Phenotypic Selection Compared to Restricted Combined Index Selection for Many Generations

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Andersson, E.W., Spanos, K.A., Mullin, T.J & Lindgren, D. 1998. Phenotypic selection compared to restricted combined index selection for many generations. Silva Fennica 32(2): 111–120.

A breeding population has been subjected to repeated selection and crossing by simulation. Unrestricted phenotypic selection and restricted combined index selection were compared at the same effective number for five generations. Results show that phenotypic selection often achieves the gain and diversity possible to achieve by combined index selection but the relative efficiency is different for different family sizes and heritabilities. When phenotypic selection was compared with restricted combined index method at low heritabilities, both methods performed almost equally in terms of gain at the same effective number in small family sizes, although in large families, phenotypic selection was less efficient. At high heritabilities phenotypic selection was as efficient as combined index selection. Phenotypic selection was more efficient in conserving additive variance than combined index selection over five generations compared at the same gain and effective number. The introduction of a dominance component to the total variance had little effect. An increased breeding population size by a factor of ten resulted in an increased additive gain by app. 15 %. The conclusion is that even though combined index selection is superior in identifying and extracting the potential for breeding achievements, it is generally not performing better than mass selection when compared at the same effective population size in small families.

Keywords phenotypic selection, index selection, status number, heritability, genetic diversity

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Received 15 May 1997 **Accepted** 8 May 1998

1 Introduction

In breeding, it is important to obtain a high genetic gain while sustaining genetic diversity (Ledig 1992). Genetic gain and conservation of genetic diversity are goals breeders are forced to combine, and this leads to reformed procedures in selection and breeding (Namkoong 1983). Combined-Index selection (*CI*) is based on an individual index value formed from within and between family heritabilities and it is known to maximize gain (Falconer 1989). In phenotypic selection the individuals are ranked and the best are chosen on their phenotypic behavior irrespective of their relationship to other individuals. Phenotypic selection is a classical method and can be considered as simple and cost efficient (Cotterill 1986). Genetic diversity described as effective population size is affected by sib type, heritability, selection intensity, family number and family size (Falconer 1989). A way to maintain genetic diversity at a desired level is to restrict the number of progeny a certain pair of parents is allowed to provide to the next generation of breeding efforts (Falconer 1989; Wei 1995). In that way the loss of effective number is decreased, but at the cost of prospective gain. Wei and Lindgren (1991) reported that combined index selection was inferior to phenotypic selection if compared at the same effective population size but in this comparison selection intensity was allowed to vary. Comparisons have also been applied to infinite populations (Wei and Lindgren 1993). By restricting the family size the methods can be compared at the same effective population size. Wei (1995) made such a comparison for one generation of selective breeding, but calculations in most cases assumed families of infinite number and size.

The additive variance maintained for the trait, or index of several traits, subject to selection, is one measure of genetic diversity, while the effective population size is a measure of the overall diversity. The effective population size expressed as status number by Lindgren et al. (1996), can be seen as the number of unrelated, non inbred, genomes in the assessed population at a specific moment, thus the genetic status of that population. In breeding this is a measure for the genetic variability, which is randomly subjected to the breeding efforts and represents the overall genetic variability. The objective of this study is to compare two principles for ranking and selecting material for multi-generation breeding advancements.

2 Methods

In the first generation, selection from a population consisting of unrelated, non-inbred founders was performed. In latter generations various degrees of relationship and inbreeding occur between individuals subject to selection. After some generations, this leads into a complex web of kinship between individuals. The complexity of multi-generation breeding inevitably lead into simulation of stochastic processes (Mullin and Park 1995; Levin 1969). Simulation is an accepted and flexible method of studying questions of complex character. To achieve our objective comparison were made by using the quantitative breeding simulator POPSIM version 2.3 (Mullin and Park 1995a, 1995b), as described in Andersson et al. (1998). This software is used to generate genetic and environmental effects for a base population, which are crossed according to a breeding plan. The mean and variance for the trait studied is assigned to the simulator and values for genetic and environmental effects are randomly added to form the performance of each phenotype. The model was designed to utilize identical individuals as founders in the comparisons, in order to retrieve unbiased results.

