

## CONTROLLING PARENT CONTRIBUTIONS DURING POSITIVE ASSORTATIVE MATING AND SELECTION INCREASES GAIN IN LONG-TERM FOREST TREE BREEDING

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### ABSTRACT

Forest tree production populations resulting from breeding strategies that combine positive assortative mating (PAM) with a variety of mating designs and selection methods were investigated over five generations by Monte Carlo simulation. Equal parent contributions were compared with strategies where better parents contributed more progeny to the next generation. Two approaches were used to accomplish this: (1) balanced mating designs producing equal numbers of crosses per parent, combined with *unbalanced selection* of more progeny from better parents (US); and (2) *unbalanced mating* to produce more crosses from better parents, followed by balanced selection within families of equal numbers from each cross (UM). In each approach, the intensity of imbalance could be adjusted from very mild, so that parent contributions were very nearly equal, to very aggressive, where parent contributions varied greatly. The resulting range of effective population sizes was measured by status effective number.

PAM increased the additive variance more for the UM strategies than for those using US. This higher variance in the breeding population led to greater gain in selected sub-populations used for seed production or clonal deployment. Differences in population structure affected the net gain in the production populations in the presence of inbreeding depression. For the progeny of a seed orchard derived from the UM strategies, net gain increased with higher contribution from better parents and declining effective size of the breeding population. In contrast, for US strategies, the net gain from orchard progeny decreased as the breeding population effective size declined. Thus, when applying PAM to breeding and selection strategies with higher contribution from better parents, the breeding population under UM has a better coancestry structure to support seed orchards with high breeding values and low inbreeding in the progeny. For both strategies, the net gain from a clone mix was generally higher at lower levels of breeding population effective size, although inbreeding increased.

**Key words:** effective population size, genetic gain, genetic variance, inbreeding depression, open-nucleus breeding, positive assortative mating

### INTRODUCTION

Non-random mating received attention very early in the development of quantitative and population genetics theory (FISHER 1918; WRIGHT 1921). In the case of positive assortative mating (PAM), individuals are mated in rank order by phenotype, so that like mate with like (Acronyms and abbreviations used are gathered in Table 1). Enhanced response to selection from PAM was demonstrated experimentally (e.g., BREESE 1956; MCBRIDE & ROBERTSON 1963), although other studies have failed to repeat these results. Inconsistent results from experiments probably come about when assumptions are not satisfied, e.g., when “unconscious assortative mating” (WRIGHT 1921) occurs in control

lines (reviewed by JORJANI 1995; JORJANI *et al.* 1997a). On the other hand, theoretical and simulation studies demonstrate that the effect of PAM on selection response is favourable (e.g., CROW & FELSENSTEIN 1968; CROW & KIMURA 1970; BAKER 1973; DE LANGE 1974; BULMER 1980; GIANOLA 1982; FERNANDO & GIANOLA 1986; SMITH & HAMMOND 1987; TALLIS & LEPPARD 1987, 1988; SHEPHERD & KINGHORN 1994; JORJANI *et al.* 1997c). Various forms of PAM have also been suggested as a means to enhance gain in forest tree breeding (e.g., COTTERILL 1984; COTTERILL *et al.* 1989; FOSTER 1986, 1993; PARK *et al.* 1993), and PAM has been investigated by simulation for typical tree breeding situations (MAHALOVICH 1990; KING & JOHNSON 1993). The interest in most of these studies was on the

**Table 1. Acronyms and abbreviations.**

Acronym	Explanation
BP	Breeding population
PP	Production population
Seed PP	Seed production population
Clone PP	Clone production population
PAM	Positive assortative mating
RAM	Random assortment of mates
SPM	Single-pair mating
DPM	Double-pair mating
GMS	Group merit selection
UM	Unbalanced mating combined with balanced selection, see table 2
US	Unbalanced selection combined with balanced mating, see table 2

potential improvement of the population mean value by PAM, and not on gain from an elite part of the population as studied by ROSVALL & MULLIN (2003).

“Nucleus breeding” can be regarded as a form of assortative mating (JAMES 1977, 1989; SHEPHERD & KINGHORN 1992, 1994), where the best trees are mated within an elite nucleus, maintained separately from the main population. In an “open nucleus”, individuals with high breeding value are transferred from the main to the elite population, and vice versa, improving genetic diversity in the nucleus and gain in both populations (JAMES 1977, 1978, 1987; RODEN 1995a, 1995b). Nucleus breeding was adapted to forest tree breeding by COTTERILL *et al.* (1989), and was first documented for *Eucalyptus globulus* and *Pinus radiata* (see references in COTTERILL *et al.* 1989, and WHITE 1993), and has now been studied and discussed by several authors (e.g., MAHALOVICH 1990; BRIDGWATER *et al.* 1993; WHITE 1993; WILLIAMS & HAMRICK 1996;) and implemented for *Pinus elliottii* (WHITE *et al.* 1993) and *Pinus taeda* (MCKEAND & BRIDGWATER 1998).

When PAM is combined with restricted selection, maintaining near-equal parent contributions to the next generation, the additive variance of the breeding population (BP) is substantially increased (ROSVALL & MULLIN 2003). This provides greater potential for gain when production populations (PP) are selected from the BP. The restricted selection – as compared to unrestricted selection – decreases variation in parent contributions, and a higher effective population size is maintained. Thus, increased short-term gain from PPs is combined with more gene diversity conserved in the BP, which serves to enhance gain in the long term. In an earlier investigation, these effects on gain and diversity were examined for single-pair mating (ROSVALL & MULLIN 2003), where parental contributions were restricted by “group-merit selection”, i.e., selec-

tion for genetic value weighted by group coancestry among the selected individuals (LINDGREN & MULLIN 1997).

PAM can be applied to any mating design, and there are many ways to vary parental contributions to the next generation, both by unbalanced selection, i.e., selecting more individuals from some parents, and unbalanced mating in combination with rules for restricting selection, i.e., making more matings among some parents and selecting proportionally more from those parents. The optimum parental contributions to selection, considering both genetic gain and diversity, are expected to be distributed approximately linearly depending on breeding value (LINDGREN 1986; WEI & LINDGREN 1995). Various weighting systems that assign mating frequencies to individuals according to their breeding values have also been investigated (KANG & NAMKOONG 1988; KANG 1989). As a rule of thumb, one might divide the population into three parts, and vary the contributions in the proportions 3:2:1 with respect to the breeding values (SÁNCHEZ 2000; RUOTSALAINEN & LINDGREN 2001).

