



Lars-Åke Dahl performing controlled crosses of Scots pine in the Brunsbergs clonal archive, spring 2009. Photo: Curt Almqvist

Number of pollen in polycross mixtures and mating partners for full sibs for breeding value estimation

Dag Lindgren, Institutionen för skoglig genetik och växtfysiologi,
Sveriges lantbruksuniversitet, Umeå

Keywords: Breeding value estimation, progeny testing, double pair mating, single pair mating, pollen mixes, backward selection

SKOGFORSK

– The Forestry Research Institute of Sweden

The mission of Skogforsk is to pursue research and development for a sustainable, profitable and ecologically sound forestry. The Institute is supported by the entire forestry sector in Sweden through member fees and a charge levied on each cubic meter of wood harvested. Financial support is also given by the government according to a special agreement and by scientific funds for certain projects.

RESEARCH

- Forest production
- Wood supply

CONSULTANCY WORK

The Institute undertakes extensive consultancy work in its fields of special competence on behalf of forest enterprises, machine manufacturers and local and central government authorities. Such projects may involve specially commissioned research or the tailoring of new methods and routines to local conditions.

DISSEMINATION OF INFORMATION

The Institute uses a variety of media and channels for disseminating the findings of its research. These include personal contact, Internet, courses and seminars, the trade press, films and its own series of publications.

Contents

Summary.....	2
Introduction.....	3
Mathematical framework.....	4
Designations	4
Different fathers in different pollen mixes.....	7
Results.....	7
Arguments to have rather many pollen parents in a pollen mix	8
Different fathers in different pollen mixes.....	10
Plants per family.....	11
Single Pair Mating and Double Pair Mating.....	12
Possible advantages of DPM over SPM are listed	12
Possible advantages of SPM over DPM are listed:	13
DPM or SPM?	13
If DPM fails?.....	14
SPM and DPM for parental testing.....	14
References	15

Summary

Formulas for correlations among true and estimated breeding values were developed for controlled crosses and poly-mixes. The formulas consider additive and dominance variation, family size and number of pollen parents. The formulas and other considerations lead among other matters to the following statements:

- It is recommended to use 25 pollen parents in a pollen mix. Then the results will be robust to variations in pollen composition and to reasonable variations in amount and quality of the different pollen sources. It will work even if dominance is higher than usual and heritability is lower and if pollen parents are variable in different mixes. The savings with lower numbers in pollen mixes are probably limited, while higher number in the most likely variations of circumstances will give only limited increase in accuracy of breeding value. It is probably often unproblematic with fewer than 25 pollen parents, the discussion helps to identify circumstances when lower numbers are likely to give accurate results..
- Test families become considerable more accurate if they are large, even 50 is not at all as accurate as an infinite number. But considering tradeoffs between accuracy of individual breeding values and the family size still results in recommendable family sizes of 30 living plants, thus 40 planted. However, these numbers must be based on optimizing considerations as a part of a continuous debate, if accuracy is given much weight it may be worth considering larger families.
- DPM can remain as a general mating design for generating the recruitment population, while it is also rather accurate for progeny-testing;
- SPM is sufficient for forwarding the breeding population and can be used in low input situations or in lower ranking strata of the breeding population;
- If one of the DPM fails, but parents still get progeny in one cross it is not worth delaying the crossing effort to complete the scheme, but instead the number of trees carried on from each cross to next generation may be increased accordingly;
- “Progeny testing” by SPM is accurate enough to be useful. DPM is better and it is better there are still more crosses (if crossings are free). Poly-mix is not essential for a reasonable good progeny testing, although it is the best alternative if parental ranking for breeding value is the only purpose of crossing.



Introduction

As a part of a revision of the Swedish Breeding Strategy I was asked to give views on some of the mating systems used in current operative breeding. The considerations discussed are not fully covering. There are other documents, many of them discussed in other parts of the breeding revision, dealing with e.g. poly-mixes for forward selection, unbalances and increasing the number of parents per grand-parent, which may result in recommendations different from those made here.

The standard model in the current Swedish model is double pair mating followed by selection of one individual from each family. Thus each individual selected for the breeding is mated with exactly two others (Double Pair Mating, DPM) and get exactly two offspring in the next breeding population. It would be simpler with Single Pair Mating (SPM), where each breeding individual get a single mate and thus no half-sibs appear. This study mainly discusses minor deviations from the DPM scheme, not major.

As a criterion for selection to the breeding population breeding values obtained by poly-crossing a number of candidates could be used. Pollen mixes are used for pollination to get more accurate estimates of breeding values than can be obtained by a few crosses with known parents. It is of interest for practical breeding to know how the accuracy of the results can be expected to change with the composition of the pollen mixes, so these mixes can be effectively composed. Breeding value estimates could also be obtained following SPM or DPM and more controlled crosses per mate, so developing the value of these designs also has an interest.

Reservation: I am not 100% sure of these calculations, it is not perfectly proof-read, neither a full list of assumptions and approximations, nor a full evaluation of the significance of those assumptions has been made, and it is difficulties formulating the logic. The formulas are believed to constitute sufficient good approximations for the accuracy predictions needed. But they are not mature for scientific publication in a refereed journal without further scrutiny, but hopefully good enough for decisions in Swedish practical breeding for Norway spruce and Scots pine. A reason to document them in "working report" is the hope that future forest geneticists will be able to improve the formulas.