Comparisons for gain or differences in gain between the two methods were made at the same level of genetic diversity as found in populations of equivalent effective size. The comparison was made at the levels of diversity given by unrestricted phenotypic selection. The balance between gain and diversity provided by unrestricted phenotypic selection is only one of an infinite number available by other selection methods and restrictions on those. We’ve chosen phenotypic selection for this comparison for its simplicity and for its wide spread use. Lindgren et al. (1995) defined the status effective number as half the inverse of the group coancestry (Θ) as defined by Cockerham (1967):

$$N_s = \frac{0.5}{\Theta} \tag{1}$$

Random single-pair mating (SPM) was used for crossing of the individuals in the breeding population. Gain and status number were calculated for a selection among progenies rising from single pair mating crossings of a defined breeding population size. In combined index selection, family contributions were regulated by imposing various restrictions to cover a large range of diversity. In order to alter the number of families while keeping the selection intensity constant and thus comparable family sizes were set accordingly to 4, 20, 200 and 500. The breeding population size was maintained at the same size by selecting the new breeding population by the proportions P = 0.5, 0.1, 0.01, and 0.004, respectively.

Individual effects were stochastically generated from normally distributed genetic and environmental effects. The total phenotypic variance was thus considered to be the sum of environmental and additive genetic components, and was arbitrarily set to 1000 for the simulations. All genetic variance was assumed to be additive; non-additive effects were assumed to be absent. Proportions of genetic and environmental variance were varied, so that the narrow-sense heritabilities varied from 0.05, 0.20 to 0.50. No restrictions on relatedness were imposed for phenotypic selection, however, a number of restrictions on family contribution (from a maximum contribution of 2, 3, 4..no restrictions) were applied to combined index selection, resulting in a range of values for gain and effective size (status number).

Simulations were made for different-sized breeding populations of 20 or 200 unrelated non-inbred trees. A simple, single-pair mating design was used to produce half as many families as parents in the breeding populations; 10 and 100, respectively. Family sizes tested were 4, 20, 200 and 500.

2.2 Gain and Additive Variance at the Same Status Effective Number

We have chosen to make the comparison at the same effective number for the following reasons. Firstly the efficiency of the selection is decided by how gain is accumulated in relation to how rapid the decay of overall genetic diversity is. This decay of overall genetic diversity can be described in terms of the accumulation of coancestry, or more conveniently, the reduction of status number as the breeding program progresses. The additive gain for combined index selection at the status number of the corresponding unrestricted phenotypic selection was given by a calculation of the distance between the value given by phenotypic points and the regression line given by the nearest restrictions for family contributions given by restricted combined index selection:

$$y_{CIS} = a + b \times x_{PS}$$

where y_{CIS} is the gain realized by CIS (combined index selection) and x_{PS} (gain realized by phenotypic selection) is the status number obtained by PS. The fixation point for this comparison was identified as the status number resulting from unrestricted phenotypic selection. Linear interpolation between the (CIS) status numbers resulting from restrictions on either side of the fixation point, was used to determine the gain for combined-index selection at the same status number as achieved under unrestricted phenotypic selection. This is comparable to a restriction for the family contribution of n in some families and n+1 in others. The gain achieved by phenotypic selection could thus be compared to those for combined-index selection at equivalent status number. 500 replications were used to improve the precision. Simulations for two breeding population sizes of 20 (BPS = 20) and 200 (BPS = 200) initially unrelated, non inbred individuals were made. This gave 10 and 100 families, respectively. Heritability levels, mating scheme and family sizes were the same as previously described. Four different mating designs were applied to the breeding population size of 20 trees to produce 10, 20, 40 & 80 families. The total selection proportion (P) was kept constant for both selection methods at value P = 0.01(20/2000) by altering the family size as shown in Table 1. The aim was to investigate to what degree the number of matings per parent affected the result.

Table 1. Family number and size produced by different mating schemes under constant selected proportion.