Here the objective was to compare two strategies to vary parent contributions in combination with PAM: (1) balanced mating schemes combined with unbalanced selection; and (2) unbalanced mating schemes combined with balanced selection.

## MATERIAL AND METHODS

Various mating and selection strategies were examined by Monte Carlo simulation. In a sequence of scenarios, each strategy was adjusted to exploit initial gene diversity at different rates, resulting in a range of BP effective sizes. Throughout the study, programme resources (in terms of the number of selection candidates generated each generation and size of breeding population) were kept constant. The strategies were compared at the same level of effective population size and inbreeding, after five generations.

### Baseline breeding strategy

The Swedish breeding strategy for Norway spruce was chosen as the basis for the analysis (DANELL 1991a, 1991b, 1993; KARLSSON & ROSVALL 1993; ROSVALL *et al.* 1998). This strategy is characterised by equal parental contributions during both mating and selection and selection precision increased by clonal testing. Each parent is crossed after random pairing to produce an equal number of offspring, while an equal number of selections are made from each cross to advance the BP.

The Swedish BP is subdivided into many independent breeding groups, and our analysis simulated progress from one such group of 48 trees. In our simulations, clonal testing of 10 ramets per genotype was used to estimate breeding values for 50 progeny per parent. In all scenarios, a combined total of 2 400 genotypes was generated and tested. Selection was used to advance the BP and to select six genotypes for operational deployment, either as seed parents or for mass vegetative propagation.

### Alternative breeding strategies

The pairing of mates was either done in rank order by clone means, positive assortative mating (PAM), or the mates were paired randomly but with selfing excluded, so-called “random assortment of mates” (RAM). The term “random mating”, i.e., an equal chance for any individual of the population to mate with any other individual, *including* the individual itself, is used here only in its strict theoretical sense.

These mating systems were applied to two alternative strategies designed to increase the contributions from better parents to various degree and generate a range of effective population sizes (Table 2):

Balanced mating designs producing equal numbers of crosses per parent, combined with *Unbalanced Selection* of more progeny from better parents (US); and

*Unbalanced Mating* to produce more crosses from better parents and fewer from poorer, followed by balanced selection within families of equal numbers from each cross (UM).

The mating and selection components of these alternate strategies, and the manner in which they were adjusted for different parent contributions to advanced generations of the BP, are detailed in the following sections, “Mating designs” and “Selection of the breeding populations”.

In each approach, the intensity of imbalance could be adjusted from very mild, so that parent contributions were very nearly equal, to very aggressive, where parent contributions varied greatly. Variation in parent contributions results in increased relatedness and a

decrease in the effective number of parents or families. Relatedness in generation  $t$  can be described by group coancestry,  $\Theta_t$  (COCKERHAM 1967), but it can also be expressed by the status effective number  $N_{st} = 1/2\Theta_t$  (LINDGREN *et al.* 1996, LINDGREN & KANG 1997), or by the proportional gene diversity ( $GD_t/GD_0 = 1 - \Theta_t$ ), where gene diversity in the source population of unrelated, non-inbred genotypes  $GD_0 = 1$  (LACY 1995). Gene diversity is the probability that two alleles sampled from the gene pool are non-identical by descent and is equal to the expected heterozygosity after random mating, i.e., at H-W equilibrium (NEI 1973). Proportional GD is a measure of the decay in GD due to increased relatedness, and is independent of the initial level of gene diversity or allele frequencies at individual loci (LACY 1995).

### MATING DESIGNS

#### Balanced mating designs

Single-pair and double-pair mating (SPM and DPM, respectively) were assessed as mating designs giving balanced representation from each BP member. Under SPM, the mating of the 48 individuals, each used in one cross, generated 24 families; while under DPM, each was used in two crosses, for a total of 48 families (Table 3). Each mating design was combined with both PAM and RAM.

#### Unbalanced mating designs

The SPM and DPM mating schemes under PAM were systematically modified, increasing the number of crosses made among better parents, in exchange for a smaller number of crosses among the less good ones (Table 3). Modifications to the balanced SPM scheme are referred to as “unbalanced 2:1:0 designs”. While in SPM all parents are used in “:1:” cross, under 2:1:0, the better parents are used in two crosses and a corresponding number of poor parents are excluded from the design. Similarly, the balanced DPM scheme with on

Table 2. Mating and selection strategies used to increase contributions from better parents in the simulation scenarios.

Strategy	Mating design	Selection
1. Balanced mating and unbalanced selection (US)	a. Single-pair mating (SPM) b. Double-pair mating (DPM)	Unbalanced group-merit selection (GMS)
2. Unbalanced mating and balanced selection (UM)	a. Unbalanced 2:1:0 mating b. Unbalanced 3:2:1 mating	Balanced within-family selection



average "2:" crosses per parent was modified to generate "unbalanced 3:2:1 designs", where the highest-ranking parents were used in three crosses, in exchange for a corresponding number of lowest-ranked parents being used only in one. The degree of imbalance in the 2:1:0 and 3:2:1 designs was increased over a stepwise series of simulation scenarios, first exchanging one pair of crosses, then two pairs, and so on (Table 3). The total number of crosses was kept constant, but parent representation became successively more and more uneven.

PAM cannot be applied in a strict rank-order fashion if the very best parent (rank order 1) is to be included in the most high-ranking crosses. We therefore modified the pairing order slightly, so that DPM crosses with the best parent under PAM were 1×2 and 1×3, while subsequent pairings were offset by one step of rank order (2×4, 3×5,...) throughout the mating scheme (Table 3). For a fair comparison, this one-step offset was also applied to the other mating designs.

### Selection of the breeding populations

Where applicable selection to the BP (and seed PP) was based on a combined-index value, where full-sib family and individual clone mean values were weighted by their respective heritabilities (as reviewed by BAKER 1986). The selected proportion was kept at 0.02 by testing 100 and 50 offspring per cross, for the 24-cross and 48-cross designs, respectively.

#### Balanced selection

For the unbalanced mating schemes, 2:1:0 and 3:2:1, selection was restricted to two and one individual per family, respectively, resulting in balanced within-family selection. Imbalance in parental contributions in these scenarios was brought about by the unbalanced mating when the best parents were used in additional crosses, in exchange for fewer crosses among the worst parents. A range of diversity-gain relationships was analysed by varying the number of pairs of crosses exchanged. The contributions per parent for the 2:1:0 design could vary as 4, 3, 2, 1 or 0 gametes and for the 3:2:1 design as 3, 2 or 1 gametes.

