Predicting Genetic Gain of Backward and Forward Selection in Forest Tree Breeding

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Abstract

In several forest tree breeding operations either backward or forward selection is used, although a proper combination of both might be more advantageous. Using calculations based on quantitative genetic theory, comparisons were made between the relative merits of backward and forward selection for individual families. In backward selection the mother was chosen based on her offspring and in forward selection the best offspring was selected from the family consisting of the mother and her children. A range of heritabilities and selection intensities in natural forest and progeny test (the latter is a function of progeny size) were compared.

It is the more favourable to select backward the higher the mother ranks. Depending on the combination of parameter values, backward selection was superior to forward selection for open pollinated progeny in 1% to 57% of the top ranking families. High intensity of selection in the forest, low heritability and small progeny size favoured backward selections. Backward selection for families with plus tree fathers was usually not favourable for more than a few percent of the families. Only when heritability was low it could be favourable to select 10% of top-ranking mothers.

The calculations show that it can often be optimal to apply backward selection for the best families and forward selection for the lower ranking families side by side. However, the difference is often small and then other considerations can be more important.

Key words: backward selection, forward selection, breeding strategy, intensity of selection, progeny size, heritability, genetic gain.

FDC: 165.3; 165.6.

1. Introduction

Progeny testing aimed at parental ranking is a commonly used method in both animal and plant breeding. Progeny testing can be used for several purposes and the term can have different meanings. In this study it is used as a synonym of parental ranking (Lindgren, 1991). In forest tree breeding, progeny testing is often viewed as a fundamental part of the whole procedure (Zobel and Talbert, 1984). It is used to obtain additional genetic gain through roguing seed orchards and establishing seed orchards with the top ranking clones. Progeny testing is also considered essential for advanced generation breeding, because the progenies of the best plus trees form the base material for the next generation breeding (forward selection). Ranking parents according to the performance of their progeny (backward selection) is especially important with characters which have a low heritability (Falconer and Mackey, 1996), as is the case with many important characters in forest tree breeding (Wright, 1976, Cornelius, 1994). Forest tree breeders have been aware of the choice between backward and forward selection for a long time; the gain may differ considerably for the different alternatives (Falconer and Mackey, 1996). However, breeders have considered it to be an "either/or" decision, and not realised that they can use different options for different families.

The original idea in many tree breeding programs was to use the progeny tests of the phenotypically selected plus trees only for parental ranking. The base material for second generation breeding was to be created by crossing the best ranking plus trees (Werner *et al.*, 1981; Pitkäntähtäyksen metsänjalostusohjelma, 1989). This plan has also been put into practice for example with Sitka spruce in Britain (Lee, 1993). However, the question that arises is whether to use the progeny tested plus trees or their offspring in long term breeding. Phenotypic selections among the progeny from plus trees may actually be a favourable option under certain circumstances (Spanos *et al.*, 1997).

Lindgren (1986) stated, as a general principle, that the best progeny tested genotypes should be selected backward and others forward. This is caused by the fact that the best genotypes in most forest tree breeding cases are mated with individuals which can be assumed to have a considerably lower breeding value. Thus the progeny have, on the average, a lower breeding value than the best parents themselves. The differential increases with increasing genetic value of the parent, whereas the within-family selection gain is independent of the parental values. Thus the gain achieved by selecting the best individual within the progeny becomes more and more difficult to balance against the difference which increases consistently with the breeding value of the parent. Therefore backward selection is the most favourable method for the best ranked parents. One contributing reason is that selection backwards does not mean the introduction of new genetic relationships but instead keeps the gene mass of the best founders intact.

The aim of this study was to develop a method for comparing backward selection and forward selection for individual genotypes as a function of their rank, and to create a firmer theoretical basis for a comparison between these selection schemes. The study also evaluates the magnitude of the difference between backward and forward selection gain, and determines which factors influence the balance between backward and forward selection.

2. Methods

2.1. *Selection alternatives to be compared*

2.1.1. Backward selection (BACKW)

Backward selection (*i.e.* reselection) means the acceptance of the best plus trees to be used as parents in the next multiplication population (ramets in seed orchards) or for breeding population (so that a new progeny is created to serve as a resource for further selections), based on the results of progeny tests. The kind of material or experimental lay-out which has been used in progeny testing is of no significance as long as the method is sound and yields accurate predictions for the breeding values of the plus trees. The offspring used to rank the plus trees are not used in creating the next generation of

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the breeding population, but it is instead based on progenies that are crosses between the highest ranking plus trees.

2.1.2. Forward selection from open pollinated progeny (FORW0)

Open pollinated seed is widely used, cheap and often rapidly available material for the progeny tests of forest trees. It can be collected either from the original plus trees or from their grafts (Zobel and Talbert, 1984). Members of an open pollinated family are assumed to be true half-sibs. However, slight deviations from this assumption will probably not have any marked influence on the model. Instead of crossing the best ranked plus trees, the best individuals from their open pollinated progenies are selected. Unimproved pollen which reduces the obtained genetic gain is the main drawback in using open pollinated material for forward selection. For a wind pollinated common tree species like Scots pine, high levels of background pollination seem inevitable even in mature seed orchards (Harju, 1995).