Number of crosses per parent	Number of families	Family size
SPM (1 cross/parent)	10	200
DPM (2 crosses/parent)	20	100
FPM (4 crosses/parent)	40	50
EPM (8 crosses/parent)	80	25

3 Results – Analysis

3.1 General

In terms of achieved accumulative gain from generation to generation, phenotypic selection measures well with restricted combined index selection in small family sizes (i.e. 4, 20) at heritability level 0.05. In Fig. 1a, this is obvious, as it reflects the only levels at which there is a substantial difference between the methods. As family sizes increase (i.e. to 200 or 500) combined index has an advantage in its ability to identify genetic variance and therefore realized up to 20 % higher gain than phenotypic selection by selecting from fewer families (uppermost curve in Fig. 1a). At higher heritabilities (i.e. 0.20, 0.50) phenotypic selection was as efficient as combined index selection Phenotypic selec-

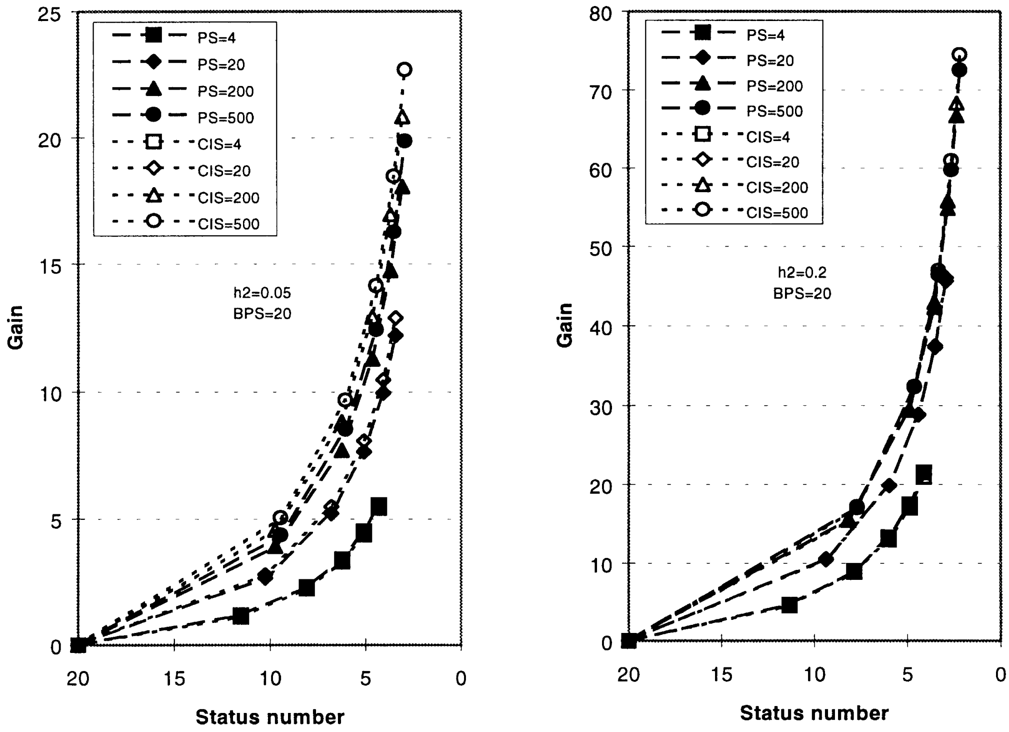

Fig. 1. Gain achieved at the same status number by unrestricted phenotypic (PS) and restricted combined index selection (CIS) from generation zero (leftmost dot) to generation five (rightmost dot) for family sizes 4, 20, 200 & 500. BPS = 20. CIS is superior only for low heritability and a relatively large BPS. BPS = Breeding Population Size. For masked symbols there is no significant difference between methods.

