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# The role of tree breeding in reforestation

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## Abstract

This article focuses on the creation of seed sources for forest planting or seeding with a special focus on clonal seed orchards supporting planting Norway spruce and Scots pine in Sweden. Supporting long-term breeding and low input breeding is discussed. The focus is not on clonal forestry, although this is discussed. Natural regeneration is not dealt with and provenance choice only briefly. It is not a manual or literature review and focus on my own evaluations, but more detailed reviews can be found in the literature cited. It is intended to contribute some familiarity with many of the relevant genetic aspects on forest plantations.

## Keywords

Seed Orchard, Long-Term Breeding, Low-Input Breeding, Domestication, Genetic Diversity, Adaptation

## Contents

## 1 Choosing among existing seed sources

The choice of source for seed collection, plant growing, and plants for individual plantation (cultivation) should be made based on actual information. The world is constantly changing. The climate changes. The knowledge changes. The experimental information increases. The goals are variable and changing. Sites are different. Some seed sources are limited but their availability can change. There are other factors than just genetics to take into consideration.

## 2 Domestication of trees

Trees have been evolving for millions of years. Tree seeds spread on the ground which causes their regeneration. The conditions for this type of “natural” regeneration differ from plantations at the beginning of tree life. In a mature forest the differences between planted trees and “natural” trees are often fairly small and probably of limited importance. Plants are raised in nurseries where many seeds develop into acceptable plants. In nature one seed among perhaps hundreds may become a plant, and one among thousands develop into a mature tree. The conditions in a nursery are optimized for producing large, healthy, and similar plants for successful plantation in an economical way. Nowadays, plants are often produced in plugs. To insure a smooth and efficient nursery operation, one seed per pot is seeded and as a result most seeds give raise to planted plants, which is very different than in nature! The plants are often prepared in some way, e.g. to resist insects. To stimulate good root development, the plants may be grown in a container with some added nutrition and sometimes mycorrhiza. Plantation (regeneration) is often done on a site with little competition from other trees, and is well prepared, where the nutrition situation is acceptable. Planting is done at a decent and prepared spot within the plantation where immediate competition is low. The plants develop into rather similar trees. Not many are outcompeted and the plants develop fast, reducing competition from other vegetation and quickly reach a size when sensitivity to different types of injuries is reduced. Young forests are usually managed by pre-commercial thinning to release competition and give room for promising trees to develop.

Seed crops for planting serve wide areas with varying conditions, where most of the production origin is from the seed crop. In nature the seeds of local trees serve a very limited area and are in constant competition with other species.

Thus, tree breeding can be seen as domestication where genotypes become adapted for the needs of the forester and environment. For this reason plants are raised in nurseries and planted on prepared and managed sites. Thus the selection of trees founding the breeding population or copied in seed orchards should preferably be done in planted forests or controlled experiments. After the selection of founder trees, domestication can be interpreted as an integration with tree breeding, as test plants are produced in nurseries and planted in test plantations followed by evaluation and selection.

## 3 Provenances and genetic tests

Plantation forestry may demand characters which justify the use of other provenances or species than the local. When the test plantation and evaluation over a range of test plantations have a larger chance of improving the material than a test with the local provenance, which may be claimed to be in their natural environment. E. g. local provenances of Scots pine on harsh, high elevation sites in northern Sweden result in a low and uncertain survival, therefore more northern origins are used for plantation. Selection based on tests can be assumed to add a benefit in tree improvement compared to local provenance.

A test plantation differentiates from commercial plantations. Exact positions are often desirable to make the test plants identifiable. Competing vegetation is removed to a higher extent than in an ordinary plantation. More attention is given to plant production and the site than in commercial plantations. Fencing may be used to avoid animal browsing more often than in commercial plantations. Test plantations are often done with denser spacing than commercial plantations to make the test smaller and thus cheaper and easier to manage. Test locations often span a wider range of locations than where the tested material is expected to be the best choice. Thus what I call domestication is not perfect but certainly important. Experimental plants in the future may be identified by their exact location or by tracking chips, which provides an easier and quicker way to remove non-experimental plants. Decisions based on testing are usually done after a short period of the rotation time. This is good breeding economy (see below). One argument as why not to wait long for using results is that the early performance in establishing a stand is important and has a value in itself. It is also important to mention that improvement should be easier in the early stages of growth where conditions are very different from the natural evolution that trees have adapted to. For mature trees it is evident that a greater size and rapid growth is an advantage. Therefore the environment in a planted forest compared to a natural forest is probably not very important for large trees, thus natural selection would have made trees suitable for the conditions in the mature forest, and it may be more difficult to make trees that grow better when they reached the mature stage. The disadvantage of not basing decisions mainly on rotation of old trees may not be as important as it appears to be at first glance.