#### Unbalanced selection

For the balanced SPM and DPM schemes with equal number of matings per parent, varied parent contribution to the next generation was performed by selecting more from better families by "group-merit selection"

(GMS) (LINDGREN & MULLIN 1997). The selection criterion used in GMS is:  $B_{\omega} = \bar{G}_{\omega} - c\Theta_{\omega}$ , where  $B_{\omega}$  is the "group-merit" of the selected subset  $\omega$ ;  $\bar{G}_{\omega}$  is the average of the breeding values of this subset;  $\Theta_{\omega}$  is the group coancestry of the subset; and  $c$  is a weighting factor converting the group coancestry to the same scale as breeding values. An iterative search was used to find the highest group merit by a stepwise inclusion of selected members (LINDGREN & MULLIN 1997). By varying  $c$ , sets of selected individuals were identified that represent different levels of relatedness, and thus different degrees of imbalance in parent contributions to the next BP. In this way, genetic gain was estimated over a range of BP effective sizes, i.e.,  $N_s$ . The highest  $N_s$  for GMS was achieved by using a value of  $c = 50\,000$ . At the other extreme, when  $c = 0$ , group coancestry is given no weight and selection is based entirely on breeding values, resulting in the lowest  $N_s$ . When both the mating and selection are totally balanced, the US and UM strategies should be identical and reach the highest  $N_s$ , i.e., when  $c = \infty$ .

### Selection of the production populations

In all scenarios, two production populations (PP) of six clones were selected, one for seed production (seed PP), which is the highest-ranking subset of the current BP, and the other as a mix of genotypes for clonal deployment (clone PP). The clone PP came from the tested progeny of the current BP, and belonged to the same generation as the progeny of the seed orchard. The seed PPs were selected without further consideration of the gene diversity or inbreeding in the subset, thus no additional restrictions on parental contributions were applied, beyond those for selection of the BP itself. The clone PP was selected on clone means without considering gene diversity or inbreeding. The purpose with applying no additional restrictions was to study the resulting properties of the extreme part of a single independent breeding group. An operational seed orchard or clone mix would generally include selections from several such groups.

#### Simulation model

Population advancement was simulated by POPSIM, a stochastic simulation software application based on a quantitative genetic model (MULLIN & PARK 1995). The software was modified to more closely simulate certain features of the operational breeding plan in Sweden (ROSVALL *et al.* 1998) and to allow for group-merit selection (LINDGREN & MULLIN 1997).

The genetic parameters were chosen to represent conditions based on the Swedish experience (DANELL 1991b). The additive breeding value for the  $i$ th individual in the founder population was sampled from a normal distribution  $N(m, V_A)$ . The initial population mean ( $m$ ) and variance ( $V_A$ ) were each set to 100. The additive value of each offspring was obtained as the average of the parents  $A_f$  and  $A_m$  plus a random Mendelian deviation sampled from  $N(0, 0.5V_{A0}(1-F_{fm}))$ , where  $F_{fm}$  is the average of  $F_f$  and  $F_m$ , which are the inbreeding coefficients of the female parent and male parent obtained from the pedigree. The dominance effect of an individual was sampled from a normal family distribution with variance equal to  $N(0, 0.75V_D(1-F_{fm}))$ , (the within-family portion of dominance variance) and with a family mean dominance effect sampled from  $N(0, 0.25V_D)$ , where  $V_D$  was set to 25, thus being  $0.25V_A$ . Environmental effects were sampled from  $N(0, V_E)$ , where  $V_E$  was set to 375 resulting in  $h^2=0.2$ .

Group coancestry ( $\Theta$ ) and average inbreeding ( $F$ ) can be derived from the pedigree.  $\Theta$  is the mean of all pair-wise coancestries ( $\theta_{ij}$ ) among individual  $i$  and  $j$  including reciprocals, plus all self coancestries of individuals with themselves [ $\theta_i = 0.5(1+F_i)$  ( $i = j$ )] (FALCONER & MACKAY 1996; LINDGREN & MULLIN 1998). Average  $\bar{\theta}_N$  for the  $N$  BP or seed PP parent trees was calculated from  $\Theta$  with the corresponding average  $F: \bar{\theta}_N = [N^2\Theta - N0.5(1+F)]/[N(N-1)]$

Wright's  $F_{IS}$ -statistic (WRIGHT 1969):  $F_{IS} = (F - \bar{\theta}) / (1 - \bar{\theta})$ , which is the ratio of average probability of gene identity within ( $F$ ) to that among  $\bar{\theta}$  individuals, was used to describe the deviation in inbreeding (or heterozygosity) due to non-random mating in a sub-population, and thus departure from H-W equilibrium (NEI 1973; COCKERHAM 1967; WANG 1997; CABALLERO 1994). Wright's  $F_{IS}$  parameter is negative, zero and positive with avoidance of close inbreeding, random mating and close inbreeding, respectively.

Inbreeding depression was simulated by reducing the individual dominance effect by  $-bF_{fm}\sqrt{V_p}$ , representing the regression of inbreeding depression on the inbreeding coefficient of the family members ( $F_{fm}$ ), where the regression coefficient ( $b$ ) expresses the reduction in phenotypic value in units of phenotypic standard deviation ( $\sqrt{V_p}$ ) for the trait in the unselected base population (BORRALHO 1994). Values for  $b$  were calculated to generate 0.5 and 1.0 % inbreeding depression per 0.01 units increase in  $F$  at additive variance coefficient 0.1. The 1.0 % rate was assumed appropriate for Norway spruce considering both growth and fitness characters (ERIKSSON *et al.* 1973, ANDERSSON *et al.* 1974, SKRØPPA 1996) and other tree species (WILLIAMS & SAVOLAINEN 1996, DUREL *et al.* 1996,

WU *et al.* 1998a, b). The influence of inbreeding depression was studied by comparing with scenarios without inbreeding depression where  $b$  was set to 0.

