



Arbetsrapport

Från Skogforsk nr. 761-2012

Inbreeding depression in seedling seed orchards

Inavelsdepression i fröplantsplantager

Ola Rosvall & Dag Lindgren



SKOGFORSK

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I Arbetsrapporter redovisar Skogforsk resultat och slutsatser från aktuella projekt. Här hittar du bakgrundsmaterial, preliminära resultat, slutsatser och färdiga analyser från vår forskning.

Titel:

Inbreeding depression in seedling seed orchards.
Inavelsdepression i fröplantsplantager.

Bildtext:

Kottar i en tallfröplantage.
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Ingegerd Hallberg

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Uppsala Science Park, 751 83 Uppsala

Tel: 018-18 85 00 Fax: 018-18 86 00

skogforsk@skogforsk.se

skogforsk.se



Ola Rosvall, konsult, tidigare chefschef på Skogforsk. Arbetar med skogsskötsel och skogsträdsförädling med speciellt intresse för förädlingsstrategier som förenar framsteg med bevarad genetisk mångfald.



Dag Lindgren, professor emeritus skogsgenetik. Har under fyrtio år arbetat vid Skogshögskolan och dess efterföljare vid SLU i Umeå, till stor del med forskning för att få genetiskt bättre utsäde.

Abstract

First we calculate the rate of inbreeding depression in the progeny for various numbers of full sib families and family sizes used as parent trees in a seedling seed orchard. Then we review different factors that influence the realized impact of inbreeding depression in the progeny and discuss a few other conditions to be considered when comparing a seedling and a grafted seed orchard. An ideal seedling seed orchard with 10 full sib families and equal contribution from all trees will in theory as a first approximation produce 10 per cent inbred seed with $F = 0.25$ from within family mating assuming that selfing $F = 0.5$ produce no viable seed. Under the same assumptions the average inbreeding in all progeny is $F = 0.025$. The influence of the sib mating of seedlings on forest stand production is reduced by unrelated pollen contamination from outside the orchard, inbreeding depression on seed production, seedling mortality in the nursery, natural regeneration in planted stands and compensatory growth from non-inbred trees. For a Scots pine seedling seed orchard in Sweden with 10 full sib families we roughly estimate that less than 4 % of the trees in a stand are influenced by inbreeding depression and that stand growth reduction is less than one percent. These effects are much depending on the number of full-sib families used.

Content

Sammanfattning.....	2
Summary.....	2
Introduction	3
Coancestry and inbreeding.....	3
From coancestry of parents in a seedling seed orchard to realized inbreeding in its offspring.....	6
From coancestry in seeds to inbreeding depression on production.....	7
What is the danger of around one percent inbreeding and inbreeding depression?	8
Advantages and disadvantages with seedling seed orchards.....	11
Acknowledgement.....	12
References	13

Sammanfattning

I den här rapporten redovisas olika faktorer som påverkar den realiserade effekten av inavelsdepression hos avkomman till en fröplantsplantage.

I rapporten diskuteras också några ytterligare omständigheter att beakta vid jämförelse av fröplantager med fröplantor och ympar. Som en första approximation kommer en idealt fungerande fröplantsplantage med 10 helsyskonfamiljer, och med lika bidrag från varje träd, att i teorin producera 10 % inavlade träd med inavelskoefficienten $F = 0,25$ från korsningar som sker inom familjerna. Om man på goda grunder antar att självbefruktning $F = 0,5$ inte ger några levande frön, blir den genomsnittliga inaveln i avkomman då $F = 0,025$.

Den negativa effekten som uppkommer från syskonparningarna på skogsproduktionen (inavelsdepression), minskas på olika sätt t.ex. av:

- Obesläktad bakgrundspollinering i fröplantagen.
- Inavelsdepression på själva fröproduktionen.
- Plantavgång i plantskolan.
- Naturlig förnygring i det planterade beståndet.
- Kompenserande tillväxt hos icke inavlade träd.