## 4 Local adaptation

“Local is best” - It is often argued that local sites have adapted for a large number of generations to the environment of the site.

There is generally a clinal adaptation to temperature and light on a national scale in Sweden which works rather fast (e.g. trees that do not harden off sufficiently when winter is approaching will not survive). Thus “provenance” behavior can sometimes be roughly predicted based on origin. However, for Scots pine in the North, the local adaptation is not sufficient for planting but a “hardier” provenance is selected. For this reason local adaptation may not be best for silviculture.

“Adaptation” has been based on historic conditions and not to the environment (site) of the actual plantation. Sites change over time with variations in climate, atmosphere transports and with changes in the biosphere and by anthropogenic influences. The adaptation is not to the site itself, but to other sites in other times. Genes can move across large distances with pollen and seeds. Thus "local adaptation" refers to an area and to past conditions in an unclear way. For plantations, seeds are wanted that are not good just for a single specific site, but for a wide range of sites and environments. Therefore, the saying "local is best" is trustworthy only when testing experience and theoretical arguments do not contradict the hypothesis.

## 5 Naturals may fill in where planted plants fail

Planted plants sometimes fail and cause "holes" in the plantation. Naturals can help to fill in the space available, this is an argument against leaving large areas without relevant seed sources, and to avoid ground preparation methods, which remove all existing naturals. Naturals may improve plantation results. Sometimes it is better to plant with wide spacing in hopes of giving room for the natural regeneration of other species that can contribute to a limited part of the production and create biodiversity on the species level.

## 6 Clonal seed orchards

Originally seed orchards were mostly made by choosing attractive mature trees in the forest and multiplying them by grafts. One hundred grafts of each tree could be planted on land suitable for seed production, cone harvest and cover an area that is sufficient for rational management and obtain a pollen cloud. By grafting, the mature characters of the mature trees were kept which promoted early and rich flowering. It was thought that the selection in the forest of "plus trees" was intense and effective.

## 7 Seed orchards – since long the major output for forest tree breeding in spite of objections

Seed orchards are a major output for forest tree breeding. They have supported industrial conifer forestry with economically important seed supply programs for over sixty years. Seed orchards are often regarded as an outdated technology that are soon to be replaced. The development of seed orchards over time has been surprisingly slow. They are usually similar and managed analogously, usually following the guidelines by Larsen (1934) in his pioneering seed orchard suggestions. Neither seed orchards seem to be very efficient. Seed yield is often only a percent of what a grain farmer could produce. From measurements in the source population (breeding population), based on which clones for the seed orchard are selected, till the last plantation originating from the seed orchard is often half a century. Thus it is a long way from the best of the breeding population to the forest. Vegetative propagation or control cross seeds offer a greater gain. Large efforts to create more efficient outlets for the breeding effort, mainly vegetative propagation, have been done, and some have succeeded like in many *Eucalyptus* programs. But less than a few percent of Swedish forest plant production uses clonal propagation techniques or controlled crosses. GMO is hardly used in the forests of the world in spite of efforts for several decades. Often a considerable part of a seed orchard crop has fathers outside the orchard. Seed orchards still remain the major supplier to forestry for improved forest regeneration material. Investments in seed orchards still are motivated and done. Swedish forestry supports seed orchard programs planned to cover the full seed need for the most important species for almost all of the forest plants produced, when all initiated seed orchards reach seed production age. The largest conifer plantation program in the world is loblolly pine in South-East USA since 1960 with around one billion tree seedlings planted annually. Approximately 85% of these originate from open-pollinated seed orchards, 8% from controlled crosses in seed orchards and 2% from tested clones (McKeand et al. 2015). An overview of seed orchards can be found in Lindgren (editor) (2008) following a seed orchard conference 2007. Information can also be found on the homepage of the IUFRO working party for seed orchards (IUFRO 2016).

## 8 Seed orchards have advantages over stands seeds besides gain from tree breeding

***Less inbreeding depression***. Seed orchards generally bring together genotypes from different stands that are unrelated. Thus inbreeding and inbreeding depression tends to be lower in forests arising from seed orchard seeds compared to seed stands. It is very probable that there is a stimulating effect from heterosis (the opposite to inbreeding, “negative” inbreeding).

