

NUMBER OF FOUNDERS FOR A BREEDING POPULATION USING VARIABLE PARENTAL CONTRIBUTION

Seppo Ruotsalainen¹ & Dag Lindgren²

¹ Forest Research Institute, Punkaharju Research Station, FIN-58450 Punkaharju, Finland

² Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, SE-90183 Umeå, Sweden

Received August 17, 1999; revised January 3, 2001; accepted January 10, 2001

ABSTRACT

This study considers a situation in which there is access to a high number of progeny tested plus trees, of which the best ranking ones are used as founders of the next generation breeding population. The question was how to obtain maximum genetic gain with a given level of genetic diversity. The level of genetic diversity was fixed to the level obtained with equally contributing within-family selection, and the resources were fixed by keeping the number and size of full sib families constant. The between-family genetic gain in establishing a breeding population was maximised by means of deterministic modelling. This was performed by selecting more founders than in the case with equal contribution and allowing them to be represented in the next generation by one, two or three offspring depending on their breeding value. The effect of variable contribution was studied by altering two parameters: selection intensity (number of tested plus trees) and genetic diversity in the resulting second generation breeding population (status number).

An increase of 20 to 23 % in the number of founders as compared to equal contribution gave the maximum genetic gain when the genetic diversity was kept constant. The optimum founder number increased with increasing number of tested plus trees and status number. The size of the highest contributing fraction of founders increased with increasing number of tested plus trees and decreasing status number. The amount of additional genetic gain obtained by variable contribution was greater with a smaller selection intensity and lower status number. In a typical case the between-family genetic gain could be increased by 7 % by increasing to the number of founders by 22 % and allowing them to contribute unequally to the next generation. Most of the additional genetic gain was obtained after the first few founders had been added.

Key words: breeding population, founder number, selection limit, genetic gain, status number, genetic diversity

INTRODUCTION

A forest tree breeding program is often initiated by choosing a number of parents – plus trees – from the forest, testing and mating them and then selecting from among their progeny. The number of founders can be based on predictions in order to keep the inbreeding and relatedness at an acceptable low level in the future, and genetic variation at so high a level that the future gains are not severely reduced (WHITE 1992). Economic compromises and other considerations also apply (LINDGREN 1991). The importance of retaining large genetic diversity depends on the time horizon of the breeding plan (WRAY & GODDARD 1994). A breeding plan aiming at continuous improvement during several generations must consider genetic diversity more than a short time plan.

One way of utilising a predetermined number of founders in a way that maximises the genetic diversity is to use within-family selection and allow each founder to contribute equally to the next generation. This

balanced within-family selection procedure is likely to maximise the long term limit of selection (DEMPFLE 1975). However, this conclusion has recently been challenged (VILLANUEVA & WOOLLIAMS 1997). The current Swedish forest tree breeding program can be described as a (mainly) balanced within-family selection procedure (DANELL 1995, ROSVALL *et al.* 1998). It is therefore interesting to have a balanced program based on within-family selection as a reference.

It has been shown that, in order to make an optimal compromise between genetic diversity and genetic gain, it is preferable to let the best selected genotypes contribute more to the next generation than the lower ranking ones (LINDGREN 1974, TORO & NIETO 1984, LINDGREN 1986, LINDGREN & MATHESON 1986, TORO & PÉREZ-ENCISO 1990). There are several possible ways of handling the trade-off between genetic gain and diversity. Some methods set a cost in terms of genetic gain for the relatedness and thus transform both quantities to the same scale (LINDGREN 1986, LINDGREN

& MATHESON 1986, WRAY & GODDARD 1994). The problem is to find the correct cost factor needed to make the transformation. TORO and NIETO (1984) presented a method for selecting the number of founders and their contributions so that the effective population size (and thus genetic diversity) is maximised with a given genetic gain. An alternative solution is to maximise the genetic gain with a given genetic diversity (LINDGREN *et al.* 1989, MEUWISSEN 1997).

The optimal proportion of a clone in a seed orchard is linearly dependent on its breeding value (LINDGREN & MATHESON 1986). The same relationship also holds approximately with a breeding population: the top ranking phenotypes should be selected from each family in linear proportion to the family average in order to obtain the maximum gain at a given effective population size (LINDGREN 1986, WEI & LINDGREN 1995). In some forest tree breeding plans the breeding population is divided into several genetically different fractions which contribute the more to the next generation the higher is their genetic value (*e.g.* WHITE *et al.* 1993). One example is the open nucleus breeding strategy, in which higher ranking trees form a nucleus that is bred more intensively than the main population (COTTERILL *et al.* 1989).

This study focuses on a situation in which a number of tested plus trees are available for mating, and the desirable next generation breeding population size and diversity have been fixed. The purpose of this study is to develop and analyse an explicit method for deciding which contributions the tested plus trees should make when generating the recruitment population for the second generation selections. In this variable contribution method such number of founders and combination of their contributions is searched for which maximises genetic gain with the given genetic diversity.

METHODS

Model formulations

We considered a situation with a number of tested plus trees in which we wanted to generate a recruitment population for the next round of selections. We assumed that this would be done by controlled crossings of the best plus trees. We will call these plus trees, which are involved as crossing partners, as founders, because they are the genotypes that can transmit genes to the following generations in long-term breeding. The number of crosses (0–3), in which a plus tree was involved in was related to its breeding value. Only one selection was subsequently made from each

family (from this point of view the system can be described as within-family selection). The number of crosses and number of selected offspring were therefore equal. This formulation was rather easy to use as a basis for the calculations.

