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GROUP-MERIT SELECTION COMPARED TO CONVENTIONAL RESTRICTED SELECTION FOR TRADE-OFFS BETWEEN GENETIC GAIN AND DIVERSITY

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ABSTRACT

The difference between group-merit selection (GMS) and conventional parental restricted selection (CRS) in a closed breeding population was analyzed by stochastic simulation. GMS, or selection for genetic value weighted by coancestry among the selected individuals, proved to be beneficial for any weight on group coancestry other than the extreme weights of zero and infinity where the methods are identical. The optimal weight given to group coancestry depends on the breeding objective and is open for consideration. A general strategy for efficiency in the use of diversity seems to be to successively increase the weight on group coancestry as the between family variance component decreases. The largest improvement by GMS was for low heritabilities, while the importance of population size and selected proportion (family size) was small. The benefit of GMS accumulated over generations. The effect of GMS compared to CRS on additive variance shifted from a decline to an augmentation with increased population size, while selected proportion had little influence. The beneficial effect on additive variance was larger with lower heritability where it increased over generations.

Key words: artificial selection, breeding strategy, coancestry, group-merit selection, restricted selection, status effective number.

INTRODUCTION

The genetic improvement obtained by recurrent selection and breeding in a closed population depends on the genetic diversity present, but since gain is obtained at a cost of reduced diversity, the potential for future gain is eroded. The accumulation of inbreeding has a negative effect on future genetic response through: (1) reduced genetic variance; and (2) inbreeding depression of individual performance and fertility. Genetic drift at each generation turnover causes a random change in gene frequencies and loss of alleles. In order to optimize short- and long-term genetic improvement, both gain and diversity must be considered simultaneously. Approaches to increase long-term selection response by also considering genetic diversity in the selection and/or mating strategy include:

(i) non-random mating schemes, such as minimum-coancestry mating, compensatory matings and factorial mating (DE ROO 1988, TORO *et al.* 1988, VILLANUEVA *et al.* 1994, SANTIAGO & CABALLERO 1995, CABALLERO *et al.* 1996)

(ii) restricting family contributions to decrease the variation in family size (TORO & PÉREZ-ENCISO 1990, GRUNDY & HILL 1993, BRISBANE & GIBSON 1995, WEI 1995)

(iii) changes in the methods of genetic evaluation based on reducing the correlation of estimated breeding values (EBV) of relatives by the use of upward-biased estimates of heritability (TORO & PÉREZ- ENCISO 1990, GRUNDY & HILL 1993, GRUNDY *et al.* 1994) or directly reducing the weight given to the family mean in the selection index (DEMPFLE 1975, TORO & PÉREZ-ENCISO 1990, VERRIER *et al.* 1993, WEI & LINDGREN 1994, BRISBANE & GIBSON 1995, VILLANUEVA & WOOLLIAMS 1997).

(iv) select a larger number of individuals, and let the higher-ranking individuals contribute more, while maintaining the same selection intensity (weighted selection) (TORO & NIETO 1984, LINDGREN 1991)

(v) include a correction of EBVs dependant on predicted error variance (WOOLLIAMS & MEUWISSEN 1993)

(vi) include a correction of EBVs for inbreeding, inbreeding depression or average relationship between its possible mates (GODDARD & SMITH 1990, LINDGREN *et al.* 1993, WRAY & GODDARD 1994a, BRISBANE & GIBSON 1995, LINDGREN & MULLIN 1997)

These methods can be combined in various ways. Simultaneously optimizing selection (ii–vi) and mating (i) by linear programming is an example (TORO & PÉREZ-ENCISO 1990). The effect on inbreeding of combining biased estimates of individual heritability (iii) and compensatory mating or factorial instead of hierarchical mating respectively (i) is approximately additive (GRUNDY *et al.* 1994, VILLANUEVA *et al.* 1994). The biased estimate reduces variance of family size and the non-random (negative assortative) mating reduces the cumulative effect of selection on inbreeding. Under certain circumstances, non-random mating (i) only postpones inbreeding, while in other circumstances it can have a permanent and cumulative effect on reducing inbreeding in mass selected populations (CABALLERO *et al.* 1996, VILLANUEVA *et al.* 1994). BRISBANE & GIBSON (1995) demonstrated the general advantage of using breeding values adjusted for genetic relationship (vi) compared to some other selection strategies, such as restricting family contributions (ii), omitting family information (iii), and increasing the index weight on individual performance when calculating breeding values (iii).

By combining a measure of inbreeding/relatedness together with the breeding value in the selection criterion, as in method (vi), the two components can be valued at the same scale and diversity becomes part of the target trait under selection. Inbreeding refers to an individual and is primarily determined by the mating system in recent generations. LINDGREN & MULLIN (1997) further generalized the breeding objective by considering group coancestry rather than inbreeding as the objective for diversity. This selection criterion, which they termed 'group-merit' (or 'population merit'), is the average of the breeding values of the selected individuals minus their 'group coancestry' (COCKERHAM 1967) multiplied by a weighting factor, '*c*'.

Cockerham's group coancestry (Θ) and its derivatives have many appealing features as measures of genetic diversity. It is defined as the average pair-wise coancestry among all selected individuals, including the relationship of the individual with itself and reciprocal relationships. Group coancestry measures the probability that a pair of genes from the same locus, sampled randomly from the population with replacement, are equal by descent, and $(1-\Theta)$ expresses the proportional gene diversity (GD), relative to the gene diversity in a founder population of unrelated, non-inbred genotypes (NEI 1973, LACY 1995, LINDGREN & KANG 1997). After random mating with equal gamete contributions, group coancestry becomes the inbreeding (F) of the progeny. Inbreeding reduces additive variance (σ_A^2) to $(1-F)\sigma_A^2$, where F is the average inbreeding of the breeding parents (FALCONER & MACKAY 1996, VERRIER *et al.* 1991). Status effective number, (N_s), is half the inverse of group coancestry (LINDGREN *et al.* 1996). Status number describes the current status of a population in terms of an equivalent number of equally represented, unrelated founders in which no inbreeding or random genetic drift has occurred (LINDGREN *et al.* 1996). Status number is equivalent to founder genome equivalent (one of the two varieties) which is used for managing genetic diversity in small captive animal populations (LACY 1995, reviewed in: LINDGREN & KANG 1998).

By plotting genetic response versus group coancestry or a diversity measure derived from it (*e.g.*, proportional gene diversity, expected inbreeding following random mating, or status number), the trade-off between genetic progress and genetic diversity can be evaluated for various breeding schemes. Genetic gain can be compared at the same level of diversity (LINDGREN 1986, QUINTON *et al.* 1992, QUINTON & SMITH 1995, WEI 1994, WRAY & GODDARD 1994, BRISBANE & GIBSON 1995, LINDGREN & MULLIN 1997), providing for analysis of 'diversity-use efficiency'.