2.1.3. Forward selection from polycross progeny (FORW+)

In some cases progeny testing is carried out with material created using a mixture of pollen collected from the plus trees (polycross). In this case the pollen parent is assumed to have, on the average, as high a genetic value as the seed parent. Thus, forward selection within polycross progeny will lead to a higher genetic gain than selection within open pollinated progeny. Open pollinated material from a seed orchard can sometimes be genetically at the same level as polycross material. This is true if the species in question is an exotic or of otherwise such low abundance that background pollination is negligible (*e.g.* Shelbourne, 1992). Background pollination can sometimes be prevented by using seed orchards located in greenhouses. Controlled polycross is still more reliable for progeny test as selfing is excluded and the different pollens are mixed to obtain equal contributions. However, the father is unknown, so several selections may have the same father, and the phenotype of relatives to the unknown father (e.g. half-sibs to the selection) cannot be used to increase the accuracy of the breeding value of the selection. The genetic gain of selections from a polycross progeny gives a considerable indication of the gain which would be achieved if there were controlled crosses with known parents.

2.2. General features of the procedure

Methods are available for comparing genetic gains from different breeding alternatives (e.g. Namkoong *et al.*, 1966; Lindgren and Werner, 1989; Shelbourne, 1992). A common feature in these methods is that the response to selection is predicted for the average of a population, using the formulae for genetic gain. Formulae predicting the selection response can be applied to any data, but a standardized normal distribution is usually used for non-experimental studies, resulting in a standardized selection response (intensity of selection). One development in this method is that predictions are made for individual genotypes rather than for the average of all selections (Lindgren, 1986). Predictions of individual values are made according to their rank, which is a conventional statistical quantity called order statistics. Breeding values are predicted for each plus tree and the best of its offspring. A plus tree which is acting as a mother forms a family together with its progeny. Either the plus tree or its best offspring is selected from each family. Hodge and White (1993) used a rather similar method for predicting genetic gain, although it differed in some details. Their comparison did not include forward selection in open pollinated progeny.

2.3. Formulae for breeding value and genetic gain

In the following calculations breeding values and genetic gains are expressed with additive genetic standard deviation (σ_A) as a unit. The calculation procedure includes several successive steps, which are presented in the following. The formulae are adopted from Falconer and Mackey (1996).

The genetic gain in phenotypic selection in the forest (wild population) can be generally expressed as

$G_1 = i_1 h^2 \sigma_P = i_1 h \sigma_A$

where

i_1 = intensity of selection in the forest
h^2 = narrow sense individual tree heritability
σ_P = phenotypic standard deviation
As $\sigma_A = 1$ by definition, this reduces to

(1) $G_1 = i_1 h,$

The following formulae (2 to 7) are applied to each family separately.

The formula for selecting a mother according to the results of an open pollinated progeny test is obtained as follows. The basic formula for sib selection is

$$R_s = i_2 \sigma_P h^2 \frac{nr}{\sqrt{n(1+(n-1)t)}}$$

where,

i_2 = intensity of selection for the particular parent
n = progeny size
r = correlation between breeding values
t = correlation between phenotypic values

By noting that $h^2 = \sigma_A{}^2/\sigma_P{}^2$, $t = rh^2$ and that for half sibs $r = 0.25$, the formula is reduced to

$$R_s = i_2 \sigma_A \frac{0.5}{\sqrt{1+(4/h^2-1)/n}}$$

Because it is question of a population with finite size, the standard deviation must be corrected by a factor $\sqrt{1-1/m}$, where m is number of plus trees (families). However, $\sqrt{1-1/m}\,\sigma_A$ becomes $\sqrt{1-1/m}$, because $\sigma_A = 1$. Finally, by noting that the formula for sib selection from open pollinated progeny gives only half the breeding value of the parent, the result must be multiplied by two.

So the formula for genetic gain when selecting a mother according to the results of open pollinated progeny test is obtained as

$$(2) \quad G_2 = 2R_S\sqrt{1-1/m} = 2i_2\sqrt{1-1/m}\frac{0.5}{\sqrt{1+(4/h^2-1)/n}} = i_2\frac{\sqrt{1-1/m}}{\sqrt{1+(4/h^2-1)/n}}$$

Analogously the genetic gain when selecting a family is

$$(3) \quad R_f = i_3 \frac{\left(\sqrt{1-1/m}\right)(1.5/n+0.5)}{\sqrt{1+(4/h^2-1)/n}}$$

where

i_3 = intensity of selection for the family.

The genetic gain when selecting the best offspring within a family (R_w) is

$$(4)\ R_w = i_4 0.75\sqrt{\frac{(1-1/n)}{(1/h^2-0.25)}}$$

where

i_4 = intensity of selection in the test when selecting the best offspring within a family (selecting the best out of n values).

The breeding value for a parent (G_3 = BACKW) is obtained as the sum of genetic gain in phenotypic selection in the forest and selection of a mother according to the results of a progeny test (operational definition for breeding value)

$$(5)\ G_3 = G_1 + G_2$$

The breeding value for the best individual within an open pollinated progeny in forward selection (G_5 = FORW0) is predicted as:

$$(6)\ G_5 = G_1/2 + R_f + R_w$$

The breeding value for the best polycross offspring in forward selection (G_6 = FORW+) includes the genetic gain in phenotypic selection in the forest as a whole

$$(7)\ G_6 = G_1 + R_f + R_w$$

The effects of the parameters on the relative order of the selection alternatives were studied in more detail by setting the formulae for backward (5) and forward selection (6) equal, and then solving the value for intensity of selection at which the alternatives give equal breeding values (formula 8).

$$(8)\ i_{\mathrm{lim}} = \frac{\left(i_4 0.75\sqrt{(1-1/n)/(1/h^2-0.25)} - i_1 h/2\right)\sqrt{1+(4/h^2-1)/n}}{\sqrt{(1-1/m)(0.5-1.5/n)}}$$

where

i_{lim} = limit value for intensity of selection (i_2 and i_3) at which $G_3 = G_5$.