When determining an efficient solution to a genetic problem the most important factors are genetic gain, genetic diversity, time and cost. Genetic gain was regarded as proportional to the selection intensity related to the choice of plus tree parents. Time was assumed to be constant. Cost was kept constant by fixing the number and size of families. The genetic diversity was described using group coancestry (θ) (COCKERHAM 1967) or, equivalently, by a measure called status number (N_s) derived from it ($N_s = 0.5/\theta$) (LINDGREN *et al.* 1997, LINDGREN & KANG 1997).

In the model case we considered a recruitment population of size N_{R1} , consisting of unrelated non-inbred progeny-tested plus trees. N_1 were selected from these N_{R1} plus trees for the first generation breeding population (the founders) according to their breeding values. These founders were then mated randomly (selfing excluded) with each other to create the second generation recruitment population. Mating design as such does not matter for the results of this study, as we are only concerned with the gene pool of the selected progeny, not with the recombination of its genes. According to the definitions given by WHITE (1987), the first generation recruitment population corresponds to the selected population, and subsequent recruitment populations to the base population. The breeding population is used in the same meaning as in WHITE (1987).

The contribution of the first generation plus trees to the next generation could be varied so that they were used in zero (rejected tested plus trees with a low breeding value), one (the plus trees with the lowest accepted breeding values), two (intermediate plus trees) or three crosses (fraction with the highest breeding values) (Fig. 1). This method of allocating parent contributions is rather similar to the unbalanced 3:2:1 mating system used by ROSVALL (1999), except that we allowed the first generation breeding population size (N_1) to vary (see details later). One offspring was selected from each cross (full-sib family) for the second generation breeding population, which had the size N_2 . The family size was the same in all the crosses. This design had the great advantage that the gain through within-family selection was kept constant, and thus did not have to be considered when searching for the optimum contribution of the founders.

The size of the second generation breeding population (N_2) can be expressed as a function of the sizes of the individual fractions of first generation

breeding population ($N_1 = n_3 + n_2 + n_1$),

$$N_2 = \frac{3n_3 + 2n_2 + n_1}{2} \quad [1]$$

where n_1 , n_2 and n_3 are the sizes of the individual fractions of first generation breeding population, with the subscript showing their contribution to the next generation (Fig. 1 and Table 1).

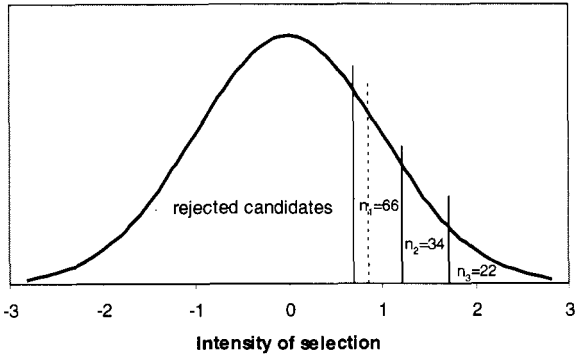


Figure 1. The first generation recruitment population (the tested plus trees = N_{R1}) arranged according to the breeding values of the trees, and divided into fractions according to the number of families for which they will be parents (0, 1, 2 or 3). The dotted line marks the limit of the breeding population in the base option, in which 100 founders have 2 families and thus 2 selected offspring each. $N_{R1}=500$, $N_2=100$, $N_{S2}=66.7$

The average between-family selection intensity for the first generation breeding population is

$$i_f = \frac{3n_3 i_3 + 2n_2 i_2 + n_1 i_1}{3n_3 + 2n_2 + n_1} \quad [2]$$

with terms as described in Table 1.

The group coancestry in the second generation breeding population (Θ_2) is

$$\Theta_2 = \frac{0.5N_2 + 0.75n_3 + 0.25n_2}{N_2^2} \quad [3]$$

This formulation can be derived as follows. Because the selected plus trees are unrelated and only one second generation tree is selected from each family, only selfing and half-sib relationships need to be considered. The first term in the numerator gives the contribution of self coancestry to group coancestry. The following

terms represent coancestries caused by half sibs in the highest and intermediate fractions, respectively. The coancestry between half sibs is 0.125, and there are three half sib combinations within the progeny of each founder tree in the highest fraction. When the reciprocal combinations are included we obtain the coefficient 0.75 ($= 0.125 \times 3 \times 2$). In the intermediate fraction each tree has two offspring, so there is only one half sib combination for each tree. When this is also taken reciprocally, we arrive at the coefficient 0.25. In the lowest fraction with only one offspring from each family there are no half sibs, and thus this fraction does not contribute to group coancestry through the half sibs (coefficient is 0).

Using formulae (1) and (3), we can express n_1 and n_2 as a function of the fixed parameters (N_2 and Θ_2) and n_3 .

$$n_1 = 6N_2 + 3n_3 - 8\Theta_2 N_2^2 \quad [4]$$

and

$$n_2 = 4\Theta_2 N_2^2 - 2N_2 - 3n_3 \quad [5]$$

The size of the first generation breeding population (N_1) is the sum of the three fractions n_1 , n_2 and n_3 . It can also be expressed as a function of n_3 and the fixed parameters Θ_2 and N_2 by substituting n_1 and n_2 with the corresponding formulae (4) and (5). This gives us the following expression for N_1

$$N_1 = 4N_2 (1 - \Theta_2 N_2) + n_3 \quad [6]$$

Simulation

We fixed the number of selections and thus the number of crosses at 100 ($N_2=100$).

