

UNBALANCES IN TREE BREEDING

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Abstract

Applications of unbalance in tree breeding are discussed. Unbalance has the potential to make the breeding more efficient. But management of unbalance is not fail-safe and requires often considerable competence. The benefits of unbalance may sometimes appear larger than they are in the long run and in the real world. On the other hand, unbalance is practically unavoidable and thus breeders have to deal with it anyway, and moderate unbalances are unlikely to have significant negative effects and thus seem fail-safe. It could be a good idea to apply unbalance with some moderation compared to what may seem optimal from individual simplified studies. When appreciable benefits seem likely, the implementation of moderate unbalance seems recommendable.

Why unbalances?

It is desirable to maintain genetic variation in breeding stock. Gene diversity is a quantitative measure of how well genes are conserved; from a conservation point of view it does not matter if they are good or bad, but to obtain high gain it is of course important to increase the representation of the good genes. Thus balanced breeding with equal contributions is not expected to be theoretically optimal.

In the gene mass of future breeding stock and propagation populations, the best part of the current breeding population will be overrepresented. It is thus more important to improve the better part of the gene mass than the worse. More resources can be spent on improving better gene mass than worse. Such a strategy will increase the realized average gain.

Unequal genetic distributions are the standard in Nature, and cannot be avoided. This is the driving force for evolution and a fundament for existence of life. It is the essence of genetic improvement that some are selected, while others are not.

Unbalanced selection offers more degrees of freedom and a more optimal consideration of essential elements of breeding (gain, diversity, time and cost).

Even a limited extra increase in efficiency (e.g., 5% increase of gain) may correspond to a huge sum of money for an expensive and important crop. Even if it is mathematically difficult and practically impossible to optimize the degree of unbalance, used with common sense and some care it ought to be possible to apply unbalance so the result become better than balance in situations when the added gain makes it worthwhile.

Utilizing unbalance may mean more gain faster, and it may be worth that even at the cost of a reduced potential for more gain later.

Against unbalances

In a closed ideal population, the gene diversity is maximized if different genetic components are equally represented. It is not fail-safe to apply unbalance; efforts may result in a worse situation than perfect balance. Breeding goals, genetic parameters and environments change over time, are difficult to predict and predictions has errors, while the effect of the unbalances may remain. Optimization of unbalance requires knowledge of certain parameters which are not accurately known and draws resources to get estimates of, larger resources the better estimates. Gains of using imbalance may be evident when measurement characters are considered, but the effects on other characters are less predictable. That means creation and optimization of unbalances may appear more favorable than it really is in the long run. Studies are often set up to demonstrate an effect and use simplifications. Results indicating considerable effects tend to be published and get more attention by both authors and readers compared to absence of effects or small effects. Therefore, if an effect is found, studies tend to overestimate the size in the real World. Safety bids that one does not change drastic at once from one extreme complete balance to the opposite extreme of strong unbalance based on a few undigested studies without much consideration about possible loopholes. It would not be politically correct to suggest the extreme, it would probably be counter-productive and raise suspicion and make it more difficult to implement a less drastic version. Striving for balance is a clear and simple strategy. Unbalance is demanding on competence and it takes time, effort and management skills to consider unbalances. Considering practicalities and difficulties to find the optimum, balanced breeding may still sometimes be regarded as best from an operational point of view when the advantage of unbalance appears marginal or doubtful.

