USING SEED ORCHARD SEEDS WITH UNKNOWN FATHERS

Jan-Erik Nilsson and Dag Lindgren
Department of Forest Genetics and Plant Physiology,
Swedish University of Agricultural Sciences, UMEE, Sweden

Abstract

The natural pollen cloud moving around with the winds in early summer may account for 50% of pollinations in mature seed orchards with high internal pollen production. The background pollen is genetically different from seed orchard pollen produced by selected plus trees. This may affect the adaptation of the seed crop and justify a modified use of the seeds, e.g. the best place to use the crop. However, even seeds from young seed orchards without pollen production may usually be useful forest regeneration material and there are reasons to limit or eliminate demands on high internal pollen production when seed orchard clones and contaminating pollen do not differ much in adaptation. Artificial freeze testing seed orchard crops of Scots pine for autumn cold hardening is often performed in Sweden to determine the area of utilization. In the same way the hardiness of the natural pollen cloud can be experimentally estimated using artificial freeze testing of progenies obtained from controlled wind pollination of selected clones. Therefore a number of permanent small clone archives of Scots pine have been established in central and northern Sweden as a basis for evaluating geographical and daily variation in the hardiness of the background pollen cloud. An archive of mobile grafts is also under establishment. One application may be long-term mapping of changes in the natural pollen cloud following climate changes and large-scale seed transfer in Swedish forestry.

Background

The major wind-pollinated Swedish forest trees (Scots pine, Norway spruce, birch) produce large quantities of pollen able to be transported wide distances by the wind. This pollen will influence seed orchards, the issue was discussed at a Nordic Genetic meeting 1991 (Lindgren 1991). Seed orchards trees produce pollen as well as seeds. In the early days of seed orchards, the hope was that once the pollen production in seed orchard started, it would outcompete pollen sources outside the seed orchard. Calculations indicated that a pollen production around 20 kg/ha would be well compatible with other pollen sources and harvest has often not been recommended until that pollen production has been reached. Later research showed that even in seed orchards with a considerable pollen production, fertilizations with fathers outside the seed orchard were important, and today we assume and accept 40-50% pollen contamination in mature seed orchards. Still cone harvest is often not recommended until the pollen production has reached 20 kg/ha, that is common in Swedish seed orchards of Scots pine and Norway spruce. A detailed evaluation of the likely quantitative consequences of utilizing the contaminated crops from young and mature seed orchard crops has never been done.

Differences between seeds fertilized by inflowing pollen versus «seed orchard pollen»

Today almost all practically used seeds in Sweden come from seed orchards with phenotypically selected plus trees. The superiority of the first generation seed orchard seeds compared to stand seeds is estimated to 10% and probably there are three sources for the superiority: (i) selection of plus trees (6%), (ii) release of inbreeding (2%) as there are relatives in a stand but not in a seed orchard (can also be expressed as hybridization as plus trees are selected from a wide area, range 100 km or more) and (iii) seed orchard seeds are more «vital», or better programmed or «physiological effects» or has a higher weight and maturity which leads to an estimated 2% «gain» (Rosvall et al 2001).

The «physiological» effects are at least in the first approximation expected to be the same whether the pollinator is a seed orchard clone or contaminant. «By definition» we define trees in *different* stands as non-related, relatedness must be «recent», the more generations back we go, the more common ancestors there will be. In advanced seed orchards, clones may be relatives and the inbreeding higher because of relatedness.

More improved seeds

Insufficient pollination can cause early conelet abortion, empty seeds and reduced production of filled seeds. In Sweden there is usually sufficient Scots pine pollen for full seed production even in absence of seed orchard pollen. But in other situations, like in environments where Scots pine is not among the dominating species, the pollen from the seed orchard can give an increased seed production of improved seeds.