The net gain in the progeny of  $N$  seed orchard parent trees in generation five was obtained, assuming no self-pollination, by adjusting the average additive effect of the parents by  $-b\bar{\theta}_N\sqrt{V_p}$ , where  $\bar{\theta}_N$  is the mean pair-wise coancestry of the parents. After random mating and equal gamete contributions,  $\Theta$  in one generation becomes  $F$  in the following. By evaluating seed orchard gain from various strategies at the same seed PP  $N_s$ , the comparison accounted for the same expected inbreeding in the progeny. If self-pollination does not occur or does not produce viable offspring it is the average  $\bar{\theta}_N$  in one generation that becomes  $F$  in the progeny.

Selection was applied to a single trait, although this could also be regarded as an index of component traits. Testing was assumed to use single-tree plots (i.e., no environmental covariances), in a single environment (i.e., no G×E interaction), with no variances associated with cloning (i.e., no C-effects). The stochastic variation in expected genetic effects and variances was described by the coefficient of variation (CV %) for 100 iterations of a given simulation scenario.

## RESULTS

### Simulation without inbreeding depression

Additive variance and genetic response after five generations of breeding and selection are presented for scenarios with successively larger contribution from better parents in Figure 1. As parent contributions became increasingly uneven, by application of either UM or US, the BP  $N_s$  retained after five generations became less and less. The US strategies that applied GMS to SPM and DPM to vary parental contributions were most unbalanced, and reached a lower BP  $N_s$  than did the UM strategies, 2:1:0 and 3:2:1, after making all possible exchanges of crosses (12) between the highest- and lowest-ranking parents. Keeping parent contributions equal, by means of balanced mating and selection, maintained the highest  $N_s$  in the BP.

The BP  $V_A$  was substantially greater under PAM than under RAM for all strategies, as illustrated in Figure 1a by comparing SPM-PAM with SPM-RAM and in Table 4 for the completely balanced case where the highest  $N_s$  was maintained in the BP. [To simplify the comparison of PAM with RAM, only SPM-RAM data are shown in the figures, as the points for DPM-RAM were very similar (data not shown).] In general, the enhancement of  $V_A$  was greater the more equal were the parent contributions, and  $V_A$  was larger for the UM

**Table 4.** The effect of PAM on the BP and PP genetic parameters after five generations for SPM and DPM under completely balanced mating and within-family selection, maintaining the highest  $N_s$  in the BP. Simulations shown without and with inbreeding depression at 1 % depression per 0.01  $F$ .

Parameters	Breeding population				Seed production population				Clone production population			
	SPM		DPM		SPM		DPM		SPM		DPM	
	RAM	PAM	RAM	PAM	RAM	PAM	RAM	PAM	RAM	PAM	RAM	PAM
<i>Simulation with no inbreeding depression</i>												
$N_s$	13.77	13.88	13.78	13.82	3.52	2.98	4.40	3.45	3.51	2.40	3.66	2.64
$V_A$	59.7	134.9	62.9	136.3								
$V_D$	22.1	21.8	22.3	21.7								
$A$	55.9	56.2	54.3	54.0	63.9	72.0	62.8	70.1	75.2	85.4	74.3	82.9
Seed PP extra <sup>1)</sup>					7.9	15.8	8.4	16.1				
$D$									6.3	5.7	6.5	5.8
$A+D$									81.6	91.1	80.9	88.6
$F$	0.021	0.048	0.021	0.034	0.025	0.070	0.023	0.049	0.034	0.098	0.029	0.075
$F_{IS}$	-0.005	0.022	-0.008	0.009								
$F_{prog}$ selfing <sup>2)</sup>					0.142	0.168	0.114	0.145				
$F_{prog}$ no selfing <sup>2)</sup>					0.068	0.094	0.034	0.069				
<i>Simulation with inbreeding depression</i>												
$N_s$	13.77	13.88	13.78	13.81	3.56	3.37	4.46	3.92	3.51	2.94	3.69	3.12
$V_A$	59.7	117.3	62.9	127.6								
$V_D$	39.2	77.2	29.8	40.2								
$A$	55.9	56.2	54.3	54.1	63.4	69.3	62.3	68.1	74.7	81.7	74.2	80.1
Seed PP extra <sup>1)</sup>					7.5	13.1	7.9	14.1				
$D$									4.9	2.9	4.7	3.6
$A+D$									79.6	84.6	78.9	83.7
$F$	0.021	0.042	0.021	0.032	0.009	0.018	0.012	0.022	0.015	0.027	0.018	0.025
$F_{IS}$	-0.005	0.017	-0.007	0.006								
$F_{prog}$ selfing <sup>2)</sup>					0.141	0.148	0.112	0.128				
$F_{prog}$ no selfing <sup>2)</sup>					0.068	0.076	0.033	0.051				