By varying the values of one parameter and fixing the others, the effects of the parameters could be studied separately. When the i_{lim} values had been solved, the percentage of families in which backward selection was superior could be obtained from the distribution of the order statistics. A modification using fixed genetic gain in selection in the forest (G_1) instead of $i_1h/2$ was also studied.

2.4. Calculation of genetic gain

The breeding values used for a population of 100 plus trees were generated by the SELEINT2 program as a function of their rank using order statistics for the normal distribution. The normal order statistics for n = 100 could also have been taken from *e.g.* the tables by HARTER (1970). SELEINT2 3) has the advantage over published tables in that it can be used for any sample size. These calculations would have been simplified if a large number of plus trees had been assumed, because in such a case the expected percentiles from the normal distribution could have been used. However, as breeders work with a finite number of plus trees we preferred the method used here, which demonstrates the handling of small numbers. More information about the statistics connected to selection from normal distributions is given by LINDGREN and NILSSON (1985). These order statistics are the predicted standardized intensities of selection for the plus trees of the ranking in question, but they can also be regarded as the breeding value of a plus tree with this ranking. Breeding values for each family were predicted for the plus tree itself (BACKW) and the best individual in open pollinated (FORW0) and polycross progeny (FORW+) (formulae (5), (6) and (7), respectively).

For each selection alternative (BACKW, FORW0, FORW+) genetic gain was calculated as a mean of the breeding values of the individual plus trees or their best offspring. This was done both for the whole population and for the top 50% of it. In addition to these three pure selection alternatives, two cases with combined backward and forward selection were studied. In BESTBAF0 the selection within each family was either the plus tree or its best open pollinated offspring, depending on which had the higher breeding value. The genetic gain for this alternative was obtained as a mean of this mixed population of breeding values. BESTBAF+ was the corresponding combination of backward selection and forward selection from polycross progeny. Backward selection was also compared with both alternatives of forward selection (FORW0, FORW+) on the family level in order to determine in which families backward selection was the preferred choice.

Three parameters affect the genetic gain in our model: intensity of selection in the forest (i_1), individual heritability (h^2) and progeny size (n). Calculations were performed with all combinations (27 cases) of three parameter value levels: low, medium and high (*Table 1*). It was assumed that the individual heritability for plus tree selection in the forest and for progeny tests was the same.

Table 1. – The parameter values used in the calculations. The parameters and values given in parentheses are secondary ones derived from the original parameters.

Parameter	Parameter value low	medium	high
intensity of selection in forest, i_1	1.8675	2.5076	3.2414
(selection ratio)	(1/20)	(1/100)	(1/1000)
heritability, h^2	0.05	0.2	0.5
progeny size, n	25	100	500
(intensity of selection in test, i_4)	(1.9653)	(2.5076)	(3.0367)

3. Results

3.1. Genetic gain for different alternatives

(a) No family selection

Forward selection in the open pollinated progeny test was usually superior to the phenotypic plus tree selection in the forest (FORW0 > BACKW) when the whole population was included (no family selection) (*Table 2*). When there is no family selection it is not strictly justified to call BACKW backward selection, since this alternative merely describes the effect of phenotypic plus tree selection. Forward selection from the open pollinated progeny (FORW0) was unfavourable at the

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3) SELEINT2 is authored by DAG LINDGREN in 1990 and is available on the internet via http://linne.genfys.slu.se/breed/breed.htm

Table 2. – Genetic gain (as per cent of the gain in BACKW) for forward selection or combination of forward and backward selection with two population compositions and sizes (all phenotypically selected 100 or top ranking 50 plus trees)[1]).

i_1 (selection ratio)	i_4 - n	h^2	The population of all selected 100 plus trees or their progeny ($\bar{i}_2 = \bar{i}_3 = 0$)				The population of best ranking 50 plus trees or their progeny ($\bar{i}_2 = \bar{i}_3 = 1.844$)			
			FORW0	BEST BAF0	FORW+	BEST BAF+	FORW0	BEST BAF0	FORW+	BEST BAF+
1.8675 (1/20)	1.9653 - 25	0.05	128	137	178	179	93	103	119	121
		0.20	129	134	179	180	99	105	128	128
		0.50	133	135	183	183	106	109	139	139
	2.5076 - 100	0.05	151	165	201	206	93	105	113	118
		0.20	153	157	203	203	106	110	133	133
		0.50	157	158	207	207	118	119	150	150
	3.0367 - 500	0.05	173	189	223	230	95	107	113	118
		0.20	175	178	225	225	115	118	141	141
		0.50	180	180	230	230	132	132	163	163
2.5076 (1/100)	1.9653 - 25	0.05	108	119	158	159	87	100	116	118
		0.20	109	117	159	159	91	101	123	124
		0.50	112	116	162	162	96	102	132	132
	2.5076 - 100	0.05	125	140	175	179	87	102	112	115
		0.20	127	132	177	177	97	104	128	128
		0.50	130	131	180	180	106	109	141	141
	3.0367 - 500	0.05	141	157	191	197	90	104	111	116
		0.20	143	147	193	193	105	109	135	135
		0.50	147	147	197	197	117	118	152	152
3.2414 (1/1000)	1.9653 - 25	0.05	95	109	145	146	81	100	114	115
		0.20	96	107	146	146	84	100	120	120
		0.50	98	106	148	148	88	100	126	126
	2.5076 - 100	0.05	108	124	158	161	83	100	110	113
		0.20	109	117	159	159	90	101	123	124
		0.50	112	115	162	162	97	102	134	134
	3.0367 - 500	0.05	121	137	171	175	85	101	110	114
		0.20	122	127	172	172	97	104	130	130
		0.50	125	126	175	175	106	108	143	143