If there are two crosses per accepted plus tree ($N_1 = 100$), with one selected offspring from each family (double pair mating), the status number for these selections is 66.66... and the group coancestry 0.0075. This group coancestry is for equal parental contribution, but it can also be called the group coancestry for within-family selection. This selection scheme was used as the base option to which the alternative selection procedures were compared. It follows the guidelines for current Swedish tree breeding strategies (DANELL 1995, WILHELMSSON & ANDERSSON 1995), except that the breeding population size is twice as large (100 vs. 50). Second generation breeding population size (N_2) was set at 100 in the calculations, and the other parameters were expressed in relation to this (Table 1). A breeding population size of 100 made it possible to interpret the results

Table 1. Parameters and parameter values used in calculations for maximising genetic gain for the 2nd generation breeding population by altering contributions of the founders according to their breeding values. The parameter values which define the main alternative are given in bold.

Parameter	Description	Value	Remarks
Value fixed			
N_{R1}	Size of first generation recruitment population	$N_2, 2N_2, \mathbf{5N_2}, 100N_2$	
N_2	Size of 2 nd generation breeding population	100	
Θ_2	Group coancestry of 2 nd generation breeding population	0.0083, 0.0075 , 0.0067, 0.0059	
N_{S2}	Status number of 2 nd generation breeding population	$0.6N_2, \mathbf{0.66...N_2}, 0.75N_2, 0.85N_2$	$N_{S2} = 0.5/\Theta_2$
Value allowed to vary			
N_1	Size of 1 st generation breeding population (= number of founders)	Varies	Result of the calculation
n_3, n_2, n_1	Numbers of trees in high, intermediate and low fractions of N_1 respectively	Varied	The numbers are actively altered.
i_3, i_2, i_1	Intensities of family selection applied for 2 nd generation in high, intermediate and low fractions of N_1 respectively	Varies	Defined by proportions selected
-	Average between family selection intensity for the 2 nd generation breeding population	Varies	Result of the calculation

concerning N_1 and n_3 as a percentage of N_2 .

The alternative procedures used a breeding population that was divided into three differently contributing fractions according to the breeding values of their trees, as described earlier (Fig. 1). The costs were maintained at the same level as in the base option by keeping the number of crosses and family size the same. It was assumed here that the number of progeny tested first generation plus trees (N_{R1}) was considerably higher than the number of founders needed (N_1). Often such plus trees are stored in clone archives during progeny testing and are thus available with little or no extra costs as additional founders, if needed. The main alternative studied was defined by the parameter values $N_{S2} = 66.7$ ($Q_2 = 0.0075$) and $N_{R1} = 5N_2$. Some other alternatives with different status number (N_{S2}) and recruitment population size (N_{R1}) were also studied, but less intensively.

In the search for the greatest genetic gain with a fixed diversity and costs, the borderline between the rejected candidates and the lowest fraction belonging to the breeding population could be changed and more trees included in the breeding population. Also the fraction division within the breeding population could be altered in order to maximise the genetic gain. In the

following this selection procedure is called *variable contribution*, and it was compared with the *base option* in which all the trees contributed equally to the next generation and the breeding population size was constant.

Starting with the values of the fixed parameters (Table 1) and varying the values of n_3 within the desired range, the values for n_1 and n_2 were calculated using formulae (4) and (5), respectively. The average between-family selection intensity was then calculated for the different alternatives using formula (2). The n_3 value giving the highest genetic gain was noted and the corresponding N_1 value was calculated. With the given restrictions n_1 and n_2 are functions of n_3 , and thus only n_3 needs to be varied. The within-family selection intensity was not considered in these calculations. Due to the constant family size and one selection per family its expectation is the same in all the families and selection alternatives so that it does not affect the ranking of different solutions. The selection intensities for the different fractions were calculated using function for infinite population size (LINDGREN & NILSSON 1985). This function was easier to program, and as the differences between the true selection intensities and those obtained by the infinite function

Table 2. Founder number (N_1) and the size of the highest contributing fraction (n_3) when the selection intensity reached its maximum at different levels of genetic diversity (N_{S2} and θ_2) and recruitment population size (N_{R1}).

		Founder number (N_1)				Size of the highest fraction (n_3)			
		N_2	100 ^a			100 ^a			
N_{R1}	N_{S2} θ_2	60 0.0083	66.7 0.0075	75 0.0067	85 0.0059	60 0.0083	66.7 0.0075	75 0.0067	85 0.0059
100	= N_2	97	100	-	-	30	0	-	-
200	= $2N_2$	102	120	140	166	35	20	7	1
500	= $5N_2$	102	122	143	167	35	22	10	2
10000	= $100N_2$	103	123	144	168	36	23	11	3

^a The breeding population size (N_2) 100 allows the values for N_1 and n_3 to be interpreted as per cent of N_2 .

were smaller than 0.01, the function could be safely used.

RESULTS

Number of founders and size of the highest fraction

The size of the highest contributing fraction (n_3) which gave the highest selection intensity varied depending on the size of the recruitment population and especially on the group coancestry (status number) in the second generation progeny (Table 2). When the size of the recruitment population increased, the maximum genetic gain was reached with a larger founder number and larger number of trees in the highest contributing fraction. This effect was, however, trivial when the recruitment population size was more than 1.5 times N_2 (Fig. 2).

When the status number in the second generation was allowed to differ from that in the main alternative ($N_{S2} = 66.7$), the founder number and the sizes of the

individual fractions were greatly influenced (Table 2, Fig. 3). The increase in status number (decrease in group coancestry) in the second generation greatly increased the total number of founders. At the same time, the size of the highest contributing fraction decreased and the lowest increased, until, finally all trees contributed only one offspring to the next generation (Fig. 3). In contrast, when the status number was decreased from that in the main alternative (more coancestry allowed), the total founder number decreased and an increasing number of trees belonged to the fraction which contributed 3 offspring to the second generation.