För en fröplantsplantage av tall i Sverige med 10 helsyskonfamiljer uppskattas, att mindre än 4 % av träden i beståndet är påverkade av inavelsdepression, och att tillväxtförlusten i beståndet är mindre än 1 %. Effekterna beror i hög grad på hur många helsyskonfamiljer som används.

Summary

We review different factors that influence the realized impact of inbreeding depression in the progeny of a seedling seed orchard and discuss a few other conditions to be considered when comparing a seedling and a grafted seed orchard. An ideal seedling seed orchard with 10 full sib families and equal contribution from all trees will in theory as a first approximation produce 10 % inbred seed with $F = 0.25$ from within family mating assuming that selfing $F = 0.5$ produce no viable seed. Under the same assumptions the average inbreeding in all progeny is $F = 0.025$. The influence of the sib mating of seedlings on forest stand production is reduced by unrelated pollen contamination from outside the orchard, inbreeding depression on seed production, seedling mortality in the nursery, natural regeneration in planted stands and compensatory growth from non-inbred trees. For a Scots pine seedling seed orchard in Sweden with 10 full sib families we roughly estimate that less than 4 % of the trees in a stand are influenced by inbreeding depression and that stand growth reduction is less than one percent. These effects are much depending on the number of full-sib families used.

Introduction

Grafted clonal seed orchards have been seen as the general way for mass propagation of seed for the major species Scots pine and Norway spruce in Sweden. Options to use seedlings in low input seed orchards was for example reviewed by Rosvall & Lindgren (2003) but not considered as an alternative when planning the third round of seed orchards, TreO. However, seedling seed orchards are used in Sweden for the introduced contorta pine, and there are other situations where seedling seed orchards may be of interest. This includes minor species as well as the mayor ones. The experimental seed orchard of Scots pine at Sävar demonstrates that seedlings produce much cones and pollen but after a significant delay in time as compared to grafts of older trees.

The recent review of the Swedish conifer breeding program identifies the need for new ways of mass propagation (Rosvall, 2011). When using forward selection in new breeding generation field experiments selected trees will be young and have small crowns. To reach the stipulated numbers of orchard trees, the limited amount of conventional scions on a small tree for orchard graft production has to be compensated for by time consuming cycles of graft propagation. If instead seed can be produced on selected trees, seedlings are much cheaper as seed orchard trees and will reduce establishment costs. Denser planting allow for genetic thinning based on next generation progeny performance (However, the experience so far is that selection intensity is reduced by management constrains). Any simple and cheap propagation method of selected trees will facilitate using trees close to the breeding frontier enhancing realized gain per unit time.

The objective in this analysis is primarily to investigate the effect on coancestry, inbreeding and inbreeding depression by using related trees, primarily full sibs in a seedling seed orchard. How many families are appropriate to be planted if to avoid too much inbreeding? How is inbreeding decreased by natural selection? These results and discussions also apply to seed production stands with open pollinated progenies.

Coancestry and inbreeding

To study effects of inbreeding the coancestry among each pair of trees (including self-coancestry) of the seed orchard or breeding group is noted in a square matrix. When mating among all trees in the matrix take place coancestry becomes the inbreeding of the progeny. This is the first approximation, and divergences will be discussed in later sections. If there are many genotypes the matrix becomes large, but it is usually easy to make simplifying short-cuts.

The group coancestry (θ) can be calculated as the average value of the elements of the matrix. The average (or group) coancestry can be divided into two terms, the self-coancestry (θ_s = the part depending on the coancestry of genotypes with themselves) and the cross-coancestry (θ_c = pair-wise coancestry, depending on the coancestry among different genotypes).

We assume a seedling seed orchard with n full sib families with m members each, thus nm trees. All trees are non-inbred (self-coancestry = 0.5) and nonrelated (coancestry = 0) except for among the full sibs (coancestry for full sibs = 0.25). The situation is symmetric, thus all trees are equal. The average coancestry for one tree with the trees in the orchard is the same as the average coancestry of the seedling seed orchard:

$$\theta = \frac{0.5 + (m - 1)0.25 + (n - m)0}{nm} = \frac{0.5 + (m - 1)0.25}{nm}$$

For the cross-coancestry part:

$$\theta_c = \frac{0.25(1 - 1/m)}{n}$$

If all combinations of genotypes are equally common in the offspring of the seed orchard (random mating), the average coancestry (θ) of a population becomes the inbreeding (F) of its progeny. If selfing does not give viable progeny, the cross-coancestry part (θ_c) becomes the inbreeding among the seeds in a conifer seed orchard. This approximation is sufficient to guide seed production considerations.