Different unbalances

There are different types of unbalances, which will be discussed to a varying degree:

- Unbalance in components (parents);
- Unbalance in resources;
- Structure of breeding population (e.g. mating probability; PAM, Positive Assortative Mating, which means that similar parents are mated)

Unbalances in the propagation population

The simplest case is the propagation population, where only unbalance in components (clones) matter. The basic idea that unbalanced representation of genetic materials could offer advantages in forest tree breeding was first introduced for deployment of clones in seed orchards. The first speculation that unbalances may be favorable was done by Lindgren (1974). The propagation population was a seed orchard, which is the most common propagation population. Mathematical development showed that a linear relation between the amount of deployed genetic units (clones) and their breeding value resulted in an optimal balance between effective number (status number, gene diversity) and breeding value, the first suggested application was formulated by Lindgren and Matheson (1986). It was widened to deployment of clones for clonal forestry (Lindgren, Libby and Bondesson 1989) and developed to be applicable for genetic thinning by Bondesson and Lindgren (1993) and Prescher et al. (2004). The advantage and characteristics of the method have been mathematically quantified (Lindgren 1991, Lindgren 1993).

Further on to the production population

The production population is generated from the propagation population, but there are some steps between propagation population and production population. The propagation population is typically an open pollinated seed orchard. Unequal number of ramets will occur even if it is not directly intended, e.g. current clonal seed orchards are usually characterised by unequal number of ramets of different clones (Kang 2001). Thus equal representation is hardly a realistic alternative, neither does it offer advantages. It may be true that - given the clone number - the effective clone number is highest if clones have equal number of ramets, but a moderate increase in clone number is almost always a better way to meet a demand for increased effective clone number. Many other factors than ramet number contribute to the unbalance in seed orchard crops (Bila 2000, Olsson 2001, Kang 2001). Genotypes in a seed orchard differ in reproductive success, and there are differences between the male and female success, and male and female may be correlated to different degree. There is pollen migration into the seed orchard. Related genotypes may occur. Only some clones may be harvested. There are phenomena also after the cone harvest contributing to unbalance: seed extraction, seed fractionation, germination, nursery mortality, field mortality, natural in plantations... The details about these phenomena occurring in the steps between the propagation population and production and possible responses are beyond the scope of this study.

Unbalances at the set up of a tree improvement program

Given a population with a structure of unrelated families it was possible to identify an optimum unbalance in selecting individuals from different families (Lindgren, Wei and Bondesson 1993). Optimum unbalance in deployment of individuals from different families is close to linear deployment, thus the number of selected from a family will be approximately linear related to the breeding value of the family, for at least some cases (Wei and Lindgren 1995).

The optimal number of families at the start of a breeding program was calculated as a function of cost components, heritability and desired effective population size (Lindgren, Wei and Lee 1997). The optimization allowed for unequal contribution from families, but the calculations were keeping the effective number constant and did not focus on unbalance. If the price of families (plus trees to use for crosses) is high, it may be worth investing a large share of available resources to get many unrelated families to start with. If the cost per family is low, it is advantageous to have a much larger number of families at the start than the effective number headed for.

Some studies mentioned below have been done more or less based on the Swedish breeding program, thus some information about that is given. The Swedish breeding stock is structured in 46 subpopulations of Scots pine and Norway spruce, the long term breeding population size (number of trees contribution to the next generation breeding stock in one of the populations) is planned to be 50. Ruotsalainen (2002, popularized in Swedish by Rosvall et al. 1999) studied the possible advantage of different contributions from different plus trees at the establishment of the breeding population. A comparison between unbalanced and balanced is done in Table 1. In the example there are 200 tested plus trees available for a population, which is rather typical. The highest ranking ones are used as founders and the contribution of the founders to the subsequent F1 breeding population is either 1, 2 or 3 (the standard variant of the Swedish tree improvement program is 2). The contribution of plus trees which are not used as founders and do not contribute to the breeding population is of course 0. This was organized so that one and only one individual was foreseen selected in each full sib family (within family selection). The compared alternatives (unbalanced versus balanced) use the same amount of resources: the

Table 1. Comparison of unbalanced versus balanced initiation of tree breeding

Unbalanced		Balanced	
Rank of plus tree	Progenies (full sib families)	Rank of plus tree	Progenies(full sib families)
1-10	3	1-50	2
11-30	2	-	
31-60	1	-	
61-200	0	51-200	0
Gain	1.368		1.271

same number of crosses (full sib families); the same number of test plants; the same number of F1-selections. The alternatives result in the same gene diversity. But the gain differs. The gain is given as selection intensity of parents.