The largest founder number (68 % greater than N_2) in the studied alternatives was obtained when both the status number and the recruitment population size were the greatest (Table 2). Correspondingly, the smallest founder number (3 % smaller than N_2) occurred with the opposite parameter combination. The size of the highest contributing fraction (n_3) could not be deduced directly from the size of the founder population. Its greatest size (36 % of N_2) was obtained with the lowest

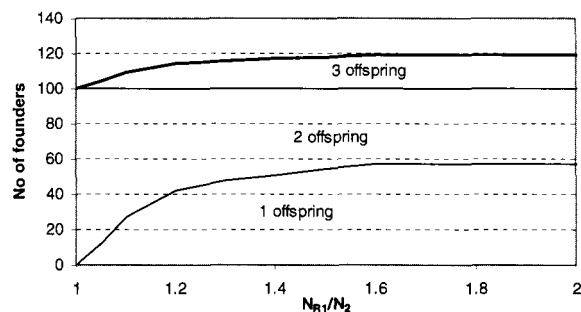


Figure 2. Optimal founder number (size of first generation breeding population) and the sizes of different fractions of the breeding population as a function of relative recruitment population size. $N_2 = 100$, $N_{S2} = 66.7$.

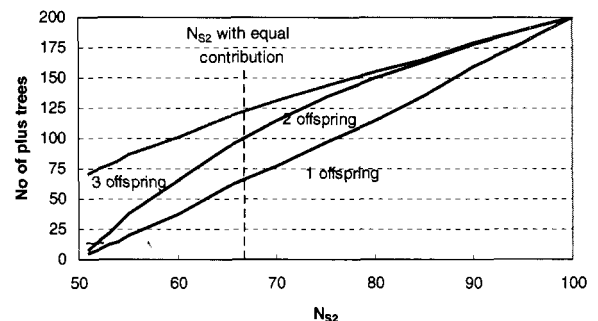


Figure 3. Optimal founder number and optimal allocation of founders to differently contributing fractions as a function of the desired status number in the new breeding population. $N_2 = 100$, $N_{R1} = 500$.

Table 3. Maximum between-family selection intensity achieved with different recruitment population sizes (N_{R1}) and second generation status number (N_{S2}), when second generation breeding population size (N_2) is 100.

		Maximum selection intensity					Maximum selection intensity in % ^a			
		Base option		Variable contribution			Variable contribution			
N_{R1}	N_{S2} Θ_2	66.7	60	66.7	75	85	60	66.7	75	85
		0.0075	0.0083	0.0075	0.0067	0.0059	0.0083	0.0075	0.0067	0.0059
100	= N_2	0	0.3753	0	-	-	-	-	-	-
200	= $2N_2$	0.7979	1.0127	0.9095	0.7506	0.5186	127	114	94	65
500	= $5N_2$	1.3998	1.5619	1.4931	1.3892	1.2465	112	107	99	89
10000	= $100N_2$	2.6652	2.7694	2.7296	2.6693	2.5867	104	102	100	97

^a The relative values are calculated from the base option ($N_1 = N_2 = 100$, $N_{S2} = 66.7$, two crosses per tree, one selection per family).

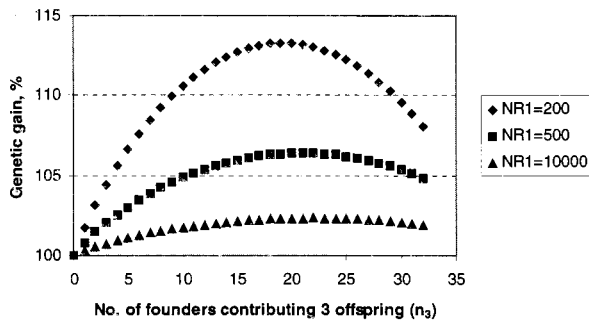


Figure 4. Genetic gain of family selection (in relation to base option) as a function of the size of the highest contributing fraction (n_3) of the breeding population at three different recruitment population sizes. $N_2=100$, $N_{S2}=66.7$.

status number and the greatest recruitment population size. The highest contributing fraction disappeared completely with the opposite combination: high status number and small recruitment population size.

Amount of maximum gain

The effect of the founder number and variable contribution on selection intensity was influenced both by the size of the recruitment population and by coancestry (status number). With the larger recruitment population the effect of a variable contribution of founders on selection intensity was smaller both in absolute and relative terms (Table 3, Fig. 4). However, there was a different trend in the relative selection intensity with a low and high status number. With a low status number the obtained selection intensity in relation to base option decreased with increasing recruitment population size. With a high status number this relative selection intensity increased in the same direction (Table 3).