Mathematical framework

DESIGNATIONS

Symbol	Meaning
$V_A = \sigma_A^2$	Additive variance
$V_D = \sigma_D^2$	Dominance variance
$V_E = \sigma_E^2$	Environmental variance
N	Number of plants in a family (poly-cross half-sib or full-sib)
M	Number of Mates, could be pollen parents in a pollen mix or the number of full-sibs with a common parent
M_E	Effective number of pollen parent in a pollen-mix
r_{FS}	Expected correlation between measurement of a full-sib family and the breeding value of its parents
r_{PCI}	Expected correlation between measurement of half-sib families with the same pollen parent (a common tester of a poly-cross with a single pollen parent) and the breeding value of the seed parent.
r_{FSM}	Expected correlation between the true breeding value and the average of M full-sib families a parent is mated with.
r_{PCS}	Expected correlation between the true breeding value and a poly-cross family with the same M contributors
r_{PCD}	Expected correlation between the true breeding value and a poly-cross family with M different contributors
K	A coefficient to make genetic gain compatible to observations, K is considered constant within this study. K considers relation between observation character and goal character, juvenile-mature correlations and genetic by environment interaction.
G_{HS}	Genetic gain by selecting based on half-sibs performance
G_{FS}	Genetic gain by selecting based on full-sibs performance

Assumptions: Mothers and fathers are sampled from the same population. It is critical that fathers but not mothers come from “the same population”, and the assumption is made to get the formulas and reasoning easier and more transparent. The population is regarded as ideal, but it is not critical that it is “exactly” ideal, and its range of deviation is debatable. The population of plus trees selected for a Swedish subpopulation is probably sufficient for the results to be relevant. It is regarded that one mother is pollinated by several fathers. The extra gain by information possible to get from connectedness is usually disregarded. Genotype by environment interaction is not considered, thus the entries can be seen as if experiments were extended over the relevant range of environments.

Genetic gain and measured characters: The genetic gain of the goal character (increase in breeding value) contributed by a selected tree is depending on the correlation between the goal character (breeding value of the goal character) and the measurement. The measurement may be an index and the goal something like

value for forestry, but it can be practical to see goal as volume production per unit area over the range where the material will be used without change in other tree characters (or rather adjusted to change in other tree characters). The gain depends on the selection intensity, the correlation between the measured trait and the trait the improvement is measured for (juvenile-mature correlation is an important component in that), the genetic variation in the trait improved and, finally, the *correlation between the estimate of the value of the measured trait and the true value of the measured trait* (this can often be seen as the square root the heritability or r_{IT}). This can be seen as a measure of accuracy will often be referred to just as accuracy. This study is concerned only with the measurement accuracy, the influence of the other components are just seen as a value K , which can be regarded as a constant in this study. The measurement accuracy is a function of number of mates, additive variance, dominance variance and family size.

Let us first recapitulate some formula for simple standard cases. The gain of selection backwards (pair of parents) based on a single family can be expressed following Lindgren & Werner (1986, 1989). Formulas developed from in these studies are also found in Rosvall, et al. (2001).

$$G_{FS} = K 0.5 \sigma_A / \sqrt{0.5 \sigma_A^2 + 0.25 \sigma_D^2 + \frac{0.5 \sigma_A^2 + 0.75 \sigma_D^2 + \sigma_E^2}{N}} \quad [1]$$

Selection backwards of “perfect” half-sib families (thus an infinite number of pollen parents).

$$G_{HS} = K 0.5 \sigma_A / \sqrt{0.25 \sigma_A^2 + \frac{0.75 \sigma_A^2 + \sigma_D^2 + \sigma_E^2}{N}} \quad [2]$$

Considering these formulas, the accuracy can be visualized as the correlation among observed and true values. This correlation is proportional to the genetic gain possible as a function of number (or effective number) of pollen parents, size of families, additive, dominance and environmental variation, while other factors need not be considered in the following. For single and double pair matings and pollen mixtures, approximate formulas were first developed by Lindgren (1978). These have been slightly modified (improved). The measurement accuracy between a full-sib and the breeding values of its two parents, r_{FS} is as in formula [1] except the coefficient. Both the nominator and denominator are divided by the (root of) the additive variance to make the inputs of dominance and environmental variance related to that of additive variance and thus make the inputs dimension independent. The formula becomes:

$$r_{FS} = 0.5 / \sqrt{0.5 + 0.25 \sigma_D^2 / \sigma_A^2 + \frac{0.5 + 0.75 \sigma_D^2 / \sigma_A^2 + \sigma_E^2 / \sigma_A^2}{N}} \quad [3]$$

Now the case that all tested trees are mated with the same pollen parent is considered. It is not a question about correlation among full-sibs and their parents, but full-sibs and their single common parent. That is like common testers with a single common tester. The testing population will become half-sibs. It can also be seen as a special case of poly-cross with a pollen mix consisting only of a single pollen parent. The correlation becomes:

$$r_{PC1} = 0.5 / \sqrt{0.25 + 0.25\sigma_D^2 / \sigma_A^2 + \frac{0.5 + 0.75\sigma_D^2 / \sigma_A^2 + \sigma_E^2 / \sigma_A^2}{N}} \quad [4]$$