<sup>1)</sup> SPP A -BP A

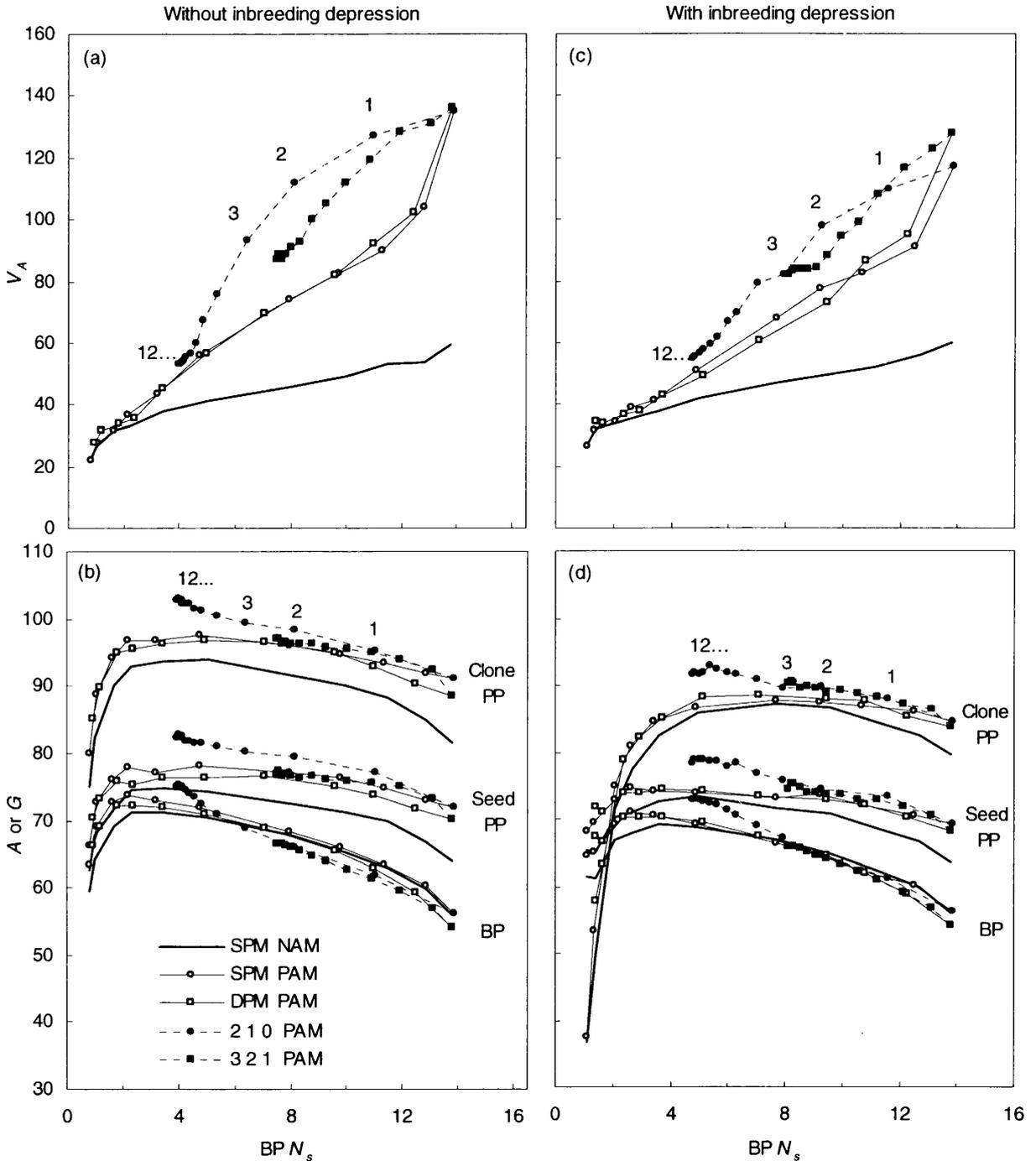
<sup>2)</sup>  $F$  in the seed PP progeny assuming selfing and no selfing, respectively

strategies than for the US strategies (Figure 1a).

Although PAM enhanced  $V_A$ , it led to greater  $A$  in the BP (up to 8 % more) only in scenarios with the most uneven parent contributions, seen in Figure 1b at low BP  $N_s$ , the UM strategy with highly unbalanced 2:1:0 mating being superior to all other breeding strategies. At higher levels of BP  $N_s$ , PAM accumulated equal or less  $A$  in the BP than RAM, the US strategies being superior to the UM strategies.

The enhancement of  $V_A$  by PAM resulted in greater gain from the selection of seed orchards and clone mixes (PPs). Under completely uniform parental contributions, i.e., when UM and US are equal, selecting the seed PPs from BPs produced by SPM and DPM, doubled the extra gain under PAM compared to under RAM (Figure 1 a and Table 4). In this way the total

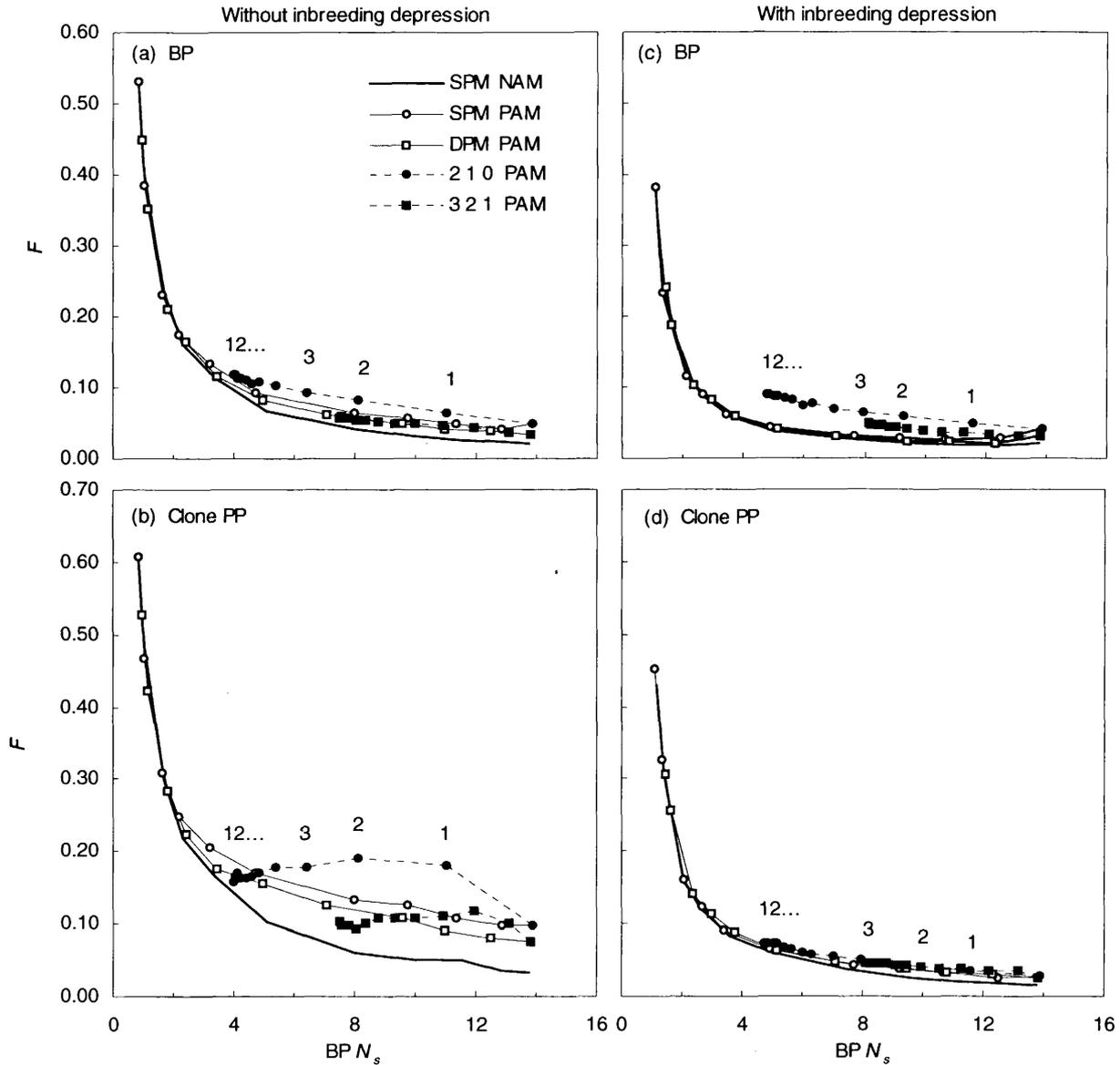
gain from the seed PPs was 12.7 % and 11.7 % higher for SPM and DPM, respectively, under PAM than under RAM. At lower levels of BP  $N_s$  and  $V_A$ , the extra seed PP gain resulting from PAM was less than at high levels (Figure 1b). For example, for the US strategy at the level where unbalanced selection retained BP  $N_s = 8.0$ , the extra total gain from a seed PP selected from a BP produced by PAM was 6.5 % and 4.7 % for SPM and DPM, respectively. The corresponding extra total seed PP gain from UM strategies 2:1:0 and 3:2:1 at BP  $N_s = 8.0$  was 9.9 % and 5.5 %, respectively. Consequently, due to the higher PP gain achieved by PAM at the maximum BP  $N_s$ , there was much less to gain in the PPs from sacrificing BP  $N_s$  under PAM than under RAM and, in general, much less in the PPs than in the BP (Figure 1b).