An increase in status number greatly decreased both the absolute and relative selection intensities (Table 3,

Fig. 5). The decrease was more pronounced with a lower recruitment population size. The greatest relative increase in selection intensity (27 % compared to the

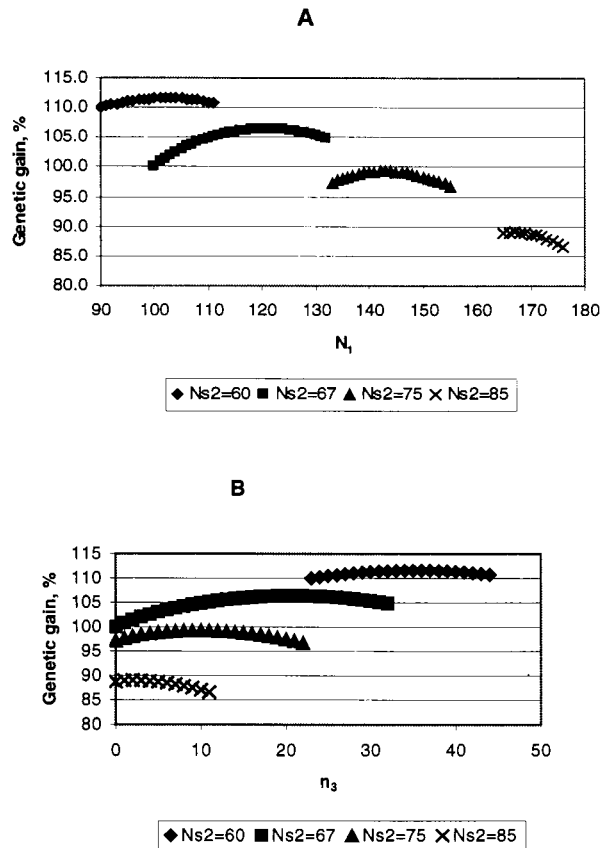


Figure 5. Genetic gain of family selection (in relation to base option) as a function of total founder number (A) and the size of the highest contributing fraction of the founders (B) at four different levels of diversity (status number). $N_{R1}=500$, $N_2=100$.

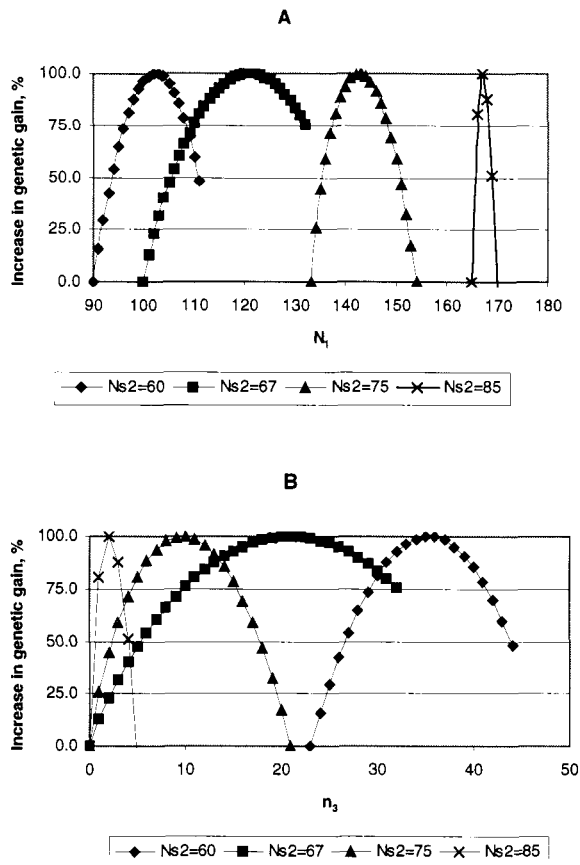


Figure 6. Relative increase in genetic gain as a function of total founder number (A) and the size of the highest contributing fraction (B) at four different levels of diversity (status number). The values are relative to the total increase between the lowest possible value of n_3 and that giving the maximum gain.

base option) was obtained when both the status number and recruitment population size were smallest. The smallest increase (in fact a decrease of 35 %) occurred with the smallest recruitment population size and greatest status number.

When the status number was high the total number of founders needed was also high, but only a few of them could contribute three offspring to achieve the greatest genetic gain. However, when the number of founders was further increased a situation arose in which genetic gain was lower than with equal contribution (Fig. 6).

The greatest part of the total increase in genetic gain obtained by increasing the size of the highest contributing fraction of founders was achieved already after adding the first few trees (Fig. 6). When the status number was 66.7, 50 % of the maximum increase was obtained after adding only six trees (or 6 % of N_2) to the highest contributing fraction, even though 21 trees (21 % of N_2) had to be added to that fraction in order to

reach the maximum genetic gain. With a status number of 75, the corresponding level (50 %) was achieved already after the addition of two trees (%), whereas the maximum was reached at 10 trees (%) in the highest contributing fraction.

DISCUSSION

The obtained results show that, by using a simple method to control the contribution of the founders, genetic gain can be increased without sacrificing any genetic diversity compared to the situation with equal contribution. This was achieved by allowing the best founders to contribute more to the next generation than those with a lower breeding value, as suggested by LINDGREN (1986) and similar to the finding of LINDGREN and MATHESON (1986). Our method divided the breeding population into three fractions which contributed to the next generation in the ratio 3:2:1 beginning from the fraction with the highest breeding value.

The contributions of the founders were approximately the same, as suggested by the model of linear deployment (LINDGREN *et al.* 1989). However, linear deployment assumes that genotypes can be deployed in any rational numbers. When we are discussing founder contributions through offspring, we are dealing with small integer numbers and, from that point of view, the current analysis is more accurate.

In a case with genetic diversity at the base option level, the number of founders should be increased by around 20 % from the original number in order to obtain the maximum genetic gain. The increase in the number of founders was, at the same time, the number of founders belonging to the highest contributing fraction. Using the model for linear deployment the increase in the number of founders was more than double (LINDGREN *et al.* 1989, Table 2). However, this model resulted in a large number of low ranking founders with very small contributions that could not be utilised when using trees as parents for a new generation. TORO and NIETO (1984) also observed that, although theoretically it would be advisable to use all the potential founders, the founders with the lowest ranking made such a small contribution that they had no practical significance.