Most recent analyses using group-merit selection, or similar concepts, have been performed for animal breeding strategies with the objective to maximize gain while constraining inbreeding below a point where problems are likely to arise (MEUWISSEN 1997, VILLANUEVA & WOOLLIAMS 1997, GRUNDY *et al.* 1998). Forest tree breeding populations are typically in the very early generations of domestication and have not yet lost much of their initial variation, either by selection (BULMER 1971) or by drift. Forest tree breeding populations are generally separated from the commercial production populations. When trees from unrelated sublines of a structured breeding population are established in a seed orchard, inbreeding depression accumulated in parents will vanish in progeny of among line crosses. This allows more inbreeding to develop within the breeding population, without detrimental effects in the forest plantations. Since many tree species are monoecious and can be vegetatively propagated there are only few limitations to family structure. The size of their progeny groups can be virtually unlimited. Larger family sizes make possible more intense within-family selection for trees than is possible for most animals, and clonal testing in addition to progeny testing can increase heritabilities substantially.

The objective of this study was to examine the trade-off between gain and diversity and to investigate the relative superiority of group-merit selection (GMS) compared to conventional restricted selection (CRS), and how this superiority is affected by the weight applied to relatedness, population size, family size (selected proportion), and heritability.

MATERIALS AND METHODS

Monte Carlo simulation was used to compare various breeding scenarios using GMS and CRS, for a variety of population sizes, family size and heritability values, and with different weights on diversity or restrictions on within-family selection.

Selection criteria

(1) Group-merit selection (GMS)
The group-merit criterion used in GMS was described by LINDGREN & MULLIN (1997):

$$B_\omega = \bar{G}_\omega - c\Theta_\omega \qquad [1]$$

where B_ω is the 'group merit' of the selected sub-set ω, G_ω is the average of the breeding values of the selected subset, Θ_ω, is their group coancestry, and c is a weighting factor converting the group coancestry to the same scale as breeding values. B_ω has a maximum, which can be identified by comparing all possible ω. For all but the smallest populations, an algorithm must be used to find the maximum efficiently. In this study, we used an iterative search for the highest group merit by a stepwise inclusion of selected members (LINDGREN & MULLIN 1997):

$$\max B_{ij\omega} = G_{ij} - c\Theta_\omega \qquad [2]$$

where $B_{ij\omega}$ is the prediction of the group merit that will result if the i^{th} member of the j^{th} family is added to (or subtracted from) the already selected group so that the new selected group becomes ω. G_{ij} is the predicted breeding value for this individual and Θ_ω is the resulting group coancestry. This selection criterion was recalculated for each candidate added to or subtracted from the selected group. Although all possible sets were not evaluated, the search process is likely to maximize the target function (LINDGREN & MULLIN 1997).

(2) Conventional restricted selection (CRS)
CRS was performed by limiting the number of progeny selected per family. Selections were added to the breeding population sequentially on the basis of their combined index breeding value. The restriction did not require equal numbers of selections from each family, only that the contributions from any given family not exceeded the specified maximum number.

The simulated breeding population

A stochastic quantitative genetic infinitesimal breeding simulator POPSIM (MULLIN & PARK 1995) was used for the comparison of GMS and CRS. POPSIM version 3.02 was modified to include the GMS criterion, as described by LINDGREN & MULLIN (1997). Breeding value was estimated on the basis of a combined index, where the performance of the individual and its relatives are weighted by their respective heritabilities (BAKER 1986). The founders were assumed to be unrelated and non-inbred. In all scenarios, all genetic effects were considered to be additive (*i.e.*, non-additive gene effects regarded as absent), with mean and variance each set to 100 in generation zero (*i.e.*, additive standard deviation was 10 and coefficient of additive genetic variation was 0.1). The phenotypic value of an individual, P_i, was the sum of its breeding value, A_i, and an uncorrelated random environmental effect, E_i. In each generation t subsequent to the base, individual progeny breeding values were generated as

$$0.5(A_f + A_m) + r\sqrt{0.5(1 - 0.5(F_f + F_m))\sigma^2_{A0}}$$

where A_f and A_m are the breeding values of the female and male parents respectively, F_f and F_m are the corresponding inbreeding coefficients at t–1, r is a random normal deviate and σ^2_{A0} the initial additive variance in the unselected base population at $t = 0$. The individual environmental effect was generated as $r\sqrt{\sigma^2_E}$, where σ^2_E is the environmental variance assumed to be equal in all generations. Selection was carried out among the progeny. The accumulated additive effect, A_{eff}, and variance, V_A, for the selected group were calculated from the generated data. Group coancestry, Θ, and average inbreeding, F, were calculated from the pedigree. The selected trees of the breeding populations were mated randomly by single-pair mating, excluding selfing. Selection and breeding were carried on for five generations.

Simulation runs were performed for population sizes (N) 4, 12 and 40 and family sizes (n) varying between 15 and 200 (corresponding to selected proportion 0.13–0.01). Initial levels of narrow-sense heritabilities (h^2) were set at 0.05, 0.20, 0.50 and 0.80, by changing the level of environmental variance, σ^2_E. The simulations were repeated 300–500 times in order to ensure precision of estimated average effects. The variability of individual runs was analyzed by the standard deviation.

The emphasis on diversity under GMS was varied in the simulation by using values of c ranging from zero (equivalent to selection on estimated breeding values, (EBV)) to infinity (equivalent to within-family selection). The simulations were repeated with different values of c between these two extremes to plot a smooth curve for the relationship between genetic gain and genetic diversity. Similarly, the maximum number of contributions per family was varied from 2 to N. Restrictions on CRS must be set as a discrete number of contributions per family (parent), while the c value of GMS can be given any value. Therefore, a family contribution limit of 3 individuals (CRS-3) was chosen as a baseline for the comparisons with GMS. CRS-3 represents a typical compromise between genetic gain and diversity. Status effective number, calculated as $N_s = 0.5/\Theta$ (LINDGREN *et al.* 1996), was used as the measure of genetic diversity for graphical presentation of the data.

RESULTS

Effect of N, n and h^2 on the trade-off between gain and diversity

The additive gain increased with population size (N), family size (n), and heritability (h^2) (Figure 1). At the highest and lowest diversities (N_s), GMS and CRS gave the same gain, as the methods are equivalent at these points (LINDGREN & MULLIN 1997). An infinitely high weight (c) assigned to group coancestry (Θ) in GMS and the restriction of exactly two selections per family in CRS correspond to balanced within-family selection. A c of zero in GMS and no restrictions on the family contribution in CRS correspond to selection on EBV, here estimated by a combined index. For all other levels of diversity induced by varying c, GMS was superior to CRS.