**Figure 1.** (a) Additive variance ( $V_A$ ) for the breeding population (BP) and (b) genetic response for the BP (A), seed PP (A) and clone PP (A + D) respectively after five generations for various breeding strategies, assuming no inbreeding depression, and (c, d) the corresponding results with inbreeding depression simulated (1 % per 0.01  $F$ ). The variation in BP genetic diversity ( $N_s$ ) of SPM and DPM US strategies was achieved by varying parent contribution by GMS, and of 2:1:0 and 3:2:1 UM strategies by varying the number of crosses exchanged from low to high ranking trees (indicated by 1–12 for the 2:1:0 mating scheme).

Average inbreeding ( $F$ ) in the BP increased, as parent contributions became more uneven (Figure 2a). Compared at the same BP  $N_s$ , PAM increased  $F$  more than RAM resulting in a departure from H-W equilib-

rium as indicated by the positive  $F_{IS}$  under PAM (Table 4). This demonstrates that under PAM average coancestry ( $Q$ ), and by that means  $N_s$ , was more influenced by  $F$  (after mating trees that were more related

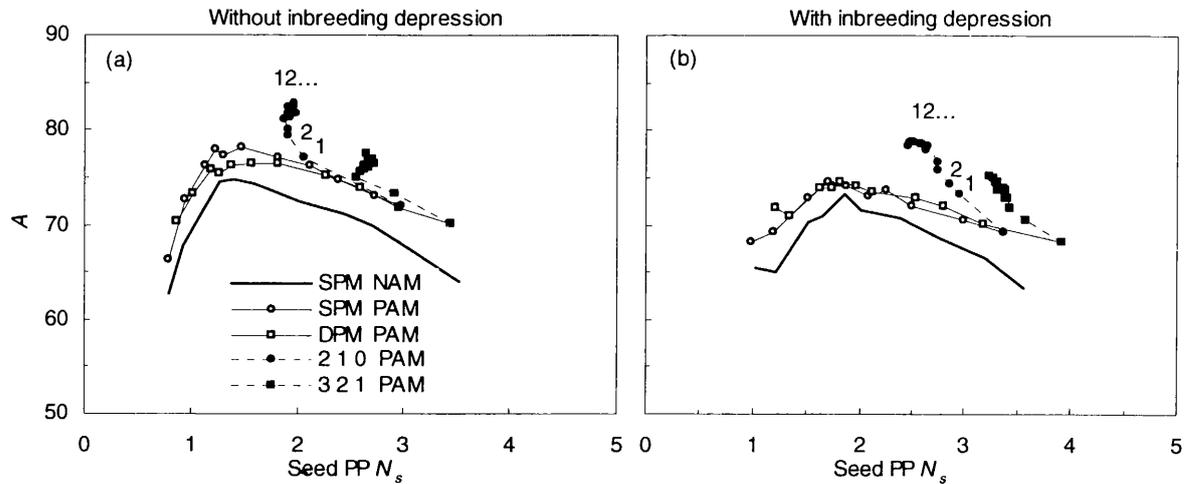


**Figure 2.** Inbreeding ( $F$ ) after 5 generations in (a) the BP and (b) the clone PP of various breeding strategies assuming no inbreeding depression and (c and d) with inbreeding depression simulated (1 % per 0.01  $F$ ). The variation in  $BP N_s$  of SPM and DPM US strategies was achieved by varying parent contribution by GMS, and of 2:1:0 and 3:2:1 UM strategies by varying the number of crosses exchanged from low to high ranking trees (indicated by 1-12 for the 2:1:0 mating scheme).