Pollen from native or transferred populations

In Swedish forestry large-scale transfer of trees has been carried out by forest owners for many decades. For Scots pine the transfer direction has been mainly from north to south, which is in the opposite direction to the main wind direction and natural pollen flow during the flowering period. As the transferred forests grow up and become fertile their pollen will contribute to the natural pollen cloud with a different genetic composition compared with pollen released from native stands in the same region. Today pollen from transferred forests does contribute much to the natural pollen cloud, and its influence on the seed orchard crops should still be relatively small, although this influence is increasing.

Breeding value

The seed orchard parents are selected while the parents of the background pollen are not selected. Breeding value of a seed with a plus tree mother and a father from outside the seed orchard is expected to be exactly half of that if the father was a seed orchard clone. If the outside father has a different geographical origin than the seed orchard father, the genetic value of the seed might be either higher or lower than half of that of a seed obtained from pollination with a plus tree father. However, unlike pollen from forests transferred by man, tree breeding has not yet advanced long enough to make contribution from bred trees in the general pollen cloud important. For the breeding values in the 3rd-batch seed orchards estimates by Lindgren and Prescher (2005) were considered.

Selfing

Trees of the most relevant species produce both pollen and seeds and are able to self-fertilize. As male and female structures are not very distant an estimated amount of 10% self pollination seems reasonable. Most selfed zygotes die and most selfings results in reduced production of filled seeds. The selfing frequency among germinating seeds or young seedlings is measurable and it is likely to be in the magnitude 4 percent (although figures such high as 25% has been reported), different in different investigations and under different circumstances. The selfed individuals are discriminated during the whole life cycle and few remain to the mature stand.

Selfing in a clonal seed orchard can occur in two ways, either selfing with a ramet's own pollen, or one ramet pollinates another of the same clone. The chance that the later will occur depends on the number of clones in the seed orchard. Lindgren and Prescher (2005) have developed methods for estimation of selfing effects. The estimates of the influence of selfing within ramets on a production compatible scale for Scots pine by Lindgren and Prescher (2005, 1.6%) in table 1 are in hyphens. Rosvall et al (2001) makes estimates which are half as high. The analysis by Lindgren and Prescher was for evaluating suitable clone number and to reduce the risk that the recommended clone number is too low and may overestimate selfing, so the production loss is assumed 1%.

Contaminating pollen can not cause self-fertilization in seed orchards; the rate of selfing will increase when the internal pollen production increases. The lower situated cones get higher rate of selfing than the higher, as the male reproductive structures are in the lower part of the crown. Because lower cones are easier to harvest, the selfing rate in a harvested seed orchard crop may be higher than in the biological crop.

Diversity Loss

The biological production in a forest may decrease if it is insufficiently diverse. Diversity also has an immaterial PR-value. The diversity losses for seed orchard crops in Table 1 are estimated by

Table 1. Summary of quantitative estimates for stand seeds and seeds from young and mature 1st batch and 3rd batch of seed orchards.

Parameter	Stand seeds	1st batch seed orchard		3rd batch orchard	
		Young	Mature	Young	Mature
Contamination (%)	50	100	50	100	50
Clones number	?	50	50	20	20
BV-clones	0	6	6	20	20
BV-seeds	0	3	4.5	10	15
Physiological	0	2	2	2	2
Selfing – within ramets	-1.0 (-1.6)	0	-1.0 (-1.6)	0	-1.0 (-1.6)
Selfing – among ramets	0	0	-0.2	0	-0.7
Relatedness	-2	0	0	0	0
Diversity loss	0	-0.2	-0.4	-0.5	-1.1
Adaptation uncertainty	0	-2	-1	-2	-1
Sum	-3.0 (-3.6)	2.8	3.9 (3.3)	9.5	13.2 (12.6)

methods developed by Lindgren and Prescher (2005) and using their quantifications for Scots pine seed orchards.

Adaptation loss and uncertainty

The seed orchard crop is made up of one seed crop from internal pollination and one seed crop from background pollination. Because the two seed lots are in practice impossible to separate a seed orchard crop can be considered and handled as a single seed lot with a wider adaptation than a seed orchard crop from pure internal pollination. With the wider adaptation follows that pollen contamination reduces the maximum adaptation of the seed orchard crop to a specific climate.