In the early generations, a high c in GMS or lower limit of selections per family in CRS resulted in less response to selection (Figure 1). For low and intermediate heritabilities, the greatest gain from either method was achieved when relatedness was ignored during selection both in early and later generations. At high heritability, the greatest gain was reached at intermediate levels of diversity in later generations. This lower future gain potential when diversity is given little effect' (BULMER 1971). The loss of gain caused by decreased V_A, due to inbreeding, was little influenced by heritability, but appeared earlier and was more

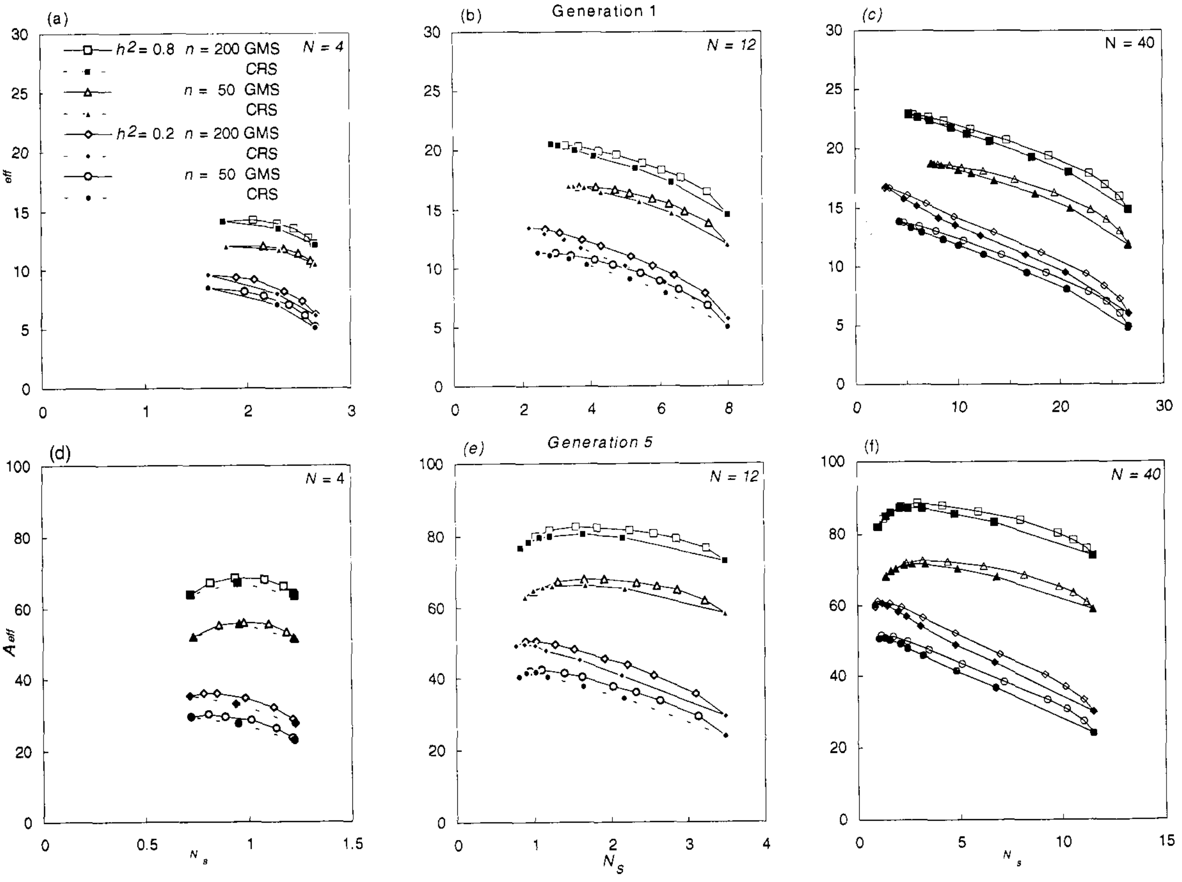

Figure 1. Additive effects (A_{eff}) of GMS and CRS compared at a range of diversities (N_s), after (a, b, c) one, and (d, e, f) five generations for $N = 4$, 12 and 40, $n = 50$ and 200 and $h^2 = 0.2$ and 0.8. The range of N_s results from a series of c-weights ($0 - \infty$) given to Θ in the selection criterion of GMS, and a series of limiting numbers of progeny per family ($N - 2$) allowed to be selected for CRS. Leftmost symbols correspond to unrestricted selection and rightmost symbols to within family selection. The values of CRS are connected with a broken line.

consideration and heritability is high is caused by the sharp reduction of among-family variance in the early generations due to more efficient selection, the 'Bulmer pronounced at smaller population sizes due to the faster increase in F at smaller N.

The standard deviation (*sd*) for additive effects (the precision of a single run) was fairly stable for various levels of diversity, while it was lower for high h^2 and large N (data not shown). When h^2 was increased from 0.2 to 0.8, *sd* decreased from approximately 40 to 15%, 20 to 5%, and 10 to 3% for $N = 4$, 12 and 40, respectively. The *sd* was much greater at h^2 less than 0.2, especially at small N and for small n, implying a strong random component in the selection.

Relationship among diversity parameters (Θ, F, N_s, GD, V_A) after five generations

The principal relationships among diversity parameters for the breeding population after five generations are shown in Figure 2. The higher the c, the lower the group coancestry (Θ), average inbreeding (F) and the loss of gene diversity become (*i.e.*, higher GD). The additive variance (V_A), among the selected individuals was larger with increased weight on Θ. Most of the reduction in V_A is caused by selection and is due to linkage disequilibrium (BULMER 1971). The V_A retained in the population is therefore larger and reduced only in proportion to F (VERRIER *et al.* 1991), as indicated by (1–F) V_A in Figure 2, assuming no reduction in among-family variance. Under random mating, F in generation five is expected to be equal to Θ in the previous generation, but the exclusion of self-mating and restrictions on family contribution delayed inbreeding (Figure 2) for up to approximately three generations (data not shown).

The size of the breeding population was critical for conservation of diversity, but h^2 and n were also important factors, as indicated by the diversity parameters when c is equal to zero or infinity (Table 1). Especially in early generations, scenarios with little consideration of diversity in the selection criterion retained higher N_s and GD, and lower F, in the breeding population at higher levels of h^2 and smaller n (Table 1 and at the left end of the curves in Figure 1a, b, c). At higher heritability, greater weight is put on individual performance in the combined index. The selections are thus more evenly spread among families, resulting in slower accumulation of Θ. A small n will also tend to distribute the selected individuals more uniformly among families.