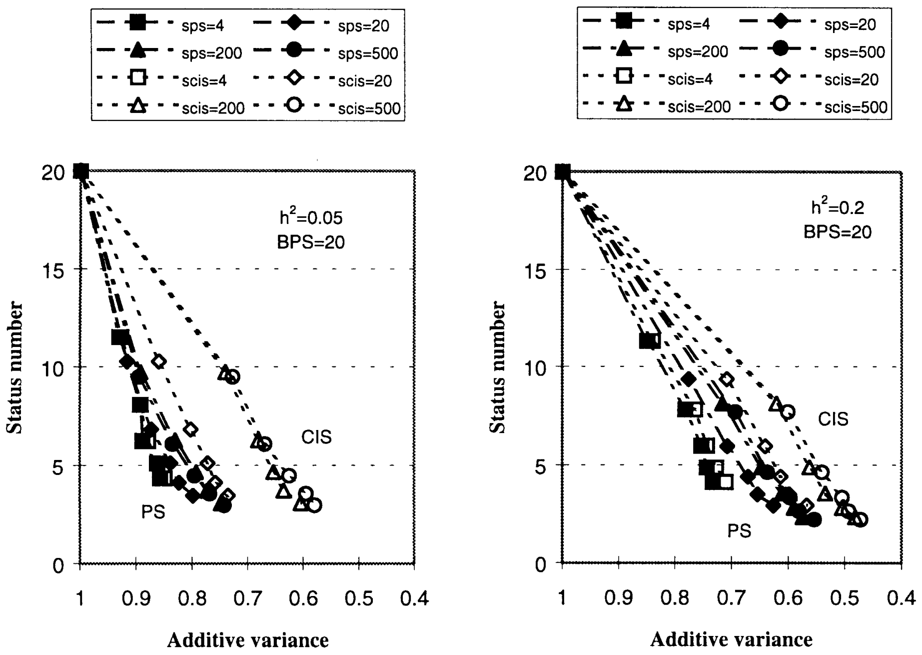

Fig. 2. Additive variance maintained at the same change of genetic diversity (status number) at heritability 0.05 (a) and 0.2 (b) by unrestricted phenotypic (PS) and restricted combined index selection (CIS) from generation zero (leftmost dot) to generation five (rightmost dot). sps, scis = family size for phenotypic and combined-index selection, respectively. BPS = breeding population size.

tion was more efficient than combined index selection in preserving additive variance from generation to generation. This was particularly emphasized at the low heritability 0.05 and in the large family sizes 200 and 500 (Fig. 2a, Tables 2 & 3), but also true at higher heritabilities (e.g. 0.20 & 0.50).

3.1 Presence of Dominance Effects

The presence of dominance variance (25 % of the total phenotypic) was found to have a small positive effect (less than 1.5 %) on the difference in gain between the two selection methods (Fig. 3). No significant difference in the outcome was recorded in the first generation shift. Nevertheless, the relative superiority of phenotypic selection was enhanced by the interference of dominance variance in latter generations for heritability 0.5.

3.2 Breeding Population Size

An increase of the breeding population size by a factor of ten (BPS = 20 → BPS = 200) resulted in an increased gain up to 15 % for phenotypic and up to 17 % for combined index, respectively (Tables 2 & 3). However, the large population size (200) conserved more additive variance, up to 22 % for phenotypic and up to 10 % for combined index selection, respectively (after 5 generations selective breeding) in comparison to the small population size (20) (Tables 2 & 3).

3.3 Effect of Family Number on Gain and Diversity under Constant Selection Proportion

An investigation of the influence of the number of crossings with a constant total population size was performed. Thus, the family size was re-

