

Since the plans were first developed, concern over climate change as well as other changes has become more pronounced and urgent. In this chapter, the Swedish breeding plans are based on a strategy to cope with any climate change.

CHANGING CONDITIONS

Swedish breeding. The utilisation of forest ecosystems has diversified, including more emphasis on environmental services such as biodiversity, recreation, and forests as carbon sinks, as well as raw material for new biomaterials, biochemicals and bioenergy. Wood-based composite materials like bioplastics from nano-cellulose, pharmaceuticals, biofuels, etc., are examples of "new" forest-product types. Silvicultural practices have changed in the past and are likely to change in the future. We see climate change and new forest products as important changes, needing consideration in an upgraded breeding plan.

Climate change. Measures to prepare for climate change were already important components of the Swedish approach to tree breeding. Multiple populations are allocated to different adaptation targets, defined by measurable parameters describing light and temperature gradients. The main selection criteria describe growth rhythm, giving optimum synchronisation of the vegetative-growth period for the intended deployment area. The distribution of adaptation targets for the breeding populations over temperature gradients encompass an area broader than the current temperature range in Sweden, enabling improved material for "new" climate conditions to be ready for propagation. Within each population, trees are tested and selected based on performance in multiple conditions and test sites.

We consider this should remain the main strategy, but suggest increased focus on characterising breeding populations by their response to climate parameters. In future breeding work, testing and selection for adaptation should be made under defined environmental conditions, rather than testing on sites characterised only by their geographic location. We also suggest that future climate uncertainty should be addressed by increasing plasticity/adaptability and resistance of bred materials. Genetic testing should be carried out over a wider range of climate conditions than today (even expanding to other countries) and selection made to favour generalist genotypes, to increase plasticity/adaptability. Temporal variation should also be implemented in testing by establishing tests over multiple years. This will yield a more robust assessment of performance in environments under change.

Climate change is also expected to increase the risk of damage from pests and diseases. This calls for increased emphasis on testing and selection aimed at improving tree resistance and tolerance to these damaging agents.

Changing conditions is also an issue for forest plantations and seed orchard establishment, and for how the use of given seed sources should be applied as conditions are changing.

In addition, we stress the need for research on adaptation and growth rhythm, since the relationship between temperature sum and the duration (start and termination) of the vegetative growth period are expected to change as climate evolves. Conditions for dormancy, rest and quiescence may also change under future climates and thus need to be elucidated.

Forest utilisation. Even though the utilisation of forests and forest products has widened (e.g., carbon sink, biomaterials, biochemicals, bioenergy, etc.), there is little motivation to change the breeding objectives or traits. The primary goal traits (adaptation, productivity) remain relevant to these new forest product areas; however, we expect rotation ages will become shorter, accelerating economic returns, reducing risk from calamities, increasing flexibility, etc., and all made possible by the faster growth from breeding, silviculture and global warming. Further, increased domestication of forest trees and new regeneration techniques will put new demands on regeneration material. Fast and secure establishment will be still more critical for the economy of forestry. These chan-

PHOTO: ISTOCKPHOTO.COM

ges will be considered when developing economic weights for the various breeding objective traits.

Objective traits. For our main species, the following objective traits should be considered:

- Vitality, resistance to biotic and abiotic stress, including ability to recover from damage;
- Dry biomass production of stem wood per unit area, including growth capacity and efficiency in both volume and basic wood density;
- Stem-wood quality, considering biomass allocation, straightness, branching properties and fibre characteristics; and
- Plasticity/adaptability, superior performance over a range of environments.

We see continued use of index selection (combining several traits based on their economic values and heritability) as more efficient than individual-trait selection. The index weights for different objective traits will vary among species and intended areas of deployment. Research is needed to develop the economic weights. Each breeding population is directed towards a particular area of use, some of which may be peripheral to what we find in today's forestry.

Focussing on safe and rapid stand establishment (vitality, canopy-closure) provides flexibility in rotation period and silviculture, especially as a strong correlation between early- and full-rotation growth has been confirmed. Safe and rapid stand establishment substantially increases the progress and benefit of tree improvement and may even be considered as a specific objective trait.

In this section we evaluate the opportunities for new molecular and other advanced biotechnologies to improve Swedish tree breeding and mass propagation in the near future (i.e., the next decade). The emphasis is to find methodology to be considered in Skogforsk's planning for operational breeding and mass production.

MOLECULAR AND OTHER BIOTECH METHODS – OPTIONS FOR SWEDISH TREE BREEDING

Bengt Andersson
Dag Lindgren

MOLECULAR BIOTECHNOLOGY

It is not only molecular biotechology that progresses over time, but also other biotech methods for selection and breeding, i.e., techniques for flower stimulation, controlled crosses, testing, evaluation, as well as quantitative genetics and the strategies and tactics for optimising and managing operational breeding. These kinds of biotechnology are considered also in other sections.

There has been much hope that "advanced molecular biotech" would revolutionise forest tree breeding. Retrospectively, these techniques have not been important for forest tree breeding over the past 70 years and molecular biotech has limited impact on current operations. Early biotech attempts, like triploids and mutations, have mainly failed and others like flowering induction and laboratory-based early testing can work, but are used in practice to a lesser extent than was originally hoped. Swedish planting stock is dominated by Norway spruce and Scots pine, while much of the "molecular" research to-date on trees has focused on broadleaved trees, which constitute less than 1% of current Swedish nursery production.

Genetic marker technology has advanced and there now exist more powerful tools that are directly linked to the genetic code, creating new possibilities. Progress, however, has turned out to be slower than expected. For example, it is more than three decades since the first genetic map of Scots pine was reported. Today, the maps are still not dense enough for efficient marker-assisted selection.

Most forests in Sweden have a long rotation time. The average age of a tree at final harvest is over 100 years and the growth rate is rather slow. The time interval between breeding and final harvest implies that it is of little interest to fine-tune trees to end products, and there is little reason for Swedish tree breeding to be at the "leading edge" in developing biotech applications. Most applications will be developed elsewhere under conditions of shorter rotations. Meanwhile, Swedish tree breeding should closely monitor what is successfully applied in another place and consider its potential under Swedish conditions.

TIME LAG FROM RESEARCH TO IMPLEMENTATION

It would not be prudent to suggest a new biotech method for large-scaled implementation in operational breeding before it has been successfully tested on a portion of the Swedish breeding population. For example, before implementing marker-assisted selection (MAS) on a large scale, it should have already been demonstrated as appropriate in a few operational field tests. Ideas resulting from this review can give rise to research efforts financed by research grants, but implementation will require major funding support for operational breeding (the government-industry framework programme).

Even if a biotech method fulfils all expectations, it will complement rather than replace traditional breeding work. Often, biotech can target only a few specific traits, while breeding objectives require that all characters are considered and either improved or at least kept under control. Biotech may help in making predictions of future performance, but these must be verified in long-term field experiments under forest conditions. Biotech may be used to reduce the time to sexual reproduction, but the need for long-term tests remains.

PHOTO: ISTOCKPHOTO.COM

Genetic-marker techniques can be used in two principally different ways: (1) markers for identification of individuals, relatedness among trees, etc., and (2) markers associated with phenotypic and genetic performance. While DNA markers for identification are available for both Scots pine and Norway spruce, those for phenotype associations have not become simple, precise and cheap enough for routine application.

GENETIC MARKER TECHNIQUES

Markers for identification. Identification of relationships by genetic markers is well developed; its use depends more on cost, available competence and convenience. Verification of ID in seed orchards, clone archives, etc., is technically possible and the application is a matter of whether or not the information is worth the effort. Techniques are developed sufficiently to initiate a project to assess the reliability of recording identities in common breeding procedures and to evaluate genetic fingerprinting in routine work. It is possible to apply the methods when a problem appears (an example is the question of what comes out from hybrid larch seed orchards).

A recommendation worth serious consideration is to store DNA from the entire founder population represented in the Swedish programme. It may be enough to store tissue containing DNA, like needles or even seeds. The costs and practicality of this action should be evaluated. The technique to determine the "genetic contributions" of each founder at any time in the future will probably be developed, but if the sampling is not done now, the option will be lost when founders are no longer maintained in archives. Furthermore, development of genome-wide scans will require association with a broad base of phenotypic information relating ultimately to the founder population. The limiting factor in developing effective associations may be an archive of founder DNA.

Marker technology makes it possible to gain better understanding and quantification of relatedness, reduction of effective population size, and loss of gene diversity. Such possibilities could be considered for routine use in operational breeding within a decade. Markers can also be used to improve breeding value estimates by constructing an identity-by-descent (IBD) matrix, which will add information on relatedness, in parallel to the coancestry matrix, i.e., MA-BLUP.

Markers also offer possibilities to dissect evolutionary processes and the influence of human society on the genetic structure of the forest. This is of particular importance as provenance and genotype transfers are included in the debate concerning "alien" genotypes.

Marker-aided identification can be used for paternity analyses in orchards, revealing the degree of imbalance in paternal contributions to the seed orchard crop, as well as the amount, pattern, and nature of pollen contamination (. Such analyses can be used to mitigate those orchard dysfunctions, which are a major problem hampering the benefits from breeding. Somatic clone variation associated with vegetative propagation could be revealed by DNA markers, but may require additional basic research.

Parental identification in open-pollinated progeny can replace controlled crosses as a method to evaluate coancestry in some tree improvement strategies – breeding without breeding, BWB (El-Kassaby and Lstibůrek 2009). It is possible to identify both parents among 30 potential parents at the scale of many hundreds of progeny genotypes. This is a new method of "breeding", which could influence operational tree breeding within a few years. Even if the method works technically, it is uncertain if situations exist in Sweden where BWB really is better than the current breeding methods; however, it is worthwhile to make efforts to identify possible applications (Wang et al. 2010).

A related option already available for operational tree breeding can identify paternity of progenies from polymix crosses to facilitate forward selection of trees with known relatedness ("Polymix with paternity analysis", PMX/WPA). Pollen mixes for such applications should represent a sufficient number of better trees, and probably use several pollen mixes in parallel (Lindgren 2009: Appendix 1).

Some of these applications have been available for decades, but not much used. Now they are somewhat more simple, cheap and precise. Others have only recently become available. It is generally uncertain if it is cost-effective to employ the methods in an operational setting.

PHOTO: ISTOCKPHOTO.COM

Markers for associations. The genome can be mapped with markers. Some markers will occur close to or within genes or regulatory sites that influence tree characters of interest to tree breeding – quantitative trait loci (QTL). Instead of selecting on phenotype, selection can be done directly on the marker (MAS). Many genes have effects on more than one character (pleiotropy), and one character is often affected by many genes (polygenic). Genes interact with each other and with the environment. Therefore genes that sometimes appear important may not be of significance for all trees or under other circumstances. This makes it difficult to establish associations between phenotypic performance and markers.

So far, most quantification of phenotype-maker associations has been done within a full-sib family and the relative importance of such QTLs may be quite different in other families. Even if a marker is close to a good gene on a gene map, it may be close to a bad gene variant in one family and close to a good variant in another. Simple marker-assisted selection is thus effective only in a specific family; the procedure must be repeated for every family and forest tree breeding deals with thousands of families. Furthermore, field performance characters such as growth rate, survival, etc., probably arise from the joint action of many genes, but information from one or a limited number of markers will only explain a minor part of the genetic variation. At present, simple MAS seems too expensive and too complicated to implement at an operational level.

Detecting linkage disequilibrium in larger populations is theoretically possible by techniques like association mapping and genome-wide mapping, offering the possibility to make associations between phenotype and large numbers of gene markers (single-nucleotide polymorphisms, SNPs). These techniques have found their way into animal breeding, where "genomic selection" is now applied in dairy breeding by using tens of thousands of SNPs in a full-genome scan (Meuwissen et al. 2001, Meuwissen 2009). The methods are very new, and the genome size of most forest trees is many times larger than that of livestock animals. While much larger numbers of SNPs may be required for application in forest trees, the concept of genome-wide selection is by far the most interesting use of genetic markers so far and deserves much attention.

Even if a promising application for marker-based selection is developed, tests are needed on a segment of the breeding population before it can be implemented into operational breeding. The positive experiences over the last three decades are generally from breeding of shorter-lived species and are mostly for traits controlled by relatively few loci, like resistance to a particular disease. For population improvement of forest trees in Sweden there is two decades of rather intensive research efforts without getting close to an application of marker-assisted selection on an operational scale, although current research is identifying associations that are more widely dispersed in populations. This requires much denser gene maps and depends on improved genome scan technology. Over time, these high density maps will be realised and they will also facilitate genome-wide selection applications, but are not yet applicable for Swedish pine or spruce.

In conclusion, no application of association marker technology for operational breeding is expected to be ready for use in the next five to ten years. However, if cost-effective markers are developed for population-wide application, they can easily and rapidly be applied in current breeding programmes for e.g. pre-selection among the seedlings of the new breeding generation. Pre-selection based on markers followed by field testing of the candidates may increase selection intensity and genetic gain without taking any risks. Another alternative is to pre-select phenotypes in field tests, followed by using molecular tools to investigate characters which cannot be observed directly, like mature wood quality or pest resistance.

FOTO: CURT ALMQVIST

GENETIC ENGINEERING AND THE USE OF GMO IN FOREST TREES

In principle, new gene constructs can be inserted into an individual with genetic engineering methods affecting genotype and gene expression, giving rise to a Genetically Modified Organism (GMO). These techniques are used commercially on a wide scale for herbicide resistance, insect control and several other characters in agricultural crop species.

When these techniques found commercial application in agricultural crops, the hope was great that they would also find application in forestry in the foreseeable future. However, progress has been slow and the application in operational forest tree breeding in Sweden seems much further away now than it did a decade ago. Hundreds of forest tree experiments have been established globally during the last decade, but almost all are small and short-term, and not similar to Swedish forest genetic field tests. Test plantations of GMO hybrid aspen were established in southern Sweden in 2010. Technically it has been possible for more than a decade but it was the first serious field test experiment of a GMO tree in Sweden. However, this adds little to the evaluation of the feasibility of practical plantations. More than twenty forest GMO tree releases have occurred in the European Union, but the number per year has declined since 1998. A semi-commercial operation with black poplars in China has been the only known commercial forest operation, and this has not been well documented.

The use of genetic engineering in operational breeding requires that the stability of gene expression be verified in long-term field trials, during which the desired goal is achieved and no negative side effects occur. There are special procedures and requirements for GMO field trials by OECD countries. Commercial use of GMO requires that the gene dispersal to wild relatives is unlikely, or have no undesirable impacts on the environment. GMO is currently generally not accepted by "green" certification of forestry operations. While commercial use of GMOs is in principle legal, in practice it may be a time-consuming, expensive and an unpredictable process to get a commercial license.

A greater obstacle for GMO technology is to find a suitable gene construct, rather than the modification technology itself. GMO also requires a system for propagation of transformed tissue, and somatic embryogenesis is most commonly suggested for this purpose, but is currently is more easily applied to Norway spruce than Scots pine. The semi-natural forestry practises and long rotations for Norway spruce and Scots pine in boreal forests make them less suitable as GMO candidates for the foreseeable future.

Before GMO applications are considered further by Swedish forestry, commercial uses should be well-established elsewhere with conifers, such as *Pinus taeda* in the southern US. The shorter rotation time in warmer climates makes it possible to evaluate the effects of GMOs faster. In addition, the first GMO field trials with trees are likely not to be welcomed by the public. Even the debate about potential use of GMO in forestry may create problems for long-standing breeding practice, e.g., conventional seed orchards have recently been questioned in British Columbia as being a form of genetic modification. In conclusion, GMOs are not of interest for operational breeding in Sweden, at least for the next decade.

PHOTO: ERIK VIKLUND

VEGETATIVE PROPAGATION

Somatic embryogenesis (SE) is one of many options for vegetative propagation, and it has received much attention for Norway spruce as the technique develops. When cell cultures are cryo-stored in liquid nitrogen, there is no loss of juvenility, which is crucial for successful rooting of Norway spruce cuttings. The clone performance does not change during storage (at least in theory) and the clone can be multiplied on a large scale when required. At present, large investments are being made to develop and apply the method in Sweden and elsewhere.

With current Swedish labour-intensive methodology, it is possible to get a few hundred clones multiplied. For the scale required for operational breeding and testing, protocols must be further developed for successful propagation and storage of much larger numbers of clones. Current methodology is thus too expensive to motivate production of trees for large-scale clonal field testing, until such time as commercial procedures for mass propagation of reforestation material by SE are available.

Elsewhere, SE is already in commercial use, e.g., southern US, eastern Canada and New Zealand. In the US it has reached perhaps 1% of the market (9 million plants). SE seedlings are available on the open market and the added unit cost is below 2 SEK, although this is probably not the full price needed to cover costs and give a profit for the supplier. As it has been possible to get SE into operational use for a conifer in US, it will likely be technically and biologically possible to introduce commercial applications in Swedish spruce in the near future, but the cost is likely to be too high for the major commercial planting stock market.

Current Swedish research and development efforts may make SE more cost-efficient. SE plants could meanwhile be used as donor plants for rooted cuttings, as is currently done for *Pinus radiata* in New Zealand, reducing the cost for commercial deployment of tested SE lines. This may also help avoid possible adverse SE propagation effects. Skogforsk should continuously consider to what extent SE could replace or supplement cuttings from zygotic seedlings for routine clone testing.

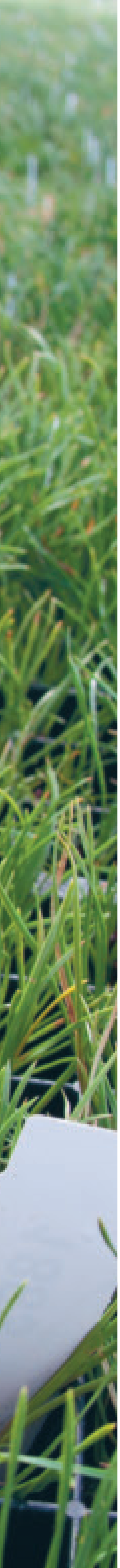
There are SE spruce clones in Swedish field tests, and it seems likely that the best of these clones will be used to some extent by the forest companies involved. There are legal constraints for the use of clones in Sweden (5% of the area of a land holding). If commercial interest develops in large-scale application of SE seedlings, it is reasonable to initiate a process to relax the constraints, using recent advances in knowledge.

The introduction of commercial SE propagation does not require clonal field tests to be mature enough for evaluation and selection. The added gain from full-sib crosses among the best tested parents can be multiplied by bulk propagation, well before seed orchards can mass-produce zygotic seedlings of similar quality. Cloning for field tests by SE technology rather than by rooted cuttings also offers advantages. If the best segment of a breeding population is tested as clones maintained as cryo-stored SE lines, the option for mass vegetative propagation of the best tested clones is maintained. Thus, Skogforsk should encourage clone testing that utilises SE technology. This research should include studying any eventual propagation effects that can affect commercial use.

Rooted cuttings. Earlier initiatives for commercial mass multiplication of the major species by rooted cuttings failed, in spite of large and repeated efforts. The reasons were mainly economic and administrative, rather than biological or technical. Initially the extra gain was less than it is today. Forest owners at that time were not willing to pay the extra cost or make the extra effort to capture the extra gain. Nevertheless, for Norway spruce the techniques are sufficiently well developed to be used for operational breeding. Clonally replicated field testing of Norway spruce with rooted cutting is now a standard procedure and genetic gain has much improved. The benefit of clone testing to improve selection accuracy in a breeding programme has also initiated research and development to apply rooted cuttings for field testing also in the Scots pine and lodgepole pine breeding programmes.

Since genetic gain has increased in current regeneration stock and forest owners put more emphasis on tree growth, it seems worthwhile to revisit the commercial viability of rooted cuttings for forest establishment.

PHOTO: ERIK VIKLUND



OTHER BIOTECHNICAL/MOLECULAR TOOLS

The fast expansion of genomics and the knowledge gained by the recently initiated mapping of the Norway spruce genome will certainly give rise to new and better-developed ideas for application to forest tree breeding. Nevertheless, the practical large-scale application of these innovations in operational breeding seems unlikely in the near future.

DNA-based tool kits for assessment of traits such as flowering competence, disease resistance and winter hardening have the potential to be developed into useful diagnostic tools. Such tools may soon be evaluated for use in operational breeding. Microarrays are an example of a research tool that can help to develop measurement kits.