[1]) Four selection alternatives are compared as follows: FORW0 = forward selection of the best tree from each open pollinated progeny; BESTBAF0 = in each family either the plus tree or its best open pollinated progeny is selected, depending on their breeding values; FORW+ = the best selection from each polycross progeny; BESTBAF+ = as BESTBAF0, but comparison between the plus tree and its best polycross progeny. i_1 = intensity of selection in the forest, i_4 = intensity of selection in the test when selecting the best offspring within a progeny, n = size of progeny, h^2 = individual narrow sense heritability. $\bar{i}_2$ = average intensity of selection for the plus trees, $\bar{i}_3$ = average intensity of selection for the families

whole population level only in the case of the highest intensity of selection in the plus tree selection and the lowest intensity of selection in the test. FORW0 gave a maximum of 80% higher genetic gain than the plus tree selection (BACKW). Forward selection was most advantageous in cases where the intensity of selection was low in the forest and high in the experiment and when the heritability was high.

Forward selection from the polycross material (FORW+) increased the genetic gain by 45% to 130% over the phenotypic plus tree selection (BACKW). The parameter values (i_1, h^2, n) influenced the relative genetic gains in the same way as with open pollinated progeny, except that intensity of selection in the forest had only a slight effect on the genetic gain. In absolute values intensity of selection in the forest did not influence the amount of genetic gain with which FORW+ exceeded phenotypic plus tree selection. However, because the level of genetic gain was higher with a higher intensity of selection in the forest, the relative values for FORW+ correspondingly decreased.

A combination of backward and forward selection (BESTBAF0, BESTBAF+) increased the genetic gain in some cases by more than 10% compared to the best single form of selection. The greatest additional gains through combination were obtained at those parameter values when neither of the pure alternatives was excessively superior, *i.e.* cases in which backward selection was used in about one half of the families utilized in breeding. When the material was of polycross origin, the possibilities for additional genetic gain were limited due to the superiority of forward selection. Heritability made a surprisingly small contribution to the effect of combining backward and forward selection, and did not follow any clear general pattern.

(b) Selecting the top 50% of families

In the case of a stronger selection comprising half as many selections as the initial number of plus trees, forward selection was less favourable than when no family selection was used (*Table 2*). Only when selection in the forest was less intense, heritability high and the families large did forward selection in open pollinated families show any overall superiority over backward selection. Combination of both selection alternatives gave a maximum increase of 7% in genetic gain. In the best 50% subpopulation too, forward selection in polycross material (FORW+) was always better than backward selection, but its superiority was considerably diminished compared to the calculation at the whole population level.

3.2. *Backward vs. forward selection at the family level*

The proportion of top ranking families in which backward selection (BACKW) was better than forward selection from open pollinated material (FORW0) ranged from 1% to 57% (*Table 3*). The effect of the parameter values parallelled those on genetic gain. Thus, backward selection was most favourable when the intensity of selection was high in the forest, but low in the test. Low heritability also favoured backward selection.

Table 3. – Percentage of top ranking families in which the plus tree has a higher breeding value than its best offspring (*i. e.* backward selection better than forward selection). Plus trees are compared both to open pollinated (OP) (alternative FORW0) and polycross (PC) progeny (alternative FORW+). Altogether 27 combinations of parameter values are presented. The parameters are as in *table 2*.

i_1 (selection ratio)	i_4 - n	h^2	plus tree better than best offspring in	
			OP progeny	PC progeny
			% of families	
1.8675 (1/20)	1.9653 - 25	0.05	29	6
		0.20	23	2
		0.50	13	0
	2.5076 - 100	0.05	28	12
		0.20	16	3
		0.50	5	0
	3.0367 - 500	0.05	25	13
		0.20	10	1
		0.50	1	0
2.5076 (1/100)	1.9653 - 25	0.05	42	6
		0.20	38	2
		0.50	30	0
	2.5076 - 100	0.05	35	12
		0.20	25	3
		0.50	13	0
	3.0367 - 500	0.05	31	13
		0.20	16	1
		0.50	4	0
3.2414 (1/1000)	1.9653 - 25	0.05	57	6
		0.20	57	2
		0.50	56	0
	2.5076 - 100	0.05	44	12
		0.20	38	3
		0.50	28	0
	3.0367 - 500	0.05	37	13
		0.20	25	1
		0.50	12	0

If polycross progeny is available, backward selection will rarely produce a higher predicted gain than FORW+. Only in the cases of the lowest heritability and medium or large families, can slightly over 10% of the top ranking plus trees be selected backward. As would be theoretically expected, the relationship between BACKW and FORW+ was not affected by the genetic gain in phenotypic selection in (*Table 3*). A typical situation describing the three selection alternatives is shown in *figure 1*. In the case of medium parameter values backward selection was better than forward selection from open pollinated progeny in 25% of the top ranking families (BACKW and FORW0 crossing at this point). On the other hand, backward selection was superior to FORW+ in only the best 3% of families. As can be seen from the curves for BACKW and FORW0 close to the crossing point, the difference between these alternatives is small with a large number of families.