But to consider in detail the effect of selfing on seed yield, the formula translating coancestry to inbreeding becomes more complicated. This matters for a seedling seed orchards with few trees, but not if there are many trees. The formula for average coancestry (θ_{c*}) assuming that selfing does not result in seeds is:

$$\theta_{c*} = \frac{nm}{nm - 1} \theta_c = \frac{0.25(m - 1)m}{nm - 1}$$

The inbreeding depending on full sib mating estimated by θ_{c*} is exemplified in Table 1.

Table 1.

Cross-coancestry ($\theta_{c*} \approx F$ in the progeny) for a seedling seed orchard as a function of number of full sib families (n) and family size (m).

Orchard trees (nm) and (orchard size)	Number of unrelated full sib families (n) in equal shares					
	1	2	5	10	25	100
100 (0,2 ha)	0,2500	0,1237	0,0480	0,0227	0,0076	0,0000
1 000 (2 ha)	0,2500	0,1249	0,0498	0,0248	0,0098	0,0023
∞ (10 ha)	0,2500	0,1250	0,0500	0,0250	0,0100	0,0025

It is seen from Table 1 that 10 families corresponding to 20 unrelated parent trees will result in $F=0.025$ in the progeny of a large orchard. Family size (orchard size) has a less significant influence on F . Using 20 unrelated parent trees for 10 full-sib families is about what is used in a conventional clonal seed orchard but in that case resulting in $F=0,00$ in the progeny. Crossing all 50 trees in a Swedish breeding population to form 25 full sib families for a seedling seed orchard will decrease inbreeding to $F=0.01$. In a real seed orchard mating is more frequent among neighbors. Thus, the spatial arrangement can change the realized inbreeding.

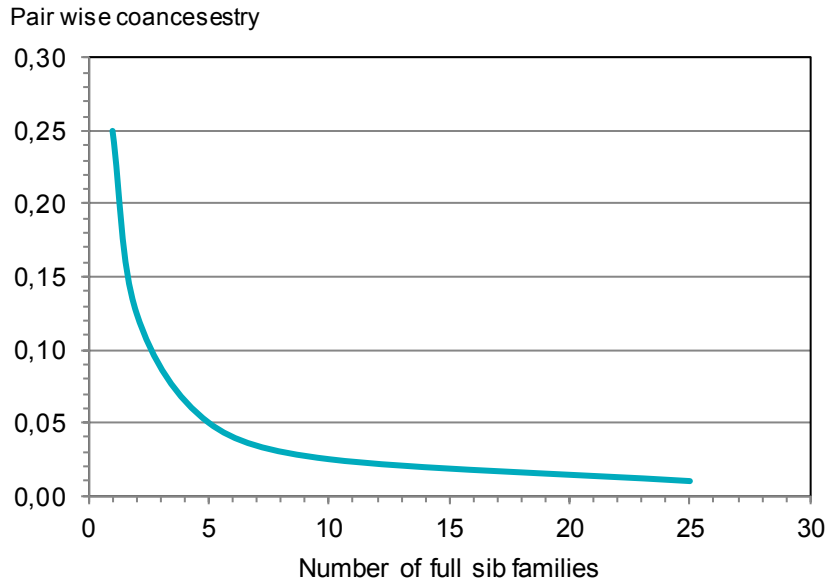


Figure 1.
Pair wise or cross coancestry ($\Theta_c \approx F$ in the progeny) for an infinitely large seedling seed orchard as influenced by the number of full sib families used.