Some biotech applications for flower stimulation have been developed in forest tree breeding and others may be developed. Flower-inducing hormones (gibberellins) have been investigated for many decades. They have found some practical applications, but are not used on a massive scale, despite many promising results. It has turned out to be difficult to obtain legal approval to commercialise manufactured hormones for use in seed orchards. Genetic engineering techniques for transferring flower-enhancing genes are still basic research and have not reached the stage where applications are available for operational breeding. While genetic engineering approaches to prevent flowering may be technically feasible and relevant for breeding, their use will only be acceptable when very long-term stability of gene expression has been demonstrated as well as rather detailed environmental evaluations undertaken.

The current Swedish breeding strategy was based on a comprehensive compilation of current knowledge when it was developed in the late 1980's (Danell et al. 1993). Over the last 20 years, research has continued, to further develop breeding techniques and strategies for selection and mating. Some of the research has been in close cooperation with Swedish breeders and the Swedish breeding programme has been a model for a great number of research efforts.

UPDATES FROM RESEARCH ON SELECTION AND MATING STRATEGIES

Ola Rosvall
Curt Almqvist
Dag Lindgren
Jon Hallander
Mats Berlin

The doctoral research of breeders like Erik Andersson (1999), Ola Rosvall (1999), Thúy Olsson (2001), Seppo Routsalainen (2002), Milan Lstibůrek (2005), Jon Hallander (2009) and Mats Berlin (2009), as well as recent research by Dag Lindgren and Darius Danusevičius, have all had the objective to study consequences and suggest improvements to the Swedish breeding strategy. In this section, we report the studies we find to be of greatest interest in considering a revision of the Swedish breeding programme.

For less-important species and situations other than Scots pine and Norway spruce in Sweden, the methods suggested by this research may be too complicated and expensive. Instead low-input methods can be considered with options for long-term breeding (Lindgren and Wei 2007). Such techniques include absence of controlled crosses, grafts and field maps, mass selection, combination of the different components of tree breeding in one single stand (recruitment, recombination, selection, seed production).

Over the years, numerous strategies and methods that vary founder contributions have been investigated to improve genetic gain, within the constraint of a given genetic diversity objective.

PHOTO: ISTOCKPHOTO.COM

UNEQUAL VERSUS EQUAL GENETIC CONTRIBUTIONS IN TREE BREEDING


PHOTO: ERIK VIKLUND

Descriptions of the Swedish breeding strategy are often simplified to depict only within-family selection, as this is a basic concept in long-term breeding. In reality, much effort has been expended to find a suitable level of imbalance in selection, within the limits set by the objectives of increasing gain and maintaining genetic diversity. In a Swedish breeding population, the target is to keep effective population size Ne to not less than 50. By applying within-family selection exclusively (equal contribution from all parents), Ne will be 100, so there is room to vary founder contribution by allowing some selection among families, while still maintaining Ne≥50. Another simplification when describing the principles of the Swedish breeding strategy is that generations are discrete, while as time goes on the generations will, in fact, overlap.

There are in principle two different types of imbalance in breeding strategies to be considered. First, and in general, imbalance in a breeding population is about carrying out selection and breeding in a way that makes the contributions of founders unequal. Selecting and mating more trees from excellent parents and fewer trees from less good parents is an example. Variation in founder contributions will reduce population effective size and gene diversity, although this can be compensated by increasing the number of founders and parents in the breeding population, i.e., its size, and by developing a more favourable relationship between genetic gain and diversity following various principles such as optimum contribution and linear deployment.

The second type of imbalance involves varying selection intensity and selection accuracy without affecting founder contributions and gene diversity. Increasing the family size from the best parents to allow higher selection intensity in exchange for lower selection intensity in smaller families is one example. More precise progeny testing of higher-ranked candidate trees is another example. Generally, greater gain achieved by investing more resources to one part of the breeding population is offset by less gain from proportionally less investment in the remainder, leaving the population mean unchanged or slightly decreased. Such imbalance can, however, result in a substantial increase in gain from an elite portion of the population used for short-term mass propagation.

NUMBER OF FOUNDERS FOR A BREEDING POPULATION USING VARIABLE PARENTAL CONTRIBUTION

When establishing trees in a seed orchard, it is favourable to have a higher representation of the best-ranking individuals, and less from lower-ranking selections. It is optimal to have the representation vary in a linear fashion, proportional to breeding value, i.e., "linear deployment" (Lindgren and Matheson 1986).

Routsalainen and Lindgren (2000) demonstrated that the theory of linear deployment also holds when initiating a breeding population. In a calculation example reported by Rosvall et al. (1999), the gain was shown to increase with no loss of diversity by adding about 20% more trees to the breeding population. In the Swedish case, this would increase the breeding population census size from 50 to 60, applying founder contributions proportional to breeding values. An idea for generating new recruitment populations could be to make as many crosses as the future breeding population, an average of two per breeding parent (50 for double-pair mating), while allocating three crosses to each of the top sixth ranking parents, two crosses to each parent in the next-ranking third, and only one cross to each in the bottom half.

PHOTO: STEFAN ÖRTENBLAD/SKOGENBILD

It is well-established in breeding theory that unequal contributions from selected parents might enhance genetic gain at the same level of relatedness (e.g., Toro and Nieto 1984, Lindgren 1991, Sanchéz 2000). To find an optimal balance between genetic gain and diversity, algorithms have been developed in the tree breeding literature, such as "group merit selection" (GMS; Lindgren and Mullin 1997). After selection has been carried out, imbalance among selected trees has been imposed using algorithms such as linear deployment.

OPTIMUM CONTRIBUTION SELECTION IN TREE BREEDING

One alternative algorithm that simultaneously selects individuals and confers imbalance (i.e., optimises contribution) at a given level of group coancestry has been termed "optimum contribution" (OC; Meuwissen 1997). The basic idea that underpins the OC algorithm is that of simultaneously selecting the optimal cohort of trees and their respective contribution to the next generation given a constraint on relatedness. The method maximises the selection differential conditional on predicted breeding values and pedigree by adjusting the number of selections to the specific situation. For example, if the heritability of the character of interest is low in the population, the predicted breeding values of relatives would be highly correlated. What OC does in this situation is select a larger number of trees, than if the heritability had been high, in order to maximise the selection differential given the restriction on relatedness. The adjustment to the specific situation makes the OC algorithm a dynamic selection method as opposed to methods where the number of selections is declared beforehand. Kerr et al. (1998) introduced the OC algorithm into a tree breeding context by adjusting the algorithm to consider monoecious species. It has recently been implemented in MATEPLAN™ by PlantPlan Genetics Pty Ltd.

Typically, OC will select a greater number of trees compared to most traditional selection methods so that a minimum of good performing trees are wasted (e.g., Hallander and Waldmann, 2009). For example, in a particular family that is known to perform well, OC might select several good genotypes contributing at different proportions, as well as trees from lower-ranking families, which traditional methods would likely not select. One could say that the OC algorithm utilises genetic variation efficiently to maximise the genetic gain given the restrictions on relatedness. Hallander and Waldmann (2009) tested the OC method on a real pedigree of Scots pine (Skogforsk id: S23F7110264 Vindeln) and compared genetic gains obtained to corresponding levels obtained by restricted truncation selection. They found that OC increased the gain by between 8 and 30%, depending on the heritability of the traits and the constraint on coancestry.

To find an optimal balance between genetic gain and relatedness, OC uses group coancestry to restrict the relatedness. Depending on the preference of the breeding manager and if random mating is assumed, the rate of inbreeding in the breeding population could replace group coancestry by using standard quantitative genetic formulas. Either way, the "weight" used in OC is directly connected to the pedigree and does not directly rely on different economic or biological conditions (i.e., cost of inbreeding depression).

A shortcoming of the OC algorithm is that contributions (mating proportions) are given as a fraction for all selected trees. Contributions need to be multiplied and rounded off to derive the number of crosses in which each tree should participate. A more convenient way for the breeding manager would be to obtain actual number of crosses (an integer) directly for each selected trees instead, i.e., by quadratic integer programming or by stochastic approaches, such as simulated annealing. Fernandez and Toro (2001) provide other alternatives to implement the OC algorithm. Interested readers might also want to consult Hallander and Waldmann (2009) and references therein for further details of the OC algorithm.

In the current Swedish breeding programme the breeding population census size is kept at 50 in each generation. The annual genetic gain (measured at the same cost and gene diversity) was much increased when this restriction was removed (Lindgren et al. 2008). This result, together with breeding population size optimisations (e.g., Danusevičius and Lindgren 2005, Li and Lindgren 2006) and the general results by applying OC, suggest that Swedish breeding could benefit from management of larger breeding populations.

ROLLING FRONT GENERATION TURNOVER IN TREE BREEDING

Most tree improvement programmes are in their infancy and have generally used a discrete generation (DG) turnover to this point. In this situation, the breeding manager must wait until all trees in the breeding population begin flowering and produce pollen so that all trees can participate in the planned matings.

There might be considerable variation in time to obtain flowering and this makes the completion of one generation time consuming. Some authors (e.g., Borralho (1995), Borralho and Dutkowski (1996)) have suggested an alternative idea: to cross trees whenever flowers become available and place the resulting offspring into field trials directly. By using this overlapping population structure (i.e., "rolling-front" procedure; RF), the authors argued that generation intervals could be shortened, which in turn would generate enhanced levels of genetic gain per year. The RF proposal was tested by Borralho and Dutkowski (1998) by extensive computer simulations, where enhancement in gain between 25–35% was demonstrated over a discrete-generation approach. Shorter generation intervals was the most important reason for the higher gain, although higher levels of inbreeding were found for RF than for DG in all scenarios, so that comparisons were not made at the same rate of inbreeding/increase in relatedness. The authors suggested that if parents were mated according to a minimum coancestry approach, the accumulated inbreeding could be managed effectively.

As pointed out by Borralho and Dutkowski (1998), of key importance to the RF scheme is the genetic evaluation procedure, with many weakly connected field trials having a relatively small number of trees that need to be analysed.

The overlapping generation structure must be handled properly, by taking genetic trends into consideration by means of an individual-tree analysis model. Heterogeneity in variance among trials, e.g., by G×E interactions and differing additive variance within test groups, might induce bias in the analysis. Consequently, the breeder needs to conduct a mixed-model genetic analysis and be aware of the pitfalls of the procedure.

To summarise, RF has potential to increase long-term response to selection by shortening the time lag between selection, mating and testing and thus the generation interval.

PHOTO: STEFAN ÖRTENBLAD/SKOGENBILD

This could be beneficial for Swedish conditions having long generation cycle times and great variation in flowering time, in general. The individual-tree model is a prerequisite for RF, since multiple, potentially unbalanced field trials that are weakly connected, need to be combined in the genetic analysis. The use of TREEPLAN® by Swedish breeders is a prerequisite. Potentially high levels of inbreeding could be managed by avoidance of mating relatives, such as minimum coancestry mating or at least avoidance of sib mating. One drawback of the simulation model of Borralho and Dutkowski (1998) is that unrestricted truncation selection is performed; this is well known to give unacceptable rates of inbreeding in selected populations. If a more sophisticated selection algorithm, such as that suggested by Kerr et al. (1998) was employed, inbreeding might be better controlled.

Similar RF ideas have been proven to work in animal breeding where generation turnovers are fast and breeding populations are distributed over large areas. In tree breeding, the RF procedure has been applied in fast-growing eucalyptus in Portugal and Australia. Indeed, many programmes originally planned as DG, have in fact become RF, where populations are stratified as they come into flower, and thus minimise time lag and spread the workload. This methodology warrants further investigation before being brought into practice.

USING VARIABLE SELECTION INTENSITY BY HAVING MORE PROGENY FROM HIGH-RANKING TREES

Milan Lstibůrek and co-workers (Lstibůrek et al. 2005) studied unbalanced selection intensity by varying the number of progeny (family size) in relation to the breeding value of the parents, using a positive assortative mating strategy.

Under single-pair mating, the extreme redistribution of progeny, where the two lowest-ranking trees had 2 progeny, both of which were selected, and the two highest-ranking trees had about 55 from which two were selected, was compared to selecting two from a fixed family size of 30 for all families. This most extreme imbalance increased gain in a seed orchard by 20%, whereas a more modest imbalance with family sizes from about 20 to 40 progeny in relation to the breeding value of the parents increased gain by 10%.

Varying family size increased gain in a selected production subpopulation, such as a seed orchard or clone mixture, without any change in genetic diversity of the breeding population. At the same time, the average genetic value of the breeding population is marginally decreased, but without practical significance. It was concluded that while moderate imbalance in family size could be used, further study of the consequences of more extreme imbalance was required.

PHOTO: STEFAN ÖRTENBLAD/SKOGENBILD

INDEX SELECTION USING A FORMALISED BREEDING OBJECTIVE

In the Swedish forest tree breeding programme, multiple traits are considered during selection, so predicted breeding values for the different traits must somehow be assessed relative to one another. In such cases, it is common to use an index, where the objective traits are standardised to the same scale by assigning economic weights and then summed to give an index value of genetic worth. This index can be called a formalised breeding objective.

Objective traits are, preferably, those that directly influence income and cost in a production system, while economic weights describe the relative economic importance of the objective traits for that system. Consequently, in order to develop a formalised breeding objective we need knowledge of the objective traits as well as how changing them affects the biological and economic system in which the gains from breeding are to be realised. Methodology to define formalised breeding objectives has been developed in animal breeding contexts (e.g., Groen, 1989; Ponzoni and Newman, 1989) and defines how a study of the system that utilises the output from breeding should be performed. The first step in such a study is to define the production conditions, i.e., the size, limit and efficiency measures of the production system.

Thereafter the process can be divided into three further steps: (i) identification of the sources and flows of income and cost; (ii) identification of the biological traits (i.e., the breeding-objective traits) that affect efficiency of production; and (iii) calculation of the economic weight of each objective trait. This process results in the development of a formalised breeding objective once the objective traits have been identified and their economic weights calculated.

In forest tree breeding, nearly all studies to date using formalised breeding objectives have related to fast-growing species with short rotations. Two major differences between these studies and Swedish conditions are: (i) the latter are associated with considerably longer rotations, causing major uncertainty with respect to future industrial conditions; and (ii) forest production systems are more complex and diverse, consisting of the entire forest products industry in a country or region. To adapt and develop the existing methodology to these conditions, a framework consisting of separate modules for different industrial subsectors (each representing a specific industrial segment) was developed for Swedish forestry (Berlin, 2009). With this structure, it is possible to calculate economic weights appropriate for the sector and serving as a platform to assist strategic breeding decisions under situations where there is uncertainty.

Considering the diverse uses of wood and the uncertain nature of the forest production system, an appropriate set of objective traits should be applicable over a wide range of site conditions, silvicultural regimes and industrial subsectors. As far as possible, these should describe underlying biological traits and general characteristics of the trees associated with basic properties in forest cultivation and of the different industrial processes. In particular, key conceptual objective traits for boreal conditions are suggested to be those that describe: (i) biomass production, including the cultivation phase, which is important for all possible industrial uses; (ii) the basic chemical content of the wood, which is important for pulping and for bioenergy and biofuel purposes, (iii) stem form and branch properties, which are mainly important for solid wood products; and (iv) wood properties that can be identified as important for certain industrial uses.

Objective traits may be expressed throughout the rotation, at thinning and at final harvesting; some are only expressed after industrial processing. Thus, objective traits are often not expressed until late in the rotation and they may be difficult and expensive to measure. To optimise gain per unit time, tree breeders often use traits that are measurable early in rotation on standing trees and are genetically correlated with the objective traits. In contrast to the objective traits, these are sometimes called selection criteria or measurement traits. Index selection is then performed by combining information on economic weights, objective traits, selection criteria and genetic parameters.

Recently two case studies have been performed to increase knowledge about economic weights for Swedish conditions:

The first case study examined how to calculate the economic weight of tree survival relative to volume production, taking patchiness into account. In five Scots pine breeding populations in northern Sweden the relative economic weight of survival varied markedly, increasing more than three-fold with decreasing survival and increasing patchiness. As a conclusion survival was an important objective trait in harsh areas, whereas survival had a small effect on volume production at medium harsh and milder sites.

The second case study defined a breeding objective for a vertically integrated forest company in northern Sweden that cultivates forests and supplies timber to its own sawmill. Results showed that a compound growth indicator (height and diameter) was a very important selection criterion, while a wood density indicator was of moderate value and vitality and straightness indicators were of negligible value.

The studies performed are first steps in developing formalised breeding objectives for Swedish conditions but a number of challenging tasks still lie ahead:

- Studies of more sawmills and pulp mills, and eventually studies of the biofuel and bioenergy sectors, should be performed and bioeconomic models developed. It is vital that stakeholders within the breeding programme are involved to provide the necessary inputs (e.g., economic information and perspectives relating to the future use of wood). In addition, performing these studies requires multi-disciplinary collaboration involving stakeholders and researchers in areas other than forest genetics (e.g., economists and wood engineers).

- Suitable selection criteria related to the objective traits also need to be identified (e.g., pilodyn measurements/ bore cores, spiral grain measurements).

- Genetic parameters necessary for genetic selection need to be estimated (i.e., correlations between objective traits and selection criteria and genetic variances of objective traits).

PHOTO: BO GÖRAN BACKSTRÖM/SKOGENBILD

PHOTO: BO KARLSSON

POLYMIX BREEDING WITH SELECTION FORWARD

Conventional progeny testing with a pollen mixture of fathers (polycross or polymix) provides reliable breeding value predictions for the seed parents. Differences among pollen parents and their interaction with the seed parents even out as many pollen parents are mixed. Selection forwards on polycross progeny is not efficient, as the father is not known. Using modern marker technology, however, the father can be identified among a number of expected fathers and polymix progenies can become a resource for continued breeding.

Polymix breeding with paternity analyses (PMX/WPA) was suggested by Lambeth et al. (2001). The idea is to pollinate with a mixture of pollen, and later to identify and utilise the male parenthood of promising candidates. A variant of the system was used operatively by Weyerhaeuser Company, where Lambeth worked. It is not known to have been used by other breeding organisations.

For the purposes of Swedish breeding, an approach to PMX/WPA was developed and discussed in Appendix 1 (Lindgren 2009). A surplus of trees are selected as candidates for breeding and pollinated with a pollen-mix of selected fathers. Later in the progeny field trial, candidates are selected forward in the best maternal families and their paternity determined with the aid of genetic markers. Combined selection for further breeding is used and is partly based on pedigree revealed by markers.

Polymix breeding applied in an optimised way has the potential to be more powerful than the current Scots pine breeding strategy. To increase the possibility to select among pollen parents it seems worthwhile to use more pollen parents than in the conventional Swedish breeding and to distribute them over several pollen mixes in the same breeding population. A possible design is totally 125 pollen parents in five pollen-mixes of 25 for a breeding population. The pollen-mix and the seed parents might belong to different compartments of the breeding population. PMX/WPA deserves to be more carefully explored by both theoretical tools (like POPSIM simulations) and pilot trials with a limited part of an operational breeding population. If the method is implemented for pine it should also be considered for spruce.

The particular algorithms and procedures needed for efficient polymix breeding do not need to be developed until a material is sufficiently mature for selection. Recent experience in using parental identification demonstrates that the method works, and that paternity determination methods will improve during the period that progeny plantations develop. Generally, if a polycross is made for any reason, it is recommended that it be carried out it in a way allowing for forward selection, rather than as a dead-end progeny test.

In this section, suggestions for improving the technical and methodological breeding work are presented based on the experiences from past operational breeding in Sweden. It includes experiences with operational genetic evaluation, field testing and carrying out controlled crosses. We begin the discussion with the long-term consequences of the Swedish breeding strategy, as evaluated by computer simulation.

METHODOLOGICAL AND TECHNICAL EXPERIENCES FROM THE SWEDISH BREEDING PROGRAMME

Ola Rosvall
Curt Almqvist
Dag Lindgren
Tore Ericsson
Lars-Göran Stener
Gunnar Jansson
Karl-Anders Högberg
Jörgen Hajek

EXPERIENCES GAINED BY COMPUTER SIMULATION

The long-term development of genetic gain and genetic diversity in the Swedish breeding programme was analysed by computer simulations for a variety of conditions. In addition, the efficiency of numerous breeding methods was investigated (Rosvall 1999, Rosvall & Mullin 2003, Rosvall et al. 2003, Ruotsalainen and Lindgren 2000, Lstibůrek et al. 2004a and b, Lstibůrek 2005, Lstibůrek et al. 2005, Li & Lindgren 2006). Most of these investigations and the suggestions to be implemented in the Swedish strategy were reported by Rosvall (2009). The document is included in Appendix 2 and the conclusions are summarised here.