For the intermediate and large N, the *sd* for N_s among replicated runs at generation five was less than 1% for scenarios with heavy weight on diversity, but increased to 15–20% for scenarios with intermediate weight on diversity. When N was reduced from 40 to 4, the *sd* for N_s increased from approximately 3% to 9–13%. The larger figures relate to GMS, which, in general, gave a more variable result. For scenarios with the lowest weight on diversity, the *sd* for N_s was lower than for intermediate weights (data not shown).

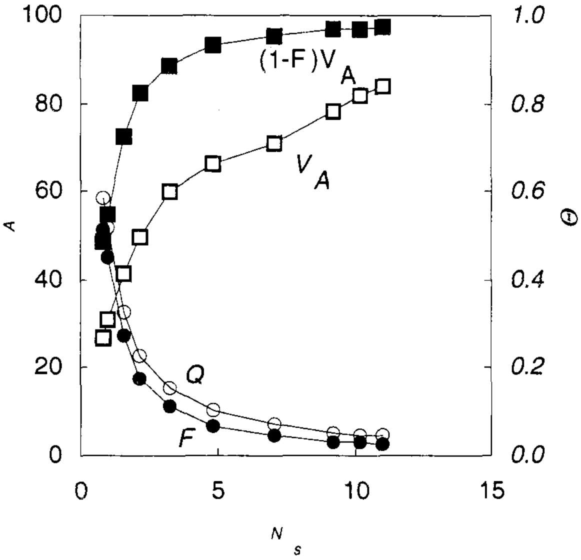

Figure 2. Relation between status number (N_s), resulting from a series of c-weights, from 0 (left) to ∞ (right), given to Θ in the selection criterion of GMS and the following diversity parameters: group coancestry (Θ), average inbreeding coefficient (F), additive variance accounting for inbreeding (1–F)V_A, and additive variance accounting for inbreeding and selection (V_A). Generation 5, $N = 40$, $n = 200$, $h^2 = 0.2$.

GMS compared to CRS for additive gain

GMS accumulated more gain over generations than did CRS, at all tested levels of diversity, with the exception of the extreme values where the methods are equivalent. The advantage of GMS was consistent over a large interval of c-weights and resulting N_s (Figure 1). An estimate of the relative difference between the methods was calculated at the diversity level corresponding to CRS-3, limiting selection to three per family (Table 2). Heritability was the most significant of the tested factors, reducing the relative advantage of GMS over CRS from 7–18% at $h^2 = 0.05$ to 1–5% at $h^2 = 0.8$. The effect of N and n on the superiority of GMS was small except for very small N, resulting in less advantage from GMS. There was little change in the relative superiority of GMS over generations (Table 2).

Table 1. Influence of population size (*N*), family size (*n*) and h^2 on status number (N_s), gene diversity (GD = 1 – Θ), inbreeding coefficient (*F*) and total additive variance $(1-F)V_A$ after one (1) and five (5) generations at zero and infinitely high weight *c* on group coancestry in the selection criterion of GMS.

Pop. size	$N_{s(1)}$			$N_{s(5)}$			$F_{(5)}$			$GD_{(5)}$ %			$V_{A(5)}$ %		
	h^2			h^2			h^2			h^2			h^2		
N	0.05	0.2	0.8	0.05	0.2	0.8	0.5	0.2	0.8	0.05	0.2	0.8	0.05	0.2	0.8
c = infinite, *n* = 50 and 200															
4	.1)	2.7	.1)	.1)	1.2	.1)	.1)	0.29	.1)	.1)	59	.1)	.1)	71	.1)
12	.1)	8.0	.1)	.1)	3.5	.1)	.1)	0.09	.1)	.1)	86	.1)	.1)	91	.1)
40	.1)	26.7	.1)	.1)	11.5	.1)	.1)	0.03	.1)	.1)	96	.1)	.1)	97	.1)
c = 0, *n* = 50															
4	1.6	1.6	1.8	0.7	0.7	0.7	0.58	0.59	0.58	31	31	32	42	41	42
12	2.2	2.4	3.3	0.8	0.8	0.9	0.55	0.52	0.47	37	40	44	45	48	53
40	3.5	4.3	7.6	1.0	1.1	1.4	0.45	0.41	0.28	48	52	65	55	59	72
c = 0, *n* = 200															
4	1.6	1.6	1.7	0.7	0.7	0.7	0.59	0.59	0.59	30	30	31	41	41	41
12	2.0	2.2	2.9	0.8	0.8	0.8	0.57	0.55	0.51	34	36	40	43	45	49
40	2.5	3.0	5.2	0.8	0.8	1.0	0.55	0.51	0.41	38	41	51	45	49	59