In reality it is not only the average inbreeding that matters but also the frequency of actually inbred trees. In the progeny of a seedling seed orchard with full sib families the progeny from within full sib family mating will have $F = 0.25$ and the progeny from among full-sib family mating will have $F = 0$. (For half sibs and cousins these figures are $F = 0.125$ and $F = 0.06$, but those relationships does not appear in the current example with full-sibs from unreated parents). However, since inbreeding depression will reduce the contribution both to seed production, seedling survival and stand growth these realized frequencies are not easily calculated for Swedish Scots pine as discussed in the following.

Although, resulting in an overestimate compared to what is realistic, an approximation is to assume that all trees contribute equally to the progeny, selfing does not produce seeds, and there is no pollen contamination. With these assumptions the percentage of within full sib progeny (P_{FS}) can be calculated with the following formula:

$$P_{FS} = \frac{m - 1}{nm - 1}$$

Calculated frequencies of progeny from within family mating are given in Table 2 for different numbers of full sib families and family sizes. With 10 full sib families from 20 unrelated parents 10 % of the progeny will have $F = 0.25$. It is the number of full sib families that is important for the percentage of mating within family members, not the family or seed orchard size.

Table 2.

Percentage of progeny from within full sib family mating (P_{FS}) with $F = 0.25$ for a seedling seed orchard as a function of number of full sib families (n) and family size (m).

Orchard trees (nm) and (orchard size)	Number of unrelated full sib families (n) in equal shares					
	1	2	5	10	25	100
100 (0,2 ha)	1,0000	0,4949	0,1919	0,0909	0,0303	0,0000
1000 (2 ha)	1,0000	0,4995	0,1992	0,0991	0,0390	0,0090
∞ (10 ha)	1,0000	0,5000	0,2000	0,1000	0,0400	0,0100

From coancestry of parents in a seedling seed orchard to realized inbreeding in its offspring

There are more uncertainties in the translation of coancestry to inbreeding. For the discussion of factors influencing realized inbreeding it is reasonable to simplify by assuming that trees from all families contribute equally many progeny. However, different degree of inbreeding usually does not contribute equally many progeny. There is inbreeding depression in the seed production itself as well as in seedling and tree survival and growth. The genetic load leads to dead seeds (in pine seeds may be empty and in spruce seeds are not formed at all). For selfing ($F = 0.5$) in conifers the seed production can be set to zero as done by Prescher et al. (2006).

Self-coancestry and selfing can be expected to be more important in a clonal seed orchard with many trees with the same genotype than in a seedling seed orchard where each genotype is unique. Thus less selfing is an advantage of a seedling seed orchard, but the effect is small and not regarded to be of any significance here.

For less severe degrees of inbreeding (F is less than 0.5) viable seeds are formed, but to a lesser extent than if they were not inbred. This can be understood by different genetic models; the simplest is by independently acting recessive lethals. Probably the genetic death of an embryo can be caused both by an individual lethal, by the accumulation of semi-lethals or just higher mortality caused by lack of heterozygosity. In conifers, the phenomenon is complicated by a system with poly-embryoni. A failed embryo can be replaced by another, which increases the proportion of non-inbred seeds among survivors and thus reduce the proportion of inbred seeds (Lindgren 1975; Griffin & Lindgren, 1985).

For this reason inbreeding is expected to be lower than the calculated coancestry if there are unrelated pollen sources within or outside the seed orchard. The quantitative effect depends on the particular circumstances and factors which are not well-known. The effect is likely to be more strongly depending on inbreeding than just linear. The underrepresentation of selfed seeds compared to selfing pollen was estimated to 0.3 by Yazdani & Lindgren (1991). As a highly uncertain but still educated guess this reducing effect on inbreeding might be a factor of 0.8 seed reduction for full sibs ($\Theta_C = 0.25$) and 0.93 reduction for half sibs ($\Theta_C = 0.125$).

Pollen contamination is common in Swedish seed orchards. For Scots pine a recent estimate is 50% (Torimaru et al., 2009). The coancestry with and among the contaminating pollen is here assumed to be zero. For typical pine and spruce clonal seed orchards in Sweden, the average coancestry of mothers and fathers is probably only about half of the coancestry among the seed orchard trees themselves. In young seed orchards coancestry may be close to zero, especially considering that pollen production starts later than cone production.