The gain will be 7.63 per cent higher for the unbalanced alternative. This difference is likely to remain in the future and cause an improvement of the magnitude of 0.5% of forest production from future seed orchard crops at a given time in the future. Another way of expressing the advantage is that 15 % less plus trees need to be selected and tested. That means that 15 % less trees can be tested and still the same gain and gene diversity can be obtained, thus the costs of the most essential part of the initiation of long term breeding can be cut by 15% by using unbalance resulting in the same size of breeding population, the same gain and the same diversity.

Ruotsalainen (2002) studied other cases. Slightly more optimal solutions can be found, but the suggested one is near the optimum for Scandinavian pine and spruce and simple to express. A «heuristic rule» is suggested for the number of offspring to different founders depending on their breeding value (cf Table 1). Founders are here plus trees with known breeding values, which transmit progeny to establish a breeding population generation with trees with known parents. The number of offspring transmitted to the breeding population is depending on the breeding value of the parent. The top 1/6 of the selected founders contributes three offspring, the 1/3 with intermediate ranking contributes two and the 1/2 with low ranking contributes one.

Andersson (1999) found, based on selection in a Scots pine progeny test, that selection resulting in different number of selections from different families with more selections from the better families had advantages (more gain at the same gene diversity) compared to within family selection.

Rosvall (1999, see below) indicated only a minor and somewhat doubtful advantage of unbalance even at the first generation of breeding. This study was not set up to investigate the initiation and this is not in focus. Thus it does not directly contradict the results by Ruotsalainen (2002) indicating that the benefits of an unbalance in the initiation of the breeding can be substantial, although it gives a reminder that the gain in seed orchards which constitutes a more intensive selection than the breeding population, may be somewhat reduced.

There are other arguments than the extra gain to let a larger number of parents by represented in the first generation of the breeding population. It remains an option to derive larger gene diversity from the F₁ population if that would appear desirable. There is a larger flexibility to respond to changes in breeding goals. The results by Andersson (1999) suggest that group merit may be higher if the F₁ breeding population is refreshed by including fresh plus trees rather than confining the selections to the related progenies of those initially selected. That may indicate a way of increasing the number of founders and to introduce unbalance if it was not done immediately.

Unbalances in long-term breeding

Since some decades the major idea in creating unbalances in breeding is by «nucleus breeding». Nucleus breeding refers to the stratification of the breeding population into distinct groups based on estimated genetic value, usually a two-tier elite and a main subpopulations. The key idea is to concentrate more of the breeding effort on the elite, where maximum gain will be achieved, with less emphasis placed on the main, which is mainly for preserving genetic variation. This system was initially used in sheep breeding (James 1977), but has later been incorporated into forest trees (Cotterill 1989). This basic idea of structuring the breeding population can be developed into something more sophisticated, e.g. PAM combined with breeding effort related to breeding value.

Short-term gain is maximized by selection for breeding value. Breeding value can be estimated based on information from relatives. A simple case is to form an index (thus calculate predicted breeding value) of the individual performance and family performance. Selection for that can be called index selection and maximizes gain. But in long term breeding the loss of gene diversity will cause a loss of additive genetic variance and thus a reduction in the response to selection. Thus maximizing genetic gain in the short term will cause reduced genetic gain in the long term. It is a matter of optimization. The longer breeding program is considered, the more important for genetic gain at the end it is to conserve gene diversity. In the real long term, the assumptions for the used models break down (e.g. as mutations occur). Novel approaches to genetic improvement are likely to take over a century ahead. Current breeders responsibility may be restricted to keep options open for the foreseeable future. Management of genetic resources of forest trees may include guarding the genetic resources for gene diversity and other aspects so a reasonable situation a century ahead seems likely, but it is debatable if the responsibility stretches beyond that. Therefore it does not seem meaningful to consider more than five generations when cycling time is several decades.