***More reliable seed supply***. Seed orchards constitute a more reliable and reproducible seed supply than seed stands. Stands and trees chosen for stand seed collection result in larger variations among seed lots than a seed orchard crop. Logistics of collection and cone handling are easier to handle in seed orchards, which also results in more reproducible seeds from seed orchards. To own seed orchards means to be less dependent of the market. Imported seeds means dependence on the authorities import regulations, national seed orchards constitute a more reliable seed supply.

***Good seeds.*** Seed orchards are established in a good climatic environment and suitable ground conditions for seed production. They are managed for sound seeds. Cone collection and handling is kept under control and easier to handle with fewer mistakes and more reproducible than stand collections. The seeds will usually be heavier, better filled and healthier, germinate faster and more uniform compared to stand seeds. That results in plant crops which develop faster and more predictable, making crops easier to manage and more uniform than stand collections. This results in a better forest that performs better in growth, value and survival and a more uniform forest plantation even in the absence of genetic gain. The non-genetic superiority of the seeds are expected to result in a stand that performs better in addition to the genetic advantages. If used for direct seeding, the higher quality of seed orchard seeds will produce a better result with fewer seeds than if stand seeds are used.

***Easier, cheaper and more controllable cone collection.*** Generally, seed orchards are pruned to limit their height, control crowns and sometimes to get cones down to the ground, which is often flat and managed. There is usually road access close by. The cone collection and operation management is similar to previous years. Cone collection can be done by anyone. Small operators were common earlier but seed orchards demand organization, continuity over a long period of time, and is requested by a certain size of operator which makes the operation more controllable by society. Because of this, cone harvest costs can be kept low. Harvesting costs are often the major component of seed cost. Over time seed supply will be rather predictable, reliable, and uniform. The origin is more precise, permanent and identifiable. It is easier for authorities to verify operations and quality.

***More robust regeneration material is more suitable as a response to global warming.*** Genetically improved material is based on selections and tests on multiple sites, which makes bred material more adaptable to environmental variations. When selections from different sites are composed to a seed orchard mix, it becomes still more robust to changing conditions. Natural selection knows only here and now, but breeders are smarter, they consider an average response over a range of environments and time. Breeders use more efficient tools than evolution and natural selection!

## 9 An example of improved Scots pine

Two photos from 10 x 10 tree plots in a Scots pine trial 30 km NE Umeå at age 15 are shown below (Fig. 1 and 2). The site index measured as upper height is 8.1 m for the improved material and 5.9 m for the stand progeny reference. The genetic gain can be considered similar to raising the site index. The improved trees look similar to the non-improved supporting the interpretation that genetic gain is similar to increase in site index.

Figure 1. and 2. Progeny from intensively selected pines (left) and Stand progeny (right). Photo by Björn Elfving

## 10 Flexibility

Neither target area nor genetic output of a seed orchard is engraved in stone once the establishment decision is made. If the environment changes, perhaps because of a warmer climate, the target area of the seed orchard can be modified. A selection of a seed orchard as seed source for a plantation need not follow the justifications for the establishment of the seed orchard decades ago.

The genetic characteristics of the crop will change when the pollen production raises and pollen contamination decreases, thus a young orchard may be used for a different area than a mature one. Genetic thinning can improve the genetic quality of the crop. Supplementary pollination can improve the genetic quality of seed orchard grafts and artificial crosses can easily be made in a seed orchard. In some cases it may be beneficial to amplify the best part of the harvest by clonal propagation. Old seed orchards should be replaced with newer, genetically improved material. But seed demand, the need for back-ups and often the need for ground for establishing new seed orchards regulate when outdated seed orchards are finally retired. Harvests from different clones in a seed orchard differ in genetic value, thus harvesting the best clones may be better than using alternative seed sources even when the average crop is no longer the best alternative.

Bred material will be better suited over a range of different environments, which is an advantage for cultivation forestry.

## 11 Social problems

Seed orchards are best placed on fertile, flat, and accessible land where pollen contamination is low. That means that former agricultural land is often most suitable. This new land-use may have difficulties when it comes to local acceptance. In mature forest tree breeding programs, new seed orchard developments are often localized to old ones. New seed orchards replace the old ones, which the neighbors are already accustomed to. There are also problems with acceptance of plantations, but this problem of acceptance is more focused on the cultivation of the forest than the actual tree improvement itself.