3.3. *Effects of parameters*

The intensity of selection in the forest (*i.e.* genetic gain in phenotypic selection) had a pronounced effect on the proportion of families in which backward selection was to be preferred (*Figure 2*). When the intensity of selection in the forest was low, the proportion of families where BACKW is superior to FORW0 was low, but with intensities of selection above 2 their proportion rapidly increased especially with a smaller progeny size.

In our main model we considered that the gain of plus tree selection in the forest (G_1) is a function of the heritability. An alternative method is to consider the average genetic gain when selecting the plus trees as fixed, and letting the heritability affect only the gain through selection based on a test. In both alternatives the proportion of families in which backward selection was a better method decreased with increasing heritability (*Fig. 3*). Compared to the situation where genetic gain was expressed as a function of heritability and intensity of selection, fixed genetic gain gave a higher proportion of backward selection at low heritabilities and a lower proportion at high heritabilities. This was caused by the fact that when genetic gain is given as a function of heritability, low heritability decreases genetic gain in the forest (G_1) and thus also decreases the genetic gain in backward selection.

Progeny size had the greatest effect on the superiority of the selection methods at the s#mallest (below 50) progeny sizes (*Figure 4*). When progeny size increased from 10 to 50 the proportion of families in which backward selection was better dropped from a maximum of 60% to 20% to 30%. When progeny size was over 100, its changes had only a weak effect on the proportion of families selected backward.

The number of families (plus trees) had practically no effect on the superiority of the selection alternatives when the proportion of families was used as the criterion.

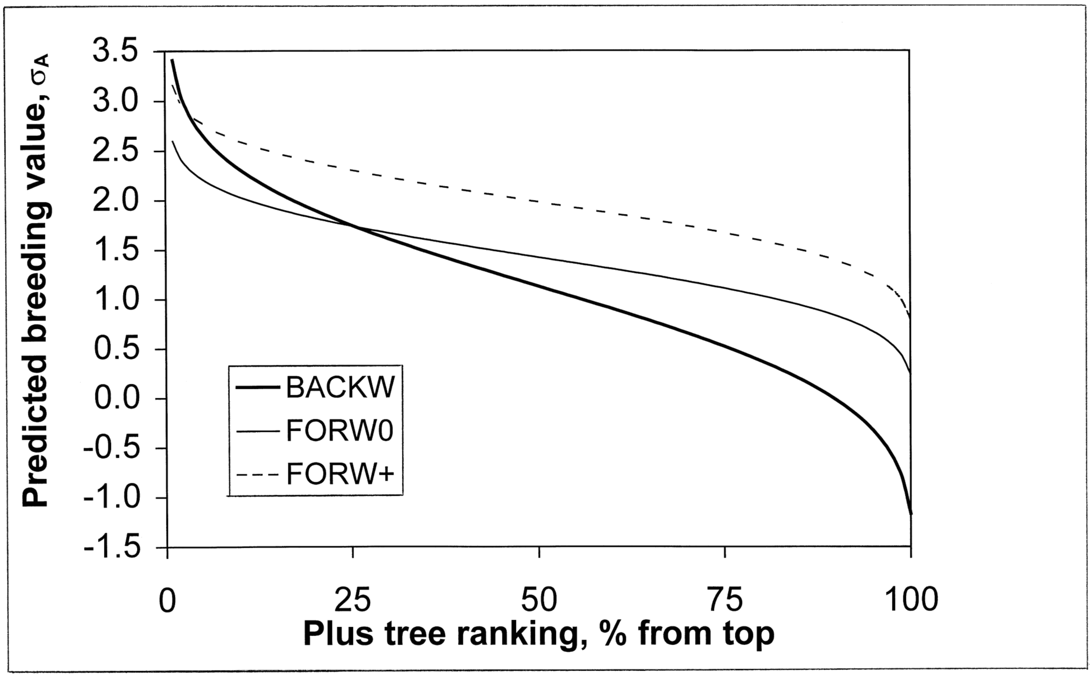

Figure 1. – Predicted breeding values for the individual progeny tested plus trees (BACKW) compared with the best offspring. FORW0 = best offspring in an open pollinated progeny of the plus tree, FORW+ = best offspring in a polycross progeny of the plus tree. This figure describes an intermediate situation in which $i_1 = i_4 = 2.5076$ and $h^2 = 0.2$.