1) no difference regardless of h^2 or *n*

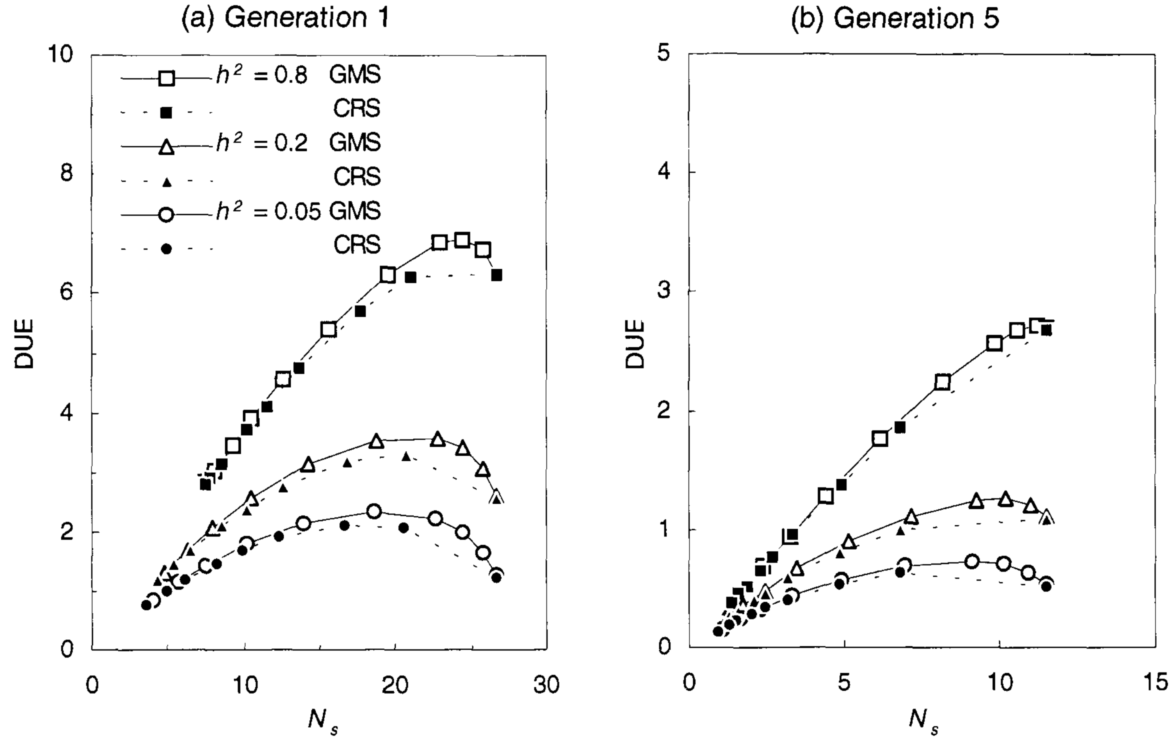

Figure 3. Diversity use efficiency (DUE) after (a) one, and (b) five generations for GMS and CRS at a range of diversity levels (N_s) for *N* = 40, *n* = 50 and h^2 0.05, 0.20 and 0.80. The range of N_s results from a series of *c*-weights (0 – ∞) given to Θ in the selection criterion of GMS, and a series of limiting numbers of progeny per family (*N* – 2) allowed to be selected for CRS. Leftmost symbols correspond to unrestricted selection and rightmost symbols to within family selection. The values of CRS are connected with a broken line. DUE = additive gain per unit increase in Θ and generation.

Table 2. The relative advantage (%) in additive gain for GMS over CRS, after 1 and 5 generations at the diversity level of CRS-3 at various population sizes (N), family sizes (n) and h^2.

Popul. size N	Family size, n											
	15				50				200			
	h^2				h^2				h^2			
	0.05	0.2	0.5	0.8	0.05	0.2	0.5	0.8	0.05	0.2	0.5	0.8
Generation 1												
4	8	6	1	2	10	5	3	1	12	6	3	2
12	10	12	8	5	15	11	7	5	18	11	6	4
40					12	9	6	4	12	8	5	3
Generation 5												
4	7	3	2	1	8	5	3	1	8	6	3	2
12	9	7	6	3	11	8	5	3	13	8	4	3
40					10	8	5	3	11	7	5	3

Diversity use efficiency

The development of diversity use efficiency (DUE), defined as the additive gain per unit loss of GD (*i.e.*, unit increase in Θ) and generation for $N = 40$, $n = 50$ and various h^2 is illustrated in Figure 3. For CRS, after a few generations any deviation from within-family selection was so large that DUE decrease from its maximum at CRS-2, except for at the lowest h^2. Maximum DUE for GMS was found between the diversity levels of CRS-2 and CRS-3, and approached within family selection as family variance declined with increased heritability and over the generations.

GMS compared CRS for additive variance

In general, more V_A was retained in the breeding population at low h^2 and large N (Figure 4), while n had less influence (data not shown). When GMS and CRS were compared at the same and intermediate levels of N_s, GMS resulted in lower, similar and higher V_A among the selected individuals for $N = 4$, 12 and 40, respectively (Figure 4). This effect of GMS on V_A was substantially greater at lower h^2 (Figure 4) and slightly greater with increasing n (data not shown). For $N = 40$, and within the limits of the study for h^2 and n, V_A was 5-25 % higher for GMS than for CRS-3. GMS also reduced the loss of V_A over generations. For $N = 40$ and at low h^2 and intermediate c, it is interesting to note the increase in V_A after the general decline in the first generation (Figure 4c and f). The *sd* of V_A after five generations was 80–100, 40–55, and 25–30 % for $N = 4$, 12 and 40, respectively, with little effect from variation in N_s, n or h^2, and with no difference between GMS and CRS.

Contributions to gain from reduced genetic diversity and GMS over generations

As a result of the decline in V_A for each generation, there was a reduction in gain. The rate of change in gain was the same for GMS and CRS under scenarios where the two methods are equivalent, but different at intermediate levels of diversity (Table 3). When c was zero or when no restrictions were put on family contributions, and for all N, n and h^2, there was generally a strong reduction in accumulated selection response from between 27–30 %, in the first generation, to 14–17 % in the fifth. There was, however, a tendency for more equal gain between generations for the smallest N and highest h^2, decreasing from 22% to 16 % from generation one to five. For GMS with $c = \infty$ and for CRS-2 (both corresponding to within-family selection), roughly the same gain (20 %) was produced in each of the five generations except at the smallest N, where inbreeding had the strongest influence on the loss of V_A ($F = 0.29$ in generation five, Table 1).

At intermediate levels of diversity (N_s), and for $N = 12$ and 40, the gain achieved by GMS decreased from a maximum of 25% in generation one to a minimum of 18% in generation five, compared to CRS-3, where corresponding figures were 23% and 18% (Table 3). Thus, the difference between GMS and CRS was greatest in the first generation. The reduction in response over generations was greater at small N and