## 12 Selfing in clonal seed orchards

In clonal seed orchards there are many copies of the selected trees. It is known that selfing is negative and efforts have been made to keep trees of the same clone apart. Inbreeding depression following selfing is on average expected to often reduce growth more than 50%, if measured as performance in large experimental plots. However, such results considerably overestimates the effect of selfing in a seed orchard. First off, there is “pollen contamination”. All fertilizing pollen does not originate from seed orchard genotypes. It often seems to be the case that half of all fertilizing pollen in a seed orchard originates from pollen parents, which are not in the seed orchard. Secondly, selfing often results in a dead embryo. This contributes to a reduced seed set and is a problem for the seed orchard manager because it increases cost and reduce production of seed orchard seeds, but does not reduce forest production. Third, all seeds are not sown and not all plants are planted. Some are discarded or outcompeted in the nursery, thus the frequency of selfing is lower among planted plants than among seeds. Fourth, if trees differ in their capacity to utilize the ecological space, the better trees will utilize more and the worse will utilize less of it. If there are selfed trees that suffer from inbreeding depression or die, they will partly be compensated by the increased growth of non-selfed trees which will utilize some ecological space that has been made available. For conifer seed orchards the forest production and reduction caused by selfing in seed orchards is seldom more than one percent (discussion e.g. Lindgren and Prescher 2005; Rosvall and Lindgren 2012).

## 13 Relatives in seed orchards

Inbreeding caused by relatedness among trees in an orchard like sibs will cause inbreeding depression. This milder inbreeding may be more harmful than selfing, as it is more likely to result in marginally handicapped trees, which may ultimately cause larger production losses in the mature forest than selfing. Trees generally have a rather high genetic load, which means that selfing seldom results in vital progeny, while milder inbreeding may result in considerable inbreeding depression. It may still be rational to have relatives in seed orchards. Seedling seed orchards require related genotypes. For advanced generation orchards it will be inoptimal to rely only on unrelated clones (Danusevičius and Lindgren 2008; Lindgren et al. 2009; Ahlinder et al. 2014). The sacrifice in the loss of potential gain by excluding all relatedness will be inefficiently high. It would be necessary to dive deep down in estimated breeding value to find unrelated clones. Rosvall and Lindgren (2012) estimated the loss due to inbreeding depression by relatives in the forest established from a seedling seed orchard to less than one percent. The gene diversity will be lower if there are relatives and this problem may be more limiting than inbreeding. For an optimal advanced generation seed orchard design it seems important to use an algorithm which allows the use of clones in different proportions and punish self-fertilization harder than sib-fertilization. This leads to increasing the proportion of some clones more often instead of including relatives in high proportions.

## 14 Seedling seed orchards

Seedling seed orchards can be an alternative to clonal seed orchards. They are cheap and easy to establish. Grafts are sensitive to different types of animal damage, whereas seedlings are often less sensitive. Most producing seed orchards of Lodgepole pine in Sweden are seedling seed orchards. Grafts were not used because of phytosanitary considerations. The risk of importing pests from Canada was seen as considerable with grafts. However, using open pollination from plus trees in the source forest for seedling seed orchards have the big disadvantage that the fathers of the seeds are not selected and unknown. Thus this type of seedling seed orchards is mainly used in low budget situations. A seedling seed orchard may in the same time be a progeny test, a source for selection of trees for the next cycle of breeding and a timber producing forest.

Comparisons of grafts and seedlings grown in seed orchard conditions by Rosvall and Lindgren (2012) have shown that grafts produce more seeds and pollen while the trees are young. As the seed orchard ages, seedlings can have a similar reproductive output as grafts.

In advanced generations, “selection forwards” is usually practiced in breeding populations and could be discussed for orchard clones as well. Trees are selected not just for their own performance, but also for the performance of their relatives. For optimizing gain, the selected trees may be rather young and small. They then produce few twigs. Preferably, the selections should not be harmed by intensive twig harvests as it is desirable to later verify their performance. Thus seedling seed orchards following crosses among selections may be an alternative in advanced generation orchards. Crosses among selections have the same expected breeding value as the selections, but the expected time till full seed production and, in particular, pollen production of seedlings may still make seedling seed orchards an inefficient alternative to grafts. Low twig production can be compensated by a cycle of grafting to get twigs from grafts. This costs time and money but may be worth it.

Selfing will be less common than clonal seed orchards in absence of genetically identical replications. Selfing in clonal seed orchards is generally a limited problem, but the problem ought to be smaller in seedling seed orchards.