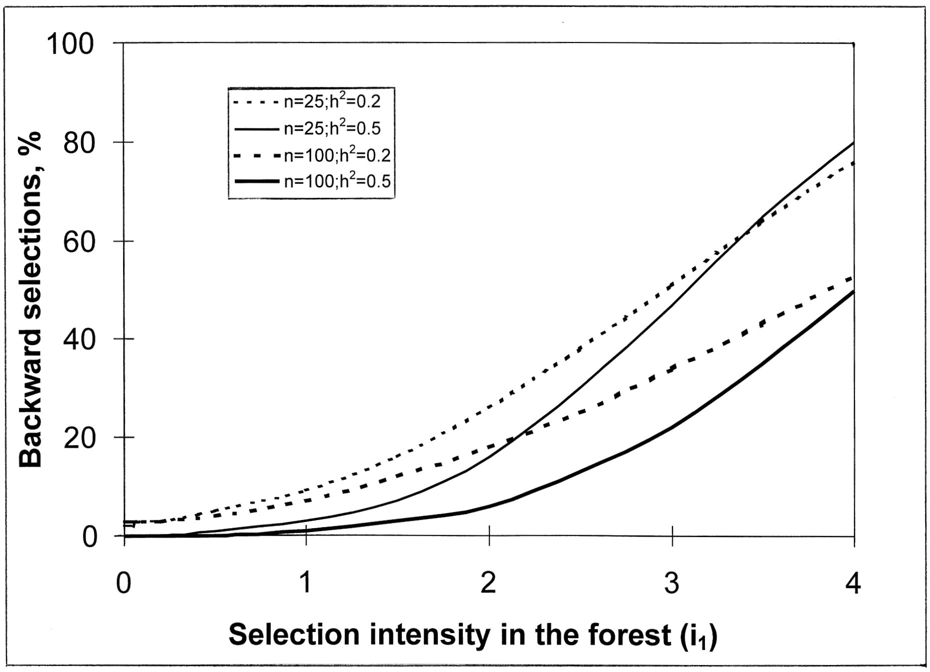

Figure 2. – Percentage of families in which backward selection (BACKW) is a better alternative than forward selection (best individual from n) from open pollinated progeny (FORW0) as a function of intensity of selection in the forest. Four different combinations of parameters n and h^2 are shown.

4. Discussion

4.1. General discussion

The proportion of families in which backward selection (BACKW) was the preferred alternative varied greatly depending on the values of the parameters (i_1, h^2, n). When BACKW was compared to forward selection from open pollinated families (FORW0) at medium parameter values, backward selection was the better alternative in some 25% of the top ranking families. A comparison with polycross families (FORW+) with the same parameter values indicated that backward selection was better in only 3% of the families. The results obtained using the same method by LINDGREN (1986) are in fairly good agreement with those presented here.

In a simulation study with full sib families (both parents plus trees) HODGE and WHITE (1993) found that the highest ranking parents were superior to the best offspring selections. They also observed that backward selection was favoured when a decreasing proportion of the original population was used. They did not allow related individuals in the offspring, and this greatly reduced the gain of the lower ranking offspring selections. According to LINDGREN and WERNER (1989), in the establishment of Norway spruce seed orchards, forward selection from full sib families gave higher general genetic gain than backward selection.

The observed regularities are rather evident. The intensity of selection in the forest influenced the balance between backward and forward selection by affecting the relative breeding value of the pollen pool. When selection in the forest has been ineffective, the unselected pollen cloud has almost as high a genetic value as the plus trees themselves, thus making forward selection from open pollinated progeny a useful option. Especially in cases where genetic gain in phenotypic selection in the forest is zero ($G_1 = 0$), forward selection in open pollinated progeny gives the same result as forward selection in polycross progeny ($G_5 = G_6$, formulae 6 and 7). On the other hand, with a higher intensity of selection in the forest the breeding value of the background pollen pool is decreased in relative terms, thus favouring backward selection. LINDGREN and

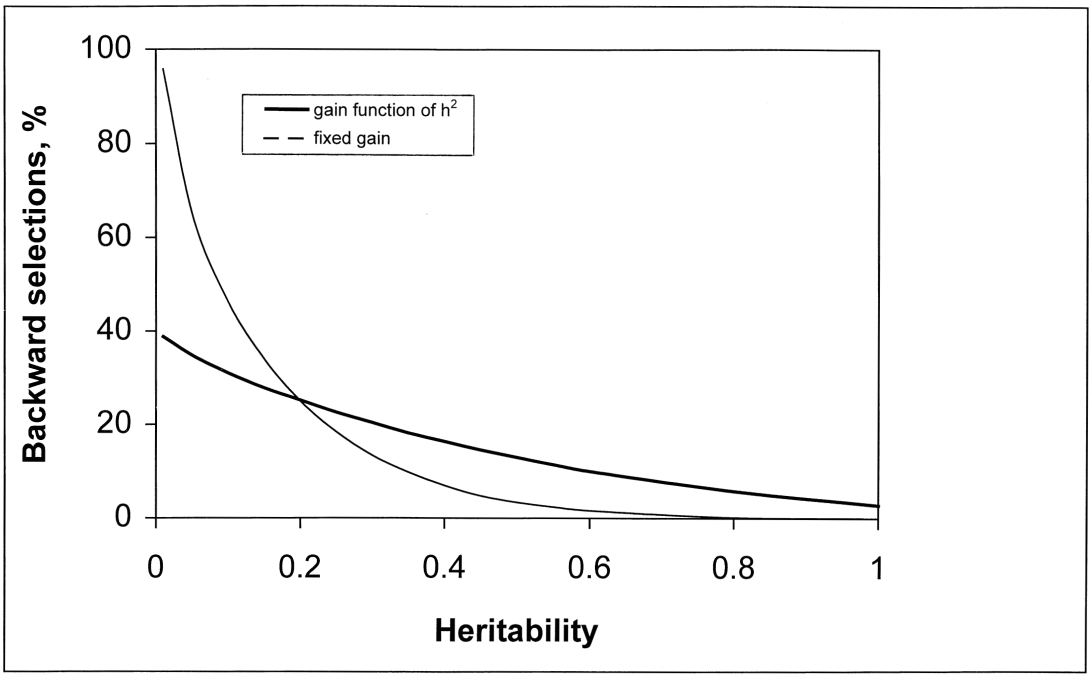

Figure 3. – Percentage of families in which BACKW is a better alternative than FORW0 as a function of heritability. A case with fixed genetic gain in the forest (G_1=1.121 σ_A) is compared with a case in which genetic gain is a function of fixed intensity of selection (i_1 = 2.5) and heritability. Size of progeny (n) is 100 in both cases.