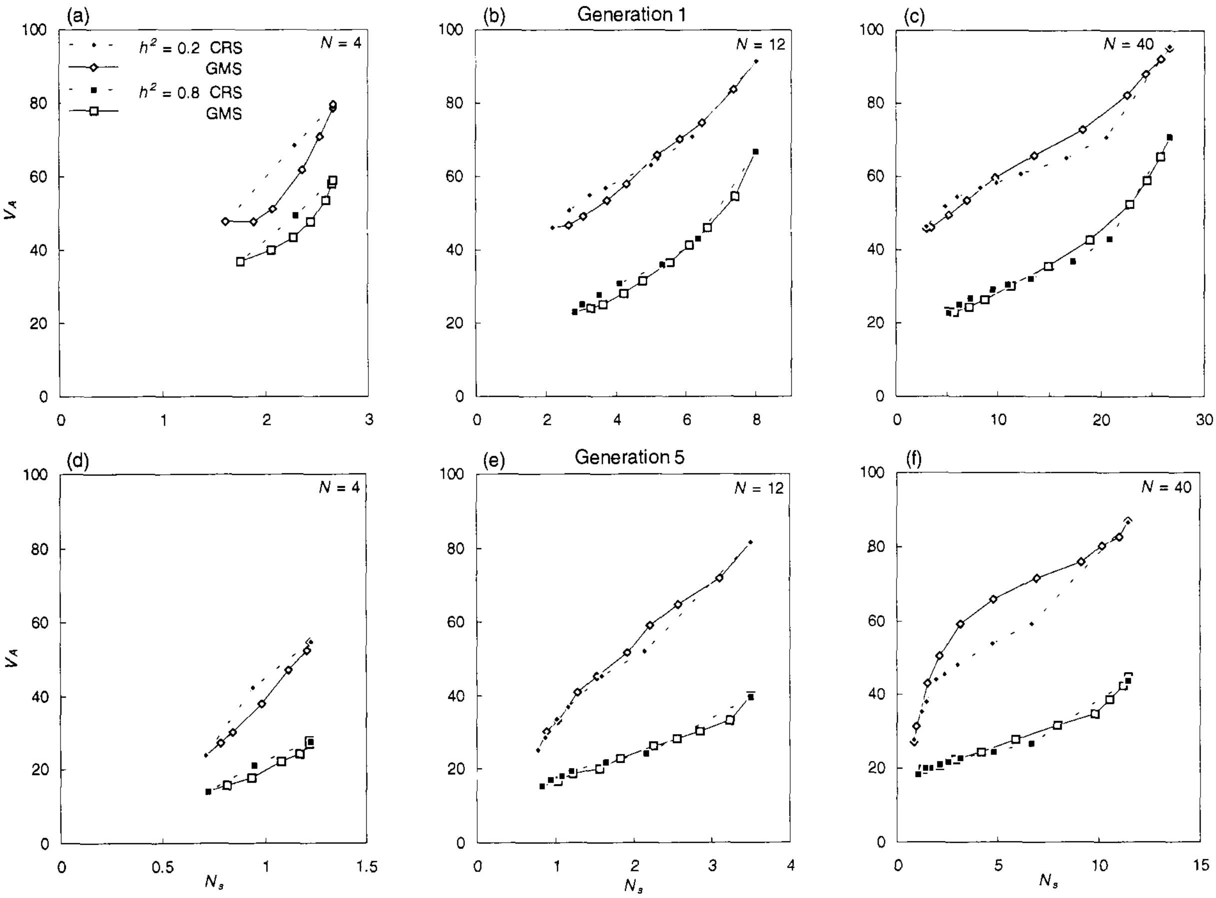

Figure 4. Additive variance (V_A) of GMS and CRS compared at a range of diversities (N_s) after (a, b, c) one, and (d, e, f) five generations for $N = 4$, 12 and 40, $n = 50$ and 200 and $h^2 = 0.2$ and 0.8. The range of N_s results from a series of c-weights (0 – ∞) given to Θ in the selection criterion of GMS, and a series of limiting numbers of progeny per family ($N - 2$) allowed to be selected for CRS. Leftmost symbols correspond to unrestricted selection and rightmost symbols to within family selection. The values of CRS are connected with a broken line.

low h^2 decreasing from 25 to 15% for GMS. The variation in response over generations between GMS and CRS corresponds to differences in the loss of N_s. For the same final N_s at generation five, GMS reduced N_s more in the first generation and less in later generations, compared to CRS (data not shown).

The relative contribution to the total gain from reduced c (trade-off with diversity) and from GMS (no loss of diversity) was examined over the generations for $h^2 = 0.2$ and 0.8 (Figure 5). For CRS, diversity was reduced by relaxing the restrictions on family contribution from 2 (within family selection) to 3 individuals per family. The corresponding N_s and additive effects for GMS were found by interpolation. In the first generation at $h^2 = 0.2$ and $n = 100$ the effect on gain of reduced weight on coancestry was 0.40, representing a 75 % increment compared to within family selection (Figure 5a). After five generations the effect was reduced to 0.30 , representing a 57 % increment. The superiority of GMS over CRS was stable over generations and was in this case 5-9 %. At $h^2 = 0.8$, gain was increased by 0.37 (28 %) by reduction of the weight on coancestry in the first cycle and by 0.16 (12 %) in generation five, while the superiority of GMS was stable over generations at 2-3% (Figure 5b). Thus, the additive gain as a result of reduced weight on diversity decreased, while the benefit of GMS was maintained in each generation.

DISCUSSION

What is a proper balance between expected gain and diversity - the value of *c*?

The weight given to group coancestry must be chosen according to the objective of the breeding program. Factors such as conservation of neutral alleles and risk of losing productive alleles, number of breeding generations and population size, and biological factors like the severity of inbreeding depression for the particular species should be considered. In addition to the trade-

Table 3. The relative distribution (%) of accumulated gain over generations (t) for various c-weights corresponding to low (zero), intermediate and high (infinite) levels of diversity, and various N, and h^2 for $n = 50$. When c is zero or infinite, gain is equal for GMS and CRS.

		Population size, N											
		4				12				40			
h^2	t	c				c				c			
		zero	intermediate 1)		infinite	zero	intermediate 1)		infinite	zero	intermediate 1)		infinite
		CRS GMS	CRS	GMS	CRS GMS	CRS GMS	CRS	GMS	CRS GMS	CRS GMS	CRS	GMS	CRS GMS
0.05	1	28	23	23	20	30	23	25	21	29	22	25	20
	2	21	22	22	22	22	20	20	20	20	20	19	20
	3	20	21	20	21	17	19	18	19	20	20	19	21
	4	14	16	16	17	16	19	18	20	17	19	18	19
	5	15	15	15	17	15	18	18	20	15	19	18	20
0.20	1	27	24	24	21	28	22	25	21	27	22	25	20
	2	23	23	22	22	21	20	19	20	20	20	19	20
	3	20	20	20	20	19	20	19	20	19	20	19	20
	4	15	16	17	18	17	19	19	19	17	19	18	20
	5	14	16	16	17	15	19	18	20	16	19	18	20
0.80	1	22	20	20	20	27	22	24	21	27	22	24	20
	2	23	22	22	21	21	20	20	20	19	20	20	20
	3	21	21	21	21	19	20	19	20	19	20	19	20
	4	17	19	19	19	18	19	19	20	18	19	19	20
	5	16	18	18	19	16	18	18	19	17	19	19	20

1) The status number of GMS correspond to the status number of CRS-3

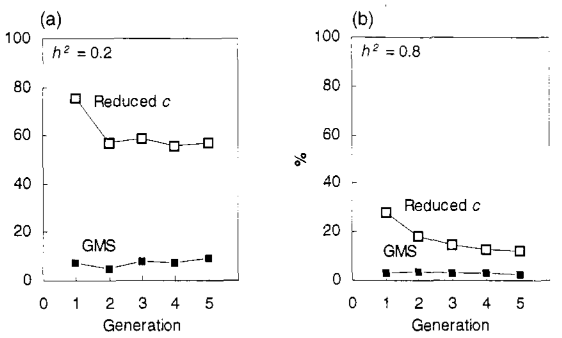

Figure 5. The increased gain per generation resulting from the separate effects of reduced weight on coancestry (reduced c) and group merit selection (GMS) respectively, at (a) h^2 = 0.2 and (b) h^2 = 0.8, for N = 40 and n = 100. The level of diversity for the comparison was at the N_s corresponding to CRS-3. The separate effect of reduced c was calculated as the difference in gain between N_s corresponding to CRS-3 and CRS-2 (*i.e.* infinite c).

off between long-term gain and diversity, there is also reason to consider the diversity of commercial forests when choosing c. The diversity of each stand should ensure efficient resource utilization and ecological stability.