It can be argued that it is not recommendable to use, as founders, those candidate trees from the recruitment population which are below the average, because the expected breeding value of an untested new selection will be higher (TORO & NIETO 1984). Such a situation is inevitable if the recruitment population is, at its highest, double the size of the breeding population. However, in practice the costs, practical difficulties and

time delays in selecting new plus trees may counteract the obtainable genetic gain. If the distribution of the breeding values in a real population differs markedly from the assumed normal distribution of this study, then the founder contributions could also be affected.

When the level of genetic diversity was increased from that of equal contribution after double pair mating, the number of founders needed increased, whereas the contributions of the intermediary founders decreased. On the other hand, when the genetic diversity was allowed to decrease, a lower number of founders was needed and their contributions increased. The same relationship between genetic diversity and number of utilised families is also observed with optimal contribution from families (LINDGREN *et al.* 1993).

The obtained increase in genetic gain when using variable contribution was close to 10 % of the between-family gain with the most relevant recruitment population sizes. This is in accordance with the increase in genetic gain obtained by optimal deployment in plantations (LINDGREN *et al.* 1989). However, it must be noted that within-family selection gain is not considered here. Thus the obtained relative increase is smaller in relation to the total genetic gain. Because the genetic gain in within-family selection is affected by *e.g.* heritability and family size, no general rules can be derived for the increase in total genetic gain.

The increase in genetic gain obtained by using the variable contribution method was larger with a smaller recruitment population size and smaller status number. This is in accordance with results concerning linear deployment (LINDGREN *et al.* 1989, LINDGREN 1991, 1993). When the recruitment population size is small, the between-family selection intensity is also usually low, and there are great differences in selection intensities between the founders. Thus it is more advantageous to manipulate the contributions of different fractions of founders than in the case with a high selection intensity when the differences between founders are smaller. In relative terms this difference is still exaggerated, because comparison in the case of a small recruitment population size is made to a smaller value than with a large recruitment population. In establishing long-term breeding populations the selection intensity from the progeny-tested recruitment population of plus trees is usually not very high. Thus there are good possibilities for increasing the genetic gain by means of variable contribution.

The influence of genetic diversity on the increase in genetic gain can be interpreted in the same way as the effect of recruitment population size. When the genetic diversity was increased by allowing more trees to contribute to the next generation, it inevitably meant a decrease in genetic gain compared to equal contribution

after double pair mating and a fixed breeding population size. This appears to be contrary to the results of MEUWISSEN (1997), whose rather similar optimal contribution method was more superior at lower levels of inbreeding. This contradiction can be explained by the fact that MEUWISSEN (1997) did not restrict breeding population size, but allowed it to vary. If this restriction is released, according to our model variable contribution will also be relatively more advantageous at greater breeding population sizes (lower inbreeding).

Most of the additional gain was obtained after adding the first few extra trees. However, because of the flat response curve of genetic gain close to the optimum, even a considerably larger number of founders than the optimum could be included without losing much of the additional genetic gain. We can see reasons to keep offspring from more founders than was found to be optimal in this study, because our definition of diversity does not fully consider the arguments of keeping offspring from many founders. One may want to include founders in the breeding population that are good in aspects other than the one (or the index) used to rank the trees. It may also be desirable to obtain a more balanced geographic representation in the breeding population. If offspring from more founders are transmitted this will also mean that more options are kept open to offer a high number of unrelated clones for future seed orchards. In all biological activities there is a risk of loss; founders may be lost *e.g.* because grafting does not work. Keeping the number of founders on the upper side of the optimum is cheap insurance against such unforeseeable losses. Thus we recommend choosing a number of founders that is slightly above the optimal found in this study.

In this study the contribution of founders to the next generation was varied by altering the number of crosses in which the trees participated, but selecting only one offspring from each family. It is also possible to alter the family size and make it dependent on the breeding value of the parents. At selection it would be more favourable to allow a different number of selected offspring from different families (*e.g.* using population merit selection, LINDGREN & MULLIN 1997) depending on the breeding value of the parents. However, genetic gain of an unbalanced mating system was equal to unbalanced selection system in breeding population, and superior in multiplication population (seed orchard) in a simulation study covering five generations (ROSVALL 1999).

The question of the best possible contribution of the founders to the next generation has also been studied earlier in both animal (MEUWISSEN 1997) and tree breeding (KERR *et al.* 1998, ANDERSSON *et al.* 1999,

ROSVALL 1999). All these studies differ from the present one in the respect that they are not searching for an analytical solution, but use either simulation or linear programming. There are also differences concerning the restrictions applied in the methods. The model described by KERR *et al.* (1998) does not have such rigorous requirements for group coancestry and costs as in our study, so closer comparison is useless. The method of ANDERSSON *et al.* (1999) is in fact optimising the contribution of families, not single founders, because it allows several selections from a family. It has options to control group coancestry and to some extent also costs (number of selections). However, the number of families is not restricted, which can result in slightly enhanced costs. The most restrictive alternative in ANDERSSON *et al.* (1999) gives both family contributions and gain increment that are in agreement with our results.

In this study the maximum number of crosses in which a plus tree participated was limited to three. Again, this is a constraint which was made to facilitate the calculations. Theoretically it would be better not to set such upper limits, but in practice this is of little importance if the size of the breeding population is not greater than 100. In a breeding populations of this size there is very little space for founders that are represented by more than three offspring if its size and status number are kept constant. For example, for a case with $N_{R1}=200$, $N_2=100$ and $N_{S2}=66.7$ it was possible to find a solution in which the highest ranking founder contributes four offspring. This solution more closely followed the optimal deployment function (LINDGREN *et al.* 1989) than the contributions with a restriction of at highest three offspring per founder, but its genetic gain was not higher.