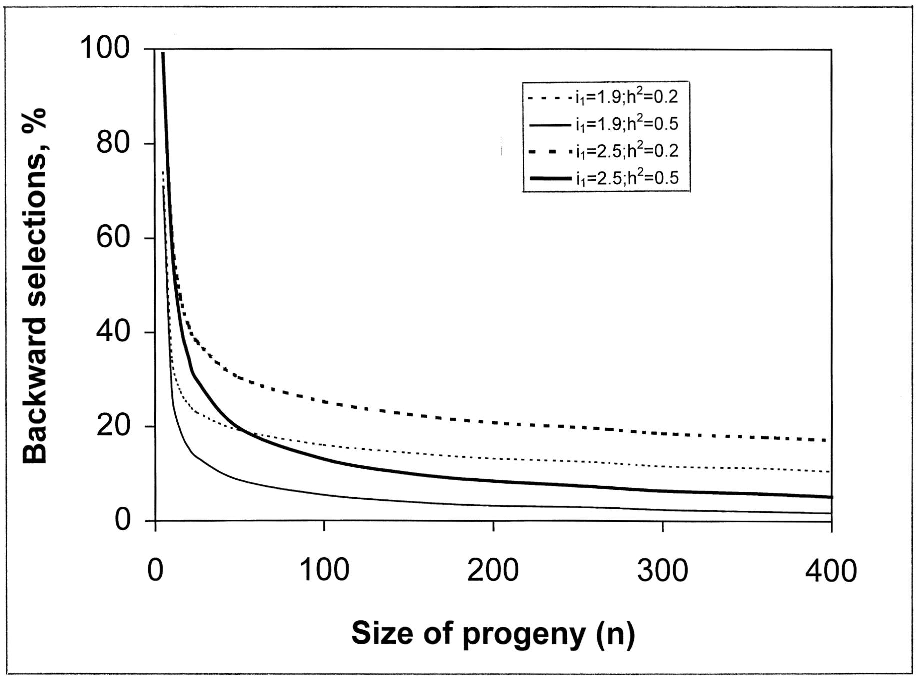

Figure 4. – Percentage of families in which BACKW is a better alternative than FORW0 as a function of progeny size. Four different combinations of parameters i_1 and h_2 are shown.

Werner (1989) also pointed out in a study on Norway spruce that open pollinated material is worth considering when genetic gain in phenotypic selection in the forest is low.

The relationship between backward selection and forward selection in polycross progenies is not affected by the intensity of selection in the forest, because both these alternatives deal only with selected material. This can also be verified analytically by setting G_3 and G_6 equal (formulae 5 and 7). As a result, the phenotypic genetic gain in the forest (G_1) is reduced from the equation.

Low heritability favours backward selection, because in such cases forward selection is not effective. This is true both with a situation in which genetic gain in the forest is expressed as a function of heritability and intensity of selection, and especially with fixed genetic gain. For practical applications it is better to study the effect of heritability with a fixed genetic gain, because in real situations one cannot change it at the time when the selections for next generation seed orchards or breeding populations are actual. On the other hand, heritability in the experiments can be influenced by experimental lay-out, tending or finally by selecting experiments according to heritability. The same relationship with heritability is also observed between backward selection and forward selection from polycross progeny. Low heritability is one of the main factors favouring progeny testing and thus backward selection (Falconer and Mackey, 1996).

Both selection backwards and forwards are affected by heritability, but the relationships are different. These combined effects can give the sort of complex dependences which are sometimes observed for BESTBAF0 and BESTBAF+ in *table 2*, although in the major comparisons forward selection became slightly better with increasing heritability. The overall impression from *table 2* is that heritability has only a slight effect, while intensities of selection are considerably more important. A parallel could be made with the studies of Lindgren (1986) and Lindgren *et al*. (1997), who conclude that heritability is of little importance for the breeding decisions studied.

Small families have the consequence that intensity of selection is reduced when selecting the best, and they thus reduce gain by forward selection. They also have the drawback that the average of the family will reflect less precisely the true family average, and thus the breeding value of the parent. This will make selection backwards less efficient.

4.2. The model and the parameters

The lowest values used for intensity of selection in the forest (i = 1.8675) may seem too low. However the intensities of selection achieved in practical plus tree selection are not necessarily very high. In Finnish plus tree selections of Scots pine and Norway spruce, the average intensities of selection for height were in the range of 1.5 to 2.0 depending on the species and area (Oskarsson, 1972). In practical selection work the intensity of selection for a single trait is lowered by selection for several traits. As a result of varying environmental conditions, reliable comparisons can only be made with a limited number of trees. Intensities of selection of 2 to 3 are realistic in the case of mass selection in uniform forest or unimproved plantation (Wright, 1976). As a consequence of this reasoning rather low intensities of selection (below 2.5) seem to be most relevant. Shelbourne (1992), for instance, used a selection ratio 1:60 (i = 2.32) in a simulation study for recurrent mass selection.

Although in some breeding programs plus trees are tested with several hundred offspring, the potential for within-family selection is limited to a much lower number of trees due to for example mortality, unsuitability of tests for selection and difficulties in making reliable comparisons between tests. Wright (1976) stated that the intensity of selection in most cases of within-family selection does not exceed 2.5 (responding selection ratio 1:100). According to Lindgren (1991), not more than 30 to 100 offspring are justified for the ranking of parents. In other simulation studies selection intensities of between 2.04 and 2.51 have been used (Shelbourne, 1992; Hodge and White, 1993). All this leads to the conclusion that the maximum intensity of selection for within family selection that can be achieved in a test is 2.5.