## 15 Protected seed production

In some species and circumstances seeds are produced under protected conditions for example plastic tents. This offer advantages, including eliminating pollen contamination, and can even be used for adding good pollen as fathers. This has not been done for most major species.

## 16 Pollen contamination

Fertilizing pollen from outside the seed orchard is important. Sweden is more or less filled with a national pollen cloud of pine and spruce therefore places with little fertilizing pollen cannot be found. General and efficient remedies have been difficult to find where this contamination is large. Reducing or eliminating such contamination will probably get a higher priority, as long-term breeding raises the potential gain and thus loss by contamination. Often seed orchard operators have to adapt to pollen contamination. Some possible reactions to pollen contamination are: to deliberately choose locations where the expected contamination has reasonable genetics, arrange for hedges around the seed orchard, let grafts in the border of the seed orchard grow tall, reduce the contamination with available methods even if they have limited effects, adjust the target area to predicted contamination, and welcome the positive effects of contamination (fewer seeds lost by selfing, more diversity and less inbreeding)! Seed collection may be done in a recently established seed orchard with superior selections even when pollen production has not started and pollen contamination is at its highest point. The genetic quality of the recently selected mothers may compensate a high impact of unimproved fathers and thus seed collection is often justified in young seed orchards where pollen production is still low (Prescher 2007). Recent results indicate that even in Sweden pollen contamination may not always be high. (Funda et al. 2015).

## 17 Keeping seed harvests from different clones separate

Clonal seed orchards may be harvested using clones. In nurseries uniform plants are obtained, which is an advantage for plant production. Genetic differences between clones can be utilized. Genetically superior clones can be used where their superiority results in the highest advantages, usually where the site index is high. Seed price may be related to genetic quality. Seeds from lower ranking clones may be kept in storage as reserves. Clones from an even lower ranking may not be harvested for years when the seed need seems limited. Harvests from low ranking clones may be used for direct seeding. When a seed orchard becomes genetically outdated, seeds harvested from the best clones may still be competitive.

## 18 Genetic diversity of the crop

Genetic diversity usually results in a higher and safer biological production. Similar genotypes interact more intensively in competition for resources and can suffer more from pests or environmental changes. Low genetic diversity results to a higher and more unpredictable interaction with the environment, thus more unpredictable crop performance. The loss in expected production (including risks) may not be high and if the low/no diversity crop is a small part of the landscape, the risk for surrounding stands and biodiversity in general is low. Genetic diversity is often demanded by legislation and it is desirable for public relations, customer and authority acceptance, and/or it may be the policy of the owner. Genetic diversity has a public relation and market value. Diversity of seed orchard crops is often expressed just as a clone number, but more sophisticated ways exist. Extra diversity in a seed orchard offers options for later genetic thinning and selective harvesting, thus genetic diversity can later be converted to gain. Sometimes seed orchards are blamed for their ecological impact, but plantation forestry may be a more proper target for such criticism rather than tree improvement itself. A product is more valuable if it is uniform and that could be a reason for low genetic diversity.

## 19 What about Environmental considerations?

Most worries about plantations are connected to the planting itself instead of the characteristics of the plants. Forest tree breeding results in better crops which establish well, and the increase in establishment ability and productivity can itself be regarded as an environmental problem. If a forest grows better and utilizes the available resources well, there is less room for others which can be regarded as a problem. Productivity can also be associated with a larger sensitivity to pests and damage makers, but on the other hand, healthy trees are generally more productive. "Breeding" means tests, and if these tests suffer, that affects selection. In that way seed orchard crops are expected to have some resistance to what they are exposed to.

The genetic variance may decrease following artificial selection depending on several mechanisms. One of these mechanisms is that the breeding population and seed orchard clone population are small and thus subject to changes due to random sampling which is known as genetic drift. A different way of seeing it is that trees become more related.