The results demonstrate that the Swedish breeding programme is sustainable, robust and efficient. The validity of the basic fundamentals of the breeding programme has been supported, although there is room for additional improvements. In the report, the background for suggested improvements is described in detail. Based on these analyses, positive assortative mating (PAM) and a new measure for genetic diversity was introduced in the Swedish breeding programme in 2001. By crossing selected trees in rank order when new breeding population generations are created, the genetic gain in seed orchards and clone-mixes is increased without compromising any genetic diversity in the long-term breeding populations.

Considering that the Swedish breeding programme has far-reaching objectives both for gene conservation and production of genetic gain, it was suggested to keep the number and size of unrelated breeding populations, as well as the strategy using near-balanced within-family selection. The structure of many unrelated breeding populations will conserve gene diversity at a higher level than that of a single large population. This benefit comes as a consequence of higher inbreeding in each single population; but keeping the breeding population effective size at Ne≥50 will manage the rate of increase in inbreeding.

In combination with PAM, near-balanced within-family selection enhances additive variance and provides an open hierarchal structure, with an “elite” within each breeding population. This elite will support production populations with the very best trees. Benefits from unbalanced selection and PAM assume that the character selected is known when the recruitment population is created. In practice this is not fully the case and therefore the advantages are quantitatively slightly exaggerated (Lindgren 2005).

Dividing a breeding population into unrelated “sublines” preserves the potential to avoid inbreeding in the production population, i.e., to produce non-inbred crosses for clonal forestry. The drawback is that smaller populations, e.g., two lines of 25, will have more inbreeding (inbreeding depression will reduce the efficiency of clonal testing), reduced selection intensity and produce less gain. Dividing the individual breeding populations into two unrelated sublines is not an attractive option for the pine and spruce programmes. These programmes already include many unrelated neighbouring breeding populations that can support an orchard and provide unrelated crosses for clonal forestry. When used, two sub-lines can be kept for a few generations without the long-term negative effect of increased inbreeding and reduced gain in the breeding population, and can later be combined. Sublining might be considered for lodgepole pine and birch with fewer breeding populations.

It is suggested to use proportional gene diversity (GD = 1 – group coancestry) and the census number of breeding trees N to measure the loss of gene diversity in the breeding populations over time. The choice of diversity measure and suitable level of diversity for a production population should consider the propagation system and species, as well as the future management and regeneration of the forest stand.

PHOTO: ISTOCKPHOTO.COM

EXPERIENCES OF GENETIC EVALUATION

PHOTO: HANS BERG/SKOGENBILD

Genetic analysis with parameter estimation (using REML) precedes the breeding value computation (BLUP). The genetic model is usually the simplest possible estimation of additive components and their correlations.

The basic tools currently available include ASReml for genetic parameter estimation from mixed-model analysis and TREEPLAN® for breeding value prediction using information from multiple generations, multiple sites, and multiple traits. We have to consider intensified efforts to optimise the analyses, including evaluation of all kinds of special/unusual genetic trials (e.g., trials where seedlings and clones with common parents are mixed).

"Post-hoc" blocking and/or spatial analysis with ASReml will be carried out to reduce environmental variation as much as possible and increase heritability. Generally, all data, including non-normal, continuous and categorical data types, are analysed without transformations, since the methods used are sufficiently robust against violations of distribution assumptions.

In older genetic tests where competition among trees becomes significant, there is a need for a "correction for competition". New models should be tested as they become available and possibilities to compare single-tree and multi-tree plots should be utilised whenever available. Development of competition models is currently a focus area for tree improvement research and Skogforsk contributes actively.

Alternative Bayesian methods for genetic analysis are known and under continuous development, but as yet they demand too much computer power for practical use. If, in the future, marker data can contribute to genetic-merit estimates, Bayesian methods are likely to be introduced.

Assessment and selection criteria. We focus on assessment traits that are efficient, i.e., inexpensive to measure and highly correlated with one or more objective traits. Common wood production measures such as height, diameter and density correlate to a varying extent with volume/biomass/

growth per unit area, while quality measures such as straightness/forks/branch angle have additional impact on tree quality and the economic yield of the forest.

Economic weights traits and matching selection criteria is critical to achieving an economic impact from breeding. Considering the rotation length of Swedish forests and the uncertainty regarding the potential areas for use of wood raw material in the future, we have to focus primarily on economic weights for the most incontrovertible objective traits of general importance, as presented in a previous section. There is an urgent need to conclude on the economic weights.

TREEPLAN. From 2009, the TREEPLAN® project entered a phase when its tools entered practical use for breeding value estimation. The combined analysis of very large numbers of trees and trials has implications for the allocation of material to genetic trials, both as regards to geographic trial location as well as genetic content in order to improve connectedness among populations as described in next section.

Databases The TREEPLAN® project has an integrated database system where all measurements and trial information from the genetic tests are stored, together with the pedigree data including all genotypes from founder trees and onwards. It is not as detailed as is the Skogforsk breeding database (Fritid), with the exception of pedigree information and measured data, but has a better structure for its purpose. Fritid is the indispensable source when information has to be searched for updating the TREEPLAN® database; they complement each other.

Breeding value reports. The form and format for breeding value reporting will be prepared according to new requirements, among other things depending on whether TREEPLAN® will evolve as the standard breeding value generator. Report generation should be (semi-)automatic and perhaps published on the web in order to be easily accessible to forest managers.

Data acquisition and use. The genetic evaluation of field trials is dependent of an adequate measurement and recording of tree data, including their validation and preparation, pedigree preparation, etc. The whole chain from measurements to TREEPLAN® run needs skilful co-operators, for:

- Organisation and performance of trial measurements
- Validation and preparation of recorded data
- Completion of pedigree information, etc. (Fritid)
- Carrying out genetic analysis with the new measurement data
- Uploading pedigree, measurement and other data into the TREEPLAN® database
- Model construction and parameter updates for TREEPLAN®
- TREEPLAN® runs and breeding value prediction
- Result presentation.

Relevant competency and co-operation is essential for all involved in planning, data collection, analyses, etc. All must be aware of a common responsibility to avoid misunderstandings with regards to naming conventions, classifications, and so on.

EXPERIENCES OF FIELD TESTING

PHOTO: BO KARLSSON

There are a number of objectives for field testing besides estimating breeding values and genetic parameters for selection in the breeding programme. In commercial forestry, groups of intensely selected trees or their progeny are grown together under competition and other conditions that differ from the ordinary genetic test situation. Therefore it is necessary to find experimental designs to estimate breeding values and genetic parameters for per-unit-area growth and performance of families (or clones) as well as finding test designs to estimate realised gain of mixtures used as planting stock.

Basically the problem deals with competition among genetic entries and is most emphasised when there are large differences in growth among the test lots as for different kinds of unimproved check lots. In the long run, comparisons with unimproved material can't be done either in single-tree plots or plot experiments with too small plots. Therefore comparisons of improved and unimproved plant material have to rely on some kind of experiments using large plots.

In this section the current test methodology for estimating breeding values is reviewed and a variety of test designs for other purposes are discussed.

TEST DESIGN FOR ROUTINE ESTIMATION OF BREEDING VALUES

The current statistical test design for all field trials is basically a totally randomised design with single-tree plots. In terms of genetic entries and number of trees, this design is dimensioned for good estimates of genotypic values, breeding values and basic genetic parameters. The current mating plan is appropriate for estimates of additive, but not for dominance or epistatic effects. In order to improve accuracy, environmental variance can be further controlled by using the randomised (complete) block concept or by imposing post-hoc blocking. Spatial analysis and competition modelling can further complement these approaches.

Distribution of the test material. Preparation for climate change is an important component of the current breeding strategy, and recently climate change has become an even more urgent concern. The unpredictability of future climate requires genotypes that are stable across spatial and temporal climatic gradients. Breeding populations should thus be tested across a

wide range of climate conditions for selection of superior and stable genotypes.

Four test sites would normally be used, irrespective of whether the tests are for clonal or seedling test material. With the need now recognised to improve knowledge of environmental stability, we should probably consider increasing the number of sites for some populations. Two test sites should normally be established within the population target area and the remaining tests established in the border area or within adjacent population target areas. The objective is to identify sites with different environmental conditions but within the range of what is normal for the species.

A general testing strategy in the north would use a factorial design with the two basic climate factors temperature and photoperiod. Summer drought may be a factor of increasing importance, especially in south-eastern Sweden. If possible, the sites should be selected or at least be defined (after establishment) based on environmental and climate conditions, rather than merely being defined by their geographic location. To get a measure of similarity in temperature sum or risk-of-frost among test sites, a data logger is recommended at each site. Resource-use efficiency is a general breeding objective and various designs and treatments can be used to explore genetic variation in light, water and nutrient use efficiency. Spacing is a fundamental treatment since it determines the total resources available for each tree and the development of competition among trees.

Another possibility is to assign one of the trials of each population to special test areas ("garden trials") that are fenced and intensively managed, in order to reduce micro-site variability. This might be of special interest if a forward selection based on individual phenotype will be used. Since there is little experience with such artificial test environments in Sweden this should not be a standard option, although worth considering. Estimates of GxE among the different test site types will tell if such sites are suitable or not.

Population connectedness among genetic tests. Each breeding population has distinct pedigrees, normally without connection. Clonal selection for mass propagation will target several deployment areas and include trees from several breeding populations, so it is necessary to have breeding populations connected in combined trials. These combined trials are best arranged in border regions between neighbour populations.

It will be normal to include candidates from adjacent populations in the same trial. Any population should be represented by not less than some ten families, but this quantity requires further consideration. We recommend this become the main method of introducing connectedness among breeding populations.

Genetic tests normally include check lots such as standard crosss, provenances or commercial lots to monitor genetic gain that will generate some linkage as well, but this is not their main purpose. If at some later stage connectedness among populations is found to be insufficient, there is an option for establishing special linkage trials with left-over materials.

Following the rolling-front strategy in order to optimise the genetic gain per time unit, genetic tests may be established before all tress selected for breeding in a population have been crossed. Then, for practical and efficiency reasons, several populations may be put together in the same trial, "automatically" creating linkages among populations.

PHOTO: ERIK VIKLUND PHOTO: BO KARLSSON

Furthermore, when using a clonal replication strategy, there will always be clones that cannot provide a sufficient number of vital cuttings at first attempt. A second cutting production will be carried out and planted together with another population and thus create additional linkages. In addition, establishment of the same material in multiple years will make it possible to capture the effect of extreme weather conditions at planting time, thus giving more information about stability of clone performance. This could be used for species regenerated by seedlings too, by sowing half of each family in different years (family stability).

In this way future trials can include varying numbers of families from different populations. The most-represented population will be the basic target at trial establishment. There are many cases where three or four breeding populations can be more-or-less equally represented in the same trial, in which case at least one trial should be established within each population's target area. All four trials belonging to the same trial series need not be identical; for example, the most northern population may not be represented in the most southern trial and vice versa.

Testing period and number of measurements. The most efficient time for trials to be measured should be based on age-age correlations and heritability development for the traits of concern, but these parameters are not well known. So far, experience indicates that measurements carried out at roughly 20% of the expected rotation time.

Trials can be measured up to three times to produce breeding or genotypic values. The first assessment is carried out after one year's growth, when survival and vitality are scored, to get a baseline to correct for seedling quality, planting quality, etc. The second assessment, which is the basis for selection and breeding (height, damage, stem quality), is normally carried out after 6–10 years in the south and 10–20 years in the north, i.e., at a mean height between 3 and 5 m. At this stage of development, height can still be measured in a cost effective way with a height-pole. If carried out, the third assessment should take place when a stable diameter measurement is possible and, if desired, when wood properties can be evaluated. Extra measurements will occasionally be carried out after different kinds of extreme occurrences in the trials, such as outbreaks of a specific damage. Additionally, measurements can be made to improve breeding values when selecting for mass propagation.

TEST DESIGNS FOR UNIT-AREA YIELD TRIALS

The usual test designs used in Sweden are based on cost-efficient single-tree plots. This design is not adequate for reliable estimates of genetic gain in terms of unit-area production (m3sk/ha) at final rotation age, which is the most important objective trait. There is a complementary need for specially designed field tests to be established in parallel with the usual genetic tests, but less frequent. Such long-term tests should be designed to manage among other things:

- Estimates of genetic variance in long-term unit-area production.
- Estimating genetic relationships between early measurements in single-tree plots and measurements in multiple-tree plots at full rotation time, in order to get reliable correlations between selection and objective traits.
- Studies of interaction effects of trees within families during the different phases of stand development.
- Serve as a long-term warning system over the generations by enhancing visualisation of complicated performance characteristics, as well as reactions to biotic and abiotic stresses and how these develop on a plot basis
- Demonstration of genetic effects within families, among families and between improved and different standard materials (i.e., seed orchards, local stand seed).

- Facilitate development of models that describe competition

One idea to be considered is establishment of additional multiple-tree plot trials with the same genetic material as in the usual testing programme for a small sample of the breeding populations. Depending on resources, this can be done with one trial in southern and one trial in northern Sweden every 5th and 10th year for Norway spruce and Scots pine, respectively. The single-tree and multiple-tree plot experiments should be planted as close as possible. If more than one site is needed, an option is to establish a number of blocks of each test design at each site.

Two pairs of trials, each including one single-tree and one multiple-tree plot design with the same test material, are established during two consecutive years. This is in agreement with the normal testing on four locations for the breeding populations. In this way, the trial series will take into account differences in annual climate at the time of establishment.

For reliable estimates of parameters and realised gain, the number of families, or actually the number of parents included in the tests, should be large and large plots are a prerequisite. For practical reasons, it seems reasonable to establish at least 30 families (i.e., a full breeding population with 50 trees crossed by single-pair mating). The precision of estimates will be insufficient for a single set of trials, but will gradually improve as results from several trials of this design are accumulated. The tests over years are to be connected by a number of families in common.

Detailed test design – spruce. A total of at least 30 families are used. From each family, 35 plants are cloned with 16 ramets per clone. Half of the ramets will be used for each of the two test designs.

The single-tree plots are designed as a total randomisation of all clones (30 families x 35 clones) within each of four blocks, i.e., following the normal test procedure; however, two (not one) ramets per clone will be planted in each block. By putting a red label on every second ramet, it will be possible to consistently plant a red-labelled plant next to a non-red-labelled plant. This will give a systematic pattern, which can be used at the two thinnings in such a way that at least one ramet per clone is easily kept in each block. In this way, the original clone representation can be maintained for a longer time.

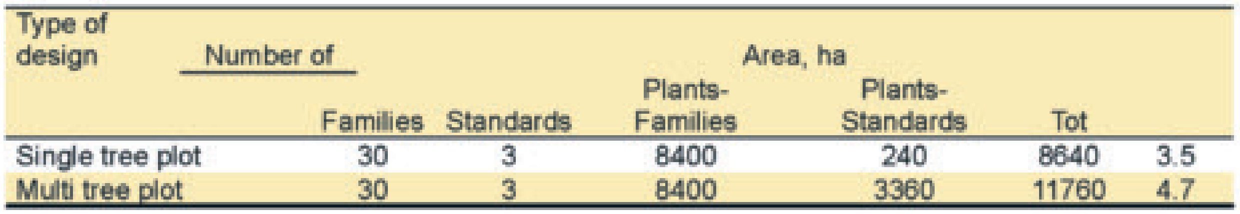
The multiple-tree plots are arranged as family plots, i.e., each plot consists of one family including 35 clones and 2 ramets per clone. The clones are planted randomly within each plot in the same systematic pattern as described above, making it possible to maintain original clone representation after the two thinnings. Each family plot is replicated four times (four blocks). The plot size will be 7x10 trees, resulting in 14 x 20 m plots at 2x2 m spacing. Since this area (280 m2) is too small for estimating of unit-area production during a full rotation, a suggestion is to arrange the family plots according to their mid-parent breeding values. Thus plots of families with the 4 best mid-parent BV's are clustered together, the next 4 best families are placed together and so on. These larger plots will consist of 14x20 trees, i.e., 28m x 40m=1120 m2 in each of the four blocks.

Apart from 30 breeding families some controls such as standard crosses, seed orchard material and local stand seed, should be included. The plot size for each of them will be the same as for the four family plots adjacent to each other (14x20 trees).

This design where plots of similar growth potential are grouped is a compromise where per ha production is given priority while other objectives are less emphasised. It deserves further discussion and should be tested before brought into application.

Detailed test design – pine. The same concept as for spruce can be used in the future when a reliable method is established for vegetative propagation of pine. Until then,

Table1. Estimated trial area required for spruce, for each of the test designs according to the assumptions given in the text.



Type of design	Number of Families	Standards	Plants-Families	Plants-Standards	Tot	Area, ha
Single tree plot	30	3	8400	240	8640	3.5
Multi tree plot	30	3	8400	3360	11760	4.7

the following test strategy can be used assuming application of within-family forward selection. The single-tree plots are designed as a total randomisations of all 30 families. The number of plants per family is here assumed to be 100. The actual number to be used will be given by results from the "pine simulation" project. The multiple-tree plots are arranged as family plots, i.e., each plot of 8x8 trees consists of one family. Each family plot is replicated in 4 blocks, for a total of 256 seedlings from each family. In total, 356 seedlings per family are used.

Since a plot area of 256 m2 (2 x 2 m) is too small for estimating unit-area production during a full rotation, the family plots will be arranged according to the mean breeding value (BV) of the parents. Thus plots of families with the 1-4 best BV's are placed together, the next 5-8 best families are placed together and so on. These bigger plots will consist of 16x16 trees, i.e. 32 m x 32 m=1024 m2 in each of the four blocks.

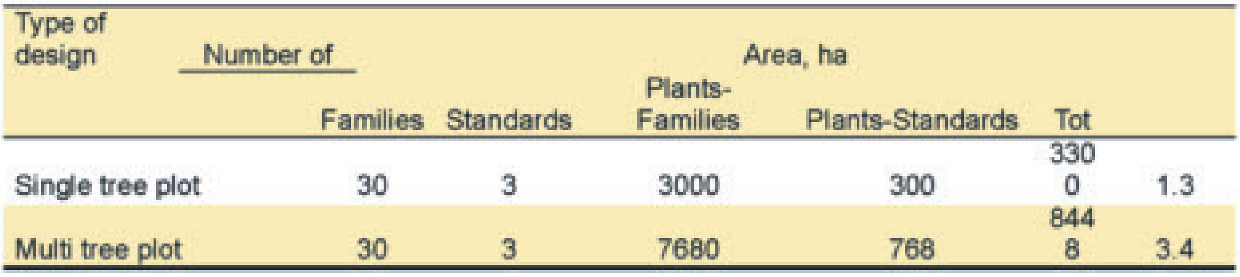
Apart from 30 breeding families, some standards such as seed orchard material and provenances including some local stand seed should be included. The plot size for each will be the same as for the four family plots adjacent to each other (16 x 16 trees).

Detailed test design – Lodgepole pine and silver birch. For lodgepole pine and silver birch, the same concepts can be used as for pine and spruce, respectively. Since these species are less important, we advise to delay establishment of multiple-tree plots, until experience is gained from the main species.

Realised gain trials for deployed mixtures. In operational silviculture under Swedish conditions, single families or clones are seldom planted to form a stand. Instead, seedlings from seed orchard seed or mixtures of vegetatively propagated clones are planted. To assess the operationally realised genetic gain from this kind of mixture, there is a demand for specially designed experiments and survey investigations. The experimental design by Ye et al. (2009) is a good example. Two mixtures of progeny are produced, each from about 20 parents (10 single-pair crosses) according to their breeding-value rank order, i.e., elite and intermediate. These two mixtures were compared to one unimproved seed source on plots of size 100, replicated 6 times on each of 5 experimental sites. In this study, two planting densities (772 and 3 086 trees per ha) were tested and had a significant effect.