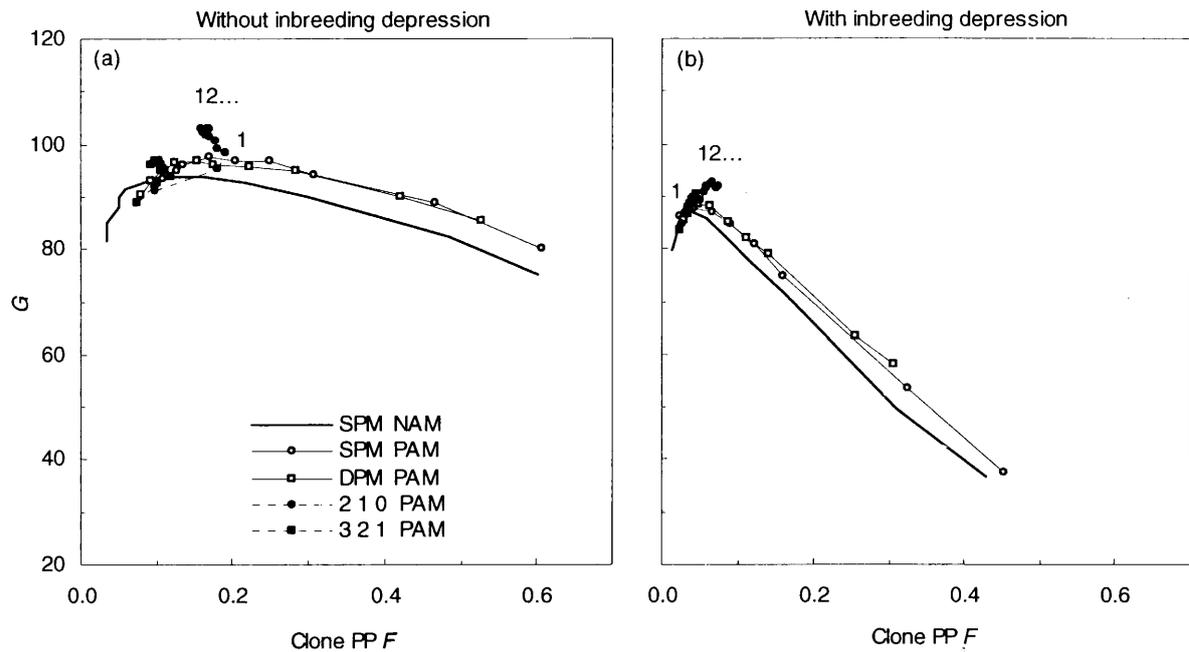
than average) than by pair-wise coancestry ( $\bar{\theta}$ ). The avoidance of selfing under RAM resulted in a slightly negative  $F_{IS}$  (Table 4). These effects on  $F_{IS}$  was consistent when compared at the same  $N_s$ , at intermediate and high levels of  $BP N_s$ . Breeding strategies with two crosses per parent, i.e., DPM and 3:2:1, resulted in the lowest  $F$  in the BP under PAM. In the PPs, as shown for the clone PPs in Figure 2b,  $F$  increased for weakly unbalanced UM strategies with up to two crosses exchanged, but decreased for more unbalanced mating schemes. In spite of this decrease, the PPs resulting from the 2:1:0 mating scheme had the highest  $F$  over

most of the range of  $BP N_s$ , while the PPs from the 3:2:1 mating scheme had values of  $F$  more similar to those produced by the US schemes (Figure 2b).

Maximum  $N_s$  for the six clones in the seed PP (which was achieved when selected from a BP with uniform parental contributions and two crosses per parent) was somewhat reduced by PAM (Table 4 and Figure 3a). This resulted in the very lowest inbreeding in the progeny of the seed PP ( $F_{prog}$ ) being higher under PAM than under RAM (Table 4). If we assume no selfing in the seed PP,  $F_{prog}$  at the highest seed PP  $N_s$  is 0.068 and 0.034 for SPM and DPM, respectively, under



**Figure 3.** Additive effects ( $A$ ) after five generations for the six best trees (seed PP) from BPs of various breeding strategies compared at the same seed PP  $N_s$  assuming (a) no inbreeding depression and (b) with inbreeding depression simulated (1% per 0.01  $F$ ). The variation in seed PP  $N_s$  was achieved by varying parent contribution in BP selection; for SPM and DPM US strategies by GMS, and for 2:1:0 and 3:2:1 UM strategies by varying the number of crosses exchanged from low to high ranking trees (indicated by 1–12 for the 2:1:0 mating scheme).

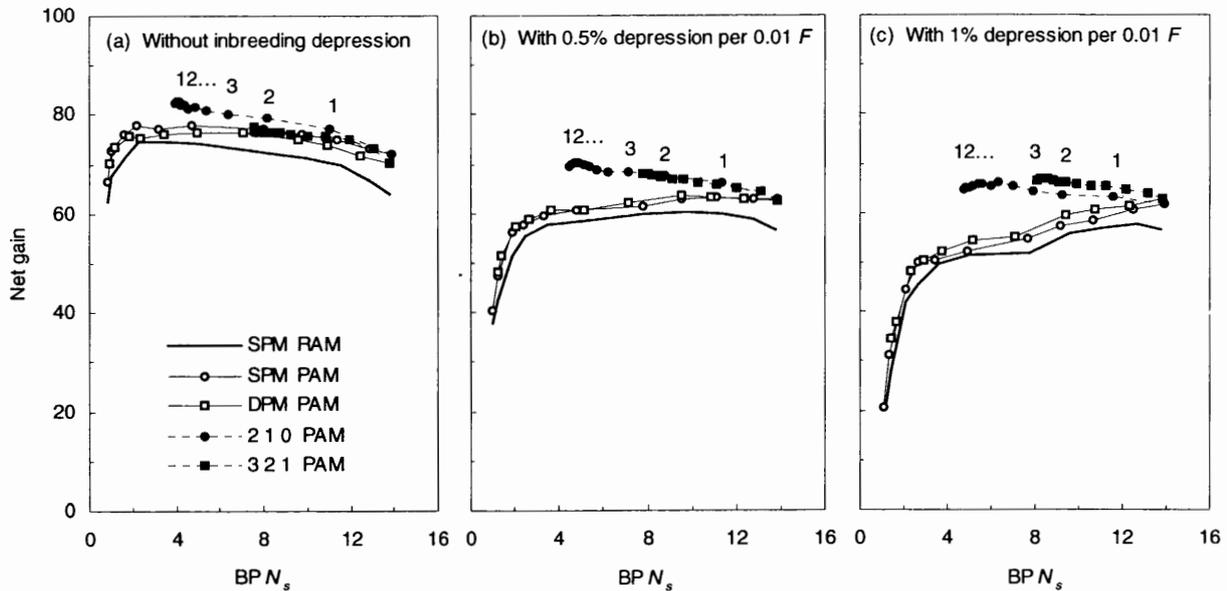


**Figure 4.** Total genetic effects ( $G$ ) after five generations for the six best clones in a Clone PP from progeny of BPs of various breeding strategies compared at the same Clone PP  $F$  assuming (a) no inbreeding depression and (b) with inbreeding depression simulated (1% per 0.01  $F$ ). The variation in Clone PP  $F$  was achieved by varying parent contribution in BP selection; for SPM and DPM US strategies by GMS, and for 2:1:0 and 3:2:1 UM strategies by varying the number of crosses exchanged from low to high ranking trees (indicated by 1–12 for the 2:1:0 mating scheme).

RAM, increasing to 0.094 and 0.069, respectively, under PAM (Table 4).