Once the breeding population is closed, the ultimate long-term response is maximized by balanced within family selection (Dempfle 1975). However this ultimate limit is irrelevant for trees, as it lies a large number of generations ahead.

Breeding can be seen as a balance between gain and gene diversity. Earlier the needed number crunching power did not exist and that put strong constraints on what could be done, much of the theoretical basis some decades ago appeared rather abstract. For forest tree applications an essential landmark was the PhD thesis of Wei (1995). It became evident that tree breeding maximizing breeding value and not considering loss in gene diversity (build up of relatedness) had the potential to erode the diversity severely. For managing unbalances the application of «status number» (group coancestry) was essential (Gea 1997, Lindgren and Kang 1997).

Rosvall (1999) used the breeding simulator POPSIM (Mullin and Park 1995) to simulate a case relevant for the planned Swedish long-term breeding of Norway spruce. (The latest version of POPSIM is referred to in Lstiburek, 2005). The value of the breeding population was seen as its capacity to support seed orchards. Higher gene diversity in the breeding population makes it more able to support selections with high breeding value to seed orchards (Figure 1). Different ways of introducing unbalance was used. Unbalance appeared to offer only minor advantages (e.g. Figure 1).

Rosvall (1999) assumed testing of the recruitment population, which means high heritability. Balance is more favorable when heritability is high as then the family component of selection becomes unimportant. An option for long term Swedish Scots pine breeding is selection of untested genotypes for the breeding population, and in that situation the advantage of unbalance can be