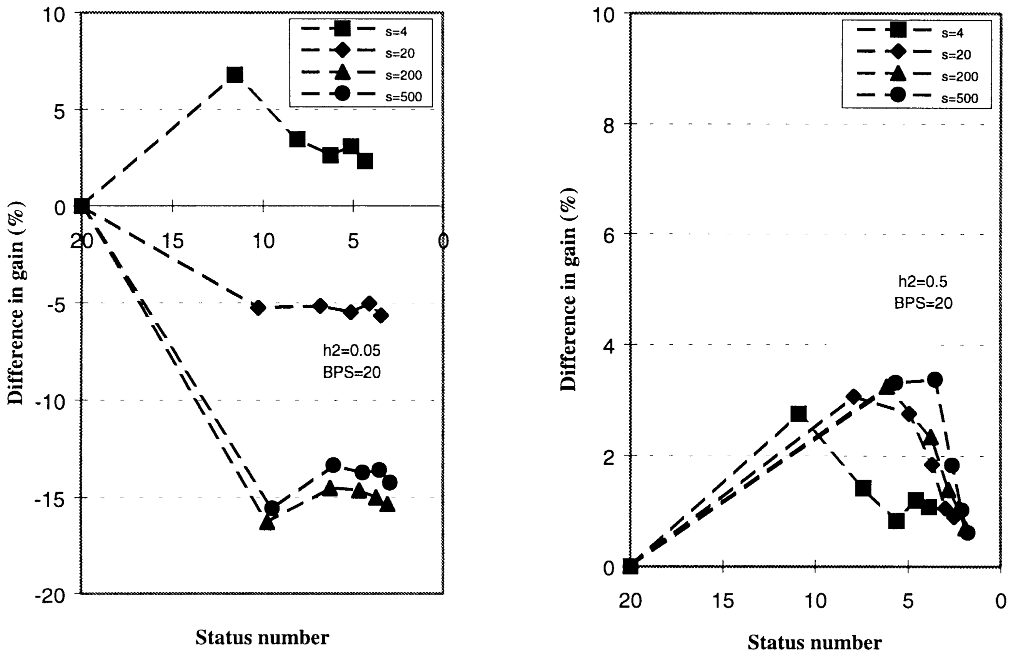

Fig. 3. Difference in gain at the same status number between the two selection methods (PS – CIS) without or with dominance variance from generation one (leftmost dot) to generation five (rightmost dot). BPS = 20.

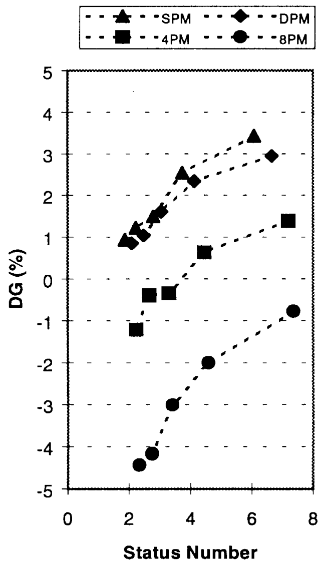

Fig. 4. Effect of family number on the difference in gain (DG) between the two selection methods from generation one (rightmost dot) to generation five (leftmost dot). SPM =10 families, DPM = 20 families, 4PM = 40 families, 8PM = 80 families.

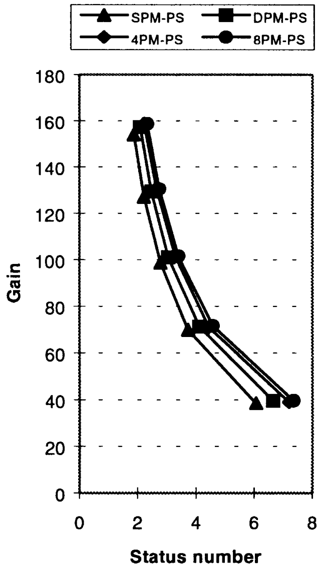

Fig. 5. Effect of family number on gain achieved by phenotypic selection from generation one (rightmost dot) to generation five (leftmost dot). SPM = 10 families, DPM = 20 families, 4PM = 40 families, 8PM = 80 families.

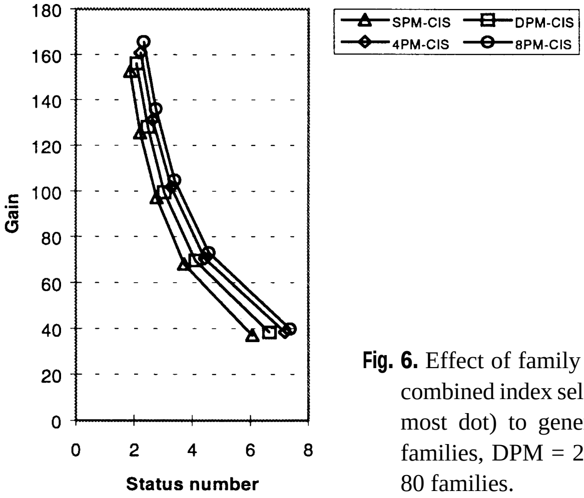

Fig. 6. Effect of family number on gain achieved by restricted combined index selection (CIS) from generation one (rightmost dot) to generation five (leftmost dot). SPM = 10 families, DPM = 20 families, 4PM = 40 families, 8PM = 80 families.

Table 2. Percent superiority in gain (ΔG) and variance (ΔV) of phenotypic selection in a breeding population of 20 trees, compared with restricted combined-index at the same status number.