Gene conservation

N_s gives information about the allele-carrying capacity of the population in terms of the expected number of founders that would be required to provide the level of allelic diversity existing in that population if the founders were equally represented and if no genetic drift had occurred (no alleles lost) (BALLOU & LACY 1995, LINDGREN *et al.* 1997). For a given increase in group coancestry, status number decreases more at low coancestry levels than at high. This reflects the greater probability of losing rare neutral alleles by drift in early generations when trees still are unrelated. The drop in status number for scenarios with infinitely high weight on diversity from 4, 12 and 40 founders to 2.7, 8.0 and 26.7 (–33 %) in generation 1, and 1.2, 3.5 and 11.5 (–60 %) in generation five, respectively, represents the minimum loss of diversity by genetic drift when neutral genes are sampled over generations (Table 1). This also occurs under balanced selection of two individuals per family, which keeps the expectation of equal gene contribution of all founders (BALLOU & LACY 1995). Despite this large probability of losing alleles, 59, 86 and 96 % of initial GD and 71, 91 and 97 % of initial V_A is still present after five generations in populations of size N = 4, 12 and 40, respectively (Table 1). By decreasing the weight on group coancestry, the GMS selection criterion will accept greater relationship among the selected individuals, the higher their contribution to average gain. After five generations, the lowest status number reached for N = 4, 12 and 40 was N_s = 0.7, 0.8–0.9 and 1.0–1.4, respectively (2–18 % of initial N_s), depending on n and h^2, indicating a high probability of losing alleles (Table 1). This corresponded to GD varying between 31–65 % and levels of initial V_A between 41–71 %. Thus, considerations concerning the probability of losing neutral alleles and the loss of genetic variance cannot be compared on the same scale, as the number of alleles retained or lost have little impact on current GD or V_A (ALLENDORF 1986). However, in the long run, the frequency of rare alleles may be increased and thereby contribute more to genetic variance. Therefore, to reduce the risk that drift will cause loss of productive genes and increase in deleterious genes, a high weight c on group coancestry should be chosen.

Maximum gain for a predetermined number of breeding generations

Although the relative value given to gain and diversity can be chosen by the preferences of the breeder, there is, for any specified number of generations in any breeding scheme, an optimum level of diversity resulting in the highest gain (WRAY & GODDARD 1994). This optimum balance can be found by testing a range of c, as done here and previously by BRISBANE & GIBSON (1995) among others, using inbreeding rather than status number as a measure of diversity. The optimum weight for a given time horizon can also be calculated analytically, but this prediction of c can only be approximate (WRAY & GODDARD 1994).

After one generation, the highest gain is always associated with the greatest erosion of diversity, and is the result of ignoring relatedness (*i.e.* selection only on EBV). In the following generations the substantial coancestry accumulated in the population becomes inbreeding, and thereby permanently reduces additive variance. In addition, in the short term, the among-family variance component is considerable reduced by selection. Although temporary, this loss of variance resulting from linkage disequilibrium, persists as long as selection is maintained (BULMER 1971). The overall loss of additive variance reduces the potential future gain. Therefore, maximum gain after some generations is reached by maintaining a higher level of diversity. The more generations considered, the higher is the level of diversity required in order to reach maximum gain. At an infinitely high c, (within-family selection) group coancestry and inbreeding will be minimized. However, the optimum selection for maximizing the selection limit may differ from within-family selection which was suggested by DEMPFLE (1975), since some positive weight should be given to family information to reach the limit according to VILLANUEVA & WOOLLIAMS (1997). For the generation interval 0–5 studied here, the requirement to conserve higher diversity to achieve maximum gain in later generations is greatest at very small population sizes, where inbreeding is accumulating most rapidly, and at high heritabilities, where the among-family variance is most rapidly eroded by selection and non-assortative mating.

Constraining inbreeding and inbreeding depression

MEUWISSEN (1997) argues that breeders know approximately the acceptable rates of inbreeding, but do not have a conception of c as a cost factor. Considering inbreeding *per se*, or if the relationship between inbreeding depression and inbreeding is known, an acceptable rate of increase in inbreeding can be used to find a c-value that corresponds to the inbreeding obtained following random mating (MEUWISSEN 1997, VILLANUEVA & WOOLLIAMS 1997). Commonly in forest trees, self-pollination ($F = 0.5$) reduces long-term productivity by 25–50 % through inbreeding depression (WILLIAMS & SAVOLAINEN 1996). This corresponds to a 0.5–1.0 % loss of gain per 0.01 unit increase in F. If a trade-off of 1 percentage point gain per generation is acceptable, a high c is needed to limit group coancestry to 0.05 after four generations, corresponding to $F_5 = 0.05$ after random mating. This will reduce short-term additive gain, but allow higher realized gain in the long run and avoid serious inbreeding depression.

Fine-tuning diversity efficient selection

With a limited number of crossings in the breeding population CRS has a few discrete outcomes, while there is a very large number of compromises available for any level of diversity by GMS (LINDGREN & MULLIN 1997). By decreasing the selection restrictions from 2 to 3 trees per family, there is a considerable drop in diversity from the highest possible. In this interval the extra gain of GMS increases from zero to close to its highest value. If diversity use efficiency (DUE) is considered, the highest marginal increase in gain per unit loss of diversity (increase in coancestry) can be found through fine-tuning GMS in this interval as was suggested by LINDGREN and WEI (1994). The positive contribution to gain will compensate the negative to coancestry only for sibs of the very best families and only if family variance is substantial. For CRS at reasonably high heritability, any deviation from within-family selection is so large that DUE will decrease. For GMS the maximal DUE approaches within family selection when family variance decreases by increased heritability or selection accuracy and over the generations. DUE *per se* is not suitable as a breeding objective. It assumes an uncontrolled weight on diversity and has no simple relationship to gain, *e.g.* high DUE is seldom associated with high gain. In the long run maximum DUE will be associated with very high weight on diversity and restricted selection. However, the concept has a value as an indicator. Considerations about DUE is best done by comparing alternatives at the same and a predetermined level of diversity found by specified weighting of gain and diversity as described above. Then the alternative with the highest gain is the most diversity use efficient.