For a seedling seed orchard with 10 full sub families theoretically 10 % of the seed is from within full sib mating with $F = 0.25$ (Table 2). Due to inbreeding depression on seed yield and pollen contamination the frequency is reduced to 4 % ($10\% \times 0.8 \times 0.5$; frequency of pollen from own family \times reduced seed yield \times frequency of outside orchard pollen).

In summary considering both the effect of inbreeding depression on seed production and the effect of pollen contamination coancestry in seeds from a typical seedling seed orchard comprising of ten full sib families is estimated to be 0.01 ($= 0.8 \times 0.5 \times 0.025$) rather than 0.025. The factor 0.8 is because full-sib mating yields fewer germinating seeds than out-breeding if compared to their share in the fertilizing pollen mix. The factor 0.5 is the fraction of pollinations by seed orchard pollen and 0.025 is the expected inbreeding following random mating in the orchard. It is to be remembered that mating among relatives and selfing will cause reduced seed production of the seed orchard. This reduction in seed yield will cause economic losses to the seed orchard manager, but to a small extent and it is neglected in this study.

From coancestry in seeds to inbreeding depression on production

The fact that inbred seeds germinate to a less degree will to some extent reduce profitability in forest tree nurseries. Usually only one single seed is sown in each container cavity, and the economic loss is rather high even at a small reduction in germination percentage. But most bad seeds are sorted away before sowing by various seed treatments. Inbred seeds also have a lower germination energy resulting in slower growth and smaller seedlings. Small inbred seedlings will not fill nursery requirements and will be sorted away at lifting or not paid for, further reducing profitability for the nursery operation. However, these effects are assumed to be negligible in this study.

Seeds from a seedling seed orchard may also lose some of the growth enhancing environmental effects on seed quality as found in grafted orchards. This “seed orchard effect” (increased seed and seedling vigor) is assumed to cause a two per cent gain on production in non-inbred seedlings.

Inbred seedlings die to a higher extent from competition with non-inbred seedlings. Therefore, after plantation in the forest there will be a higher mortality and slower growth and probably more damages by pests and diseases among inbreeds. A considerable part of the higher mortality and loss of growth will be compensated for through reduced demand for resources and by this better growth of non-inbred neighboring trees. In this way there is little reduction in per hectare production.

In a planted boreal forest stand all production is not by the planted trees, but typically 20 percent is by natural regenerated trees. The figure is supposed to be a little less if the planted trees are genetically improved and also if the natural regeneration has some inbreeding. The natural regenerated trees are often, but not always another species. We assume that the contribution of natural regeneration is not influenced by the inbreeding in the planted material. In reality there is probably a small effect which would be difficult to estimate.

The variation in inbreeding in a partly inbred material is expected to result in larger genetic variation than in an out-bred material. Superior trees will take a larger part of the production than poor performing trees. The most depressed inbred trees will be removed by pre-commercial and commercial thinning operations to a higher degree than non-inbred trees. We assume that the reduction in per hectare production by using inbred material is directly related to the coefficient of inbreeding. It is probable that the depression sometimes is somewhat higher, but this assumption is simple and has some logic.

In total these stand compensatory effects are assumed to be of a factor at 0.9 for full sibs and 0.96 for half sibs. Thus the overall production loss because of inbreeding depression for a Swedish Scots pine dominated forest (100 % planted trees) originating from a seedling seed orchard with full sibs and cross coancestry among seeds being 0.01 (F corrected from 0.025 to 0.01 as found above) is expected to be $(1 - 0.2) \times 0.9 \times 0.01 = 0.007$ (1 – natural regeneration × stand compensated growth by non inbred trees × corrected F).

Thus the influence on stand production from the corrected fraction of 4 % inbred seedlings with $F=0.25$ from a seedling seed orchard with 10 full-sib families will be reduced to 3 % of the stand trees $(1 - 0.2) \times 0.04$ and their contribution to reduced production will be less by compensatory growth from non inbred trees resulting in not as much as one percent reduced per hectare production.