An alternative design using ordinary single-tree plot experiments is also worth considering. In advanced generations, single-tree plot progeny testing will be with mixtures with greater and greater performance. If unimproved reference trees are planted in the single-tree mixture they will suffer from heavy competition. If instead the unimproved trees are planted on a few large multiple-tree plots, the design will better serve for comparisons with multiple plots of highly improved mixtures. The design allows for assessments of unit-area production.

Table 2. Estimated trial area required for pine, for each of the test designs according to the assumptions given in the text.



Type of design	Number of Families	Standards	Plants-Families	Plants-Standards	Tot	Area, ha
Single tree plot	30	3	3000	300	3300	1.3
Multi tree plot	30	3	7680	768	8448	3.4

The research to develop the technology using rooted cuttings for clonal testing of the new generation in pine breeding has three components. (1) donor plant production methods to obtain one or more crops of even-sized cuttings; (2) rooting procedures and production methods to raise an even crop of rooted cuttings for field testing; and (3) technology to produce in the order of 25 000 rooted cuttings required for a full series of tests for a breeding population.


PHOTO: ERIK VIKLUND

EXPERIENCE WITH ROOTED CUTTINGS AS A TOOL FOR GENETIC TESTING IN PINE

These research objectives, including the target of 10 high-quality rooted cuttings per donor plant, will be reached by a combination of scientific experiments, repeated trial-and-error efforts to improve nursery practices and personnel skill, and pilot-scale operational propagation for an entire breeding population to develop greenhouse technology. Inspiration is found from programmes with other pine species, especially those in North America and New Zealand, but also with lodgepole pine in Sweden (Frampton et al. 1998, Frampton et al. 2000, Fries & Kaya 1996, Menzies et al. 1992).

Since 1999 at Sävar, combinations of growing space, nursery management, pruning regime and growing time have resulted in 3–10 suitable cuttings per donor plant. Recent research in Punkaharju gave an average of 16 cuttings per donor plant, which demonstrates the potential. More effort will be spent on research taking two consecutive cutting crops. Taking ”cuttings from cuttings” will also greatly reduce the main source of nursery-based C-effects.

So far, by treating the cutting and managing the rooting environment, the percentage of rooted winter cuttings from dormant seedlings is much too variable among years and nurseries, but there are explanations and the technology can be improved. In Ekebo, >50% rooting was reached in one experiment, 15–20% in another and 14% in a third. In Sävar, the variation is 35–70% in different rooting experiments. Some plagiotropic growth was observed in Ekebo in the year of rooting, but disappeared the next year and does not appear to be a problem.

The pilot-scale rooting for pine population T12 resulted in a total of 3 000 rooted cuttings established in field experiments. Problems with the first large-scale greenhouse environment caused variation in rooting that varied from 33 to 57% depending on water regime in different parts of the greenhouse. In the better part, 4.2 cuttings out of 7.5 rooted and 93% of all clones were represented.

In parallel with Scots pine, a lodgepole pine rooting project was undertaken at Sävar. The experience demonstrates that more cuttings are produced per donor plant, 9–13, and much higher rooting obtained, 80–95%. In breeding population C3, 2 578 clones and 23 328 rooted cuttings were produced and planted in field experiments. A technical accident in the nursery reduced the rooting percentage to 65% as compared with 82% in a control greenhouse.

The conclusion from the large-scale pine propagation project in Sävar in 2009 and 2010 was that the methodology could be used after further developing the water regime, although more efforts are needed to develop a robust method for the production of cuttings. The Ekebo nursery is ready for the first large-scale experiment. For lodgepole pine, rooted cuttings for clone testing is considered a robust technology, but still better management of the donor plants to produce cuttings is required.

C-effects are known to reduce accuracy and introduce bias in genetic testing. This is an important issue for further research, but not until the propagation technique works satisfactory.

FOTO: JOHAN KROON

EXPERIENCES OF BREEDING ARCHIVES AND CONTROLLED CROSSES

This section deals with controlled crosses in operational breeding, including establishment and management of breeding archives. The number of pollen parents in a polymix is investigated as well as the consequences of single- versus double-pair mating. Some of the suggestions require further investigation and discussion among breeders.

Breeding archives. Controlled crosses are best performed in a breeding archive, located in the vicinity of a breeding station with skilled personnel. In reality, there is no case where a conventional field-test plantation is well located and suitably spaced to allow controlled crosses to be carried out efficiently. In some cases, the function of a breeding archive and a seed orchard may be combined.

The breeding archive should be designed for top grafting by successively planting out and managing inter-stock grafts to meet operational requirements for progress through breeding cycles, while permitting crossing done from the ground or small ladders. Both male and female flowering must be forced. This concept for a breeding archive has to be further investigated, including management strategies, inter-stock clones, capacity figures and time schedules, etc. Preliminary experience suggests that it is possible to put as many as 10 top-grafts on each grafted inter-stock. Inter-stocks are planted at 6 x 5 m spacing (333 trees/ha).

In the case of clonal testing, there is the option of keeping one (or two) ramets in a breeding archive. With 2 000 clones, 2 ramets per clone and 1 000 trees per ha 4 ha is needed per population, or a total of 80 ha for 20 breeding populations. While at first glance this seems excessive, the option becomes more and more attractive when compared to grafted breeding archive alternatives. If planted on a carefully selected nearby forest site and following regular field experiment practices, most or all expenses of archive establishment and management can be avoided. Crosses can likely be performed before the age of 20. For lodgepole pine, there is no doubt about flowering capacity at younger ages. The option for denser plantation and genetic thinning of the archive based on, say, 10-year measurement results should be investigated. Under some circumstances this orchard can be used for genetic testing as well.

The original plan was first to select mother trees in the field trials to be grafted for female flowering and later identify male trees and bring pollen collected in the field experiments to the breeding archive for breeding. The idea was theoretically appealing, but has been found to be unreliable and ineffective. It requires too much management, waiting, attention and travelling and cannot be controlled to the extent needed for Swedish breeding. This does not preclude the collection of pollen in field trials as a complementary option.

Mass propagation archive. With current propagation techniques, the number of scions available from a tree selected for seed orchard establishment limits the speed and extent to which it can be propagated. There is a need for a propagation archive to produce larger numbers of healthy scions from potential seed orchard trees. For this purpose, traditional grafting is done on rootstock seedlings. Selected trees are replicated by 5 ramets. Trees are planted at 6 x 3 m spacing (555 trees/ha).

Clone archive. Although top grafts are suitable for crossing, they are not suitable for long-term storage of genotypes. For that reason mass propagation archives or similar kinds of archives may be needed to store valuable genotypes for breeding that will never be used for mass propagation.

Management of breeding archives. Top-grafting is a procedure where young scion material is grafted onto reproductively mature trees (Gooding et al. 2000). The “trees” into whose crowns the scions are grafted are usually grafts themselves, known as “interstocks”. This creates a “tree” with three genotypes: the rootstock, the interstock and the top-graft.

Top-grafting is now standard procedure for shortening the time to obtain flowers for crossing in Pinus taeda and Pinus elliottii breeding programmes (McKeand & Raley 2000, Medina Perez et al. 2007).

The first Scots pine study of top-grafting was published by Almqvist & Ekberg (2001) and showed that the method works also for this species. It showed the importance of selecting the right interstock clones to enhance flowering and that flowering of top-grafts can be further improved by GA4/7 treatment of the interstock.

The interstock clone affects not only the flowering of the top-graft, but also its survival and development (Almqvist 2010). Identification of good interstock clones requires screening of clones for this purpose, since flowering of the interstock itself gives no useful information about its capacity to induce flowering on the top-graft.

In an on-going Scots pine top-grafting experiment with young (4–6 years old) top-graft material, 45% of the top-grafts produced flowers two years after grafting (Almqvist, 2010).

Flower stimulation is an important tool to ensure sufficient flowers for breeding. Hormone treatment with GA4/7 is the basic flower stimulation treatment. As a complementary treatment, root pruning or stem strangulation can also be used. Girdling should be avoided due the risk of stem breakage at the girdling point.

GA4/7 treatment is performed as stem injections in a hole drilled in the trunk. GA4/7 diluted in absolute alcohol is used, and the dose is adjusted to the size of the tree. Scots pine needs higher doses of GA4/7 than lodgepole pine or spruce.

The timing of the GA4/7 treatment is important. In Scots pine and lodgepole pine, treatment at the end of the current year’s flowering period promotes male flower induction. Treatment for female flower induction follows vegetative elongation and should normally be performed during the first half of July in central Sweden. In Norway spruce, proper GA4/7 treatment time is when the current year’s shoot elongation of the terminal shoots on the uppermost branches has reached about 80% of final length. In a normal year, this means at the end of June to beginning July in central Sweden.

Root pruning and strangulation treatment should be performed earlier in the vegetative growth period than GA4/7 treatments. The end of May is suggested as a rule-of-thumb.

The technology for controlled crosses has to be further developed to facilitate carrying out large numbers of crosses in a short time. The pollination equipment should be effective, making efficient use of very small amounts of pollen. There must be adequate pollination equipment on-hand so as not to limit the crossing programmes.

NUMBER OF CROSSES AND POLLEN PARENTS IN CROSSES FOR BREEDING VALUE ESTIMATES

Approximate formulas for correlations between true and estimated breeding values were developed for controlled crosses and polymixes (Lindgren 2009, Appendix 3). The formulas consider additive and dominance variation, family size and number of pollen parents.

The formulas and other considerations led to the following statements:

- It is recommended to use 25 pollen parents in a pollen mix and at least 30 test plants per family. The results will then be robust to variation in pollen composition and to variation in amount and quality of different pollen sources. This number will be adequate, even if dominance is higher than usual and heritability is lower. The savings with lower numbers in pollen mixes are probably limited, while a larger number will give only limited improvement in the accuracy of breeding value. If it is problematic with 25 pollen parents, discussions indicate under what circumstances a lower number is possible and still useful. In general it is often possible to use fewer pollen parents.
- If polycross is used, pollen parents should be chosen to make forward selection possible, aided by marker determination of paternity (Appendix 1).
- DPM can remain a general mating design for generating the recruitment population, while it is also rather accurate for progeny-testing.
- SPM is sufficient for forwarding the breeding population and can be used in low input situations or in lower-ranking strata of the breeding population.
- If one of the DPM fails, but parents still get progeny in one cross, it is not worth delaying the crossing effort to complete the scheme, although the number of trees carried on from each cross to next generation may be increased accordingly.
- “Progeny testing” by SPM is accurate enough to be useful. DPM is better, and additional crosses are better still. A polymix is not essential for a good progeny testing, although it is the best alternative if parental ranking for breeding value is the only purpose of the cross.

PHOTO: ERIK VIKLUND

EXPERIENCE FROM THE SEED ORCHARD PROGRAMME

Ola Rosvall
Curt Almqvist
Dag Lindgren

Over the years, experience has accumulated on the importance of coordinating tree breeding and mass propagation. In this section we report on the experience from the third round of seed orchards. We also summarise an investigation on the optimal number of clones in a seed orchard.

EXPERIENCE FROM THE THIRD ROUND OF SEED ORCHARDS – "TRE-O"

In 2002, a cooperative seed orchard establishment programme involving all Swedish forest owner categories was initiated (Remröd et al. 2002). The objective was to establish new orchards before 2020. To support these large-scale activities, a number of investigations were carried out as a basis for key decisions. Most of them were published with the intent to help both the current and future seed orchard establishment.

Planning started for the establishment of the third round of seed orchards in 1999. Initially, for each seed zone of Sweden, calculations were carried out to demonstrate the potential genetic gain from seedorchards or clone mixes if established at present orin the future (Rosvall 2001, Rosvall et al. 2001 and 2002).

The economics of seed orchards were evaluated by Rosvall and Ericsson (2002a and b), and the demand for orchard seed was analysed by Hannerz and Almqvist 2000, Hannerz et al. 2000). The demand was further detailed after the delineation of new seed utilisation zones (Rosvall 2003), including the demand for seed used in direct seeding. Alternative seed-orchard concepts and establishment techniques were investigated (Rosvall and Lindgren 2002), as well as alternatives for "rolling" seed-orchard designs (Rosvall and Almqvist 2003). Finally, a work plan for the operations was outlined (Rosvall et al. 2002).

During the planning and calculation for new seed orchards, attention was paid to a number of unresolved problems and unexploited opportunities. In Appendix 4, feedback to the breeding programme is presented, including a great number of comments and suggestions. One important issue is summarised here.

The delay between the time that genetic progress is made in the breeding population and the time when that improvement is turned into large-scale planting of improved seedlings is too long and is reducing realised economic gains. Owners of seed orchards and other mass propagation facilities should be seen as the prime target group for tree breeding outputs. Since seed orchards cannot produce forever and must at some point be replaced, it is most important to synchronise the tree breeding activities with the need for

PHOTO: BO KARLSSON

new seed orchards or other installations for mass propagation to help capture as much genetic gain as possible. This need of synchronisation was also stressed by El-Kassaby et al. (2007), who suggested that it is profitable to replace pine seed orchards earlier than was considered in the past, provided long-term breeding is able to deliver genetic progress at the right time. A study on spruce seed orchards indicted optimum rotation time to be longer (Moriguchi et al. 2008).

It has been found necessary to find new ways to speed up the Scots pine breeding in general and in some areas in particular. To shorten the gain delivery time to its minimum, tree breeders should also plan for future propagation activities like scion or cutting archives, so that these are ready to produce grafts or rooted cuttings for seed orchard establishment. The financing of this should be negotiated with the customers.

Here we identify the need for new approaches to accelerate establishment of orchards when forward-selected trees are small and produce rather few scions for conventional grafting. For example, improvements in technique might permit micro-grafting with very small scions, or even propagation by rooting of needle fascicles, enabling more rapid orchard establishment of young selections. Alternatively, establishment of seedling seed orchards could bypass the requirement for grafting altogether.

OPTIMAL CLONE NUMBER FOR SEED ORCHARDS WITH TESTED CLONES

The optimal number of clones in seed orchards was investigated by Lindgren and Prescher (2005). A model was constructed to maximise a goodness criterion ("benefit") for seed orchards.

The goodness criterion was a function of:

1. the number of tested genotypes available for selection;
2. the contribution to pollination from:
    a) the ramet itself;
    b) the closest neighbours;
    c) the rest of the orchard and
    d) sources outside the orchard (contamination);
3. variation among genotypes for fertility;
4. frequency of selfing;
5. production of selfed genotypes;
6. gene diversity (= status number);
7. influence of contamination;
8. genetic variation among candidates;
9. correlation between selection criterion (e.g., height in progeny test) and value for forestry (e.g., production in forests from the orchard); and
10. the number of clones.

Numeric values of the entries were discussed, and values were chosen to be relevant for scenarios with Swedish conifers (focusing on Scots pine) and for loblolly pine in the US. Benefit was maximised considering the number of clones.

The optimum was 16 clones for the Swedish pine scenario, and somewhat less for the loblolly pine scenario. The optimum was rather wide, thus it is not essential to deploy the exact optimum, and an approximate optimum will be satisfactory. The loss in gain and diversity due to deviation from the optimal number may be greater when fewer clones are used rather than more. A sensitivity analysis was performed to evaluate the importance of the uncertainty and variation in different entries. Valuation of the benefit of gene diversity is important. Other significant considerations are the genetic variance in the objective character and the ability to predict it, as well as the impact of selfing and the variation in reproductive success among clones. The assumptions did not consider linear deployment, and somewhat higher census numbers would be appropriate if this is practiced. More clones will also allow for genetic thinning and selective harvest. Twenty clones are suggested as a rule-of-thumb for seed orchards of Swedish conifers and more if unequal proportions are used intentionally.

The Norway spruce breeding programme has reached the stage where relatedness must be considered during selection of orchard clones. The principles for optimisation when selecting among related and unrelated trees and clones have been analysed by Lindgren et al. (2009).

PHOTO: ERIK VIKLUND

BREEDING STRATEGIES

Ola Rosvall
Curt Almqvist
Dag Lindgren
Tim Mullin

One of the main reasons for a review of the Swedish breeding programme is to evaluate alternatives to the pine breeding strategy, primarily Scots pine but also for lodgepole pine. The programmes, as originally implemented, have been found to be too time consuming. In this section, a number of alternative mating and selection systems are described and evaluated in terms of time and resources used, potential genetic gain achieved and genetic diversity maintained.

The comparisons are simplified to highlight the principal differences. Each individual strategy has to be optimised by computer simulation before completing a fair comparison of alternative strategies.

The current pine strategy uses "dead-end" progeny testing of 10–20 unselected individual full-sib family seedling candidates from parents in the selected breeding population. While useful for identifying the best candidates, the progeny generated for these tests are never intended as candidates themselves for breeding. Experience has shown that producing test progeny for these candidates in breeding archives takes more than 10 years and that intensive culture to accelerate the development of flowering is complicated and resource demanding.

ALTERNATIVES FOR THE SCOTS PINE STRATEGY

The currently recognised "alternative" pine strategy is forward selection in field experiments (It has been often called "phenotypic forward selection", but will in the following be referred to as "forward selection"). To make this alternative option possible, the new generation must have also been planted in field experiments allowing for forward selection. Recently it was shown that forward selection, although much less accurate than backward selection based on progeny testing, results in higher gain per unit time since the breeding cycle is shortened (Lindgren and Danusevičius 2004, Hannrup et al. 2006).

An alternative to pure forward selection in field tests uses the concept of pre-selecting a number of candidates in field tests and testing these by progeny-testing (Lindgren and Danusevičius 2004). The authors indicate that this alternative seems slightly superior to forward selection, when considering the accumulated effect of gain, time, and cost. Another alternative is to increase the breeding population size by selecting and mating a number of full-sib candidates and use a combination of forward and backward selection. In this way, many of the related selections used for breeding in the breeding population will be rejected after evaluating their progeny and not contribute to the next generation. The principle of this strategy has been applied in Swedish lodgepole pine breeding (Rosvall 2000). A particular variant of the strategy was studied by Lindgren at al. (2008) and Danusevičius and Lindgren (2010). The results indicate a great potential to improve the efficiency of breeding. Further, genetic markers make possible the determination of paternity of candidates in polycross families. Based on this methodology, strategies based on polymix breeding and forward selection can be developed, as presented in Appendix 1 (Lindgren 2009).

Given the constraint of long-term management of the gene resource, the principal gain in the Swedish programme comes from within-family selection, i.e., selection among the full-sibs in a family from selected parents. Balanced within-family selection will maintain the highest possible gene diversity by keeping all founders equally represented. Therefore, from a theoretical perspective, the ultimate challenge is to find the best strategy for mating and selection to make possible to select as intensely and accurately as possible within a full-sib family of selected parents. To obtain additional gain in an optimised breeding programme, the restriction on fully balanced selection could be relaxed somewhat and other ways found to control loss of gene diversity, as will be further discussed. Nevertheless, the greatest challenge remains to find the best approach to within-family selection.

We have defined 6 principally different mating and selection strategies for within-family selection and outlined the schedule of operational activities, use of materials and resource in terms of number of trees used for field testing and selection, archives for breeding (flowering) and for propagation of seed orchard trees (scions). These strategies are outlined in detail in Appendix 5 and summarised in Table 3. We have also investigated the practical and economic consequences of the operational activities using the cost functions given in Appendix 6 (Almqvist et al. 2009). The results of this work are guiding breeding strategy simulations currently underway. Our findings to date are summarised in the following sections.

TERMINOLOGY AND ASSUMPTIONS

A "recruitment population" comprises all trees in a new generation that can be considered for selection. "Candidate trees" make up a part of the recruitment population, having been selected or sampled at random (unselected). Candidate trees are intended to be further evaluated before it is mated and entered in the breeding population. The term "progeny test" describes a dead-end test intended to estimate breeding values of the parents, to identify those that should be crossed to generate a new generation. Progeny testing in this way and clonal testing of a candidate itself is used before selection to the breeding population. Candidates that are not tested in either of these ways but selected and mated in the breeding population may later be rejected based on performance of their progeny in later generations. Thus, all kinds of candidate trees have a limited probability to enter or stay in the breeding population and contribute to future generations.

Phenotypic forward selection has been used in the Swedish breeding context for the case of selecting among sibs within a family where all information from relatives are the same and the only distinguishing data are the measurements of the individual trees themselves. However, breeding values estimated by BLUP include information from relatives so that values of all candidates are comparable. Therefore, when selection is made forward on breeding values the term phenotypic can be misleading; we will simply call this "forward selection".