It is assumed that the crossing design is symmetric and as much information is obtained from each full-sib. In reality the connectedness of the crossing scheme means more information, but this is neglected (and complicated as it is a function of the exact mating design). The correlation between the parents with M mates in separate full-sibs which among them are half-sibs becomes:

$$r_{FSM} = 0.5 / \sqrt{0.25 + 0.25 / M + 0.25\sigma_D^2 / M\sigma_A^2 + \frac{0.5 + 0.75\sigma_D^2 / \sigma_A^2 + \sigma_E^2 / \sigma_A^2}{NM}} \quad [5]$$

Effective number of pollen parents in a poly-mix. Pollen from different fathers is not equally effective. There will be differences in their contribution besides the Poisson distribution. The physical amount of pollen in a mixture can differ. The germination capacity may differ. Differences can be handled by “effective number of pollen parents”. It is given the symbol M_E . That is the inverted value of the square sum of the contributions from different parents (p_i). The formulas for poly-cross can be used if the effective number of pollen parents is used as an entry instead of the real number.

$$M_E = 1 / \sum_{i=1}^M p_i^2 \quad [5a]$$

For a single poly-cross family all individuals can be considered at least half-sibs as they have the same mother. The stochastic variation among a sample from a half sib family of size N is one term to consider in the accuracy. The males have the same average additive value and the stochastic variances in sample of males is disregarded, so no term for this is considered. The dominance means that each father react differently with each mother. As the dominance variance among full sib families is one quarter of the dominance variance and as different mothers get affected by the average of M_E fathers the term can be formulated.

$$r_{PCS} = 0.5 / \sqrt{0.25 + 0.25\sigma_D^2 / M_E\sigma_A^2 + \frac{0.75 + \sigma_D^2 / \sigma_A^2 + \sigma_E^2 / \sigma_A^2}{N}} \quad [6]$$

Probably a more accurate derivation is possible from analyzing the grandparents. Stochastic variation in additive variance among fathers is not considered in formula [6] and [8], but this is probably not of much importance.

The accuracy (correlation) r_{FSM} does not refer to mixes and $M=1$ and 2 are not tabulated for mixes but for single pair mating and double pair mating. There are double as many plants behind a breeding value if double pair mating as single pair mating, thus to be compatible on the same price for progeny testing, single pair mating should use double as large progenies as double pair mating or poly-cross, but this has not been considered in the comparisons in Table 1 or Figure 2.

Different fathers in different pollen mixes

It is sometimes desirable to compare mothers, which has been pollinated with different pollen mixes. Different pollen parents in different mixes constitute an additional reason for differences among poly-cross-families. To quantify this in an easy way it was assumed that different pollen parents were sampled from the same populations. That adds a term to consider variation among different pollen parent samples to the expression under the square root in formula [6]. A mother is pollinated with a mixture. That adds a variance in the average performance of the full sibs formed. A single full sib will vary from an infinite population of full sib families it is sampled from as $0.5V_A + 0.25V_D$, that is the among family part of the variation in a population, cf formula [1]. For a sample of size M_E , of pollen parents, the variation will be:

$$\frac{0.5\sigma_A^2 + 0.25\sigma_D^2}{M_E} \quad [7]$$

Thus, if different pollen parents fertilizing different females origin from different samples of a population, formula [6] is modified and the correlation becomes:

$$r_{PCD} = 0.5 / \sqrt{0.25 + 0.5 / M_E + 0.5\sigma_D^2 / M_E\sigma_A^2 + \frac{0.75 + \sigma_D^2 / \sigma_A^2 + \sigma_E^2 / \sigma_A^2}{N}} \quad [8]$$

Results

Formula [6] gives the accuracy (the correlation among observed and true values for the measured trait, which is proportional to the genetic gain possible) as a function of effective number of pollen parents, size of families, additive, dominance and environmental variation. The accuracies are listed in Table 1 and visualized for a case in Figure 1.

Table 1.

Measurement accuracy (correlation between true and estimated breeding value) as a function of number of pollen parents in the mixture, variance components and family size with the same pollen mix for different mothers and accuracy with SPM and DPM.

σ_D^2 / σ_A^2	σ_E^2 / σ_A^2	Family Size (N)	Number of pollen parents in pollen mixes r_{PCS}				r_{FSM}		
			5	10	20	∞	M=1*	M=1*	M=2
σ_D^2	σ_E^2								
0	0	10	0.877	0.877	0.877	0.877	0.674	0.690	0.791
0	0	50	0.971	0.971	0.971	0.971	0.700	0.704	0.811
0	0	∞	1.000	1.000	1.000	1.000	0.707	0.707	0.816
0.25	0	10	0.830	0.838	0.841	0.845	0.553	0.565	0.684
0.25	0	50	0.941	0.951	0.957	0.962	0.572	0.575	0.702
0.25	0	∞	0.976	0.988	0.994	1.000	0.577	0.577	0.707
1	0	10	0.725	0.745	0.756	0.767	0.392	0.400	0.516
1	0	50	0.864	0.898	0.917	0.937	0.405	0.407	0.531
1	0	∞	0.913	0.953	0.976	1.000	0.408	0.408	0.535
0	5	10	0.550	0.550	0.550	0.550	0.488	0.568	0.620
0	5	50	0.828	0.828	0.828	0.828	0.640	0.671	0.762
0	5	∞	1.000	1.000	1.000	1.000	0.707	0.707	0.816
0.25	5	10	0.538	0.540	0.541	0.542	0.435	0.492	0.565
0.25	5	50	0.808	0.815	0.819	0.822	0.538	0.557	0.670
0.25	5	∞	0.976	0.988	0.994	1.000	0.577	0.577	0.707
1	5	10	0.506	0.513	0.516	0.520	0.343	0.371	0.459
1	5	50	0.758	0.781	0.793	0.806	0.392	0.400	0.516
1	5	∞	0.913	0.953	0.976	1.000	0.408	0.408	0.535
0	10	10	0.434	0.434	0.434	0.434	0.402	0.494	0.527
0	10	50	0.733	0.733	0.733	0.733	0.593	0.643	0.722
0	10	∞	1.000	1.000	1.000	1.000	0.707	0.707	0.816
0.25	10	10	0.428	0.429	0.430	0.430	0.371	0.441	0.492
0.25	10	50	0.720	0.725	0.727	0.729	0.509	0.540	0.642
0.25	10	∞	0.976	0.988	0.994	1.000	0.577	0.577	0.707
1	10	10	0.412	0.415	0.417	0.419	0.309	0.348	0.417
1	10	50	0.684	0.700	0.709	0.718	0.381	0.394	0.503
1**	10	∞	0.913	0.953	0.976	1.000	0.408	0.408	0.535