		Heritability								
		0.05			0.20			0.50		
Family size	Generation	Status number	ΔG relative measure	ΔV relative measure	Status number	ΔG relative measure	ΔV relative measure	Status number	ΔG relative measure	ΔV relative measure
4	0	20.00			20.00			20.00		
4	1	11.52	0.07	0.00	11.33	0.03	0.01	10.90	0.00	0.01
4	2	8.08	0.03	0.00	7.83	0.02	0.02	7.40	0.02	0.03
4	3	6.24	0.03	0.01	5.98	0.02	0.01	5.61	0.01	0.02
4	4	5.10	0.03	0.00	4.86	0.02	0.02	4.56	0.01	0.05
4	5	4.33	0.02	0.01	4.11	0.02	0.03	3.85	0.01	0.06
20	0	20.00			20.00		0.00	20.00		
20	1	10.26	–0.05	0.06	9.36	0.01	0.09	7.91	0.03	0.02
20	2	6.82	–0.05	0.08	5.95	0.00	0.09	4.92	0.03	0.01
20	3	5.11	–0.05	0.08	4.39	0.00	0.09	3.68	0.02	0.02
20	4	4.10	–0.05	0.08	3.49	–0.01	0.09	2.97	0.01	0.01
20	5	3.44	–0.06	0.08	2.91	–0.01	0.09	2.50	0.01	0.01
200	0	20.00			20.00		0.00	20.00		
200	1	9.74	–0.16	0.17	8.14	0.01	0.13	6.13	0.03	0.00
200	2	6.27	–0.15	0.18	4.88	0.00	0.13	3.75	0.02	0.00
200	3	4.65	–0.15	0.17	3.53	–0.02	0.13	2.81	0.01	0.04
200	4	3.71	–0.15	0.18	2.81	–0.02	0.14	2.25	0.01	0.03
200	5	3.08	–0.15	0.19	2.34	–0.02	0.16	1.89	0.01	0.04
500	0	20.00			20.00		0.00	20.00		
500	1	9.47	–0.16	0.19	7.68	0.01	0.13	5.64	0.03	–0.02
500	2	6.07	–0.13	0.20	4.60	0.00	0.15	3.51	0.03	0.01
500	3	4.45	–0.14	0.21	3.30	–0.01	0.15	2.60	0.02	0.00
500	4	3.52	–0.14	0.23	2.61	–0.02	0.15	2.09	0.01	0.05
500	5	2.94	–0.14	0.22	2.18	–0.03	0.15	1.76	0.01	0.00

Table 3. The relative difference between the both selection methods for a breeding population size of 200.

		Heritability								
		0.05			0.20			0.50		
Family size	Generation	Status number	ΔG (PS – CIS) /PS	ΔV (PS – CIS) /PS	Status number	ΔG (PS – CIS) /PS	ΔV (PS – CIS) /PS	Status number	ΔG (PS – CIS) /PS	ΔV (PS – CIS) /PS
4	0	200.00			200.00			200.00		
4	1	113.65	0.02	0.01	111.43	0.03	0.02	107.42	0.01	0.01
4	2	78.93	–0.02	0.01	76.28	0.02	0.03	71.63	0.02	0.01
4	3	60.35	0.00	0.01	57.60	0.01	0.03	53.56	0.02	0.01
4	4	48.85	0.01	0.00	46.25	0.01	0.04	42.80	0.01	0.00
4	5	41.05	0.00	0.01	38.55	0.01	0.04	35.60	0.01	0.01
20	0	200.00			200.00			200.00		
20	1	99.54	–0.07	0.07	89.33	0.00	0.12	72.08	0.02	0.10
20	2	64.25	–0.07	0.07	52.78	–0.02	0.13	39.31	0.01	0.08
20	3	46.93	–0.07	0.09	36.73	–0.02	0.13	27.22	0.01	0.08
20	4	36.75	–0.07	0.10	28.14	–0.03	0.14	21.00	0.00	0.07
20	5	30.21	–0.08	0.09	22.73	–0.03	0.14	17.26	0.00	0.06
200	0	200.00			200.00			200.00		
200	1	91.72	–0.19	0.21	70.31	–0.02	0.23	42.24	0.01	0.15
200	2	55.71	–0.18	0.26	35.21	–0.04	0.26	19.98	0.01	0.11
200	3	39.13	–0.18	0.27	22.45	–0.05	0.25	13.62	0.00	0.09
200	4	29.78	–0.18	0.27	16.62	–0.06	0.24	10.82	0.00	0.10
200	5	24.02	–0.19	0.27	13.22	–0.06	0.25	8.93	0.00	0.10
500	0	200.00			200.00			200.00		
500	1	90.16	–0.19	0.24	64.54	–0.02	0.26	34.80	0.02	0.15
500	2	53.31	–0.19	0.29	30.66	–0.04	0.26	16.71	0.01	0.11
500	3	36.66	–0.19	0.29	19.65	–0.04	0.25	11.62	0.01	0.10
500	4	27.72	–0.20	0.31	14.42	–0.05	0.26	9.19	0.00	0.10
500	5	22.19	–0.20	0.31	11.45	–0.05	0.25	7.55	0.00	0.13