Longer field testing times are needed in harsher climates. We have divided Sweden into four regions, characterised by different testing times: south, central, north coastal and north inland. Compared to southern Sweden, field testing takes one year longer in the central region, two years longer in the north coastal region, and four years longer in north inland Sweden. In central Sweden (T26), backward selection at a dominant height of 3 m and forward selection at 4 m are expected to require 12 and 15 years, respectively.

Crosses will normally be repeated in two consecutive years to ensure sufficient success rate. In the breeding archives, inter-stocks are planted at 6 x 5 m spacing (333 trees/ha) and 10 top-grafts are grafted on each inter-stock graft. We assume it will take 2–3 years from top-grafting to collection of pollen and 2 additional years to pollination of all female flowers. It takes trees or grafts two more years to flower in the north than in the south. In the propagation archive, established to produce future scion material, selected trees are replicated by 5 ramets, planted at 6 x 3 m spacing (555 trees/ha).

COST FUNCTIONS FOR SCOTS BREEDING ACTIVITIES

Using genetically improved planting stock is similar to a technology breakthrough. Large gains are achieved at low additional cost, and sometimes at a lower cost. To optimise a breeding plan, however, the costs for all management activities have to be considered. The marginal cost for an additional parent to be tested to enhance selection intensity has a trade off by allowing fewer test progeny per cross, which reduces selection accuracy. The efficiency of a strategy can be calculated as genetic gain per unit cost and time (or annual gain under an annual budget restriction). A less cost-efficient strategy that produces more gain can still be more profitable, if compared to alternative investments other than tree breeding.

A number of cost functions were developed to determine the optimal trade-offs for resources used in field testing, selection and breeding for a number of breeding plans. The cost functions consider those costs that are variable among strategies. They include the marginal costs for each field site, field-tested tree, controlled cross, archived tree, etc., and some start-up costs for these specific activities. The basic costs for running a breeding programme with its infrastructure, field stations, competence, planning and administration, supportive research, etc., are not included; these costs are considered to be fixed and therefore independent of breeding strategy.

The cost functions are reported in Appendix 6. They include the costs for: sowing and growing candidates, flower stimulation and crossing, sowing and maintenance of progenies, trial establishment and maintenance, measurement, data analysis and reporting, grafting on root stock, top-grafting, forming a new generation, and DNA analyses.

SEVEN STRATEGIES FOR WITHIN-FAMILY SELECTION IN DETAIL

The application of the seven strategies to Swedish conditions are described in this part, as outlined in Figure 2, briefly following appendix 5.

In general, strategies 1 and 2, the current Scots pine strategy, and strategy 7 the current Norway spruce strategy, start with producing separate test material to progeny test or clone test the new F+1 generation full-sib candidates already at the seedling stage of development. All other strategies start with planting out new F+1 generation full-sib seedlings in field experiments where within-family forward selection of the final breeding population or candidate trees is made at age 10–20 years.

Strategy 1 and 2, "Progeny testing of unselected seedling candidates and backward selection – basic and intense respectively" (referred to as "Seedling candidates backward").
These are the current Swedish programmes. They start with planting a breeding archive with full-sib F+1 progeny from the current breeding population to make them flower and produce F+2 progeny (polymix pollination) for a dead-end progeny test. Selection is then made backward of the final F+1 breeding population of size 50 (the standard size of a single multiple breeding population). The F+1 full-sib seedling candidates can result from some kind of early selection, but so far the criterion has been 10–20 vigorous F+1 seedlings. In strategy 2 "intense", F+1 seedling development is forced by intense cultivation, top-grafting and flower stimulation, in order to reduce the overall cycle time.

Figure 2. Flowchart of activities required to implement the 7 breeding strategies.

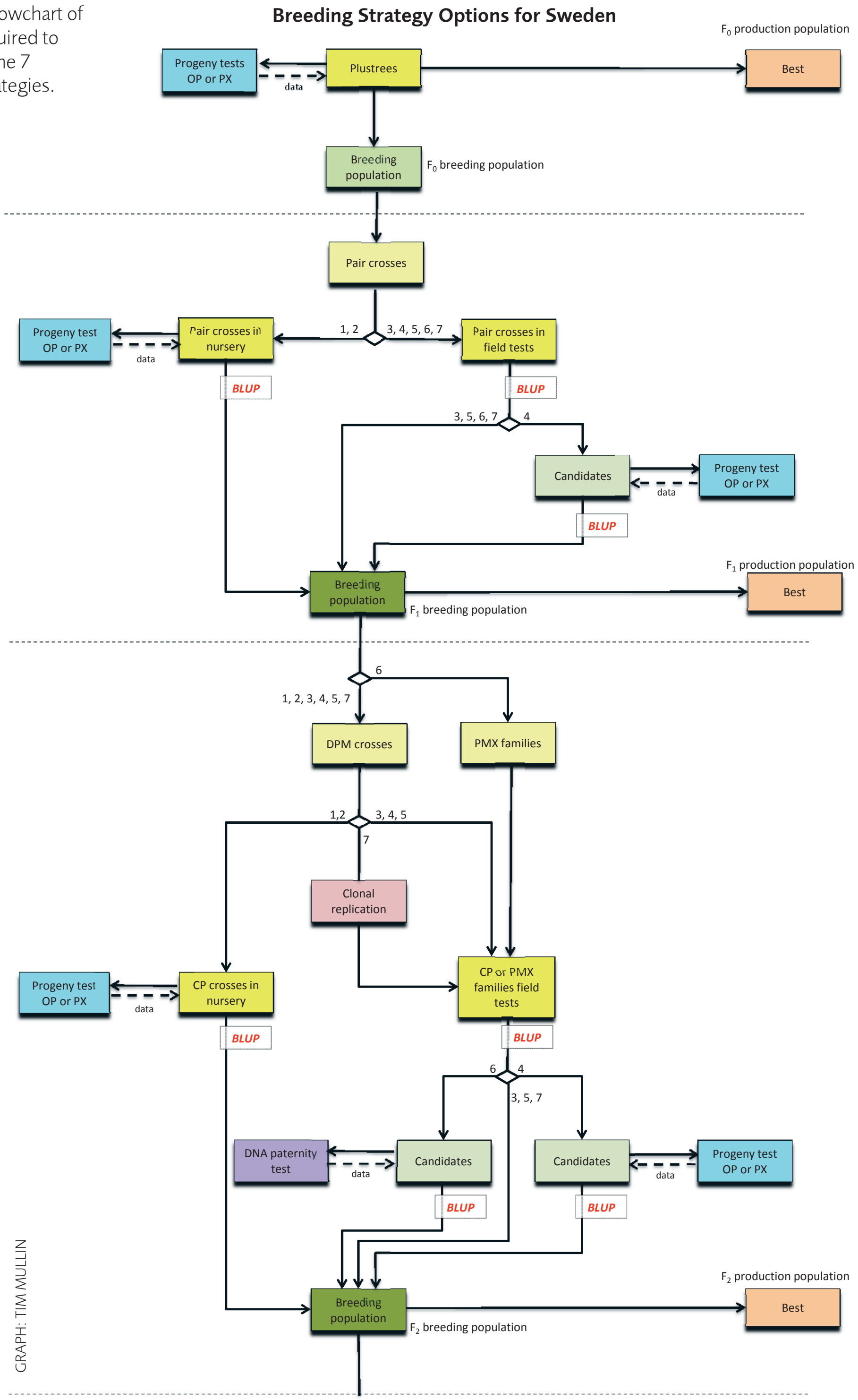


PHOTO: BJÖRN SVENSSON/SKOGENBILD

GRAPH: TIM MULLIN

Strategy 3, "Forward selection – current alternative programme" (referred to as "Field forward") The F+1 breeding population of 50 trees is directly selected within-family by forward selection in F+1 field experiments and selected trees are mated to produce a new generation to be planted in new field experiments.

Strategy 4, "Forward selection of candidates, progeny testing and backward selection" (referred to as "Field candidates backward"). A number of F+1 candidates are selected within-family and tested by a dead-end progeny test (open pollination or controlled polymix pollination) before backward selection of the final F+1 breeding population of size 50.

Strategy 5, "Forward selection of candidates, testing pair crosses for combined family and individual selection" (referred to as "Field candidates pair-wise forward") The concept of strategy 5 can be explained in different ways. Following the basic ideas of strategy 3, forward selection in a field test is performed within family to obtain a number of F+1 selections (rather than just one) and these are mated to unrelated selections from different families under PAM (a necessity), to produce an F+2 recruitment population. In the F+2 population, the family component of selection based on F+2 family information (parental BLUP BV) is in principle within-family selection of the previous generation, i.e. "backward" selection among the F+1 individuals. Forward selection of new F+2 candidates are within-family of the current generation. If "backward" selection among the F+1 parents is strictly within-family the scheme will maintain equal founder contributions, as in previous schemes. Retrospectively, 50 trees in the F+1 generation have contributed to the F+2 generation.

This scheme can also be understood as increasing the BP size from 50 up to 100–300 trees, including all relatives of each F+1 full-sib crossed. Variation in founder contribution and effective population size can be controlled by including genetic diversity in the breeding objective. BLUP breeding values and coancestry are considered jointly by using group-merit selection (GMS) or the optimum contribution algorithm (OC).

Strategy 6, "Forward selection of candidates, testing polymix crosses with a mix of selected fathers for combined family individual selection (BLUP) aided by paternal control" (referred to as "Field candidates poly-mix forward") This strategy can be applied in many different ways. First we describe a variant expanding from strategy 3. A polymix of some portion of F+1 fathers (most likely two mixes, each with 25 fathers rather than one with 50, due to current marker technology) is used to simultaneously test the F+1 candidates (i.e., 50 candidates) and produce F+2 progeny for forward selection. DNA markers are used to determine the F+1 pollen parents of the pre-selected F+2 trees, before the final forward selection of 50 F+2 parents with restrictions on parent contributions. This and other options for polymix breeding are outlined in Appendix 1 (Lindgren 2009).

This strategy can also be applied as a variant expanding on strategy 5. In the field tests, 300-500 candidates are selected (rather than just 50) and mated by the polymix to produce F+2 progeny for forward selection. As above, DNA markers are used to determine the F+1 pollen parents of the pre-selected F+2 trees, before the final forward selection of 50 F+2 parents with restrictions on parent contributions. In each subsequent cycle, a large number of new candidates (i.e., 300-500 candidates) are selected forward and polycross bred.

In a third variant, the best 50 F+2 trees are selected forward in the best F+1 PX-families and are pair-crossed to produce F+3 progeny, among which many candidates are selected for polycross breeding. Thus, in this variant, 50 trees are pair-crossed in every second generation and up to 500 candidates are polycross bred in every other generation.

For practical reasons, pollen from recent-generation selections can be assigned to unrelated pollen mixes of 25 parents per mix. Different sets of the mothers can be pollinated with different pollen mixes.

In summary, for strategy 5 and 6, the additional dead-end progeny test experiment of candidates in strategy 4 is replaced by tests that provide good estimates of parental breeding value, yet allow effective forward selection.

Strategy 7, "Testing unselected cloned pair cross candidates for forward selection" (referred to as "Seedling candidates clonal forward") F+1 full-sib progeny are

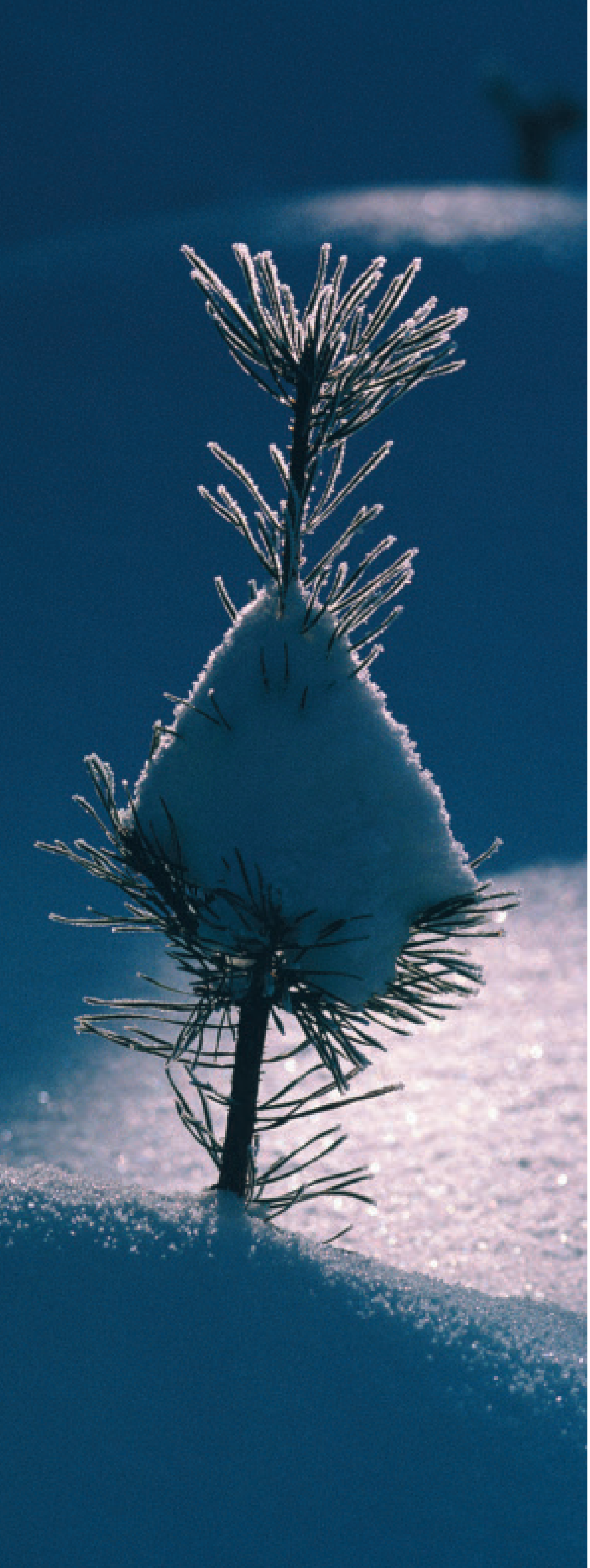


PHOTO: STEFAN ÖRTENBLAD/SKOGENBILD

cloned to produce a recruitment population for forward selection. Best clones within each family are selected for a new BP of size 50.

In strategy 7a, scions for grafting and perhaps pollen need to be transferred from the field trials to a grafted breeding archive to facilitate crosss, while in strategy 7b copies of each clone are kept in a parallel breeding archive.

Comparing strategies. Based on the alternative mating and selection schemes described above and detailed in Appendix 5, Table 3 was constructed to summarise the use of time and resources assuming that 25 000 trees per cycle are planted in field experiments under all strategies. This resource is not optimally portioned among types of field tests and number of candidate trees tested or selected for breeding, but can serve as a basis for comparing at a given total use of test resources. To illustrate the effect of varying resource distribution, figures are given for both expanding the breeding population from 50 trees to 100 and 300 trees to be crossed in strategy 5, “Field candidates pair-wise forward”.

Strategy 3 “Field forward”, 5 “Field candidates pair-wise forward” and 6 “Field candidates polymix forward” have the shortest cycle time, using 21 years, and strategy 4 “Field candidates backward” the longest, using 36 years.

From Table 4 it is evident that the total cost per population for all strategies is about 2 million SEK per population, while strategy 3 (Field forward) is about half of that, 1 million SEK. Strategy 6 (Field candidates polymix forward) is the most expensive due to the cost of paternity analysis.

If the cycle time is considered, as it is in the last column of Table 4 where these per population costs are translated into annual costs for all 24 Swedish pine populations, strategy 3 (Field forward) will be the lowest cost at 1 million SEK per year, followed by the current strategy 1 (Seedling candidates backward) and strategy 4 (Field candidates backward) with 1.3 million SEK per year. Strategy 5 (Field candidates pair-wise forward) with 300 trees in the breeding population and 6 (Field candidates polymix forward) with short turnover times will be the most expensive at about 2.5 million SEK per year. Strategy 5 has high costs arising from many pair crosses while the simpler polymix strategy 6 has higher costs for parental

DNA analysis. It can be observed that the costs for DNA analysis are uncertain. If in strategy 5, 100 instead of 300 trees are used in breeding the annual cost is reduced to about 2 million SEK. It is interesting to note that strategy 7 (Seedling candidates clonal forward) with its high cost for rooted cuttings combines a short generation turnover time and a moderate annual cost of 2.0–2.2 million SEK. This is in the same order as the current strategy 2 (Seedling candidates backward intense).

In conclusion, there are a number of alternatives to the current breeding strategy which have about the same cost per generation, with the exception of strategy 3 (Field forward). This is because the costs are largely determined by the number of trees in field tests. Since strategy 3 (Field forward) can't fully benefit from very large family sizes, it is cheaper; it uses 10 000 instead of 25 000 trees in field tests. The cycle times have a large impact on annual costs resulting in somewhat higher costs for strategies with shorter cycle times; however, the annual costs of the most interesting strategies are roughly the same and similar to the current main strategy 2 (Seedling candidates backward intense).

Table 3. Summary of alternative mating and selection schemes approximately following the examples given in Appendix 5. Breeding archive sizes assume top-grafts of both mothers and fathers. bw and fw is backward and forward, respectively. op and px is open pollination and poly-mix crossing, respectively and cp is controlled single pair pollination. The figures are chosen to give 25 000 trees in field experiments. This resource is not optimally portioned among types of field tests and number of candidate trees tested or bred, but can serve as a basis for comparing the use of resources.

Alternative mating and selection strategies	Cycle Time	Field tests				Crosses		Archives			
		Candidates	Trees per family	Test sites	Trees in test	BP = BP size	Progeny testing	Breeding		Propagation	
					(2 500/ha)	(DPM)		(333 trees/ha)		(500 trees/ha)	
	Years	Trees	Trees		Trees	Crosses	Crosses	Trees	Ha	Trees	Ha
1. Seedling candidates backward - basic[1]	33	500	50 bw	4	25 000 bw	50 cp	500 px			500	1-1.5
2. Seedling candidates backward - intense[1]	26	500	50 bw	4	25 000 bw	50 cp	500 px	250	0.75	500	1-1.5
3. Field forward[1]	21		200 fw	2	10 000 fw	50 cp		25	0.08	80	0.2
4. Field candidates backward	36	300	200 fw 50 bw	2 4	10 000 fw +15 000 bw	50 cp	300 op	25	0.08	80	0.2
5. Field candidates (300) pair-wise forward (100)	21	300	83 fw	4	25 000 fw	250 cp		150	0.45	80	0.2
		100	250 fw			100 cp		80	0.24		
6. Field candidates polymix forward	21	300	83 fw	4	25 000 fw	300 px		150	0.45	80	0.2
7a. Seedling candidates clonal forward without breeding archive	26	2 500	10 fw	4	25 000 fw	50 cp		25	0.08	0	0
7b. Seedling candidates clonal forward with breeding archive	23	2 500	10 fw	4	25 000 fw	50 cp		0	0	4 000	8.0

[1] Current Swedish programmes

PHOTO: ISTOCKPHOTO.COM

Table 4. Variable cost components for one breeding population and the annual variable cost for all Swedish pine populations with cycle time and dimensions from Table 3 according to Almqvist et al. (2009). Propagule costs include: cost of sowing and growing candidates (Cc), cost of flower stimulation and crossing (Cf), cost of sowing and maintenance of progenies (Cn), cost of forming a new generation (Cng). Field trial costs include: cost of trial establishment and maintenance (Ct), cost of measurement (Cm), cost of data analysis and reporting (Ca). Grafting and archive costs include: cost of grafting on root stock (Cg), cost of top-grafting (Ctg). DNA analysis cost includes: cost of DNA analyses for paternity determination (Cx).