** The formula may give too low value of the correlation when V_D is high.

* Two values are given for single pair mating. The difference is the family size. The left column refer to the family size tabulated and the right column to double as high family size, which makes a more fair comparison to the other values as each family give breeding value of two parents for SPM.

Arguments to have rather many pollen parents in a pollen mix

Probably it is not problematic to collect and manage the magnitude of 25 different pollen parents. Equipment to keep them separate exists, sampling of 25 clones will not take unreasonable amount of time, establishments like seed orchards and breeding orchards contain usually more than 25 clones, and collections can exclude bad pollen producers. Selfing should be avoided since it increases uncertainty in the analyses, but for mixes of many pollen parents it may be possible to tolerate to pollinate a clone with a mix containing that clone.

There are a number of investigations on using pollen parents in equal mixtures, and the results vary. The effective number versus the real number of pollen parents was calculated to 0.64 based on the relative success of different pollen parents in a mixture obtained in a study by Wheeler, et al. (2006) and I suggest to use that value ($M_E=2/3$) when equal amounts of pollen are used. But a more careful literature study may be justified. Skröppa & Lindgren (1994) found considerable differences in paternal success in mixtures, while Wiselögel & Hattemer (1988) found no deviation from the equal paternal success hypothesis. Kumar, et al. (2005) reviewed around 10 studies, most of them finding unequal contributions after pollination with an equal amount of pollen in a poly-mix. They found that a single pollen parent dominated after pollinating radiata pines with an equal mix of 15 pollen parents and they also found some contamination. Pollen germination differences can give important contributions Nikkanen, et al. (2000).

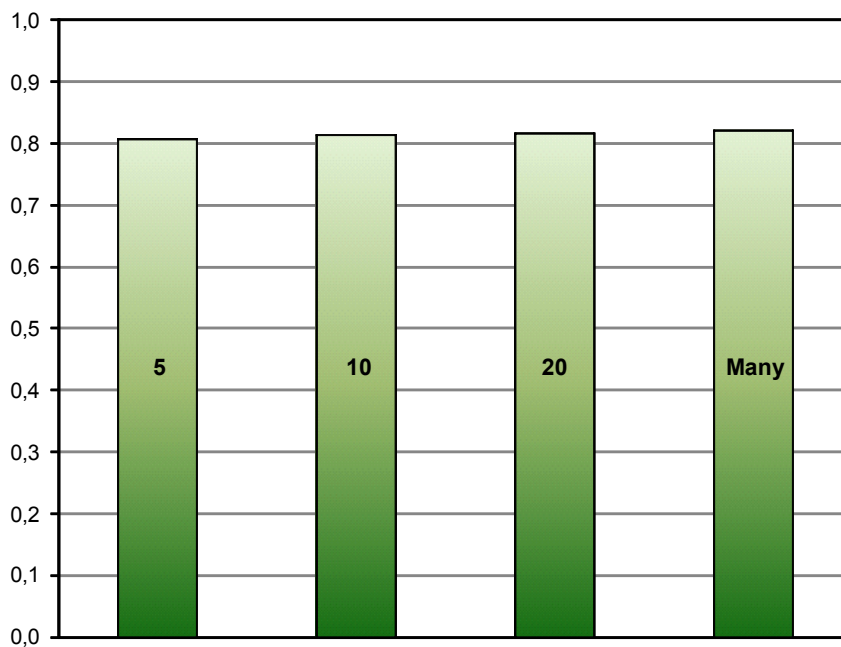


Figure 1. Accuracy (correlation between observed and true) selecting tested female parents with variable number of pollen parents in the polymix cocktail (given in bar) for the values: family size =50; $V_D=0.25V_A$; $V_E=5V_A$.

The number of fathers does not seem to be an important factor, but of course it is the only component which can be manipulated by the breeder. Dominance variation is not an important factor for the accuracy, and not so important for the number of pollen parents to be used.