Because the contaminating pollen may vary in origin and frequency due to changes in weather conditions (temperatures, winds, rain etc.) before and during female receptivity, crops from a seed orchard exposed to pollen contamination are more uncertain and less reproducible than a crop from a seed orchard less affected by contamination.

Nilsson (1991) presented a model to estimate effects on survival of seed orchard crops planted on different latitudes/altitudes from varying background pollination rates and origins. The model can handle daily variations in both rate and hardiness of the contaminating pollen (assuming a normally distributed quantitative trait) as well as for pollen and female gametes in the seed orchard. By careful studies of timing of pollen dispersal and female receptivity and estimation of breeding values of the seed orchard clones relevant parameters for the seed orchard genotypes can be determined for input into the model. However, little is still known about what parameter values are relevant for the complex background pollen.

Daily variation in origin and adaptation of background pollen

In a seed orchard female receptivity may be extended over a period of one week or more. It is reasonable to assume that changes in weather condition and wind directions might cause significant changes in the origin of long distance pollen invading a seed orchard in different days of the receptive period. Nilsson (1995) found that the background pollen in a coastal clone archive of Scots pine had a geographical origin and cold hardiness (estimated from artificial freeze testing of progenies from controlled wind pollination and progenies from pollination with reference pollen) approximately one degree latitude north of the archive. The most likely explanation was that immediately before female receptivity occurred in the clone archive a heavy rain washed out pollen from the air and the earlier southern winds were changed to northern ones carrying pollen from early flowering non-coastal northern localities. With a more interior localization (less influence of the cold Gulf of Bothnia on early summer temperatures means earlier receptivity) or if the sudden change in weather conditions had occurred a few days later more southern pollen would probably have contaminated the archive and reduced the hardiness of the seed crop.

Discussion

Today it is usually recommended for Scandinavian conifer seed orchards to start seed collection when pollen production is above 20 kg/hectare to assure a sufficient reduction of pollen contamination from outside the seed orchard. It is suggested that the demand is relaxed for seed orchards where the contaminating pollen is not drastically different from the seed orchard clones. The seed orchard material can often be assumed to be the best available for reforestation even in cases with 100% non seed orchard pollen.

The gain from a young 3rd batch of seed orchards compared to a mature first batch seed orchard is considerable when adaptation pattern of the contaminating pollen is the same as the orchard clones, and is thus not likely to be inferior as long as there are not large problems with the adaptation of the contaminating pollen.

Selfing

Estimates of selfing are mainly done on rather young seed orchards, whereas pollen production per graft and thus selfing may be larger in mature seed orchards. It is possible that the 3rd batch of seed orchards will be subject to more selfing as they are planned for more intensive pruning. The repeated pruning may raise the male strobili in the tree crowns and move them on average closer to the female strobili and thus increase selfing, as has been found a problem with lodgepole pine seed orchards in British Columbia (Owens et al. 2005).

Testing seed orchard crops

The adaptation pattern of each actual crop could be tested. Such tests are sometimes done routinely, e.g. artificial freeze testing of seed orchard crops during autumn cold acclimation using seeds of known adaptation pattern as references. There may also be variations among years due to variable contribution from different clones, the effect of this would be decreased by freezing tests. This problem will increase with the 3rd round seed orchards as they will have fewer clones, and there may thus be a larger variation among years. A possible problem with progeny testing of young seedlings occurs if the testing method catches up «after-effects» which are physiological rather than genetic. One way to circumvent this problem is to postpone testing of seedlings until possible after-effects are insignificant. In freeze testing for autumn cold acclimation after-effects have been found small already for one-year progenies, and non-significant for two-year progenies. Anyway, we suggest a mixture of reliance of test results and predictions based on origin and common sense when deciding the area of use of tested seed orchard crops.