Of course these estimates are highly uncertain, but indicate the magnitude and highlights relevant factors.

What is the danger of around one percent inbreeding and inbreeding depression?

In principle about one percent inbreeding and inbreeding depression seems to be acceptable in an improved forest stand. It is less than expected by using seeds from natural stand collections and a much lower amount than the genetic improvement itself. Variation between stands in genetic value and level of inbreeding is also expected to be larger than one percent (Lindgren, 2008).

Inbreeding of this magnitude will also be practically unavoidable in future clonal seed orchards, if not measures which seems contra-productive to genetic gain are taken (Lindgren et al., 2009). Thus some inbreeding can be considered as optimal.

Full sib mating may be rather rare under natural conditions and does not explain much of the inbreeding depression in nature. It could be some risk to have this type of handicapped trees in a forest stand besides the inbreeding depression in it. However, their frequency will be low (a few percent, see example with 3–4 percent above). For less inbred trees ($F < 0.25$) it is more certain that they are common in nature and that their characteristics overlap with non-inbred trees. Fully selfed trees ($F \geq 0.5$) exist in natural forests and plantations. Their occurrence varies and is likely to be more than two percent in a typical young forest, although they contribute very marginally to total production. Serious effects of selfed trees besides the very evident would probably have been observed or at least speculated about since long in forest genetics if the risk was considerable.

Half-sib mating must be common under natural conditions. A phenotypic variation with a range of magnitude of 25% or more in e.g. tree size must be rather common. 10% suppressed trees is common. The genetically superior trees are growing 25% better, but some fraction of them may not be faster growing than unimproved trees because of inbreeding depression. The seed crop from a seedling seed orchard could be seen as a mixture of seedlings with 25% better growth, 12.5% better growth (father contamination in the orchard) and 0% better growth (inbreeding depression). The 0%-level is the same as for the natural unimproved trees that occur in stands planted with improved trees. Thus the forests from seedlings seed orchards can be claimed to be slightly but not much more genetically diverse.

Seedling seed orchards are not an uncommon method and have been used for lodgepole pine in Sweden. There is much empirical experience. We are not aware of that inbreeding caused by sib mating has been reported as a serious problem anywhere.

The question is rather if it is optimal to use seedling seed orchards than if it is dangerous. However, it may be some doubts about the optimality with high input breeding programs like Scots pine in Sweden.

Results from a seed orchard experiment.