It is rather arbitrary exactly what to recommend according to table 1. For $M_E \geq 5$ for all tabulated values with $V_D \leq V_A$ the accuracy is at least 91 % of that with an infinite number of fathers. For $M_E \geq 10$ the accuracy is 95 % of that with an infinite M_E . For $M_E \geq 10$ allowing $V_D \leq 0.25V_A$ it is at least 98 %. Values of dominance variance $V_D=0.25V_A$ seems most typical (Fries 1987 and Rosvall 1999, dissertations). Thus, it seems to be little benefit in using more than 10 fathers and

even that may be much for the typical situation. I recommend twelve pollen equally mixed by volume, probably corresponding to an effective number of reproductive successful pollen of 8, but even if it is more unequal pollen contribution, the loss of accuracy will not be high.

The table assumes equal amounts of pollen from each father and that the same pollen mix is used for all mothers. The recommendation is not a guarantee for a high accuracy under all circumstances, but the accuracy cannot be much larger by adding more pollen parents. But the gain maybe somewhat increased (or even rather much increased under some not that likely circumstances which will not be known then the decision is taken) if a higher number of fathers is used, so the recommendation is to be interpreted as a minimum. There is no disadvantage to use many pollen parents apart from the practical troubles involved in collection and management. Therefore, if the troubles involved are limited, I see no disadvantage to use higher numbers than recommended. If the opinion concerning the degree of dominance should change increasing dominance variance, an increase of the minimum number of parents may be debated but it does not seem critical. A higher number of pollen parents in a mix make it less sensitive to replacements of some pollen parents in the future (see below).

Pollen from different parents need not necessarily be mixed in equal amounts, but if unequal amounts of pollen are used, the number of pollen parents should be increased. The more pollen used, the less critical it is how the proportions vary. If more pollen sources are available there is no penalty in gain to use them even if the amounts in the mix of the added pollen should be smaller. An effective number of pollen contributors can be estimated based on the square of the sum of proportions divided by the square sum of the proportions (formula [5a]). An estimate is better done at the spot rather than a thumb rule, as the variation in pollen produced per clone can vary very differently among different years and establishments. It may be more important but also easier to use more clones (all in a seed orchard rather than just a few) than using the minimum suggested in equal proportions.

Different fathers in different pollen mixes

Different pollen parents in pollen-mixes pollinating different mothers, which are compared for breeding value, is an additional reason for differences among poly-cross-families. But using a high number of different pollen parents sampled from the same population, comparisons may still be efficient.

Using formula [8] for calculating accuracy values (r_{PCD}), Table 2 was obtained. The number of fathers to get a certain correlation is roughly double as large as if the father gametes were sampled from the same set of pollen parents. Thus if I suggested 8 and 12 pollen parents when using a single pollen mix, now I suggest 16 and 24 when using different pollen mixes for different mothers.

Table 2.

Correlation between true and estimated breeding value (measurement accuracy) as a function of the number of pollen parents in the mixture, variance components and family size when using different pollen mixes for testing different mothers (r_{PCD}).

σ_D^2 / σ_A^2	σ_E^2 / σ_A^2	Family size (N)	Number of pollen parents in pollen mixes (M)			
			5	10	20	∞
0	0	10	0.767	0.816	0.845	0.877
0	0	50	0.828	0.891	0.928	0.971
0	0	∞	0.845	0.913	0.953	1.000
0.25	0	10	0.725	0.778	0.810	0.845
0.25	0	50	0.796	0.867	0.911	0.962
0.25	0	∞	0.816	0.894	0.943	1.000
1	0	10	0.632	0.690	0.725	0.767
1	0	50	0.718	0.806	0.864	0.937
1	0	∞	0.745	0.845	0.913	1.000
0	5	10	0.520	0.535	0.542	0.550
0	5	50	0.733	0.776	0.801	0.828
0	5	∞	0.845	0.913	0.953	1.000
0.25	5	10	0.506	0.523	0.533	0.542
0.25	5	50	0.711	0.760	0.789	0.822
0.25	5	∞	0.816	0.894	0.943	1.000
1	5	10	0.471	0.494	0.506	0.520
1	5	50	0.654	0.718	0.758	0.806
1	5	∞	0.745	0.845	0.913	1.000
0	10	10	0.419	0.426	0.430	0.434
0	10	50	0.665	0.697	0.714	0.733
0	10	∞	0.845	0.913	0.953	1.000
0.25	10	10	0.412	0.421	0.425	0.430
0.25	10	50	0.648	0.685	0.706	0.729
0.25	10	∞	0.816	0.894	0.943	1.000
1	10	10	0.392	0.405	0.412	0.419
1	10	50	0.604	0.654	0.684	0.718
1	10	∞	0.745	0.845	0.913	1.000

Plants per family

The accuracy for using 10 test progeny (family size N in table 1 and 2) is low. Increasing the size of test progeny can result in considerable additional gain. Skogforsk (Almqvist 2009) suggests 40 as a main alternative till further results become available and as a main alternative for future considerations. Danusevicius & Lindgren (2002) find 17 surviving plants optimal in optimization of a 2 stage selection of Scots pine where the first step is phenotypic forward selection within full-sibs and the second step is progeny testing these trees by a poly-cross. To allow for mortality, asymmetries and tests at different sites, at least 30 planted trees could be assumed to be optimal, but 40, as suggested as the standard alternative, may be good for polycross progenies. However, the accuracy can be increased rather much by increasing the progeny size, the sizes mentioned are low because it

is a trade off between accuracy of a tested unit and number of tested units. Thus progeny sizes lower than 50 should only be used after careful considerations of the trade offs, not as a thumb rule used without consideration. To optimize plant number in long term breeding additional considerations for selections forward has to be done, which are not dealt with in this study.