If the breeding population size is considerably larger than 100, the solutions obtained by this method would deviate from the optimum one obtained by not limiting the contribution of the best trees to any fixed number. However, in such a case the optimum solution would be difficult to calculate using the methodology presented here, but it could be approximated by using linear deployment (LINDGREN *et al.* 1989).

For long-term breeding it is important to consider the genetic contributions from the founders to the breeding population some generations ahead. Gain can be expected to be proportional to the contributions, and diversity to the square of the contributions (WOOLLIAMS 1998). It can thus be assumed that the optimal long-term impact of a founder on gain versus that on diversity is obtained by using linear deployment in analogy with the case for clonal deployment for the multiplication population (LINDGREN 1986). This can justify the mating of founders with a similar breeding

value (positive assortative mating), as it will make it easier to obtain similar genetic contributions from these founders in the future. In the first rounds of breeding and selection it will probably be optimal to get founder contributions that are linearly related to their breeding values. In later generations favourable genes from different founders may be differently selected and are subject to drift in such a way that the genetic contributions are less informative as regards the distribution of valuable genes. At the same time information about the breeding values of later generation genotypes provides new bases for selection decisions. For this reason future generation breeding will most likely primarily focus on selection while keeping an approximate balance of the founder contributions. On the other hand, in the initial steps of breeding efforts should be made in the matings and selections to obtain a founder contribution that is linearly related to the breeding values of the founders.

Increased contribution of the best trees makes the best fraction of the breeding population to be more related to others than lower ranking trees. If repeated over many generations this leads to increased inbreeding. However, this did not abolish the additional genetic gain obtained by unbalanced mating system in a five-generation simulation study (ROSVALL 1999). Unbalanced mating is a better method than unbalanced selection for increasing contribution of best trees, as it creates less relatedness between selected trees, and gives thus better opportunities for future selections. For the same reason two crosses per tree are more recommendable than one (ROSVALL 1999).

The results presented here cover only the first round of selection, but the final goal is long-term improvement. However, even the first generation genetic gain is important as such, especially with such breeding objects as trees, since they have rather long generation intervals. It can also be argued that the gain obtained in the beginning of the breeding program will not be lost, irrespective of the decisions made in later generations. Several studies with stochastic simulations have shown that selection methods implementing the contribution of parents in relation to their breeding values also produce, after many generations of selection, higher genetic gain than equal contribution, with equal or lower inbreeding (TORO & NIETO 1984, WRAY & GODDARD 1994, LINDGREN & MULLIN 1997, MEUWISSEN 1997, ROSVALL 1999, ROSVALL & ANDERSSON 1999). Experimental results from a six-generation selection experiment with *Drosophila melanogaster* have shown that a method that optimises mate selection and contribution at the same inbreeding level gives a higher genetic gain than an equally contributing and random mating system (SANCHEZ *et al.*

1999). Continuously improving genetic gain by optimising the genetic contributions of the parents thus seems to be possible.

Exactly which method is used to allocate the contributions of the founders to the next generation is not essential, but what is most important is that the contributions approximately increase along with breeding value (WEI 1995). Small deviations from the theoretically optimal contributions do not greatly impair the result. The contributions giving maximum genetic gain with retained diversity can be approximated by the following rule of thumb. Rank the recruitment population trees by their breeding values and select 20 % more founders than is the intended later generation breeding population size. Then divide the obtained breeding population into six sections of equal size. Let the highest section trees contribute three offspring to the next generation, the two following sections two offspring and the last three sections one offspring. This variable contribution method makes it possible to increase the genetic gain without losing genetic diversity and with essentially no extra costs. The number of crosses remains the same and, in most tree breeding situations, the additional founders needed in this method already exist *e.g.* in clone archives. It therefore only requires some more technical documenting when the number of founders is increased and all the founders are not contributing equally.

Variable contribution makes better use of the available genetic resources by saving more of the available gene pool and thus increasing the ultimate selection limit. This study confirms that the relationship between genetic diversity and gain is not fixed, but can be influenced by sound planning of the number of founders and their contributions.

ACKNOWLEDGEMENT

We acknowledge the financial support from Föreningen Skogsträdsförädling and the Nordic Academy for Advanced Study (NorFa) for this study. Erik D. Kjær has contributed valuable comments. The language was revised by John Derome whose help we greatly appreciate.