Theoretically, directional selection makes trees more uniform for the selected characters, but this does not have a large effect for the low number of generations involved with tree breeding. Narrowing occurs only in the selected and associated characters but not for other characters. Even if trees are selected only for a single character, e.g. for height growth, the selection of a tree is done among a small sample of trees in a small non-systematics sample of environments at a certain age with a specific tree history. Forest tree height will not be in the same conditions and the genetic explanation to the height may vary, thus genetic variation is not much reduced. The characters of an individual tree are more dependent on the environment than its genes. Even if part of the selection is done based on a large number of progenies compared in large trials, character still depends on many genes interacting with the environment. The real genetic variation is often larger than assumed. Most (if any) characters are not target characters. Target characters are usually a combination of characters, and reduction in variation of the individual components of the selection index is less than for the index itself. Variation closely correlated to target characters is much less affected by selection than the initial mean of the characters variation and characters which are not closely correlated to the said target character is hardly affected at all. Generally the variation of bred trees overlap the variation of non-bred trees, thus for the first generations of breeding it can be stated that seed orchard crops contain trees with characters which occur in a non-bred forest.

The first phase of forest tree improvement often may be regarded as restoration to a more natural state. For several centuries forests have been creamed for trees that fit “the industry” and less desirable trees have been left to regenerate the site. The first phase of tree breeding is to select good looking trees in the forest, and that selection is likely to compensate for earlier intentional removal of such trees.

Seed orchards constitute a technique for creating future forests. This technique can be used to balance different public/state/owners desires and those desires are partly different from “production”. Thus criticism against the current seed orchards may not be criticism against the technique itself, but how the goals usually are set and balanced.

## 20 Seed orchard rotation time

It is generally inefficient to use a seed orchard for a very long time. One reason is that the cost and effort of harvesting the seeds often increases steeply with the height of the trees. Harvest costs are often the dominating factor when it comes to the cost of the seeds, which is usually more than the capital costs themselves. Another reason as to why it is inefficient to use seed orchards for a long time is that a seed orchard gets genetically outdated, as new and improved breeding stock become available. Normally, a seed orchard program should be supported by a long-term breeding program. The potential to harvest gain from that breeding program increases over time. The age of some Swedish seed orchards seem to indicate that an optimally short rotation has not been planned. Seed orchard establishment should interface with breeding efforts so the breeding stock can be efficiently creamed when selections have to be done for a planned seed orchard. The replacement of retired seed orchards serves to introduce new clones as “parents” to forests, and thus contribute to genetic diversity on a regional level. As thumb-rules for Sweden, the operative optimal rotation times of seed orchards for Scots pine has been suggested to be 30 years and for Norway spruce 40 years (Prescher 2007). It may be a good idea to maintain the mature seed orchard for a couple of extra years just in case the performance of the new orchards should fall below expectations or the demand for seeds increases. The seeds harvested from the best clones of a mature seed orchard might still be genetically compatible with harvests from a young seed orchard. When seed orchards get genetically old, often a good idea would be to renew a portion of it. Besides reusing the land, the pollen cloud fertilizing the young orchard trees will be improved.

## 21 Bred crops – response to an uncertain future!

Advanced generation breeding and production is a response to an uncertain future. The future has always been uncertain, now more than ever because of the heavy, rather unpredictable, impact of human activities. This was recently manifested by the Paris agreement December 2015 regarding climate. Reasons why improved forest trees are important for the unforeseeable future: 1) more available raw materials; 2) less dependence on finite fossil resources; 3) less carbon released into the atmosphere; 4) less deforestation; 5) a greener, more sustainable economy based on sunshine; 6) increased probability that the recently established forest will develop into a good, mature forest.

## 22 Seed orchards and the future of Mankind

Forests create the very materials that Man needs from air, water, and sunshine and recycles it back to the air and water. Seed orchard forestry is not mining, but it is sustainable and renewable. Seed orchards improve the green production apparatus each time they are harvested and create additional resources in an environmental friendly way. Seed orchards form the foundation for much of the future physical and ecological realities in our countries and are part of what we give to future generations, and so it may be seen as a moral activity.

Seed orchards are used for land managed as production or cultivated forest by planting or direct seeding. Good seed orchards raise the production and thus give more room for other land uses including “conservation” needs. Better economic output from cultivated forests will offer forest operators more room to use land for other purposes.

Seed orchards constitute a well-known, safe and rather mature technology. There is still room for improvement with the development of technologies like genomics, flower stimulation, exotics, hybrids and GMO. Seed orchards are not dependent on new innovations. Clonal propagation or crossing technology may replace seed orchards and geneticists see advantages in that. Most of these high expectations have, however, failed in the past, and a cautious attitude seems advisable until the benefits of these new approaches can be shown to supplement the need for the well-established benefits of seed orchards.