Single Pair Mating and Double Pair Mating

Note that a considerable part of the gain by selection is obtained if the parents of a full-sib are selected based on the performance of the full-sib (Table 1). A still larger fraction of the gain can be obtained following double pair mating, higher than table 1 indicates as the tabulated case assumes the two parents pollen are mixed and form only a single family (cf. Lindgren, 1978). But this underestimates the power of SPM and DPM, as they test two parents while the poly-cross only test one parent, thus they are considerable more efficient if compared at an equal cost level.

Possible advantages of DPM over SPM are listed

- A higher connectedness will usually occur, which makes it possible to use information from all the breeding stock more efficiently when calculating genetic parameters like dominance variance and breeding values. The value of this added information is often not important; the gain in information is small and can not be used if parental balance is applied. The DPM can be done in different ways, and in itself does not guarantee a good connectedness.
- Specific combining ability and maternal effects can be better evaluated and utilised. However, the estimates of the influence of SCA versus GCA will be highly uncertain and contribute little to the gain. Specific combining ability appears rather unimportant in most Swedish cases, which reduces the relative advantage of DPM over SPM.
- Better BV estimates for the parents, and as the parents are seed orchard candidates, slightly better seed orchards are likely.
- Slightly better BV estimates of progeny and slightly larger genetic variation. As progeny are seed orchard candidates and clonal forestry candidates and family forestry candidates, slightly higher gain transferred to the forest can be foreseen.
- A slightly higher selection intensity at a constant breeding population size over generations (thus the single best of 50 is not expected to be as good as the average of the two best of 100).
- More families to choose among which could mean a slightly higher gain if family forestry with tested families becomes important, but this scenario does not seem likely.
- Higher robustness, thus even if some crosses fail or are not realised, still parental genes will be transmitted, and the chance is higher that a crossing program need not be extended more years.

- It has advantages if an individual is used once as a mother and once as a father. If crosses are done with similar samples of male or female gametes, maternal effects or just “after-effects” may be interpreted as breeding values, but if both gender are as common, such effects level out. With SPM probably always a genotype is only represented by one gender.
- Increased probability of mating two good parents for forward selection
- Opportunities to select and cross less related trees. Under balanced selection two parents result in two selected half-sibs in their progeny as compared to two selected full-sibs under SPM

Possible advantages of SPM over DPM are listed:

- Positive Assortative Matings can be easier implemented with SPM as matings can be done exactly according to the ranking of breeding values and adjustments because of e.g. scarce flowering are easily done, and thus the breeding population is somewhat easier structured to support mass production population.
- The relatedness pattern will be less complex and more manageable.
- SPM is the simplest possible mating design.
- SPM is the easiest design to set up, DPM is more difficult to implement and less flexible and may not be perfectly realised.
- SPM may be the most efficient design for some cases and is not expected to be bad for any realistic situation.
- Cheaper (half as many crosses).
- Somewhat simpler field design (half as many entries).
- In scenarios where the breeding population is expended far above the number of founders, or include many founders, SPM is interesting, as it is the cheapest way to involve many parents.
- A clearer and more manageable relatedness structure in the next recruitment population (trees are either full-sibs or not sibs).

No of the reasons mentioned is expected to be quantitatively dramatically strong and the preference of DPM or SPM is not critical.

DPM or SPM?

Note that this study focus on breeding value estimates rather than breeding strategy and thus does not intend to give a complete picture, although still some other aspects that breeding values are comparatively briefly mentioned. DPM (or still more mates) can be reserved for strata of the breeding population where the trees have a higher value for some reason and SPM can be used in less valuable strata. Strata may refer to species (Norway spruce and Scots pine have a high value and most deciduous trees have a low value) or parts of the breeding population. If a large breeding population is desirable at a small effort, SPM seems to be the best option. If costs or availability of genders (possible seed vs. pollen parents) vary, one can think in terms of “ $1/2$ DPM”, thus some genotypes get two mates and

some one, e.g. the same pollen parent is used for two females, the pollen parents are DPM but the seed parents SPM.

If DPM fails?

If a planned DPM scheme is not filled, but all parents are represented in crosses, it is not worthwhile to wait many years to fulfil the design. But to make the selection more efficient and optimal, the number of selections per family and family size could be adjusted (in principle double as many selections from SPM families as for DPM families, thus two selections instead of one, but in a more complex world, more sophisticated adjustments has to be considered).

SPM and DPM for parental testing

It is an old pre-justice that SPM and DPM do not give useful information about the parents, although it was demonstrated by Lindgren (1978) that they give rather efficient information (Figure 1 and Table 1). Otherwise untested parents to SPM and DPM families can be used in seed orchards and be regarded as fairly well tested, and a substantial gain will occur based on selection among those tested breeding population members. Thus, a breeding strategy based on selection of phenotypes with no replicates, which are crossed with SPM or DPM can support a seed orchard program using clones tested in this way. The function of test accuracy on variance components and family size is tabulated in Table 1 and Figure 2 is actually unfair to SPM, because compared at the same number of parents tested the plant number of trees is half as many for SPM. To obtain a sufficiently reliable testing it seems to be motivated to try to attain at least 50 living progeny to each parent.