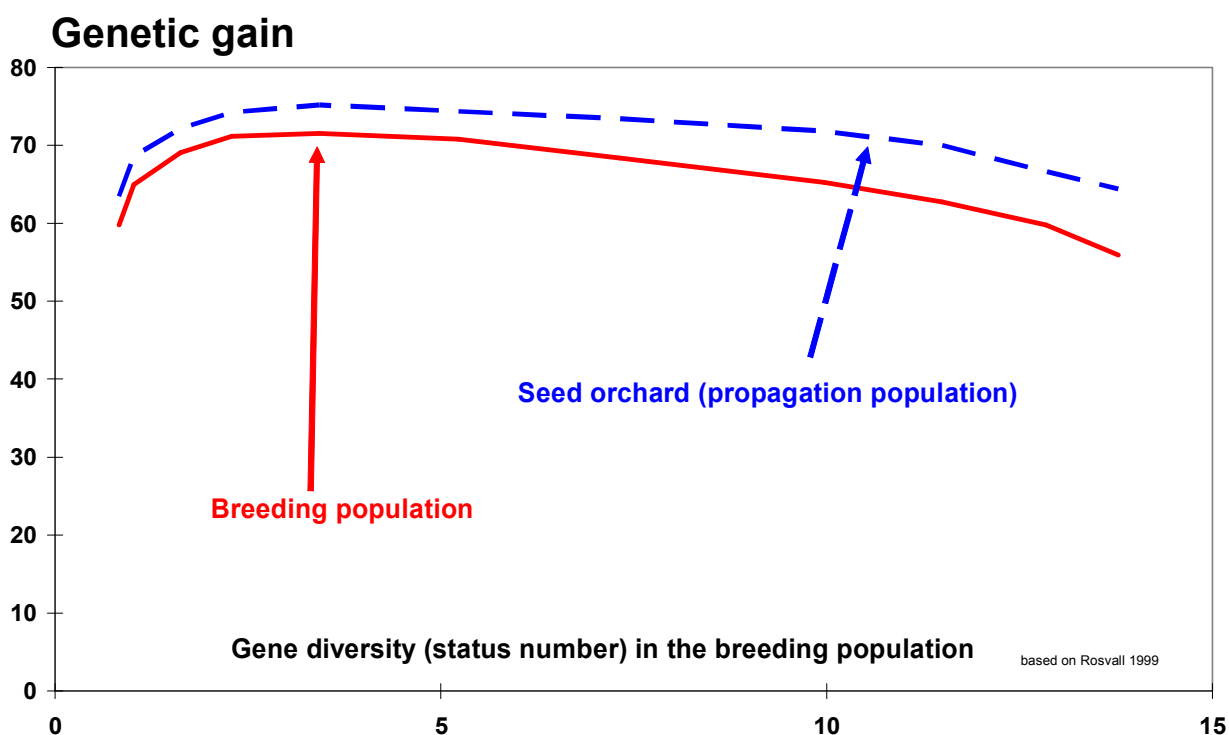


Figure 1. Genetic gain as a function of gene diversity remaining after five generations in a simulation of a program similar to Swedish Norway spruce breeding. (Single pair mating, progeny size 50, high heritability with clone testing.) The rightmost diversity values correspond to maximizing balance (strict within family selection, each member in the breeding population get exactly two offspring transferred to next breeding population generation). Some of the genetic gain lost in the breeding population, when that is run for high genetic gain, is recovered then forming seed orchards. The extra genetic gain obtained by applying unbalance becomes rather small. The figure is based on Rosvall (1999).

expected to be larger. An advanced generation «seed orchard» is likely to be designed in a complex and sophisticated way, thus the idea of classifying the «goodness» of an advanced breeding population by a seed orchard derived from it could be developed and it does not seem impossible that unbalance in the breeding population will carry a smaller penalty with such a more developed measure.

It may be noted that the balance becomes less important the higher the breeding population size is, thus unbalance may be more justified in breeding programs using large breeding populations.

Sanchez (2000) concluded, based on quantitative simulation, that a slight unbalance could be more favorable in breeding than complete balance, as it leads to more gain without a corresponding loss of genetic diversity.

Lindgren and Wei (1994) studied the effect of selection in a population composed of an infinite number of equally sized unrelated families. The selection criterion was a weighted average of family value and individual value. By using different weights of family versus individual, a gain/diversity relation was developed. Among family selection and within family selection appeared as extremes, and index selection where family and individual are optimally weighted to maximize gain of cause appears as a peak. They got results, which indicated an unfavorable gain/diversity relation for completely balanced within family selection. Their study was based on infinite populations and normal distributions, while later studies have used limited population and populations truncated by selection, and also other inputs closer to forest tree breeding. Even if a

drop in efficiency has been observed also in later studies, its magnitude seemed smaller than noted by Lindgren and Wei (1994).

It is practically easier, more transparent, less competence demanding and more fail-safe to manage balanced selection than intentionally unbalanced in the first breeding generations, so advantages of the magnitude observed by Rosvall (1999) may not be regarded as sufficient motive to apply intentional unbalance in the long term breeding.

Population-wide PAM appeared, based on POPSIM simulations, to offer advantages compared to structuring of the breeding population in elite and main (Lstiburek 2005). The advantage of PAM was emphasized if test effort was linearly related to breeding value (see below).

Change per generation at a given breeding population size does not say everything

Perhaps it should not be the loss of gene diversity per generation but the annual loss, which should be in focus. Both annual gain and annual diversity loss are affected by both the degree of unbalance and the duration of a generation. More unbalance and longer generation time may possibly result in both higher gain and less loss in gene diversity at a certain time. A high degree of balance is one way of increasing gene diversity but another way is to increase breeding population size, and there may be trade-offs. An optimization e.g. maximizing gain per year at a given gene diversity loss per year allowing variation in testing time, breeding population size and degree of unbalance simultaneously has never been done and unbalance may appear favorable. Using fixed generation times and breeding population size may be somewhat misleading. Application and extension of the methods used by Wei and Lindgren (2001) and Danusevicius and Lindgren (2005) could be helpful in more sophisticated studies. Multi-generation studies usually assume that the breeding population is managed in the same way over generations, but the optimum may be to deal with them differently, and that may give larger room for unbalance.