Changed weight on diversity over generations

Since the increase in group coancestry is not proportional to the increase in gain over generations, a fixed weight, c, on group coancestry in the selection criterion would mean a change in relative weight between gain and diversity at each generation shift. The relative weight on diversity will also vary with heritability, since heritability has a high impact on the development of gain but not on diversity. In order to keep the relative weights constant, the c value must be revised for each breeding cycle. However, as diversity and gain change over generations, this gives an incentive to change the relative weights. In particular, the sharp reduction in among-family variance during the first generations by selection should be considered. The loss of variance is greater when the evaluation method is more accurate, under higher h^2, and when family weight in the combined index is high (BULMER 1971, GOMEZ-RAYA & BURNSIDE 1990). Since the gain from reducing the weight on group coancestry comes only from the among-family portion of the additive variance, this contribution to gain decreases in each generation. The associated cost in terms of diversity-lost per unit-gain-achieved, becomes larger as long as among-family variance decreases, but there is no cost in diversity for within-family selection in addition to that of genetic drift. The best strategy for an efficient use of the genetic diversity seems to be to successively increase the weight on diversity following the decrease in among-family variance. This will reduce the contribution from the genetically poorest founders in the first generation when among family variance still is high. In later generations, diversity use efficiency is kept high by turning more to within-family selection and allowing a higher contribution only from the genetically most superior families.

Economic considerations

Since gain now is more valuable than gain later, this should be incorporated in the choice of c. If the breeding objective is formulated in terms of economic income this can be achieved by discounting gain over a future time period (WRAY & GODDARD 1994b). Maximizing diversity-use efficiency will probably not maximize returns on investments in breeding.

Group-merit selection

The objective of GMS is to maximize the group-merit. Thus, GMS ought to be superior to other selection objectives under all circumstances (except when it coincides with the totally restricted and unrestricted selection of the reference method ($c = \infty$ or $c = 0$, respectively) (LINDGREN and MULLIN 1997). Therefore, it was not of interest to study the statistical significance of the superiority (the standard error of the difference), but rather the size and how it is affected by different factors. In spite of the standard deviations for the additive effects being of the same magnitude as the effect of GMS, the large number of replicate runs produced very small standard errors and thus the magnitude of the difference between GMS and CRS was estimated with considerable precision.

GMS can be applied to various selection strategies. Here, the strategy was to keep the breeding population constant and to vary the contributions from families. For the number N of breeding individuals chosen, the results obtained represent the maximum gain for any level of diversity. However, given a certain number of candidates ($N \times n/2$ for single pair mating), there is also an optimal number of individuals to be selected for breeding the new generation, which gives the maximum gain at a given level of diversity (QUINTON & SMITH 1995, MEUWISSEN 1997, VILLANUEVA & WOOLLIAMS 1997, ZHENG *et al.* 1997). Furthermore, the mating design will affect the loss of additive variance by changing the rate at which inbreeding develops. Compensatory mating, where individuals with many co-selected relatives are mated to those with few relatives, will reduce the variance of the long term founder contribution and thus the rate of inbreeding and loss of variance, as will minimum-coancestry mating and avoidance of sib mating (CABALLERO *et al.* 1996). The mating design also has an impact on among-family variance. Positive assortative mating can counteract the loss in variance by the Bulmer effect (TALLIS & LEPPARD 1988, SHEPHERD & KINGHORN 1994). Thus, a total optimization should include the number of breeding trees, their contribution to the next generation and the mating design.

In a combined family-individual selection index, the index weights themselves can also be optimized (VILLANUEVA & WOOLLIAMS 1997). Since we used simulation to study the effect of GMS, optimized index weights were calculated from the results. This was seen by the effect of heritability on the diversity level for maximum response as a result of lowering the index weight on family. GMS can be seen as if the weights given to family information will differ for each individual (WRAY & GODDARD 1994).

Earlier studies have shown that application of GMS at a fixed population size can give up to 10 % higher gain than various forms of conventional restrictions (BRISBANE & GIBSON 1995, LINDGREN & MULLIN 1997, ZHENG *et al.* 1997). This is equivalent to a reduction in population size with 10–30 %, while maintaining the same gain and diversity (BRISBANE & GIBSON 1995). Compared to tree breeding populations, the animal populations of BRISBANE & GIBSON (1995) were larger and progeny sizes smaller.

While proposing the GMS technique LINDGREN & MULLIN (1997) used $h^2 = 0.05$ and $N = 40$ in their only example, the present study indicates a substantial benefit by GMS for much smaller population sizes and, as family sizes had little influence, the benefit is consistent with the selected proportion. This is of interest to forest tree-breeding programs where many small sub-lines are managed to avoid inbreeding depression in forest plantations (BURDON & NAMKOONG 1983). Heritability is the most important factor affecting the additional benefit realized by GMS. The relative superiority of GMS is largest when heritability is low, and is significantly less at high heritabilities, although the absolute effect of GMS remains substantial.

The inbreeding depression likely to develop within small sub-line populations will, after only a few generations, preclude effective phenotypic selection or clonal testing, and require the program manager to perform progeny tests by outcrossing with trees outside the sub-line. This will increase heritability and accuracy but, if resources are fixed, will also result in smaller family sizes and selected proportion, thus decreasing the advantage of GMS. In general, the advantage of GMS will be most significant in programs applying phenotypic selection for traits with low to intermediate heritability, and the advantage will be less for programs applying clonal testing or progeny testing.

Although highly variable among simulation runs, the larger additive variance retained by GMS at large population sizes contributes to the advantage of GMS. Under these circumstances, additional gain can be attained by further selection of production populations. In order to keep this option and to control inbreeding in the deployed planting stock, diversity must be maintained by means of a high *c* weight on group coancestry. Finally, it is worth emphasizing that any measure taken leading to an increased heritability (given fixed additive variance) is the best way to increase diversity-use efficiency, since there is no loss of genetic diversity resulting from this procedure. This can best be obtained by efficient genetic testing. If individual heritability is improved from 0.2 to 0.8 by clonal testing or improved progeny testing, the additive mean is more than doubled at the same level of diversity.

CONCLUSIONS

In order to manage the trade-off between gain and diversity efficiently in the early generations of a breeding population, increasingly more emphasis should be given to conservation of diversity in each generation by means of controlling the accumulation of relatedness. However, irrespective of the breeding objective in terms of the weight given to genetic diversity, GMS results in equal or superior gain over generations compared to CRS. This superiority is consistent for all population and family sizes as well as variance patterns of practical importance

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