Alternative mating and selection strategies	Cycle Time	Total variable costs per population (thousand SEK)[1]					Annual variable costs for breeding programme (thousand SEK) [2]				
	years	Propagule costs	Field trial costs	Archive costs	DNA analysis	Total costs	Propagule costs	Field trail costs	Archive costs	DNA analysis	Total costs
1. Seedling candidates backward - basic[1]	33	574	1 266			1 840	418	920			1 338
2. Seedling candidates backward - intense[1]	26	544	1 266	290		2 099	502	1 168	267		1 937
3. Field forward[1]	21	158	690	66		915	181	788	76		1 045
4. Field candidates backward	36	328	1 565	66		1 959	219	1 043	44		1 306
5. Field candidates (300)	21	600	1 265	251		2 116	686	1 446	286		2 418
pair-wise forward (100)		363		95		1 772	415		108		1 968
6. Field candidates polymix forward	21	412	1265	251	300	2228	471	1446	286	343	2 546
7a. Seedling candidates clonal forward without breeding archive	26	825	1 265	40		2 130	762	1 168	37		1 966
7b. Seedling candidates clonal forward with breeding archive	23	832	1 265			2 097	868	1 320			2 188

[1] Variable costs for one breeding population with cycle time and dimension according to Table 3.

[2] Variable annual costs for the Swedish Scots pine breeding programme, 24 breeding populations, with cycle time and dimension according to Table 3.

Work is underway to compare the alternative strategies using a stochastic parametric simulation tool, POPSIM (Mullin and Park 1995). This investigation is considering cost and cycle time analysis and will add optimisation of resource distribution and accurate calculations of genetic gain and diversity to guide the choice among strategies.

ADVANTAGES AND DISADVANTAGES WITH THE ALTERNATIVE STRATEGIES

Initially, the strategies will be compared at three resource levels representing 10 000, 20 000 and 40 000 trees per generation. Comparisons will also be made at fixed numbers of trees per year and fixed cost per year.

Some results are also available from deterministic simulation studies. Recently, Lindgren et al. (2008) and Danusevičius and Lindgren (2010) published research giving support for higher gain per unit time for strategy 5 (Field candidates pair-wise forward). Strategy 4 (Field candidates backward) seems to be at least equivalent to the current strategies 1 and 2 (Seedling candidates backward) and 3 (Field phenotype forward) (Danusevičius and Lindgren 2002a, 2002b and Danusevičius and Lindgren 2003). It is also known that strategy 7 (Seedling candidates clonal forward) gives the highest gain possible under Swedish breeding conditions, provided that test material can be clonally replicated in an efficient manner (Rosvall 1999).

Based on the literature, experience, current discussions and investigations, and preliminary simulation studies, some comments can be made on the alternative strategies.

Important characteristics of the different breeding strategies are summarised in Table 5. Genetic gain per unit time depends on selection intensity and accuracy, and the time required to complete the breeding cycle. Resources to increase selection accuracy in genetic tests will always compromise selection intensity. The greater the number of progeny used for testing each selected tree, the fewer are the parent trees that can be tested. Testing also adds time to the cycle. Using the concept of “realised selection intensity”, we consider how selection restrictions and conditions limiting the opportunity to select the best trees also affect finding good mate pairs and how this influences selection intensity. By “complexity” of the breeding archives, we consider that managing top-grafts of both sexes is more complicated than simply planting trees for breeding purposes.

Strategy 3 (Field forward) as implemented here for within-family selection, is an extreme in terms of high selection intensity and short cycle time, but it is the least accurate strategy because a tree is never replicated or tested across environments. Progeny testing and backward selection is the other extreme, characterised by low selection intensity and high accuracy, but requiring a long cycle time. The other alternatives are compromises in terms of selection intensity, accuracy and cycle time, by using combinations of forward selection and various ways for testing the candidates. Clonal testing combines high accuracy with moderately high selection intensity and short cycle time, and is thus the most efficient method of testing in terms of test progeny per candidate tested. The mating design has no importance with respect to long-term average genetic gain in the breeding population. However, the mating design (and unequal family sizes) can be used to create a within-population structure to enhance gain in a part of the breeding population, and thus increase potential gain in the production populations, i.e., by using PAM. Strategies using backward selection will result in a list of trees with accurate breeding values that could be used for selection of the 50 final breeders and to develop a mating design with precise assortment. Strategies that plan the mating on breeding values of selected trees from forward selection will have less precise assortment, due to less precise breeding values.

In strategy 5, however, to save time and avoid progeny testing, an excess of less-accurately forward-selected candidates are mated “on speculation”, with the option for correction by future selection. The reduction in “backward” selection options due to undesired mate combinations and reduced forward selection intensity in the less desirable families has to be compensated for by accelerating the cycle. In this case, more than one mating per candidate and positive assortative mating is a prerequisite for increasing the probability of mating the best trees in the breeding population and avoid mating a good tree with those that will later be rejected. Thus, the less precise mate assortment causes selection restrictions that will decrease realised selection intensity.

Strategy 6 has a high accuracy for the “backward” selection option and moderately high backward selection intensity. In the polymix progeny trial, there will be few progeny trees per father mated to each mother (averaging 4) but many trees per father (averaging 1 200) over all mothers. It will be interesting to study by computer simulation what the effective selection intensity can be for fathers by optimising selection of fathers over all polymix families. It will also be interesting to see how many trees must be DNA tested before finding an acceptable representation of fathers. More has to be learned also about the variation in mate success of fathers in a pollen-mix.

The strategies also differ in the breeding population’s ability to support selection to production populations, such as seed orchards and clone mixes. Progeny testing and clone tests give rise to more accurate breeding values, which may be preferred in a production population as compared to forward selected trees with a slightly higher, but less accurate individual breeding values. Seed orchards, however, are assembled from many selections resulting in expected high mean orchard value, despite a large variation in true individual breeding values. As a practical concern, trees selected forward will often be small and produce few suitable scions, while backward selections often are represented by many older grafts, providing a better supply of scion material for orchard establishment. Such differences have to be considered when the best options for long-term breeding are chosen.

PHOTO: ERIK VIKLUND

Table 5. Characteristics of the alternative breeding strategies. Realised selection intensity considers the influence of selection and mating restrictions. Mate plan considers the opportunity to mate final selections and find suitable pairs. The complexity of the breeding archives considers managing top-grafts of both sexes.

Strategy	Realised selection intensity	Selection accuracy	Mate plan	Number of crosses	Breeding archive	Field testing	Cycle time	Cost per year	Potential gain per year
1. Seedling candidates backward – basic	Low	High	Precise	Many Two rounds	Simple	One	Long	Low	Moderate
2. Seedling candidates backward – intense	Low	High	Precise	Many Two rounds	Intense	One	Long	Moderate	Moderate
3. Field forward	High	Low	Moderate	Few	Complicated Small	One	Short	Low	Low
4. Field candidates backward	High	High	Precise	Few Many OP[1]	Complicated	Two	Long	Low	Moderate
5. Field candidates pair-wise forward	Moderate	Moderate	Moderate under PAM	Moderate	Complicated	One	Short	High	High
6. Field candidates polymix forward	High for mothers Low for fathers	High and low	Moderate	Moderate	Complicated	One	Short	High	High
7a. Seedling candidates clonal forward without breeding archive	Moderate	High	Precise	Few	Complicated	One	Short	Moderate	High
7b. Seedling candidates clonal forward with breeding archive	Moderate	High	Precise	Few	Simple Large	One	Short	High	High

1) OP is open pollination

PHOTO: BO GÖRAN BACKSTRÖM/SKOGENBILD

SPECIES-SPECIFIC PROGRAMMES

In this section, we summarise suggestions to be considered when revising the Scots pine strategy. We also give some suggestions to be considered when continuing the current plans for Norway spruce and broadleaved species. Since the original programme suggested for lodgepole pine was changed before being put into practise, the new strategy already implemented is presented in more detail.

Ola Rosvall
Curt Almqvist
Dag Lindgren
Per Ståhl
Bo Karlsson
Bengt Andersson
Johan Kroon
Tore Ericsson
Lars-Göran Stener

SCOTS PINE BREEDING STRATEGY

Based on the experience and investigations summarised in this report, we present some general recommendations for development of a new pine strategy. The final revision of the pine strategy can be confirmed when computer simulations are complete.

Generally, for the best use of resources, an alternative to the present Scots pine breeding strategy should be a flexible combination of alternative strategies, rather than just one prescription. The strategies can vary among populations as well as among parts of a population. Regardless of the strategy chosen, the time schedules for field experiments, breeding archives and propagation archives must be carefully planned and prepared in advance, so that sequential activities of testing, selection and mating can be effectively synchronised.

Three stages of development for Scots pine breeding populations can be distinguished where different strategies are appropriate:

1. For those populations of Scots and lodgepole pine that are about to be crossed in the near future, and generally in the long term, clonal testing is of greatest interest, as described in strategy 7 (Seedling candidates clonal forward). The results so far have been sufficiently good to warrant gathering experience on an operational level. In addition to directing effort towards clonal testing, more resources should also be spent on improving this technology to support operational activities. The supportive research should include managing clonally replicated breeding archives on forest sites close to breeding stations.

2. For most of the pine breeding populations, the next activity is to select and breed F1 trees located in field experiments. For these situations, there is a choice between selecting 50 trees by forward selection, as in strategy 3 (Field forward), or to select additional candidates for further testing before breeding the new generation, as in strategy 4 (Field candidates backward), 5 (Field candidates pairwise forward) and 6 (Field candidates polymix forward). To gain experience, it is worthwhile to carry out all these options as large-scale experiments at the size of a whole population, even if the simulation studies may prefer one over the others. For this purpose, it should be planned to select about 100–300 candidates for breeding and not just the 50 needed for strategy 3.

If following strategy 4 (Field candidates backward), and if open pollination is not used for progeny testing, polymixes should be from selected trees and used to allow for forward selection, i.e., following strategy 6 (Field candidates polymix forward).

For all these alternative strategies (3, 4, 5 and 6), the operation starts with selecting young trees in a field experiments followed by grafting into an archive, so that breeding can be done without loss of time. A carefully planned breeding archive with field-grown trees for top-grafting must be established in advance. There is no time to lose for developing these breeding archives. Research resources should be directed in parallel to support these activities and to improve the technology for controlled crosses.

PHOTO: MATS BILDSTRÖM/SKOGENBILD

3. For breeding populations already following the current main strategy 1 (Seedling candidates backward) with an established archive, and in those cases where no F1 field experiment is available for forward selection, it would be preferable to either make pair crosses, as in strategy 5, or to use a polymix composed of selected pollen parents for progeny testing, as in strategy 6. In both cases, this allows for both forward and backward selection.

The final optimisation of resource allocation for these strategies and a fair comparison among them by computer simulation is yet to be completed. To put any optimised strategies into practice, new tools are required to enable optimised-contribution selection, rolling-front population management, linear deployment, etc., and the consequences of applying these tools require further investigation. A step in this direction will be to evaluate MATEPLAN as a complement to TREEPLAN®.

Finally, the cost of the time delay between achievement of gains in the breeding population and delivery of the improvement as regeneration material should be emphasised. It is urgent to take any means to shorten this delay by means of propagation archives for seed orchard trees, rooted cuttings for clonal testing of the new breeding generation and ultimately to develop vegetative propagation methods such as somatic embryogenesis.

SPECIES-SPECIFIC

NORWAY SPRUCE BREEDING STRATEGY

In general, the current breeding strategy for Norway spruce is already the best strategy from all perspectives, genetic as well as economic. This has been demonstrated repeatedly by computer simulations. Experiences from practical breeding also favour the programme.

Operational problems with implementation generally centre on time to promote flowering and complete the prescribed DPM crossing scheme. Improving nursery practices for growing of seedlings and replicating them by cuttings while avoiding C-effects has been a continuous task.

At this time, there is no recommendation to change the Norway breeding strategy, however, this investigation suggests considering more flexibility by relaxing the DPM mating system and the number of ramets planted per clone, in favour of increasing the number of clones to be tested. It also suggests that a detailed operational plan is required for the breeding activities, including timing of field measurements, planting the breeding archive, top-grafting selected clones, flower stimulation, etc. The cost functions could be extended and used to show the value of investing in methodology that shortens the time from measurement/selection to planting the next-generation trees.

PHOTO: LE CARLSSON/SKOGENBILD

LODGEPOLE PINE BREEDING STRATEGY

The initial breeding plan for lodgepole pine was similar to that for Scots pine (SP) and the two plans were originally presented together (Danell et al. 1993, Wilhemsson & Andersson 1993). Based on research findings, operational experience and analysis of different breeding strategies, a new breeding plan for lodgepole pine has evolved and been put into practice.

Lodgepole pine (LP) is the most-used exotic tree species in Swedish forestry. Today it covers some 600 000 hectares. After a peak of planting LP in the late 1980s, the annual planting decreased – a trend that has only recently reversed. forest production has led to increased planting of LP. Changing tree species to LP is now recognised as the most efficient way to enhance forest production in northern Sweden (Rosvall et al. 2004, Simonsen et al. 2008). LP is also considered to have limited environmental consequences when deployed under current guidelines (Andersson et al. 1999, Engelmark et al. 2001).

LP is easy to handle in almost any breeding strategy, due to its early male and female flowering, and relative ease of propagation through rooted cuttings, making it amenable to clonal testing and short generation turnover.

INITIATION OF A LP LONG TERM BREEDING PROGRAMME

The introduction of LP in Sweden has been accompanied by extensive collections of material and much research. Systematic provenance testing started in the 1960's. The first plus-tree selection in natural forests in Canada for grafting trees into seed orchards in Sweden was initiated by two forest companies in the early 1970's. A third company used plus-trees selected in the oldest Swedish plantations. In the late 1970's, a cooperative of forest companies initiated and financed a seed orchard programme to make Sweden self-sufficient in genetically improved LP seed. This programme included new plus-tree selection in natural forests in Canada, genetic field testing, and establishment of seedling seed orchards.

The largest number of Canadian plus-trees selected in the late 1970's by Skogsförbättring (now Skogforsk) (Bartram 1979) originates from the recommended provenance areas for LP in Canada (Figure 3). The main selection areas were interior British Columbia, the Yukon Territory and to some extent also in Alberta. Due to phytosanitary trade restrictions, plus-trees from this second round of selection could only be imported to Sweden as seeds. Trees selected earlier and imported as scions were incorporated into the new long-term breeding programme, which started in the late 1980's (Ericsson 1993).

FOUNDER POPULATIONS

There are a total of 3232 plus-trees available as candidates for the LP breeding population. These include plus-trees imported as grafts, selected progenies from plus-trees, and selections in commercial Swedish plantations. Depending on their origin, these can be separated into three groups:

- old Canadian tested plus-trees from the first selection in Canada and grafted in Sweden;
- young Swedish untested plus-trees selected in regular Swedish plantations; and
- young Swedish F1 plus-trees selected in best open-pollinated (OP) families in Swedish progeny tests of the second plus tree selection in Canada.

The old Canadian plus-trees (128 trees) were selected mainly in mature natural stands in Canada. Scions and OP seeds from these trees were imported into Sweden to establish the first seed orchards in the 1970's and 80's. They were grafted into seed orchards (SCA), and into clone banks (initially STORA, now Bergvik Skog AB), and later progeny tested together with the imported OP seeds from the Canadian plus trees selected later (see below).

The young Swedish untested plus-trees (193 trees) were selected in commercial LP plantations in northern Sweden and grafted into clone archives at Sävar.

The young Swedish F1 plus-trees (2911 trees with up to 5 sibs per OP family) were selected from field-planted OP progeny from the second batch of Canadian plus trees. OP progenies from 1142 of these newly selected Canadian plus-trees were used to establish seedling seed orchards and OP family tests. The young Swedish F1 plus-trees were selected in the best 941 of these OP families. The selected trees are grafted into clone archives at Sävar and Brunsberg. A portion of the F1-population, selected in the southern-most seed orchards, is also available in a F2-test series (a total of 379 tested F1s).

This plus-tree material covers much of the native distribution range of LP north of latitude 50°N in Canada, and represents an excellent starting point for Swedish long-term breeding. In addition, it is possible to include some more trees by selection in full-sib families from crosses among the first imported Canadian plus trees. These crosses were carried out in three of the oldest seed orchards by the Swedish University of Agricultural Sciences (SLU) in the 1980–90's and put out in field tests (Fries 1987).

FORMATION OF BREEDING POPULATIONS

Currently, the plan is to structure the LP breeding populations as 11 advanced-generation breeding groups that cover the climate variation in northern Sweden (Figure 4, Wilhemsson & Andersson 1993). This is a smaller number of populations than for Scots pine and Norway spruce (NS), since LP:

- will not be used for planting in the same scale as the native species;
- is more broadly adapted to climate gradients than SP; and
- long-term gene conservation is carried out within its native distribution in Canada.

Each closed population has at least 50 unrelated trees giving a meta population of some 550 trees.

In the original breeding plan, the LP breeding populations were to comprise trees selected based on progeny test

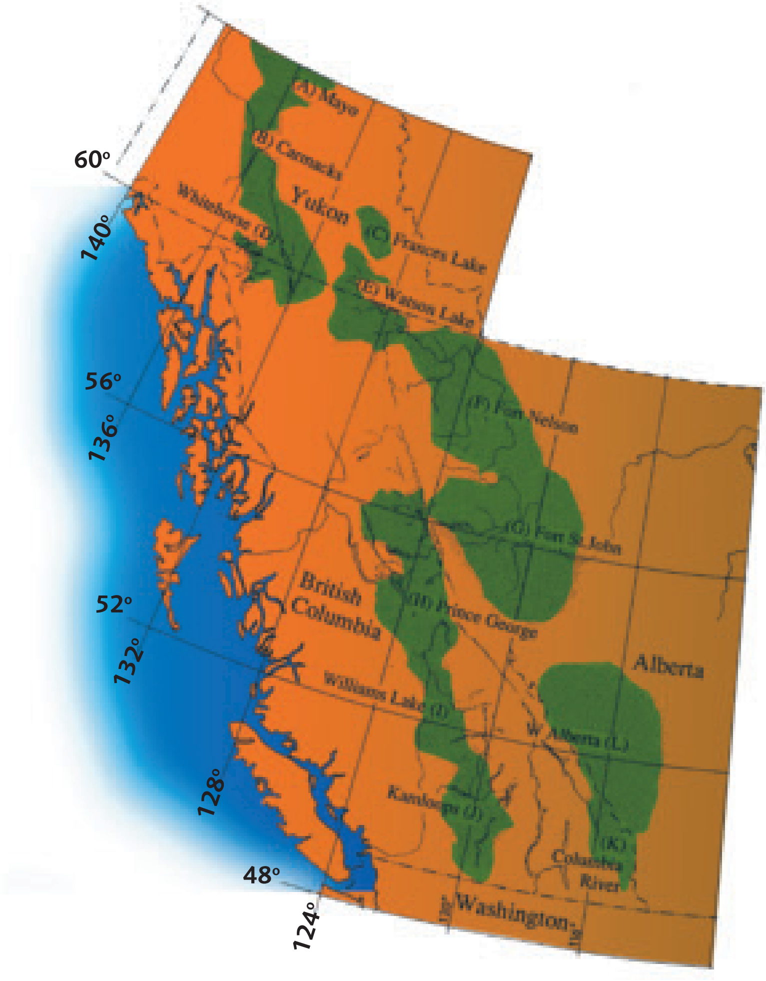


Figure 3. Provenance origin of lodgepole pine in Sweden.

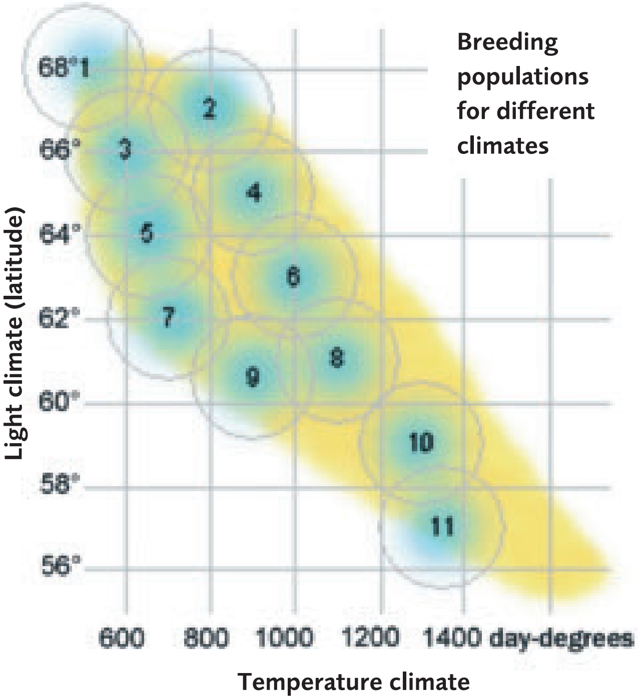


Figure 4. Breeding populations of lodgepole pine in Sweden.

results, i.e., backward selection of the young F1-candidate trees, selected in field tests and of the plus trees selected in commercial plantations. This strategy will now be changed, as outlined below, and the selection of trees for each breeding population will be by forward selection in full-sib families, facilitated by clonal replication.