Rolling front breeding

Forest Tree breeding is almost certainly better made in a rolling front system (Borralho and Dutkowski 1998) than in discrete generations turned over at the same time. It just does not work to get all needed crosses and other operations done at the same time in an operative breeding program. For Swedish breeding, the status of the breeding populations are annually reviewed (Sonesson et al. 2005), the problem of managing a breeding population synchronous is evident. In advanced breeding it will turn out advantageous to mate individuals from different generations. In rolling front breeding perfectly balanced breeding become rather meaningless and does not appear simple any more. A rolling front strategy may be optimized by using group merit annual progress as the criterion on efficiency (Wei and Lindgren 2001, Danusevicius and Lindgren 2005)

Stratified sublines with and without unbalance

Stratified sublines (Ruotsalainen 2002, Lindgren et al 2004) can be described as positive assortative mating driven to its extreme, where the process is continued several generations forming separate small sublines. Stratified sublining makes it possible to get orchards with more than 10% superior gain compared to conventional sublining, it ought to get still higher improvement by using higher breeding efforts on the highest ranking sublines, while the low ranking sublines could have a still stronger emphasis on diversity.

Stratified sublining will be implemented in the recently developed Finnish breeding strategy (Lindgren et al. 2004). To further boost the effect of stratification and to obtain additional genetic gains from future seed orchards, the Finnish breeding strategy involves the idea of distributing breeding, testing and selection efforts unequally, making the effort positively dependent on genetic value of the material being improved. This principle is implemented throughout the breeding cycle. In the first generation turnover, the founders forming the first-generation breeding population are single-pair mated with regard to breeding value (in the way described above). Those of the founders that are ranked to the highest quarter are, however, double-pair mated to allow more options for recombination of their gene mass and reduce the risk that their gene mass is degraded by an unfortunate choice of partner, as well as a way to increase the number of offspring. Furthermore, the target sizes of F_1 families are larger for the best quarter of the parents than for the average parent or for the lowest quarter of parents. The F_1 families (the recruitment population) are grown in forward selection trials that last from 5 to 10 years depending on species. At this age, the best individuals within each full-sib family are phenotypically selected for further testing. Roughly three times as many selections (candidates) are drawn from within the larger families (representing offspring of the best parents) than from the smaller ones. The number of candidates selected from each full-sib family to the new breeding population varies in relation to the mean breeding value; three individuals are selected from the best full-sib families (determined as the mean breeding value of the top 3 candidates), two individuals from the average families, and one (possibly none) individual from the lowest ranking families (Ruotsalainen 2002). As a result, the second generation breeding population, will have an unbalanced structure where the size of the stratified subline is six, four or two trees for the highest ranking, the average and the lowest ranking candidates, respectively. This method results in an overrepresentation of the gene mass of the best founders whereas a high number of low ranking founders will still be represented, but with relatively small genetic contributions.

Unbalances in deployment of resources to families

Lstiburek (2005, a popular presentation in Swedish by Mullin et al 2005 is based on Lstiburek's thesis) made a study with the tree-breeding simulator POPSIM. The recruitment population was created by PAM single-pair among selected tested parents. The family size was linearly related to the families breeding value (thus a form of «linear deployment»). The next breeding population was selected by within-family selection. The criteria of goodness of the strategy were the genetic gain of the best share of the breeding population selected for mass multiplication (seed orchard) at a given diversity. The comparisons were done at the same resource (the same number of trees planted). Different degrees of unbalance were used; on one extreme was balanced selection when all families are of size 30 and the other extreme strong unbalance when family sizes varied between around 2 and 60. Moderate unbalance implied differences among family sizes of the magnitude 20-40. The gain compared to balanced selection increased by 20% using strong unbalance and 10% if intermediate unbalance was used. There is no associated disadvantage from increased resources or lost diversity for these gains. It seems very logic that allocating more resources to improving the genotypes which are more likely to be selected to seed orchards and less to those which are there more for assuring diversity in long time breeding will boost seed orchard selections. The advantage is large compared with what was indicated by earlier similar efforts, e.g. Rosvall (1999). That is probably explained by that Lstiburek (2005) in the simulation used REML and BLUP, thus more precise methods making more efficient use of available information (like a modern breeder would do).