Adaptation correction

The seed orchard parents are selected as they are expected to match the adaptation demands in the target area for the seed orchard. The target area can be where the average of the seed orchard clones is best adapted. However, the pollen contamination is so large in mature seed orchards, so the matching of seed source and intended area of use will assume 40-50% pollen contamination. If the orchard clones have different adaptational pattern than the contaminating pollen, the target area can be modified considering the adaptation. For Scots pine the adaptation can be expressed as latitudes, and the adaptation of origins could be modified by one degree latitude for 300 m difference in altitude of origin. The target area of the mature seed orchard crop could be calculated as the average of the target area for the clones and the contaminating pollen.

If the difference in adaptation of the seed orchard clones and the contaminating pollen is not much larger than what corresponds to one latitude of origin, it is suggested that the loss is neglectable. If it were 1 latitude, the mature seed orchard adaptation would be changed 0.25 latitudes because of the contamination, now the adaptation would change 0.5 latitude instead, thus a difference in the adaptation peak of the seed orchard crop of 0.25 latitude. Clone origins in a seed orchard typically have a range of 1.5 latitudes. The intended target area of the orchard ranges slightly more than one latitude.

Individual seed crops from the same seed orchard vary. Let us assume that adaptation varies with a standard deviation of 0.4 latitudes. Seen against these ranges and fluctuations and also uncertainty, a change in adaptation caused by the decreasing amount of pollen contamination seems marginal. The contaminating pollen is also variable among years, both in extent and in origin, so that is a disadvantage with a larger share of contaminating pollen. Quantitatively the production loss is likely to be below one percent, as the loss of adaptation by recruiting plus trees from a range of two latitudes instead of recruiting from the same latitude is less than one percent (Lindgren and Ying 2000).

Lindgren and Cheng (2000) calculated adaptational loss as a function of seed orchard size using data for Swedish Scots pine. The worksheet is found at:

http://www.genfys.slu.se/staff/dagl/Breed_Home_Page/SiteNrRange/ADAPTATION.XLS

The math discussed here should be valid for Scots pine plantations on adjusted latitudes 59 and 66.5 (thus not the highest elevations in the far north). Some figures are derived from that which a perfectly adapted provenance is assumed to perform 100%. To indicate adaptedness latitude is used, but this latitude is to been seen as adjusted for altitude. Seed orchards are composed of a mixture of provenances; the plus trees are assembled over a range assumed to be two degrees latitude. That means that if the seed orchard material is used where it has its adaptational peak it produces 99.3% of its production capacity because of the heterogeneous origin of the plus trees, while a provenance at its adaptational peak produces 100%. A seed orchard crop used over a range of 1.5 latitudes (± 0.75 latitudes from where it is «targeted») has an adaptational value of 98.9 % on average over the range of use of the seed orchard material. But 0.75 latitudes away from the target the value is 97.4% and one latitude away from the target it is 95.6 %. Let us say that the contaminating pollen has an adaptation for X latitudes south of the adaptation of the seed orchard clones (designed X0). This would change the adaptational goal for the seed orchard. For 50% and 100% contamination the goal would be changed (X0-0.25*X) and (X0-0.5X), respectively. If seed usage assumes 50% contamination but the contamination is 100%, the seeds would be out of target with 0.25X. The consequences are summarized in Table 2.

Table 2. Expected effect from differences in geographical origin of seed orchard clones and contaminating pollen assuming 50 % pollen contamination (model from Lindgren and Ying, 2000)

Difference between seed orchard average and contaminating pollen	Difference between recommendation for mature crop and best use of young crop	Value if young seeds are used based on an area assuming a mature 50% contamination (%)	Expressed as loss (%)
0 latitudes	0	99.6	0.0
1 latitude	0.25	99.4	0.2
2 latitudes	0.50	98.6	1.0
3 latitudes	0.75	97.4	2.2
4 latitudes	1.00	95.6	4.0

The losses expressed by this method give approximately the same but marginally larger losses compared to suggestions by «Val av skogsodlingsmaterial» www.skogforsk.se). A few percent can be seen as marginal. There are few cases where the difference between the orchard clones and the contamination origin is likely to be larger than 3 latitudes and even if it is not expressed in official recommendations it is still likely that some considerations may be done. The «loss» will lead to a higher increase in mortality but that is partly compensated for by a better growth. However, the losses will be relatively larger if the area of use is on the fringe already with assumption of 50% contamination.