Carbon dioxide is recycled which is a problem, but ways may be found to remove it from the cycle or perhaps delay its release. The rotation time of the forest can be prolonged so that the carbon in the growing stock is larger, but that means that the delay between creaming the breeding population and the end product will be longer. The products can last long (buildings, bridges), thus store the carbon longer. The carbon may be more permanently attached to the soil. Forests remove carbon dioxide from the air, bred forests remove an even higher amount, and the problem to keep it stored somewhere after being kept away from the air for a longer period of time seems solvable.

## 23 Long term breeding

Continuously improved forests require long term breeding as a source for improved material to be deployed into forests in the future. Long-term breeding requires organization, interactions, documentation, activity and reasonable continuity. Breeding could be initiated with, for example, selections and establishments of a seed orchard, an activity restricted to what could be called short term breeding. For a reasonably sized, long-term forest operation, it is desirable to develop long-term breeding programs beyond meeting short term demands. Long-term breeding should include a sufficient genetic base which may take some time. After a few generations, the breeding population should avoid refreshment with new material. The infusion of fresh material results in a reduction in gain. It is better to assure sufficient initiation material in the first decades. Genetic diversity in breeding stock is the raw material for long term breeding and a valuable resource, which should be managed with care in a sustainable way and should not be exhausted. The genetic diversity and relatedness in the breeding stock should allow the best genetic material to be creamed for deployment to seed orchards with a high degree of improvement and at the same time desired, sufficient, or optimal diversity for deployment to forestry. To be able to deploy selections efficiently to forests with limited relatedness and sacrifice in genetic diversity in coming generations, it is important that the breeding population is large enough to limit genetic drift and that the build-up of relatedness within the breeding population is minimal. A breeding program may appear more efficient in a shorter period of time if it sacrifices diversity for gain, but much of that seemingly extra gain in the breeding stock will be lost later as the gain in the final selection step from breeding population to the forest (seed orchard) will be low if the target genetic diversity for the forest should not be problematically low. Inbreeding will accumulate if the initial base is too small and narrow and the breeding stock will not be sustainable for generations to come.

In high budget programs, which is recommended for circumstances where the value of harvested trees will be high (like major pines and spruces), I recommend to keep known pedigrees. This generally means using controlled crosses where both parents are known. Knowing pedigree, gene diversity, and relatedness can be computed and optimized. Long term organization and documentation is possible; knowledge and breeding materials shall be maintained.

***Make trees less egoistic!***

Evolution favors selfishness. “The egoistic gene” has no other goal than replicating itself. There are mechanisms modifying that, e.g. that it favors the selfish genes if relatives (in particular children) get help to prosper as they partly carry the same genes. If doves and hawks are mixed in simulations, some doves will remain as the hawks spend too much energy fighting each other. Too much egoism is inherent in individuals to function optimally in a group. For trees, the group is a stand where different genotypes interact. Individual trees benefit from taking sunlight and nutrition from their neighbors. Smart tree breeding has potential to create trees that work better together in a stand. Tree breeding techniques are still far from optimal from this aspect.

***Clone testing can be good for long term breeding!***

Clonal forestry has always looked attractive, but often failed when it comes to commercial forestry. Clones have been very successful for producing seeds for commercial forestry. Clones have a niche for multiplying a limited number of seeds with good parents. An important use of clones may be for genetic testing and selection of seed orchard clones, even where deployment in forestry has not been successful (Lindgren 2009a). Theoretically, clone testing is faster and cheaper than progeny testing and more reliable than selecting individuals “forwards”. For Norway spruce in Sweden, a huge investment in clone testing was done to choose clones for forestry, but these clones has not been much used for plantations. That “failed” investment turned out to be very fortunate! The best tested clones became seed orchard parents. Individuals from controlled crosses among the best clones are cloned and field tested. Selections from those tests will be used for new seed orchards. The main goal in long-term breeding is to make crosses between the top ranking selections and test-cloned full-sibs as a recruitment population for long-term breeding and seed orchards.

## 24 Low budget breeding

There are many breeding programs that suffer from low and unpredictable budgets with an unstable organization. Lindgren and Wei (2007) discuss this situation. Operations like controlled crosses, grafting, keeping complicated information alive and updated over many decades seem too demanding and unrealistic. The development of tree breeding as a science has mainly been driven by the needs identified by the large high-input programs. Consequently, methods suitable for high-input programs are often too implemented into low-input programs. Sophisticated or futuristic tree improvement requires plenty of resources, stable funding, efficient monitoring, control, competent and permanent technical and scientific staff and a well-developed infrastructure, is well represented in qualified literature, in scientific research, in available expertise, in speakers at conferences and in formal training programs. Methods particularly suitable for breeding with limited resources may be neglected or used inefficiently as little thought is given to adequately develop, implement, and optimize these methods. Tree breeders generally feel more motivated to focus on how things can be done well, rather than how they can be done cheap but sloppy.