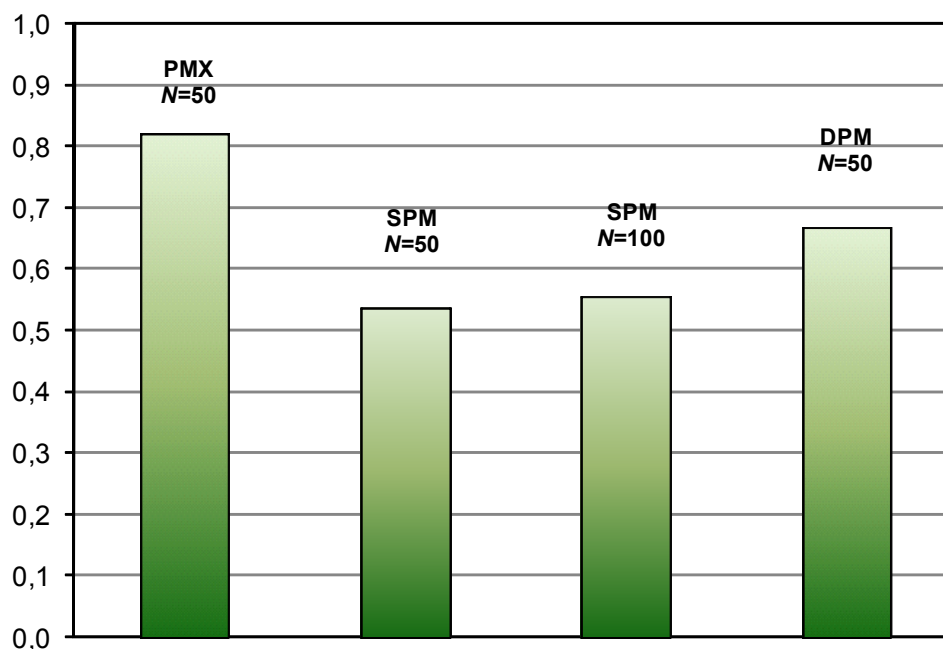


Figure 2. Example of expected gain following selection on estimated breeding value with a pollen mix with a large number of pollen (PMX), single pair mating (SPM) and double pair mating (DPM). The family size is 50 but for SPM a value for family size 100 is also given to make SPM compatible at the same resource per tested parent basis. Note that the pollen mix does not give that very superior accuracy for estimating breeding values $V_D=0.25V_A$; $V_E=5V_A$.

Acknowledgement: Discussions with the Swedish breeding revision theme and in particular Ola Rosvall and Curt Almqvist are acknowledged.

References

A website which currently have relevant information and links for the problem:

<http://www-genfys.slu.se/staff/dagl/Foradlrevision07/MainPageForRev.htm>

- Almqvist, C. 2009. Alternative strategies for Scots pine breeding in Sweden. Description of strategies for Scots pine breeding that should be considered in the revision of the Swedish breeding programme. Document dated 090212.
- Danusevičius, D. & Lindgren, D. 2002. Two-stage selection strategies in tree breeding considering gain, diversity, time and cost. *Forest Genetics*. 9:145–157.
- Fries, A. 1987. Genetics of plus tree progenies of lodgepole pine (*Pinus contorta* spp. latifolia), and possible implications for a breeding program in Sweden. Ph thesis.
- Lindgren, D. 1978. Genetic gain by progeny-testing as a function of mating design and cost. – Third World Consultation on Forest Tree Breeding 2:1223–1235.
- Lindgren, D. & Werner, M. 1986. Hellsyskonklonplantage – ett sätt att få bättre granfrö. Årsbok, Institutet för skogsförbättring. s. 155–186.
- Lindgren, D. & Werner, M. 1989. Gain generating efficiency of different Norway spruce seed orchard designs. (including an appendix by Ö. Danell). In Stener, L.-G. & Werner, M. (eds) Norway spruce; provenances, breeding and genetic conservation. Institutet för Skogsförbättring. Rapport 11: 189–206.
- Kumar, S., Gerber S., Richardsson T. E. & Gea, L. 2005. Testing for non-random contribution of pollens using nuclear- and chloroplast SSR markers in polycross families of *Pinus radiata* D. Don. *Tree Genetics & Genomics* 3:207–214.
- Nikkanen, T., Aronen, T., Haggman, H. & Venäläinen, M. 2000. Variation in pollen viability among *Picea abies* genotypes— potential for unequal paternal success. *Theor Appl Genet* 101:511–518
- Rosvall, O. 1999. Enhancing Gain from Long-Term Forest Tree Breeding while Conserving Genetic Diversity. *Acta Universitatis Agriculturae Sueciae. Silvestria* 109 65pp+4 chapters.
- Rosvall, O., Jansson, G., Andersson, B., Ericsson, T., Karlsson B., Sonesson, J., Stener L-G. 2001. Genetic gain from present and future seed orchards and clone mixtures. The Forestry Research Institute of Sweden, Rep. 1: 36–41.
- Skröppa, T. & Lindgren, D. 1994. Male fertility variation and non-random segregation in pollen mix crosses of *Picea abies*. *Forest Genetics* 1:13–22.
- Wheeler, N.C., Payne P., Hipkins V., Saich R., & Kenny S. 2006. Polymix breeding with paternity analysis in *Populus*: A test for differential reproductive success (DRS) among pollen donors. *Tree Genetics & Genomes* 2: 53–60.
- Wiselogle, A.E. & Buijtenen J.P. van. 1988. Probability of equal mating in Polymix pollinations of loblolly pine. *Silvae Genet.* 37:184–187.