Conclusion: it should usually be possible to generalize so the recommended seed use is the one assuming 50% contamination even for the early crops.

Localization of seed orchards

Seed orchards are preferably established on localities that favors rich flowering, large seed crops and high seed quality. For northern latitudes this usually means more southern localities at lower elevation and closer to the coast than the plus tree origin. A consequence of the southern location is an increased risk of exposure to pollen populations that are poorly adapted to northern environments. The increased risk of southern localization has two sources: shorter geographical distance to southern pollen sources, and less time separation between flowering in the seed orchard and the timing of pollen dispersal in southern stands. Coastal localization of seed orchards may delay flowering about one week compared to localization in the warmer, less costal localities on the same latitude. Except for the mountain areas in the west that are unsuitable for abundant seed production for other reasons, the coolest early summers in central and northern Sweden are probably found on islands in the sea. Such localization of a seed orchard should mean that female receptivity can be delayed another week or more compared today's localization in coastal mainland (Figure 1).

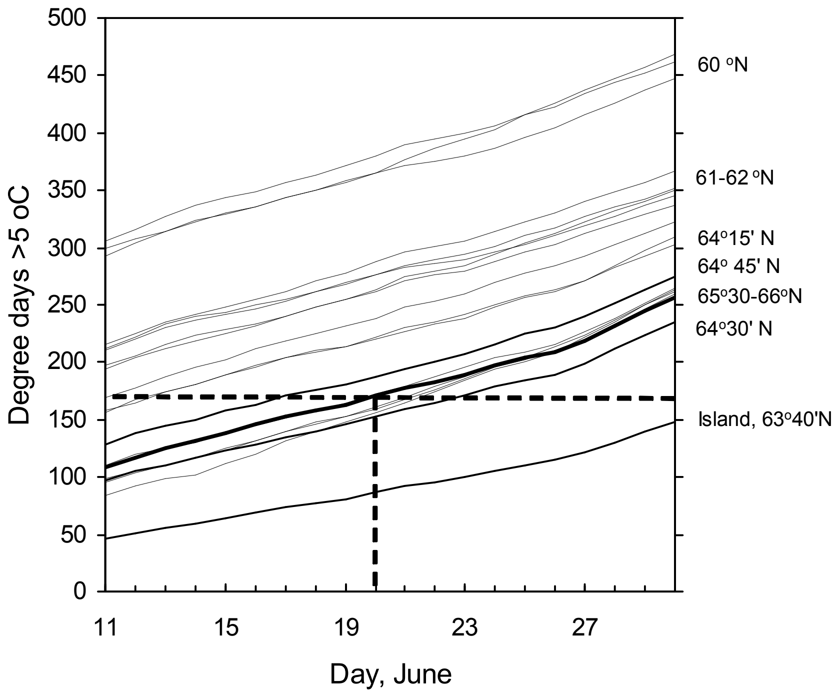

Figure 1. Degree days (> 5°C) in June 1998 on 19 weather stations (SMHI) between latitudes 60 and 66 °N Sweden. The bold curve indicates Umee (lat 63°48'N), the dotted lines indicate date and degree days for onset of pollen dispersal in mature seed orchards close to Umee.

Localization on islands in outer archipelagoes would usually reduce the influence of southern background pollen and enhance the influence of northern background pollen on the seed orchard crop. However, so far we have too little knowledge about how the geographical origin and genetic composition of the background pollen are affected by weather and winds to make more than very approximate statements about effects of seed orchard localizations on the adaptation pattern of seed orchard crops.