duced accordingly, when the number of crosses increased. Simulations were carried out where family number was increased by using each parent in several crosses (Table 1). This is an attractive approach since the crosses alone generate a desirable multitude of new genetic combinations of which some are superior. Fig. 5 shows that an increasing number of families lead to superiority of combined index selection (King and Johnson 1993). Multiple crossings per individual give the possibility to better performing families. This tendency is better identified by combined index selection. The quotient ({PS – CIS}/PS) shows negative values indicating superiority of combined index method. In spite that were only minor differences in gain when family number was altered, one effect is worth pointing at: A large number of crossings per individual in the breeding population (i.e. 4, 8) conserved the status effective number at a higher level.

4 Discussion

The efficiency in the tradeoff between overall genetic variability for genetic gain can be reflected by the performance of the breeding material with respect to the increase in group coancestry. The results of this study demonstrated that at high heritability phenotypic selection was almost equal to combined index selection for gain in small family sizes and only slightly inferior for large family sizes. At low heritabilities it seems as if phenotypic selection is not as rewarding as combined index selection for family sizes larger than twenty are. The information from families is of greater importance if heritability is low and there are many sibs taking ore information into account. At higher heritabilities (i.e. 0.20, 0.50) phenotypic selection was as efficient as restricted combined index selection. This can be explained by the fact that the correlation between the observed phenotype and the actual genotype increases when the genetic component grows proportionally larger.

Phenotypic selection proved to be an efficient method for preserving variance from generation to generation and this was particularly emphasized at low heritabilities and large family sizes. If variation was caused by dominance instead of environment, it favored phenotypic selection relative to combined index selection, but the effect was minor.

There is a possibility to increase the family number by utilizing each parent in multiple crosses. King and Johnson (1993) pointed out that an increasing number of families resulted in a relative superiority of combined index selection. Multiple crossings per parent give the possibility of gaining better performing families and this tendency is better identified by combined index selection. In absolute measures, there was only a minor increase in gain when family number was altered. Large number of crosses per individual (i.e. 4, 8) conserved the status number to a higher extent from generation to generation in a comparison with small numbers of crossings per individual (i.e. 1, 2). Thus, which mating scheme the breeder chooses to utilize depends upon costs and time of performing controlled crosses.

The stability of the results available from comparing means of 500 replicates of simulations shows no significance except for the largest differences (low heritabilities and large family sizes) with the methods at hand. The conclusion is that for most cases in breeding there is no significant loss in efficiency if selection is performed on the phenotype or if the pedigree information of the breeding population is incomplete. If a rapid progress is desired this requires more sophisticated methods, but the enhanced selection intensity is giving progress in breeding at the expense of diversity. This investigation gives no other suggestion than that the efficiency of breeding in terms of gain per unit diversity is fairly constant irrespective of selection method.

Phenotypic selection has several advantages such as simplicity, low cost, less risk for errors, conservation of additive variance, consistency for altered breeding objectives and flexibility for breeding systems characterized by variable resources and fluctuation in management intensity. For an optimal selection procedure over many generations, a combination of methods, from generation to generation, might prove feasible. For combined objectives, compromising between desired genetic improvement and preservation of genetic diversity, phenotypic selection was proven to be an acceptable option for one generation breeding (Andersson et al. 1998; Wei and Lindgren 1991). The perspective of five generations is considered to be sufficient for most long-lived species.

This work has shown that long term outcome in breeding is affected by all decisions taken in the design and accomplishment of a breeding program. Allocation of resources between choice of methods, number of generations, number of crosses and family size and structure are central.

Acknowledgements

We gratefully acknowledge support from the Kempe foundation and the Organization for Economic Co-operation and Development (OECD), Directorate for Food, Agriculture and Fisheries - Biological Resource Management for enabling this study.

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