In a review covering several species and traits, Cornelius (1994) found that for growth traits the average heritabilities were between 0.2 and 0.3, and more than 75% of the heritability values were less than 0.4. According to Haapanen *et al*. (1997), the mean weighted heritability value for height was 0.24 in 16 Scots pine progeny trials in Finland. In individual trials heritability values of as high as 0.77 were observed. In a similar simulation study, Shelbourne (1992) used heritability values of between 0.1 and 0.4, and Hodge and White (1993) 0.2. It can be stated that heritability values of between 0.2 and 0.4 are realistic for this kind of calculation. Actually, we have made a simplification which is probably not realistic by assuming that the heritability in the plus tree selection is the same as in the progeny test. A more realistic but also more complex model which uses G_1 (the genetic gain in phenotypic plus tree selection in the forest) as an independent entry could be considered.

The fixed values for phenotypic genetic gain in the forest (G_1) cannot easily be compared to real values, because not many published genetic gains have been expressed in terms of additive genetic standard deviation (σA). However, some information can be obtained by analysing the values of heritability and intensity of selection yielding the used value. The value used for genetic gain (1.121) can be regarded as realistic, because it is a result of *e.g.* rather typical parameter values of $h^2 = 0.2$ and $i = 2.507$.

4.3. Combination of the generations

When the whole population was considered, a combination of generations was in many cases favourable. However, because some degree of family selection is almost always utilized in advanced generation breeding and the establishment of seed orchards, results dealing only with the better half of the population are more relevant. In this case the additional genetic gain obtained with a combination of generations was small. The smaller the proportion of families needed for the next generation or seed orchard, the less use there is for a combination of the generations, because selection is then performed backwards in a higher proportion of families. This is in accordance with the results of a simulation study with full sib families (Hodge and White, 1993). A seed orchard which combined the best material from parent and offspring generation was about one percent better in a small breeding population than corresponding orchards which utilized only one generation. In a large breeding population the combination of generations did not increase the genetic gain, because there were more than enough superior parental selections.

4.4. Application to real situations

The limit between backward and forward selection can be solved for each situation if the essential parameter values are known. Using the most realistic set of parameters ($i_1 = 2-2.5$, $n = 50-100$ and $h^2 = 0.2-0.4$) it can be estimated that some 20% of the originally selected plus trees are generally superior to their best open pollinated offspring. If polycross progeny is available, only a few per cent of the best plus trees will outperform their best offspring. However, this information only has practical value if the relatedness can be sufficiently controlled after selection in polycross progenies. The practical consequences of this result depend greatly on the size of the breeding population compared to the number of originally selected plus trees. If the size of the breeding population is only 20% or less of the total number of plus trees, then all selections can be made backward. On the other hand, if considerably more than 20% of the phenotypic plus trees are needed, then the use of the best open pollinated offspring instead of the lower ranking plus tree itself is a good alternative. The difference in the breeding values of the plus tree and its best offspring is rather small around the critical value, so there will be a rather large number of families where the question whether to select backward or forward can be solved on practical grounds.

It should be noted that the variation among the forward selections will be greater than that of the backward selections, and in some cases there may be some additional gain to harvest. HODGE and WHITE (1993) pointed out that the precision of the breeding value estimates of the offspring of tested plus trees is lower than that of the parents themselves, but higher than untested phenotypically selected plus trees. This higher uncertainty in using forward selections can limit their use in seed orchards. On the other hand, it makes it rewarding to progeny test such selections, because the breeding value at selection is uncertain. The results presented here can most straightforwardly be applied to seed orchard situations. In breeding populations more intricate developments are probable; for instance, selecting several offspring from one family or selecting a plus tree and its offspring.

In addition to the genetic gain several other factors also affect the feasibility of the selection alternatives. Parent trees are often grafted in seed orchards or clone archives and thus are ready for crosses for the next generation, whereas forward selected offspring often need to be grafted. This causes extra costs and a time lag, which can cancel out the small additional genetic gains predicted by theoretical calculations. Biological characteristics of the species in question and other practical restrictions highly influence the optimal solution. In creating breeding populations of radiata pine in South Australia slight family selection was followed by forward selection within families (COTTERILL, 1984). On the other hand, forward selection within a late flowering species like Sitka spruce in Britain was not a justified option in composing breeding populations (LEE, 1993).

The handling of parental and offspring material as a basis for advanced generation breeding can cause practical difficulties beyond those associated with using only one generation. However, according to HODGE and WHITE (1993), the combined parent and offspring seed orchards for pine in southeastern USA are a flexible and straightforward option. Combinations can be made in such a way that the backward selections are grafted clones which can be used as seed parents, while the forward selections for long term breeding are young trees in progeny tests, that are harvested for pollen only and used as pollen parents.

The use of open pollinated offspring as a base material for advanced generation breeding has the disadvantage that it is impossible to keep record of the pedigree of the trees. However, if the pollination is mainly derived from outside the seed orchard, it can be presumed that the risk of a high proportion of common ancestors in the offspring is low. Also if the seed for open pollinated progeny tests is collected from original plus trees that are widely separated from each other there is practically no risk that the selections will be related through a common male parent. Background pollination can even be regarded as an advantage because it increases genetic diversity.

Breeding is not only a question of producing gain, but also controlling diversity. Less related individuals can be considered as more valuable for long term breeding. For this reason reliance on polycross selection is questionable. Selection should take into account not only breeding, but also relatedness (ZHENG *et al.*, 1997).

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6. References

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