Clone archives for pollen cloud observations

In the early 1990's nineteen small clone archives of Scots pine, each with the same ten clones, were established in central and northern Sweden between latitudes 61 and 67°N with the intention that the female flowers would catch up the background pollen on the different localities. From the seeds produced by wind pollination, progeny testing can be performed to study geographical variation in adaptation patterns between pollen clouds. To reduce pollination from neighboring stands the archives were established in areas without adjacent Scots pine forests. The ten clones originating from between latitudes 62 and 67°N in Sweden are represented by five grafts in each archive. Clone selection was made in mature seed orchards for abundant female flowering but no pollen production. In addition an archive of potted grafts of Scots pine clones was recently initiated as a mobile complement to the permanent field archives allowing future studies of background pollen on any places.

Some of the permanent clone archives on mild localities up to latitude 64°N have now started to produce female flowers and seeds to allow progeny testing of background pollinated progenies. Therefore the first artificial freezing experiments for autumn cold acclimation are now performed to give experimental indications on differences in cold acclimation patterns between natural pollen clouds of Scots pine on different localities in Sweden.

Norway spruce

With Scots pine and northern Norway spruce «origin» can be related to mainly «latitude» and that makes the contamination rather manageable. With Norway spruce in southern Sweden the critical factor is flushing phenology in early summer which is more a question of longitude of origin. Long pollen transports ought to be less frequent for Norway spruce as the pollen is heavier and less likely to stay airborne for many hours. «Local» pollen originating some kilometers from the seed orchard may cause the same contamination rate; but it would at least be somewhat more reproducible. On the other hand there may be larger variations in «local» contamination, in particular considering the large variation in origin of spruce in southern Sweden. There are observed effects in seed orchards with Eastern European clones which could indicate that the large phenological genetic differences matter for contamination. Could it be some sort of physiological effects rather than contamination?

Acknowledgements

We discussed the pollen contamination on the web prior to writing this paper. We are grateful to the participants in that discussion for their good comments, in particular Seppo Ruotsalainen.

References

Lindgren D (editor), 1991. Pollen Contamination in Seed Orchards. Proceedings of the Meeting of the Nordic Group for Tree Breeding 1991. Swedish University of Agricultural Sciences. Department of Forest Genetics and Plant Physiology. Report 10, 120pp.

Lindgren D and Prescher F, 2005. Clone number for seed orchards with tested clones. Silvae Genetica 54: 80-92.

Lindgren D and Ying CC, 2000. A model integrating seed source adaptation and seed use. New Forest 20: (1) 87-104.

Nilsson J-E, 1991. Estimating the effect of pollen contamination on the seed orchard progeny. In Lindgren D (editor). Pollen Contamination in Seed Orchards. Proceedings of the Meeting of the Nordic Group for Tree Breeding 1991. Swedish University of Agricultural Sciences. Department of Forest Genetics and Plant Physiology. Report 10: 66-85.

Nilsson J-E, 1995. Genetic variation in the natural pollen cloud of Pinus sylvestris: a study based on progeny testing. Scand. J. For. Res. 10:140-148.

Owens JN, Bennett J and L'Hirondelle S. 2005. Pollination and cone morphology affect cone and seed production in lodgepole pine seed orchards. Can. J. For. Res., 35(2): 383-400.

Rosvall O, Jansson G, Andersson B, Ericsson T, Karlsson B, Sonesson J and Stener L-G, 2001. Genetiska vinster i nuvarande och framtida frцplantager och klonblandningar. Genetic gain from present and future seed orchards and clone mixes. SkogForsk, Redogцrelse nr 1, (2001). *Remark: An English abbreviated version is found in Haapanen M & Mikola J (Eds): Integrating Tree Breeding and Forestry – Proceedings from a meeting of the Nordic Group for Management of Genetic Resources of Trees. The Finnish Forest Research Institute Research Papers 842, p 71-85.*