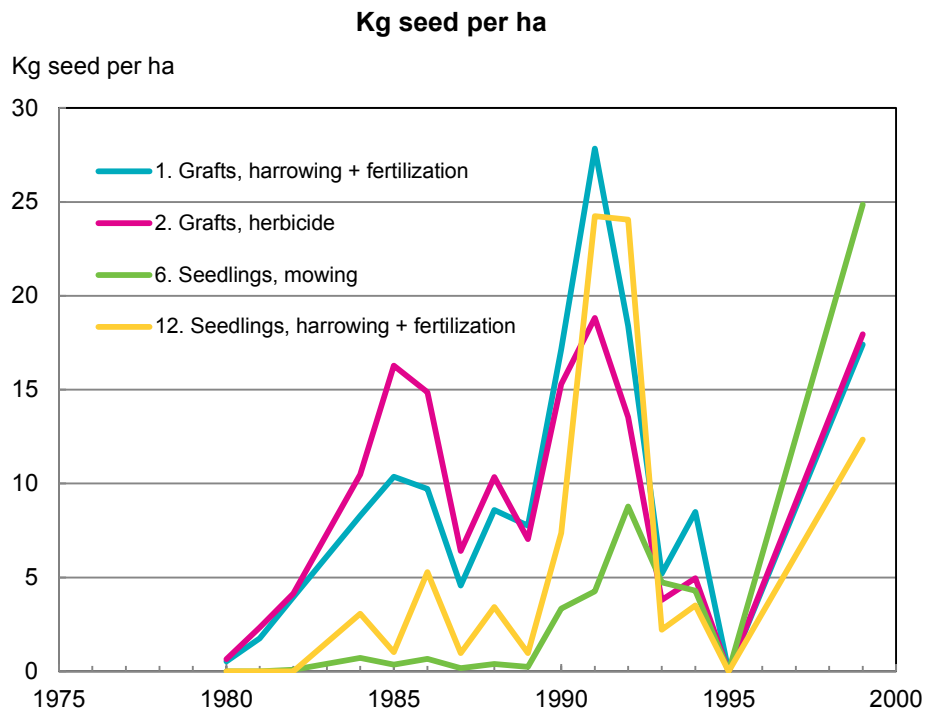
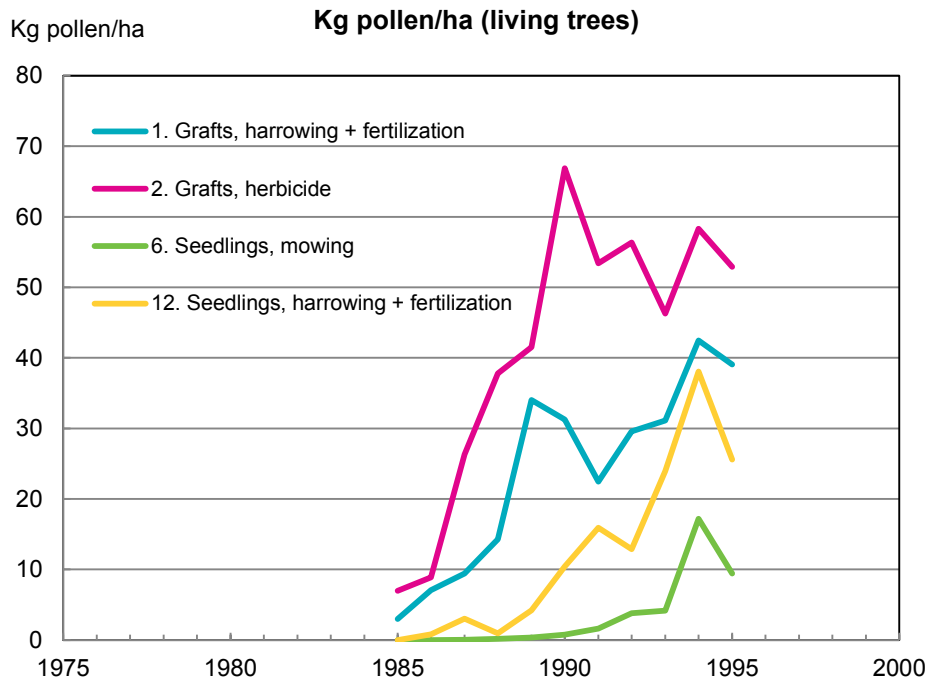


Figure 2. Pollen and seed production in a seed orchard experiment comparing seedlings and grafts at 5.5 by 5.5 m spacing (333 trees/ha).

The experimental seed orchard at Sävar was planted in 1969. By treating the seedlings with open soil and fertilizer they reached 20 kg per ha of pollen production after about 20 years. That is 3–4 years later than for comparable grafts. Seed production reached 10 kg also after about 20 years but this was 8–10 year later than for the grafts. After 20 years there are little differences between pollen and seed production on seedlings and grafts if they are in good nutritional condition.

Advantages and disadvantages with seedling seed orchards

In general the untested progeny (seedlings) from well tested and selected genotypes (grafts) can be expected to be equally good if used as parents in a seed orchard. In theory there is a loss of gene diversity in the progeny (seedling trees) as compared to the parents (grafted trees) due to random genetic drift. But since the parents contribute a large number of seedlings all genes will be sampled and there is little difference between a seed orchard with 10 full sib families and one with the 20 parents as grafts.

The greatest disadvantage with a seedling seed orchard is the much longer time to get reproductive trees from seedlings than from grafts of a tree which is sufficiently sexually mature. Thus the gain in a seedling seed orchard will be harvested 5–10 years later than the gain in a clonal seed orchard. For less mature trees the difference between grafts and seedlings might be less. That delay can be seen as resulting in a lower gain. However, the choice of starting material for a seed orchard is partly depending on the development of seed demand and the alternative ways for seed supply. Therefore in a larger context the different timing of a seedling and a clonal seed orchard may be more or less suitable.