There is no sharp delineation between low-input breeding and high-input breeding, choice of technique depends on specific circumstances that vary. Some techniques are still common only in low budget breeding. The “easiest” ways to get seeds are not regarded as long-term breeding. Low budget breeding techniques are identified seed collection stands; establishing seed resource stands without identified plants; thinning to improve genetic quality; fast screening of tree characteristics instead of careful measurements; assign several purposes for the same trees (seed collection areas or seedling seed orchards can in the same time be wood producing forests, candidate population, testing population and serve gene conservation purposes). Even simple clone-testing can be part of a low budget program if clone propagation is very easy and other circumstances are right, e.g. that several members of a clone can be evaluated and compared with other clones in the field. The principle “more of the best” can be used if good seed parents differ. Equal representation is not optimal when efficient ranking of parents is possible. The best parents could be overrepresented and more not top-ranking parents could contribute less to keep gene diversity high. It can be comforting for the low-budget breeder to know that simple phenotypic selection can be rather efficient (Harwood et al. 1996). Larger breeding populations are needed and some type of estimates how large breeding populations must be has be done, considering fertility variations in actual circumstances. Fathers, and even mothers, can sometimes be derived from good candidates for selection by DNA in open pollinated seeds. Provided access to DNA competence and experience in the species and breeding competence, low budget breeding can theoretically benefit from techniques to keep pedigree under control, but I think that will be the case in a few circumstances (Lindgren and Wang 2009). Polycross crosses are efficient for progeny-testing and DNA markers can be used to identify the father of the best phenotypes within the good polycross progenies and this can be used for breeding (Lindgren 2009b). However, this can hardly be called low-budget.

## 25 Genetic diversity in supporting breeding

It is beneficial if both the breeding (recruitment) population and the production population (seed orchards) utilizes somewhat more of the genetically better genomes and founder genomes than by truncation selection (either select or reject). It is not efficient or practical to overemphasize equal utilization of clones or genomes with motivation that for a certain number gene diversity is maximized for equal proportions. It is better to use them in a more gradual way according to their assumed contributions to genetic value and gene diversity. In that way, a better balance between gain and gene diversity can be obtained.

The most attractive share of the recruitment population for seed orchard deployment will become more related as generations pass, and that relatedness will be converted to inbreeding when selections are placed in a seed orchard. It is possible to arrange the breeding stock, for example, twenty unrelated selections will remain available, but it is not good breeding economy to deploy selections equally to a seed production population. It seems more optimal to allow slight inbreeding by deploying a few relatives. To keep such inbreeding low is an argument in favor of starting long term breeding efforts with many genotypes, to run the breeding population with a higher priority to avoid relatedness than avoiding inbreeding and to preserve gene diversity over generations. To keep sufficient gene diversity in the breeding population and sacrifice some immediate gain, pays back when a seed orchard is deployed if some gene diversity can be sacrificed for gain in the deployment keeping gene diversity in the seed orchard at an acceptable level.

## 26 Swedish Scots pine and Norway spruce

Swedish tree breeding has been reviewed and discussed by Rosvall et al. (2011). Some current typical values for the two major conifers in Sweden are given. The Swedish national breeding meta-population comprises slightly more than 1000 genotypes (founders, breeding population) structured in unrelated subpopulations of 50 each. Selection has a large “within family” component to keep losses of gene diversity low at generation shifts. The subpopulations have slightly different target areas and characteristics. A subpopulation is tested in target areas of adjacent subpopulations or a wider range of environments to create flexible genotypes and to be able to respond to changing environments such as global warming. A seed orchard is typically recruited from four adjacent subpopulations in addition to the major target for the seed orchard. It has been estimated that seed orchards will raise the national annual forest harvest in Sweden by approximately 10% until 2100. An individual new seed orchard is assumed to raise production more that 20% in the forest successfully established from the seed orchard seeds, but it is a long time gap in the system and all trees do not origin from seed orchards. A driving force for seed orchard establishment in Sweden has been the high plantation rate. According to Keenan et al. (2015) Sweden is fifth in the world when it comes to accumulated area of forest plantation after China, United States, Canada and Russia.

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