Arguments against to employ tree improvement efforts depending on the breeding value

A model predicting the profit of some action deviates always from the real world. Those deviations may be more or less severe. Unequal representation of families can have direct negative effects if the model assumptions are not full-filled. A simple example is given to illustrate one problem (Table 2). A field test has 10 trees belonging to two families. The best individual in each family is selected by within family selection.

Table 2. Average selection intensity for within family selection. The candidate population consists of two families of different sizes where the best tree is selected

	Balanced		Moderate unbalance		Strong unbalance	
	Size	Sel int	Size	Sel int	Size	Sel int
Large family	5	1.163	6	1.267	9	1.485
Small family	5	1.163	4	1.029	1	0
Average selection intensity		1.163		1.148		0.742
% of balanced		100		98.7		63.8

Genetic gain is proportional to selection intensity. The selection intensity will decrease if there is unbalance. Average gain by within family selection will be lower. The decrease in selection intensity will be marginally small if the family sizes vary intermediate, but may be important if there is large variation in family size. As the goodness is only counted on the best selections and as the best families are larger, the within family selection intensity will be higher for the selected part, and that effect is much larger in the simulation than that caused by the loss in selection intensity. But simulations differ from the real world. It is assumed that the family sizes (decided before establishment of the trial) concern exactly the same character as the selections (decided when trials are mature for selection). That is certainly not so, e.g. environments used where the propagation population is deployed will not be the same as the test environments. Sampling effect is one reason but there are many more which are likely to cause differences. The preferred selection index (selection criteria) as a combination of characters used for deciding breeding values of parents probably changes over time till progenies are selected. It might actually be optimal to use different index for different purposes. The breeding targets are probably somewhat different for the breeding population and the seed orchard population (which is used as a measure of the value of the breeding population).

If one invests resources in creating offspring from parents, it seems bad breeding economy to field test very few individuals for any families. Breeding population members and families are expensive and these costs are not neglectable compared to costs related to family size. There are costs connected to parents like clone archives and pollen management. It does not make sense to create families which are so small so all individuals have to be selected resulting in no gain at all. Just for safety reasons as an assurance against irreversible loss, it seems advisable to use a minimum size of families, so there exist some selectable trees when it is time. Linear deployment need not be optimal for deployment of the recruitment population even if it was proven good, it seems likely it is more optimal to make the smallest families a bit larger, at least in a real world.

In the simulations an average under an idealized situation is considered. The results favoring PAM and variations in breeding effort are probably less robust and more depending on the idealized conditions than Random Mating and uniform breeding effort in a single run in the real world than under simulations.

In the real world the PAM are not as perfect as assumed in simulations. Besides practical considerations reducing the degree of PAM, PAM is for the index used over the environments used, and that degree of PAM will be lower for the selection index and environments in the progeny generation. The breeding stock is often not propagated under the same conditions or tested in a single test. The crosses are usually done at different occasions and places, which may cause asymmetries. The individuals will often be selected in several steps, first based on the phenotype and later based on some test.

The uncertainties are small with intermediate unbalance. The intermediate unbalance is not larger than usually occurs unintentionally. It does not seem to exist a good reason not to apply moderate unbalance immediately (say decreasing within family selection intensity by 2%). The risk that this results in a considerable loss seems neglectable. The implementation in Finnish breeding mentioned above seems to be such a moderate application with limited risk.

It seems illogic that unbalance in testing effort should be strongly positive while unbalances in contributions small, that indicates a better balance between these two types of unbalances can be found.

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