REFERENCES

- ANDERSSON, E. W., SÁNCHEZ RODRIGUEZ, L. & ANDERSSON, B. 1999: Group coancestry controlled selection in a *Pinus sylvestris* L. breeding program. *Theoretical and Applied Genetics* **99**(1/2):73–80.
- COCKERHAM, C. C. 1967: Group inbreeding and coancestry. *Genetics* **56**: 89–104.
- COTTERILL, P. P., DEAN, C., CAMERON, J. & BRINDBERGS, M. 1989: Nucleus breeding: a new strategy for rapid improvement under clonal forestry. *In*: Breeding tropical trees: Population structure and genetic improvement strategies in clonal and seedling forestry. (eds. G. I. Gibson, A. R. Griffin, & A. C. Matheson). pp. 39–51. Proc. IUFRO Conf. Pattaya, Thailand, November 1988. Oxford Forestry Institute, Oxford, UK and Winrock International, Arlington, Virginia, USA.
- DANELL, Ö. 1995: Breeding programs in Sweden: 1. General approach. SkogForsk. *Arbetsrapport* **302**: 1–4.
- DEMPFLE, L. 1975: A note on increasing the limit of selection through selection within families. *Genet. Res., Camb.* **24**: 127–135.
- KERR, R. J., GODDARD, M. E. & JARVIS, S. F. 1998: Maximising genetic response in tree breeding with constraints on group coancestry. *Silvae Genetica* **47**(2–3):165–173.
- LINDGREN, D. 1974: Aspects on suitable number of clones in a seed orchard. Proceedings, Joint IUFRO meeting, S.02.04.1–3, Stockholm, 1974, Session V. pp. 293–305.
- LINDGREN, D. 1986: How should breeders respond to breeding values? *In*: Conference proceedings: A joint meeting on IUFRO WP on breeding theory, progeny testing and seed orchards. Virginia, October 13 to 17, 1986. pp. 361–372.
- LINDGREN, D. 1991: Optimal utilization of genetic resources. *Forest Tree Improvement* **23**: 49–67.
- LINDGREN, D. 1993: Quantitative comparison between truncation selection and a better procedure. *Hereditas* **118**:289–292.
- LINDGREN, D. & KANG, K. S. 1997: Status number – a useful tool for tree breeding. *Res. Rep. For. Gen. Res. Inst. Korea* **33**:154–165.
- LINDGREN, D. & MATHESON, A. C. 1986: An algorithm for increasing the genetic quality of seed from seed orchards by using better clones in higher proportions. *Silvae Genetica* **35**(5–6):173–177.
- LINDGREN, D. & MULLIN, T. J. 1997: Balancing gain and relatedness in selection. *Silvae Genetica* **46**(2–3): 124–129.
- LINDGREN, D. & NILSSON, J.-E. 1985: Calculations concerning selection intensity. Sveriges Lantbruksuniversitet, Institutet för skoglig genetik och växtfysiologi. *Rapport* 5. 28 pp.
- LINDGREN, D., LIBBY, W. S. & BONDESSON, F. L. 1989: Deployment to plantations of numbers and proportions of clones with special emphasis on maximizing gain at a constant diversity. *Theoretical and Applied Genetics* **77**: 825–831.
- LINDGREN, D., WEI, R. P. & BONDESSON, L. 1993: Optimal selection from families. *Heredity* **70**:619–621.
- LINDGREN, D., WEI, R.-P. & LEE, S. J. 1997: How to calculate optimum family number when starting a breeding program. *Forest Science* **43**(2):206–212.
- MEUWISSEN, T. H. E. 1997: Maximizing the response of selection with a predefined rate of inbreeding. *J. Anim. Sci.* **75**:934–940.
- ROSVALL, O. 1999. Enhancing gain from long-term forest tree breeding while conserving genetic diversity. *Acta Universitatis Agriculturae Sueciae. Silvestria* **109**, 65 pp. + app.
- ROSVALL, O. & ANDERSSON, E. 1999: Group-merit selection compared to conventional restricted selection for trade-offs between genetic gain and diversity. *Forest Genetics*

- 6:11-24.
- ROSVALL, O., LINDGREN, D. & MULLIN, T. J. 1998: Sustainability robustness and efficiency of a multigeneration breeding strategy based on within-family clonal selection. *Silvae Genetica* **47**:307-321.
- SANCHEZ, L., TORO, M. A. & GARCIA, C. 1999: Improving the efficiency of artificial selection: more selection pressure with less inbreeding. *Genetics* **151**: 1103-1114.
- TORO, M. A. & NIETO, B. M. 1984: A simple method for increasing the response to artificial selection. *Genet. Res., Camb.* **44**:347-349.
- TORO, M. & PÉREZ-ENCISO, M. 1990: Optimization of selection response under restricted inbreeding. *Genetics Selection Evolution* **22**: 93-107.
- VILLANUEVA, B. & WOOLLIAMS, J. A. 1997: Optimization of breeding programmes under index selection and constrained inbreeding. *Genet. Res., Camb.* **69**:145-158.
- WEI, R.-P. 1995: Predicting genetic diversity and optimizing selection in breeding programmes. Swedish University of Agricultural Sciences. Department of Forest Genetics and Plant Physiology. Dissertation. pp. 64+app.
- WEI, R.-P. & LINDGREN, D. 1995: Optimal family contributions and a linear approximation. *Theoretical Population Biology* **48**:318-332.
- WHITE, T. L. 1987: A conceptual framework for tree improvement programs. *New Forests* **4**:325-342.
- WHITE, T. 1992: Advanced-generation breeding populations: size and structure. *In*: Proceedings of IUFRO conference S2.02.-08 Breeding tropical trees. Cartagena and Cali, Colombia, October 9-18, 1992, pp. 208-222.
- WHITE, T. L., HODGE, G. R. & POWELL, G. L. 1993: An advanced-generation tree improvement plan for slash pine in southeastern United States. *Silvae Genetica* **42**(6): 359-371.
- WILHELMSSON, L. & ANDERSSON, B. 1995: Breeding programs in Sweden. 2. Breeding of Scots pine (*Pinus sylvestris*) and lodgepole pine (*Pinus contorta* ssp. *latifolia*). SkogForsk. *Arbetsrapport* **302**: 5-15.
- WOOLLIAMS, J. A. 1998: A recipe for the design of breeding schemes. *In*: Proceedings of the 6th world congress on genetics applied to livestock production. Armidale, NSW, Australia, January 11-16, 1998, p. 427-430.
- WRAY, N. R. & GODDARD, M. E. 1994: Increasing long-term response to selection. *Genet. Sel. Evol.* **26**:431-451.