LONG-TERM BREEDING

Current activities. Based on analysis of possible breeding alternatives, the dead-end progeny testing of candidate trees, stipulated in the original breeding plan, has been changed to pair crosses among candidate trees, allowing for combined backward and forward selection in new F2 generation field tests. This option best utilises resources already invested in the breeding, and provides options for long-term breeding and selection into seed orchards. A new generation of trees for forward selection is formed without delay.

The current mating scheme uses positive assortment (PAM) and double-pair mating (DPM) among all F1 plus-trees that were selected earlier in field trials and grafted in clonal archives. Crossing all candidates, including all selected half sibs per OP family and not just the 50 best per population, will make the best use of genes from the unknown Canadian pollen parents. Genetic variance and selection opportunities are increased in the new generation. DPM provides accuracy for backward selection and PAM will increase the probability to make good mate combinations for forward selection. In addition, clonal replication is applied on a large scale, to increase the accuracy of forward selection. Breeding and mass propagation will be facilitated through parallel establishment of field tests and a new clone archive (in a favourable environment), with all clones represented. The next generation can then be established through crosss in the clone archive, and scions can easily be harvested for grafting of seed orchard trees, without unnecessary delay.

Long-term strategy. After the initial round of field tests for selection, the general breeding strategy of LP follows the same principles as that for Norway spruce (NS) (Danell et al. 1993). The strategy optimises resources for maximum genetic gain per unit time, together with conservation of genetic diversity (Rosvall et al. 1998, Rosvall & Mullin 2003).

The selected breeding parents represent almost all families (essentially within-family selection), and are crossed by DPM under PAM to generate a new recruitment populations. Production populations such as seed orchards are assembled by intense selection from a few adjacent populations, allowing for strong among-family selection.

Although, conservation of gens is of less importance in LP, maintenance of genetic diversity remains important to assure continuous long-term gain from breeding. It is also important to manage relatedness and inbreeding within the breeding populations to avoid consequences of inbreeding depression.

BREEDING OBJECTIVES

The breeding of an exotic species like LP emphasises its capacity to adapt to its new economic and biological conditions, including both abiotic and biotic factors, all of which are likely to be affected by climate change. The breeding of LP is still in an early phase and much about its behaviour and genetics is still to be learned for an efficient breeding and domestication process. As an example, wind stability of planted LP is a major problem and has to be improved. This has now been attributed to poor silviculture practices (nursery and soil preparation practises and planting on unsuitable sites) that have resulted in asymmetrical root systems. However, LP stems are more elastic than those of Scots pine, which influences its capacity to withstand snow and wind loads. LP also has a less wide-spreading root system and a greater tendency, especially at young ages, to allocate more biomass to needles and branches than Scots pine (Rosvall 1994). Possibilities to improve weaknesses have to be considered when further developing the breeding objectives.

In general terms, the breeding of LP focuses on trees that are efficient in using limited resources, and grow stem wood more rapidly. The objectives of operational breeding today are:

- **Adaptation**

  Survival

  LP is characterised by good survival, high resistance and tolerance to most stresses. In a new and changing climate, however, high vitality and survival is paramount. LP is less sensitive to photoperiod and temperature regime than is Scots pine. Autumn hardiness develops more quickly in LP than SP, so that seed sources can be used over wider gradients.

  Resistance to wind and snow

  There has been a general problem with the stability of planted LP, especially on unsuitable soils with a dense texture. Wood elasticity affects stem stiffness and its ability to resist heavy snow and strong winds.

  Disease resistance

  A general resistance to fungi damage, e.g., the fungal pathogen Gremmeniella abietina, is important.

  Insect resistance

  A general resistance to insect damage is required. Occasional insect damage occurs, e.g., from pine weevils (Hylobius spp.), and the defoliator Neodiprion sertifer.

  Resistance to animal browsing

  Damage to LP by moose is not currently significant. It is of interest, however, to increase resistance to damage from other animals, such as field voles.

- **Production**

  Unit-area stem wood yield

  The stem is the primary source of economic returns to the forest owner and is the focus for yield improvement. Trees that combine good survival and fast growth, give high unit-area productivity and a short rotation.

  Stem-wood yield capacity and efficiency

  Rapid early development depends on tree capacity to acquire resources when abundant, while stand growth under competition depends on efficient use of limited resources.

- **Quality**

  Stem quality

  Yield and product quality are enhanced in stems with desirable branch characters and straightness.

Wood quality

Wood density and fibre quality (limited spiral grain) must be maintained to give a stable, uniform and high-value yield. Structural value is related to stiffness, as represented by modulus of elasticity.

A selection index is constructed from the measured traits, their heritabilities, and economic weights of the breeding objectives.

The methodology of vegetative propagation for clonal field testing should be studied and analysed considering C-effects (environmental effects that are "common" to a group of relatives and thus confounded with genetic effects) and dominance effects. If these effects are present, test accuracy may be reduced. However, these effects are thought to be of most concern at young ages and diminish over time.

DEPLOYMENT OF IMPROVED MATERIAL

The best available tested parents should be used when new seed orchards are to be established. If used in equal proportions, about 15 clones should be established; this is the same as for native species and gives sufficient genetic variation for commercial plantations. To maximise orchard gain, the selection of trees will be made from more than one breeding population. Using optimised deployment methods (linear deployment, etc.) will determine the absolute number of trees in proportion to their breeding value and genetic diversity. Since there is less contamination by external pollen in lodgepole pine seed orchards, gain will be higher (and genetic diversity lower) than in orchards of native species.

Current options for seed orchards. Tested trees for immediate establishment of grafted seed orchards can produce substantial genetic gain. New orchards will be composed of both old plus-trees selected backward based on progeny tests and young plus-trees selected forward in the best field-tested OP-families. These seed orchards are expected to give a total gain in growth rate of about 25% (Rosvall et al. 2001). Within 15 years, after evaluation of clonal tests, the potential gain from future seed orchards is predicted to reach 32–36% (selecting trees over three neighbouring breeding populations). Information from current clonal archives facilitates selection among the young plus trees.


THOMAS ADOLFSÉN/SKOGENBILD

There is also an option to use more intense genetic thinning to enhance gains from current seedling seed orchards.

Long-term breeding gains

Prolific early flowering and ease of clonal propagation make LP a good species for tree improvement, with shorter generations and higher rates of genetic improvement than for Norway spruce or Scots pine. In addition, lack of background pollination enhances realised gain in seed orchards.

The progeny tests also indicate that heritability for growth traits is higher for LP than for SP (Ericsson 1994). In combination with the row-plot design used in older field tests, this ought to have made the selection of the Swedish "Young" F1 plus-trees efficient (Ericsson 1993, Ericsson et. al. 1994, Ericsson & Danell 1995). At present, there are considerably more "Young" untested plus-trees than "Old" tested plus-trees – 3104 and 128, respectively. Thus, higher selection intensity in the "Young" plus-trees can potentially compensate for lower selection accuracy. Progeny test data for the young trees will be available in about 10 years.

Breeding gains for LP under alternative long-term strategies have been quantified by Rosvall (2000, 2006). Long-term gain for a programme initiated with 50 trees would give 5% gain per generation in the breeding population for individual forward selection and 11% gain for clone testing, corresponding to an annual gain of 0.26 and 0.65% per year, respectively. In general, additional gain from a seed orchard with 12 clones will be 6–7%, due to among-family selection.

PHOTO: ERIK VIKLUND

BROADLEAVED SPECIES

Breeding efforts for broadleaved species have varied considerably over time. During the period 1940–1960, there was a rather intensive start-up period, which all but ceased between 1960 and 1980. Increased interest in broadleaved species in the 1980's initiated a resurgence of breeding effort for a number of broadleaved species.

Today's planting of broadleaved species is carried out at a very low level; 2–3 million plants (mainly birch) are planted annually, compared with about 350 million conifer seedlings. There are no indications of any major change, but there is an increasing interest to develop knowledge and well-adapted regeneration material for many broadleaved and exotic species, as part of the overall strategy for adaptation to climate change. Species other than Norway spruce or Scots pine should be considered, to spread the risk of regeneration investments to meet uncertain future environmental and economic conditions. At present, there is also an increasing interest in biomass for energy production. This has increased focus on high-yielding species such as hybrid aspen and poplars. The scenario of climate change will probably increase interest in the "noble" species, such as beech and oak and to some extent ash, wild cherry, lime and maple, but the plantation area for these species is still expected to be very limited.

Overall, the breeding plan developed for broadleaved species in 1995 is still valid, although priorities for investment in the different broadleaved species requires further discussion, especially under scenarios of increased energy demand and climate change. It is thus suggested that more emphasis should be put on hybrid aspen and poplar and less on birch, while also increasing efforts on oak and perhaps beech, compared to other species.

General breeding outlines – All species

Due to the varying importance and interest in the different broadleaved species, breeding goals vary. These differences are important when dimensioning breeding programmes, and are summarised in Table 6.

Silver birch is the only broadleaved species that is currently bred with a long-term programme. Species belonging to the class "Progeny testing and selection of the best genotypes to seed orchards" (Test_Sel) are planned for 1 or 2 generations of breeding. Plans for hybrid aspen and poplars include testing and selection of existing clones for commercial use (TestC_Sel). Crossing activities to produce new aspen and poplar varieties are suggested if increased utilisation of these species is forecasted.

Table 6. Description of breeding and conservation ambitions for different broadleaved species

Species	Gene conservation[1]	Breeding level[2]	Priority	Target area
Betula pendula	B	Cont_Breed	1	Götaland, Svealand, s. Norrland
P. tremula x P. tremuloides	C	TestC_Sel	1	Götaland, Svealand, s. Norrland
Populus spp.	C	TestC_Sel	1	Götaland, Svealand, s. Norrland
Acer platanoides	C	Test_Sel	3	Götaland
Alnus glutinosa	C	Test_Sel	3	Götaland
Alnus incana	C	Test_Sel	3	Götaland, Svealand, s. Norrland
Betula pubescens	C	Test_Sel	3	Götaland, Svealand, s. Norrland
Fagus sylvatica	C	Test_Sel	2	Götaland
Fraxinus excelsior	C	Test_Sel	3	Götaland
Prunus avium	C	Test_Sel	3	Götaland
Querqus borealis	C	Test_Sel	2	Götaland, Svealand
Querqus petrea	C	Test_Sel	2	Götaland, Svealand
Querqus robur	C	Test_Sel	2	Götaland, Svealand
Tilia cordata	C	Test_Sel	3	Götaland

1 A=sufficient genetic variation for evolution (not used for these species); B=sufficient genetic variation for breeding; and C=sufficient genetic variation for mass propagation

2 Cont_Breed=Continuous long-termed breeding; Test_Sel=Progeny testing and selection of the best genotypes to seed orchards; and TestC_Sel=Clonal testing and selection of the best genotypes to mass propagation.

The main priority is for efforts on birch, hybrid aspen and poplar, and to some extent oak and beech.

Current breeding – Birch

A total of 1300 founders were selected, originating mainly from Sweden, but also Finland, the Baltic States, Poland and Germany (Figure 5). For the most part, founders are currently being tested in field trials as OP progenies (Zone B1–B4) or as cloned founders (Zone B4); testing has thus been more intensive in the southern-most zone. Today there are breeding values or genotypic values available for most plus trees, and selection of the best plus-trees to each breeding population is on-going.

Seven breeding populations cover Sweden from south to north (Figure 6). In each population, about 50 trees will be selected and bred to generate a new recruitment population. The breeding plan is currently the same in all populations, i.e., similar to the spruce breeding strategy: 50 parent clones per population, each clone represented in two crosses (families), 40 individuals within each family selected after one year, each of them vegetatively propagated (16 ramets/clone) and planted on up to four test sites, where finally the best individuals per family are selected based on their genotypic values. The breeding in zones B1–B3 (populations 1–3) has so far been carried out according to the original plan, with plus-tree selection and OP progeny testing. The next step is selection and producing crosses within each population.

The plan has been modified for zone B4 (populations 4–7), as a consequence of the low interest in birch. The efforts in each of the four populations have decreased. Instead, an elite population for the entire deployment area of Götaland and southern Svealand was created, consisting of the top 30 clones, to increase genetic gain in the short

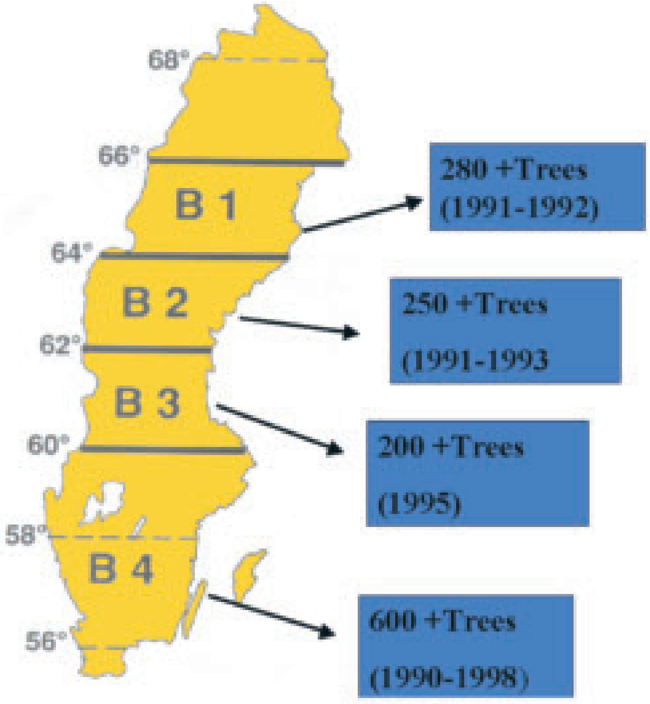


Figure 5 Administrative breeding zones for birch used at the re-start of birch breeding in 1988. These zones are now "history" and replaced by the distribution of breeding populations (see Figure 6).

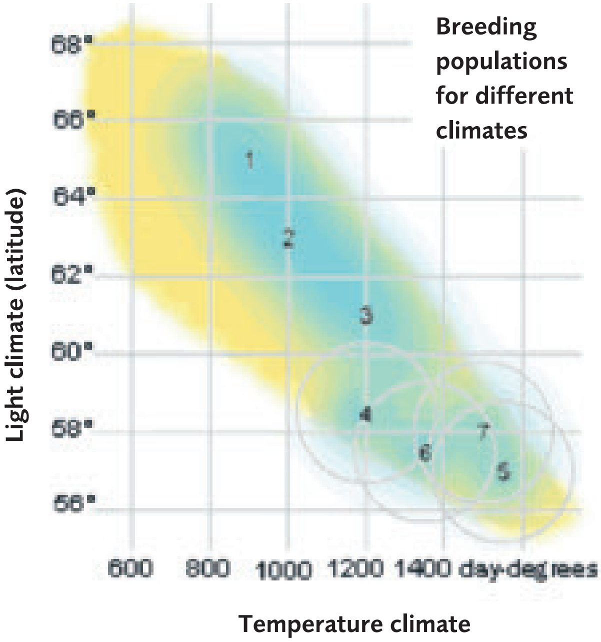


Figure 6 Breeding populations for birch.

PHOTO: BO GÖRAN BACKSTRÖM/SKOGENBILD

term. The future generations of this elite population will depend on infusion of new, unrelated material from the breeding populations, since inbreeding and sterility problems will increase after some generations of breeding.

FUTURE BREEDING – BIRCH

Given the current budget constraints and low interest in planting birch, as well as the increasing emphasis on hybrid aspen and poplars, the breeding strategy for birch should be revised. The clonal testing strategy is efficient but expensive and could be questioned as an overall strategy for all breeding populations. The use of selected clones in a clonal forestry programme was one argument for clonal testing in the current plan, although this does not seem to be realistic for birch in the near future. A more cost-efficient strategy needs to be developed that is in balance with the current deployment of birch.

Furthermore, the intensity and the strategy for birch breeding in the different zones needs to be re-examined. If the priority is set in proportion to the deployment of birch, more emphasis should then be put on southern Sweden. Furthermore, if the only purpose of birch breeding is to improve planting stock in the short term, there is an option to utilise material from Finnish seed orchards in central and northern Sweden. Finnish birch breeding has been quite intensive since the 1960's and is now in its 2nd or 3rd cycle. Tests of Finnish seed orchard materials compared to Swedish plus-tree material at four locations in Sweden (latitudes 60°, 62°, 64° and 65°) do not show many statistical significant differences among the tested materials, but generally indicate that the Finnish birch is superior. There are currently Finnish seed orchards that could cover central and northern Sweden from latitudes 59.5° to at least 63.5° (zone B3 and partly zone B2).

LITERATURE

Almqvist, C. 2010. Topgrafting Pinus sylvestris – a tool for increased efficiency in breeding programmes. In: Proceedings from IUFRO Working Party 2.09.01 conference Seed orchards and the link to long-term tree breeding in response to climate change. 8-11 September, 2009, Jeju, Korea. (in press).

Almquist, C., & Ekberg, I. 2001. Interstock and GA4/7 effects on flowering after topgrafting in Pinus sylvestris. Forest Genetics 8: 279–284.

Almqvist, C., Eriksson, M. & Gregorsson, B., 2009. Cost functions for variable costs of different Scots pine breeding strategies in Sweden. Arbetsrapport 669, Skogforsk.

Andersson, E.W. 1999. Gain and Diversity in Multi-Generation Breeding Programs. Acta Universitatis Agriculturae Sueciae. Silvestria 95: 42 pp+4 chapters.

Andersson, B., Engelmark, O., Rosvall, O. & Sjöberg, K. 1999. Miljökonsekvensbeskrivning (MKB) av skogsbruk med contortatall i Sverige. (Environmental impact analysis (EIA) concerning lodgepole pine forestry in Sweden.) Skogforsk, Redogörelse nr 1, 1999. 50 p.

Bartram, V.C. 1979. The Swedish lodgepole pine selection project (Work report no. 199, Institute for Forest Improvement, Uppsala 1988), 78 pp. Prince George.

Berlin, M. 2009. Development of economic forest tree breeding objectives. Doctoral thesis. Acta Univ. Agric. Sueciae 2009:90. SLU, Uppsala. 35 pp. ISBN 978-91-576-7437-1.

Borralho, N.M.G. (1995) The impact of individual tree mixed models (BLUP) in tree breeding. In Proc. CRCTHF-IUFRO Conf. Eucalypt Plantation: Improving Fibre Yield And Quality, 19–24 Feb., Hobart. Edited by B.M. Potts et al. CRC for Temperate Hardwood Forestry, Hobart, Tasmania. pp. 141–145.

Borralho, N.M.G. & Dutkowski, G.W. 1996. A ‘rolling front’ strategy for breeding trees, Tree Improvement for Sustainable Tropical Forestry, Caloundra (Australia), pp. 317–322.

Borralho, N.M.G. & Dutkowski, G.W. 1998. Comparison of rolling front and discrete generation breeding strategies for trees. Can J For Res 28:987–993.

Burdon, R.D. & Kumar, S. 2004. Forward versus backwards selection: Trade-offs between expected genetic gain and risk avoidance. NZ J. For. Sci. 34(1):3–21.

Danell, Ö. Wilhelmsson, L. Andersson, B. Karlsson, B. Rosvall, O. Werner, M. 1993. Breeding programmes in Sweden. Corrected reprint from: Lee, S.J. (ed.), Progeny testing and breeding strategies, Proc. from a meeting with the Nordic group for tree breeding, October 1993 (Arbetsrapport nr 302 1995, SkogForsk), 25 pp. Forestry Commission, Edinburgh.

Danuseviöius D. & Lindgren D. 2010. Efficiency of breeding strategy where grandparents - but not parents - contribute equally to the breeding population. Ann. For. Sci. 67: 404.

Danuseviöius, D. & Lindgren, D. 2002a. Efficiency of selection based on phenotype, clone and progeny testing in long-term breeding. Silvae Genet. 51: 19–26.