The problem with a grafted orchard in advanced generation breeding is lack of scions for grafting. Selected trees are typically fifteen year old, four meter tall trees and only few scions can be harvested for grafting without harming the tree. These scions are taken and top grafted on mature grafts in archives to support crossing activities. To mass produce grafts for seed orchards other forms of clone archives for multiplication is needed and this process takes time.

However, if scions were not limiting it takes more time to get seedlings than grafts. To facilitate controlled crossing operation the selected genotypes have to be transferred from the forest field experiment to a clonal archive. At a rough estimate establishment of a seedling seed orchard may be delayed by four years as compared to a grafted seed orchard. In this perspective the current development of methods to get many more scions (from each needle pair) are of greatest importance and may make it possible to get sufficient number of scions to make clonal seed orchards from young selected trees.

To increase the bulk of scions an alternative to make just one selection forward in a full sib family is to make several selections from the same family for grafting in seed orchards. That involve a reduction of genetic gain because of lower selection intensity, but it will anyway be a gain, and seed production in the seed orchard is likely to come after a shorter time. This alternative will also result in marginally higher inbreeding in the orchard, but the earlier seed production is

likely to more than compensate for that. Such seed orchards could partly function as clonal archives.

Long term archives of selected genotypes will be established and may be suitable for multiplying grafted seed orchard trees. In a decade or two these archived clones will be available for backward selection based on their progeny performance as an alternative to selecting forward in the progeny.

Seedlings are cheaper, but considering the total cost of a seed orchard that advantage may be less important. However, the delayed seed production will reduce the return of the investment. Management of seedling seed orchards of Scots pine could be further developed to increase pollen and seed production. The seed productive phase may be extended longer for seedlings than with grafts. Trees in a seedling seed orchard can be used for selections to the breeding population (before crown management) and thus be a part of a much cheaper breeding system. A seedling seed orchard can be genetically thinned based on the performance of the seed orchard trees.

Scots pine seedling seed orchards are commonly used in for example Poland as described by Kowalczyk (2008). Seeds were harvested following open pollination from individual plus trees and planted well mixed in single tree plots. There were no replications. Crown shaping is not done before evaluation. The seedling seed orchards were established in much wider spacing than forests which reduces the value of the combination of seed orchards and testing. The seed production has been lower than in corresponding grafted orchards but the trees are still young. The total Scots pine seed orchard area of Poland is composed of 279 hectares seedling seed orchards and 426 ha clonal seed orchards (Matras, 2008).

A technique for optimal deployment of related clones has been developed by Lindgren et al. (2009) and is now used in several breeding programs. It is sometimes much superior to use related clones compared to use only unrelated clones. Relatedness in a seed orchard of any kind should be considered in relation to the achievable gain.

Acknowledgement

At the breeders meeting in Uppsala on November 18, 2010 Bengt Andersson suggested to use seedling seed orchards to increase flexibility in delivering improved seed from a rolling front breeding strategy. I became interested and calculated the suitable number of full sib families to be used to avoid too much influence of inbreeding depression. Dag Lindgren then suggested numerous improvements and has contributed almost all of the discussions. This subject is one of Dag Lindgrens specialties. Tim Mullin made a relevant comment on selection against inbreeding depression due to the reproductive biology of Scots pine due to the formation of many embryos within each ovule. Ulfstand Wennström provided the seedling seed orchard production figures. Bengt Andersson reviewed the manuscript. I am grateful for all contributions.

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arbetar för ett lönsamt, uthålligt mångbruk av skogen. Bakom Skogforsk står skogsföretagen, skogsägareföreningarna, stiften, gods, skogsmaskinföretagare, allmänningar m.fl. som betalar årliga intressentbidrag. Hela skogsbruket bidrar dessutom till finansieringen genom en avgift på virke som avverkas i Sverige. Verksamheten finansieras vidare av staten enligt särskilt avtal och av fonder som ger projektbundet stöd.

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