Arbetsrapporter från Skogforsk fr.o.m. 2008

År 2008	
Nr 652	Löfgren, B., Nordén, B. & Lundström H. 2008. Fidelitystudie av en skogsmaskin-simulator. 30 s.
Nr 653	Norén J., Rosca, C. & Rosengren, P. 2008. Riktlinjer för presentation av apterings-information i skogsskördare. 70 s.
Nr 654	Sonesson, J. 2008. Analys av potentiella mervärden i kedjan skog-industri vid användning av pulsintensiv laserscanning.
Nr 655	Jönsson, P. & Nordén B. 2008. Skotare med ALS och tredelade stöttor – Studier av prestation och helkropps vibrationer i gallring. 14 s.
Nr 656	Persson, T., Almqvist, C., Andersson, B., Ericsson, T., Högberg, K.-A., Jansson, G., Karlsson, B., Rosvall, O., Sonesson, J., Stener, L.-G. & Westin, J. 2008. Lägesrapport 2007-12-31 för förädlingspopulationer av tall, gran, björk och contortatall. 21 s.
Nr 657	Stener, L.G. 2008. Study of survival, height growth, external quality and phenology in a beech provenance trial in southern Sweden. 11 s.
Nr 658	Almqvist, C. & Eriksson, M. Ökad produktion i plantage 501 Bredinge – försök med rotbeskäring och gibberellinbehandling. 13 s.
Nr 659	Rytter, R.M. 2008. Detektion av röta i bok med 4-punkters mätning av resistivitet. 14 s.
Nr 660	Bergkvist, I., Iwarsson Wide, M., Nordén, B. & Löfroth, C. 2008. Jämförande prestationsstudier – Röjsåg med klinga kontra kedjeröjsåg. 21 s.
Nr 661	Johansson, K. Snytbaggen – kunskapsläget 2008. 18 s.
Nr 662	Österman. Öd. D., Rimquist, L. & Hanson, M. 2008. Geststyrning för engreppsskördare – en första undersökning – Projektarbete Ergonomi och Design VT-2008. 64 s.
Nr 663	Westlund, K. & Andersson, G. 2008 Vägstandardens inverkan på skogsnäringens transportarbete. 58 s.
Nr 664	Hannrup, B. 2008. Slutrapport för projekt ”Mätteknik för avverkningsrester”. 52 s.
Nr 665	Rosvall, Ola., Wennström, U. 2008. Förädlings effekter för simulering med Hugin i SKA 08. 38 s.
Nr 666	Barth, A., Hannrup, B., Möller J. J. & Wilhelmsson, L. 2008. Validering av FORAN SingleTree® Method. 44 s.
Nr 667	Baez, J. 2008. Vibrationsdämpning av skotare. 67 s.
Nr 668	Björklund, N., Hannrup, B. & Jönsson, P. 2008. Effekter av förhöjt knivtryck i skördar-aggregat på barkskadorna hos massaved och följeffekter på produktionen av granbarkbollar. 34 s.
År 2009	
Nr 669	Almqvist, C., Eriksson, M. & Gregorsson, B. 2009. Cost functions for variable costs of different Scots pine breeding strategies in Sweden. 12 s.
Nr 670	Andersson, M. & Eriksson, B. 2009. HANDDATORER MED GPS. För användning vid röjningsplanläggning och röjning. 25 s.
Nr 671	Stener, L.G. 2009. Study of survival, growth, external quality and phenology in a beech provenance trial in Rånna, Sweden. 12 s.
Nr 672	Lindgren, D. 2009. Number of pollen in polycross mixtures and mating partners for full sibs for breeding value estimation. 15 s.
Nr 673	Bergkvist, I. 2009. Integrerad avverkning av grotbuntar. 21 s.
Nr 674	Rosvall, O. 2009. Kompletterande strategier för det svenska förädlingsprogrammet. 26 s.
Nr 675	Arlinger, J., Barth, A. & Sonesson, J. 2009. Förstudie om informationsstandard för stående skog. 21 s.
Nr 676	Nordström, M. & Möller J. J. 2009. Den skogliga digitala kedjan – Fas 1. 38 s.
Nr 677	Möller J.J., Hannrup, B., Larsson, W., Barth, A. & Arlinger, J. 2009. Ett system för beräkning och geografisk visualisering av avverkade kvantiteter skogsbränsle baserat på skördardata. 36 s.

Nr 678	Enström, J. & Winberg, P. 2009. Systemtransporter av skogsbränsle på järnväg. 27 s.
Nr 679	Iwarsson Wide, M. & Belbo, H. 2009. Jämförande studie av olika tekniker för skogsbränsleuttag. – Skogsbränsleuttag med Naarva-Gripen 1500-40E, Bracke C16.A och LogMax 4000, Mellanskog, Färila. 43 S.
Nr 680	Iwarsson Wide, M. 2009. Jämförande studie av olika metoder för skogsbränsleuttag. Metodstudie – uttag av massaved, helträd, kombinerat uttag samt knäckkvistning i talldominerat bestånd, Sveaskog, Askersund. 25 s.
Nr 681	Iwarsson Wide, M. 2009. Teknik och metod Ponsse EH25. – Trädbränsleuttag med Ponsse EH25 i kraftledningsgata.
Nr 682	Iwarsson Wide, M. 2009. Skogsbränsleuttag med Bracke C16. – Bränsleuttag med Bracke C16 i tall respektive barrblandskog.