Danuseviöius, D. & Lindgren, D. 2002b. Two-stage selection strategies in tree breeding considering gain, diversity, time and cost. Forest Genetics 9: 145–157.

Danuseviöius, D. & Lindgren, D. 2003. Progeny testing preceded by phenotypic pre-selection – timing considerations. Silvae Genet. 53, 1: 20–26.

Danuseviöius, D., Lindgren, D. 2005. Optimization of breeding population size for long-term breeding. Scand. J. For. Res. 20: 18-25.

El-Kassaby, Y.A. & Ritland, K. 1992. Frequency-dependent male reproductive success in a polycross of Douglas-fir. Theor. Appl. Genet. 83: 752–758.

El-Kassaby, Y.A. & Lstib□rek, M. 2009. Breeding without breeding. Gen, Res. 91: 111-120.

El-Kassaby, Y.A., Prescher, F. & Lindgren, D. 2007. Advanced generation seed orchards' turnover as affected by breeding advance, time to sexual maturity, and costs, with special reference to Pinus sylvestris in Sweden. Scandinavian Journal of Forest Research 22:88–98.

Elfving, B., Ericsson, T. & Rosvall, O. 2001. The introduction of lodgepole pine for wood production in Sweden. For. Ecol. Manage. 141 (1–2): 15–29.

Engelmark, O., Sjöberg, K., Andersson, B., Rosvall, O., Ågren, G.I., Baker, W.L., Barklund, P., Björkman, C., Despain, D.G., Elfving, B., Ennos, R.A., Karlman, M., Knecht, M.F., Knight, D.H., Ledgard, N.J., Lindelöw, Å., Nilsson, C., Peterken, G.F., Sörlin, S. & Sykes, M.T. 2001. Ecological effects and management aspects of an exotic tree species; the case of lodgepole pine in Sweden. In: Andersson, B., Engelmark, O., Rosvall, O & Sjöberg, K. (eds.), Environmental impact analysis of lodgepole pine introduction in Sweden. Forest Ecology and Management 141: (1–2), 3–13.

Ericsson, T. 1993. Provenance qualities of the Pinus contorta breeding base in Sweden (Report no. 4 1993, Skogforsk – Forestry Research Institute of Sweden), 33 pp. Uppsala.

Ericsson, T. 1994. Lodgepole pine (Pinus contorta var. latifolia) breeding in Sweden – results and prospects based on early evaluations. Dissertation Swedish University of Agricultural Sciences, Faculty of Forestry, Department of Forest Genetics and Plant Physiology. Umeå p 1–32.

Ericsson, T. & Danell, Ö. 1995. Genetic evaluation, multiple-trait selection criteria, and genetic thinning of Pinus contorta var. latifolia seed orchards in Sweden. Scand. J. For. Res. 10: 313–325.

Ericsson, T., Danell, Ö. & Andersson, B. 1994. Genetic variation in Pinus contorta var. latifolia breeding material in Sweden. Can. J. For. Res. 24:723–729.

Fernandez, J. & Toro MA (2001) Controlling genetic variability by mathematical programming in a selection scheme on an open-pollinated population in Eucalyptus globulus. Theor Appl Genet 102:1056–1064.

Frampton, J., Goldfarb, B., Surles, S. E. & Lambeth, C. C. 1999. Nursery rooting and growth of loblolly pine cuttings: effects of rooting solution and full-sib family. Southern Journal of Applied Forestry 23: 108–116.

Frampton, J., Li, B. & Goldfarb, B. 2000. Early field growth of loblolly pine rooted cuttings and seedlings. Southern Journal of Applied Forestry 24: 98–105.

Fries, A. 1987. Genetics of plus tree progenies of lodgepole pine (Pinus contorta ssp. latifolia), and possible implications for a breeding program in Sweden. Ph.D. thesis, 62+ pp. Umeå: Swedish Univ. of Agr. Sci., Dept. of Forest Genetics and Plant Physiology.

Fries, A. & Kaya, Z. 1996. Parameters affecting shoot production and rooting of cuttings from lodgepole pine hedges. New forests 12: 101–111.

Gooding, G. D., Bridgwater, F. L., Bramlett, D.L. & Lowe, W. J. 2000. Topgrafting Loblolly Pine in the western gulf region. Proceedings: 25th Biennial Southern Forest Tree Improvement Conference. New Orleans, Louisiana, USA. July 11–14. 1999. pp 60–66. Southern Forest Tree Improvement Committee.

Groen, A.F. (1989). Cattle breeding goals and production circumstances. Ph.D. thesis, Wageningen Agricultural University, The Netherlands, 167 pp.

Hallander, Jon. 2009. Novel methods for improved tree breeding. Doctoral diss. Dept. of Forest Genetics and Plant Physiology, SLU. Acta Universitatis agriculturae Sueciae vol. 2009:13. 50 pp.

Hallander J,, & Waldmann P. 2009. Optimum contribution selection in large general tree breeding populations with an application to Scots pine. Theor. Appl. Genet. 118: 1133-1142.

Hannerz, C. & Almqvist, C. 2000. Nya fröplantager behövs för att trygga tillgången på förädlat frö. (Resultat Nr 22 2000, Skogforsk), 4 s.

Hannerz, M., Eriksson, U., Wennström, U. & Wilhelmsson, L. 2000. Tall- och granfröplantager i Sverige – en beskrivning med analys av framtida fröförsörjning.

Hannrup, B., Cahalan, C., Chantre, G., Grabner, M., Karlsson, B., Le Bayon, I., Jones, G.L., Müller, Ü., Pereira, H., Rodrigues, J.C., Rosner, S., Rozenberg, R., Wilhelmsson, L. & Wimmer, R. 2004. Genetic parameters of growth and wood quality traits in Picea abies (L.) Karst. Scand. J. For. Res. 19: 14-29.

Hannrup, B., Jansson, G. & Danell, Ö. 2008 Genotype by environment interaction and optimum test size in Pinus sylvestris (L.). Silvae Genetica 57:(6) 306–311.

Hannrup, B., Jansson, G. & Danell, Ö. 2009 Comparing gain and optimum test size from progeny testing and phenotypic selection in Pinus sylvestris (L.). Can. J. For. Res. 37:1227–1235.

Jansson, G., Li, B. & Hannrup, B. 2003. Time Trends in Genetic Parameters for Height and Optimal Age for Parental Selection in Scots Pine. Forest Science 49(5): 696–705.

Johnson, G.R. 1998. Parental GCA testing: How many crosses per parent? Can. J. For. Res. 28: 540–545.

Kerr, R.J., Goddard, M.E. & Jarvis, S.F. (1998. Maximising genetic response in tree breeding with constraints on group coancestry. Silvae Genet. 47: 165–173.

Lambeth, C., Lee, B.C., O'Malley, D. & Wheeler, N. 2001. Polymix breeding with parental analysis of progeny: an alternative to full-sib breeding and testing. Theor. Appl. Genet. 103: 930–943.

Li H & Lindgren D. 2006. Comparison of phenotype and combined index selection at optimal breeding population size considering gain and gene diversity. Silvae Genetica:13-19.

Lindgren, D. & Matheson, A.C. 1986. An algorithm for increasing the genetic quality of seed from seed orchards by using the better clones in higher proportions. Silvae Genetica 35:(5–6) 173–177.

Lindgren, D. 1977. Genetic gain by progeny testing as a function of mating design and cost. Third world consultation on forest tree breeding Canberra), pp. 1223–1225.

Lindgren, D. 2003. Low-input tree breeding strategies. In Eucalyptus Plantations – Research, Management and Development, R.-P. Wei and D. Xu (eds.), World Scientific, Singapore, 149–166.

Lindgren, D. 2005. Unbalances in tree breeding. In Fedorkov A (editor) Status, monitoring and targets for breeding programs. Proceedings of the meeting of Nordic forest tree breeders and forest geneticists, Syktyvkar 2005, ISBN 5-89606-249-4: 45–56.

Lindgren, D. & Danuseviöius, D. 2004. Thoughts about possible implications for Swedish forest tree long term breeding from breeding cycler studies. http://www.genfys.slu.se/staff/dagl/Reflections/LongTerm04/default.htm.

Lindgren, D, & Mullin, T.J. (1997) Balancing gain and relatedness in selection. Silvae Genet 46:124–129.

Lindgren, D & Wei RP 2007.

Low-input tree breeding strategies. In Proceedings of the IUFRO Division 2 Joint Conference: Low Input Breeding and Conservation of Forest Genetic Resources: Antalya, Turkey, 9-13 October 2006. Edited by Fikret Isik. p 124-138.

Lindgren, D., Danuseviöius, D. & Rosvall, O. 2008. Balanced forest tree improvement can be enhanced by selecting among many parents but keeping balance among grandparents. Canadian Journal of Forest Research 38(11): 2797–2803.

Lindgren, D., Danuseviöius, D. & Rosvall, O. 2009. Unequal deployment of clones to seed orchards by considering genetic gain, relatedness and gene diversity. Forestry, 82:17-28.

Lindgren, D. Prescher, F. 2005. Optimal Clone Number for Seed Orchards with Tested Clones. Silvae Genetica 54 2: 80-92.

Lstibürek, M. 2005. Population response to positive assortative mating in forest tree breeding. Doctoral thesis, N.C. State University, Raleigh, NC. 149 pp.

Lstibürek, M., Mullin, T.J., Lindgren, D. & Rosvall, O. 2004a. Open-nucleus breeding strategies compared with population-wide positive assortative mating I. Equal distribution of testing effort. Theor. Appl. Genet. 109: 1196–1203.

Lstibürek, M., Mullin, T.J., Lindgren, D. & Rosvall, O. 2004b. Open-nucleus breeding strategies compared with population-wide positive assortative mating II. Unequal distribution of testing effort. Theor. Appl. Genet. 109: 1169–1177.

Lstibürek, M., Mullin, T.J., Mackay, T.F.C., Huber, D.A., and Li, B. 2005. Positive assortative mating with family size as a function of predicted parental breeding values. Genetics, 171: 1311-1320.

McKeand, S. & Raley, F. 2000. Interstock effects on Topgrafting in Loblolly Pine. Proceedings: 25th Biennial Southern Forest Tree Improvement Conference. New Orleans, Louisiana, USA. July 11–14. 1999. pp 121–123. Southern Forest Tree Improvement Committee.

Medina Perez, A.M., White, T.L., Huber, D.A. & Martin, T.A. 2007. Graft survival and promotion of female and male strobili by topgrafting in a third-cycle slash pine (Pinus elliottii var. elliottii) breeding program. Can. J. For. Res 37:1244–1252.

Menzies, M.I., Faulds, T. & Dibley, M.J. 1992. Production of radiata pine cuttings for plantation in New Zealand. Acta Hort. 319: 359–364.

Meuwissen, T.H.E. 1997. Maximizing the response of selection with a predefined rate of inbreeding. J Anim Sci 75:934–940.

Meuwissen, T. H. E. 2009. Accuracy of breeding values of 'unrelated' individuals predicted by dense SNP genotyping. Genet. Sel. Evol. 41(1): 2. Published online 2009 January 5. doi: 10.1186/1297-9686-41-2.

Meuwissen, T.H.E., Hayes, B.J. & Goddard, M.E. 2001. Prediction of total genetic value using genome-wide dense marker maps. Genetics 157: 1819-1829.

Moriguchi, Y., Prescher, F. & Lindgren, D. 2008. Optimum lifetime for Swedish Picea abies seed orchards. New Forests 35: 147-157.

Mullin, T.J., Lstibürek, M., Rosvall, O. & Lindgren, D. 2005. Korsa utvalda träd i rangordning – och låt dessutom de bästa få fler avkommor. I: Årsbok 2004. Föreningen Skogsträdsförädling s 2–12. Uppsala.

Mullin, T.J. & Park, Y.S. 1995. Stochastic simulation of population management strategies for tree breeding: a new decision-support tool for personal computers. Silvae Genet. 44(2–3): 132–141.

Olsson, T. 2001. Parameters, relationship and selections in pines. Acta Universitatis Agriculturae Sueciae. Silvestria. 192: 27 pp+4 chapters.

Ponzoni, R.W., Newman, S. 1989. Developing breeding objectives for Australian beef cattle production. Anim. Product. 49: 35–47

Remröd, J., Lundell, S., Pettersson, W. & Rosvall, O. 2003. Svenska skogsfröplantager 2020 – Nationell plan för den 3:e omgången fröplantager i Sverige. (Arbetsrapport 548, 2003, Skogforsk), 16 s.

Rosvall, O. 1994. Contortatallens stabilitet och motståndskraft mot vind och snö. Skogforsk, Redogörelse nr 2, 1994. 50 ss.

Rosvall, O. 1999. Enhancing Gain from Long-Term Forest Tree Breeding while Conserving Genetic Diversity. Acta Universitatis Agriculturae Sueciae. Silvestria 109: 65 pp+4 chapters.

Rosvall, O. 2000. Förädling av contortatall – preliminär jämförelse av olika teststrategier. Internal investigation document, Skogforsk, 8 pp.

Rosvall, O. 2001. Hög förädlingsvinst med nya fröplantager. New seed orchards give high genetic gain. Skogforsk, Resultat nr 1, 2001. 4 s. (also as Results No. 2, 2001.)

Rosvall, O. 2003. Zon- och ägarvisa plantagearealer för tredje omgången fröplantager i Sverige. (Arbetsrapport 549, 2003, Skogforsk), 46 s.

Rosvall, O. 2006. Långsiktig förädling av contortatall – beslutsunderlag för nystart 2006. Internal investigation document, Skogforsk, 10 ss.

Rosvall, O. & Almqvist, C. 2003. Möjligheter att "rulla" in nya plusträd i tallfröplantager. Arbetsrapport från Skogforsk nr 553, 2003. 9 s.

Rosvall, O. & Mullin, T. J. 2003. Positive assortative mating with selection restrictions on group coancestry enhances gain while conserving genetic diversity in long-term forest tree breeding. Theor. Appl. Genet. 107: 629–642.

Rosvall, O. & Eriksson, B. 2002a. Nya fröplantager i Sverige – underlag för strategiska beslut. Skogforsk, Arbetsrapport nr 499. 27 s.

Rosvall, O. & Eriksson, B. 2002b. Dags att anlägga nya fröplantager – en viktig framtidssatsning. Time to establish new seed orchards for the future. Skogforsk, Resultat nr 22, 2002. 4 s.

Rosvall, O. & Lindgren, D. 2003. Fröplantager till låg kostnad? (Arbetsrapport 551, 2003 Skogforsk), 18 s.

Rosvall, O. & Lundström, A. 2010. Förädlingseffekter i Sveriges skogar – kompletterande scenarier till SKA-VB 08. (Arbetsrapport 702, 2009, Skogforsk), 35 s.

Rosvall, O. & Wennström, U. 2008. Förädlingseffekter för simulering med Hugin i SKA 08. (Arbetsrapport nr 665, 2008, Skogforsk), 38 s.

Rosvall, O., Lindgren, D. & Mullin, T. 1998. Sustainability robustness and efficiency of a multigeneration breeding strategy based on within-family clonal selection. Silvae Genet. 47: 307–321.

Rosvall, O., Lindgren, D. & Ruotsalainen, S. 1999. Högre vinst utan diversitetsförlust. I: Årsbok 1988. Föreningen Skogsträdsförädling 9–16 ss. Uppsala.

Rosvall, O., Jansson, G., Andersson, B., Ericsson, T., Karlsson, B., Sonesson, J. & Stener, L.-G. 2001. Genetiska vinster i nuvarande och framtida fröplantager och klonblandningar. Genetic gain from present and future seed orchards and clone mixes. Skogforsk, Redogörelse nr 1, 2001. 41 ss.

Rosvall, O., Jansson, G., Andersson, B., Ericsson, T., Karlsson, B., Sonesson, J. & Stener, L.-G. 2002. Predicted genetic gain from existing and future seed orchards and clone mixes in Sweden. In: Haapanen, M. & Mikola, J. (eds.), Integrating tree breeding and forestry. Proceedings of the Nordic Group for Management of Genetic Resources of Trees, meeting at Mekrijärvi, Finland, March 23–27, 2001 (Research Papers 842, Finnish Forest Research Institute), 71–85. Vantaa. ISBN 951-40-1822-2.

Rosvall, O., Mullin, T.J. & Lindgren, D. 2003a. Controlling parent contributions during positive assortative mating and selection increases gain in long-term forest tree breeding. Forest Genetics 10: 35–54.

Rosvall, O., Peichen, G. & Simonsen, R. 2006. Den gamla skogen står i vägen för den nya. I Utvecklingskonferens 2006. Redogörelse Skogforsk nr 2, 94–104.

Rosvall, O., Wennström, U., Almqvist, C., Andersson, B., Karlsson, B. & Sonesson, J. 2003b. Underlag för operativ planering av tredje omgången fröplantager (TreO) i Sverige. (Arbetsrapport 550, 2003, Skogforsk), 43 s.

Ruotsalainen, S. 2002. Managing breeding stock in the initiation of a long-term tree breeding program. Finnish Forest Research Institute, Research Papers 875: pp 95+61.

Sánchez, L. 2000. Balanced vs. slightly unbalanced selection. Heredity 84:685–691.

Simonsen, R., Rosvall, O. & Gong, P. 2008. Lönsamhet för produktionshöjande skogsskötselåtgärder hos Holmen Skog AB. [The profitability of Silvicultural methods for raising forest increment at Holmen Skog AB]. Skogforsk, Redogörelse, nr. 2. 35 ss.

Skogforsk. 1995. Strategi för framtida skogsträdsförädling och framställning av förädlat skogsodlingsmaterial i Sverige ("Förädlingsutredningen"). (Utredning

95–06–20. Red. Urban Eriksson. Skogforsk), 259 s + bilagor. Uppsala 258 s.

Skogsstyrelsen. 2008. Skogliga konsekvensanalyser 2008-SKA-VB 08. Rapporter 2008:25. Jönköping 145 s.

Toro, M.A. & Nieto, B. 1984. A simple method for increasing the response to artificial selection. Genet Res 44, 347–349.

Torimaru, T., Wang, X.-R., Fries, A., Andersson, B. & Lindgren, D. 2009. Evaluation of pollen contamination in an advanced Scots pine seed orchard. Silvae Genet. 58: 262-269.

Wang, X.-R., Torimaru, T., Lindgren, D. & Fries, A. 2010. Marker-based parentage analysis facilitates low input 'breeding without breeding' strategies for forest trees. Tree Genetic and Genomes 6: 227-235.

White, T.L., Hodge, G.R. & Powell, G.L. 1993. An advanced-generation tree improvement plan for slash pine in the southeastern United States. Silvae Genet. 42: 359–371.

White, T.L., Matheson, A.C., Cotterill, P.P., Johnson, R.G., Rout, A.F. & Boomsma, D.B. 1999. A nucleus breeding plan for radiata pine in Australia. Silvae Genet. 48: 122–133.

Wilhelmsson, L. & Andersson, B. 1993. Breeding programmes in Sweden: 2. Breeding of Scots pine (Pinus sylvestris) and lodgepole pine (Pinus contorta ssp. latifolia). In: Lee, S. J. (ed.), Progeny testing and breeding strategies, Proceedings of the Nordic group of tree breeding, October 1993, 135–145. Edinburgh: Forestry Commission.

Ye, T. Z., Jayawickrama, K. J. S. & St Clair, J. B. 2009. Realized Gains from Block-Plot Coastal Douglas-Fir Trials in Northern Oregon Cascades. Silvae Genet. 59 29-39.

APPENDICES 1–6

Download the appendices at **skogforsk.se/tree-breeding-programme**

Appendix 1. Polymix breeding with selection forwards (Arbetsrapport 687)

Appendix 2. Kompletterande strategier för det svenska förädlingsprogrammet (Arbetsrapport 674)

Appendix 3. Number of pollen in polycross mixtures and mating partners for full-sibs for breeding value estimation (Arbetsrapport 672)

Appendix 4. Återkoppling till förädlingsverksamheten från utredningsarbetet med nya fröplantager

Appendix 5. Alternative strategies for Scots pine breeding in Sweden. Description of strategies for Scots pine breeding that should be considered in the revision of the Swedish breeding programme.

Appendix 6. Cost functions for variable costs of different Scots pine breeding strategies in Sweden. (Arbetsrapport 669)