Compared at any given seed PP  $N_s$ , i.e., the same inbreeding in the orchard progeny under random mating, PAM consistently produced higher gain than

RAM (Figure 3a). The six seed PP clones selected from the UM strategies had greater  $A$  than those from US strategies. By increasing the contributions from high-ranking trees beyond the first two cross exchanges, gain increased without further loss of seed PP  $N_s$  in both the



**Figure 5.** Net gain ( $A -$  inbreeding depression) after five generations in seed PP progeny of BPs of various breeding strategies over a range of  $BP N_s$ . (a) Simulation without inbreeding depression, (b) simulation with 0.5 % depression per 0.01  $F$  and (c) 1 % depression per 0.01  $F$ . With inbreeding depression, the parent additive effects were corrected for inbreeding depression due to inbreeding in the progeny, assuming no self pollination ( $F_{prog}$  no selfing). Any  $D$  effects among parent trees were not included. The variation in  $BP N_s$  of SPM and DPM US strategies was achieved by varying parent contribution by GMS, and for 2:1:0 and 3:2:1 UM strategies by varying the number of crosses exchanged from low to high ranking trees (indicated by 1–12 for the 2:1:0 mating scheme).

2:1:0 and 3:2:1 UM strategies, albeit at different levels of SPM and DPM  $BP N_s$ . Thus, while reducing BP gene diversity, more uneven parental contributions in the UM schemes beyond these points led to additional seed PP gain, with no further loss in seed PP gene diversity.

If the clone PP total gain ( $A+D$ ) is compared at the same  $F$ , PAM produced higher gain at most levels of  $F$  (Figure 4). Exchanging more than two crosses under the UM schemes led to no further increase in the clone PP  $F$  and, consequently, these strategies reached the highest gain at levels where clone PP  $F$  was stable.

#### Simulations with inbreeding depression

With inbreeding depression included in the simulation, performance was reduced in proportion to the inbreeding coefficient  $F$  of each full-sib family. When parental contributions were allowed to vary by family selection, inbreeding depression changed the selection pattern considerably and  $F$  was substantially reduced in the BP and especially in the PPs, resulting in similar PP  $F$  for all breeding strategies (Figure 2d compared to 2b). The smaller decrease in BP  $F$  of UM compared to US strategies by inbreeding depression was due primarily to lower family selection intensity, caused only by the degree of unbalanced mating allowed. Changes in rank order, brought about by inbreeding depression, affected the mating pattern and, consequently, the effects of

PAM.

Changes caused by inbreeding depression also increased  $V_D$  and decreased  $V_A$  of the BP (Table 4 and Figure 1c), and under certain conditions decreased both  $A$  and  $D$  in the BP and PPs (Figure 1d). At the highest  $N_s$  when selection was completely within families, the increase in  $V_D$  and decrease in  $V_A$  did not affect either BP  $A$  or  $F$  under RAM (Table 4). Also, under PAM and purely within family selection, BP  $A$  was unaffected, but  $F$  was slightly reduced.

Also at lower levels of  $BP N_s$ , the decrease in  $A$  by inbreeding depression was small. In the BP at the 1 % rate of depression, the loss in  $A$  reached up to 3 and 6 % for 2:1:0 and SPM mating schemes, respectively, and 1 and 3 % for 3:2:1 and DPM mating schemes, respectively. The corresponding figures for the seed PP of the one and two crosses per parent schemes was up to 5 and 3 %, respectively (data not shown). Thus, in general, with respect to inbreeding depression for both the UM and US strategies, the two-crosses-per-parent schemes improved their position compared to the one-cross-per-parent schemes (Figure 1d).

For the seed PPs,  $N_s$  was enhanced by selection against inbreeding depression, which further reduced inbreeding and inbreeding depression in the progeny of the seed PP (Figure 3b compared to 3a, Table 4). Under PAM, this change was greatest for the 3:2:1 strategy,

which improved its advantage under inbreeding depression. Assuming no selfing in the seed orchard, the lowest  $F_{prog}$  under PAM with inbreeding depression was 0.076 and 0.051 for SPM and DPM, respectively, which can be compared to 0.068 and 0.033 for SPM and DPM, respectively, under RAM (Table 4).

The effects on the progeny performance of the combined effect of differences among strategies in seed PP  $N_s$  and  $F$  (i.e. the resulting  $F$  in the progeny) was accounted for by subtracting inbreeding depression from the seed PP  $A$  ( $A$  in Figure 1d) and plotting the net gain over BP  $N_s$  (Figure 5). The calculation considered the  $F_{prog}$  that will arise if no selfing takes place in the seed orchard (i.e., average  $\bar{\theta}$  of the seed PP parents). For the US strategies at a 1 % rate of inbreeding depression, the greatest net gain was reached at the highest BP  $N_s$ , while for the UM strategies, the greatest net gain was reached at close to the lowest BP  $N_s$  achieved under this strategy (Figure 5c). At low levels of BP  $N_s$ , the differences between strategies reached 16 to 23 %, and the those strategies with two crosses per parent (i.e., DPM and 3:2:1) were consistently better than the analogous strategies with only one cross per parent (i.e., SPM and 2:1:0, respectively).

In the clone PP, the net gain accounting for 1 % inbreeding depression per 0.01  $F$  was seen directly as a decrease in the genotype mean ( $A+D$ ) (Figure 1d). Net gain decreased substantially when  $F$  in the clone PP was greater than 0.07 (Figure 4b), which was reached at BP  $N_s$  around 4 (Figure 2d). These levels of  $F$  were never exceeded by the UM strategies, for which the highest net gain was achieved at close to the highest  $F$  and lowest BP  $N_s$  (after exchanging 5 crosses). The two UM strategies were equally good over the range of BP  $N_s$  (Figure 1d), although the 2:1:0 mating scheme could exploit more of BP  $N_s$  than could the 3:2:1 scheme.

## DISCUSSION

### Similarity to "Open-nucleus" strategies

The mating system PAM by itself had negligible effects on effective population size ( $N_s$ ), while the two approaches used to increase contributions from the better trees caused the accumulated additive gain ( $A$ ) to increase and effective population size to decrease in disparate ways. Both strategies, but in particular the UM approach, have similarities with an open-nucleus system, the group with more crosses or increased contributions being the nucleus of a larger main population (JAMES 1977; SHEPHERD & KINGHORN 1994; RODEN 1995b; COTTERILL *et al.* 1989). The nucleus and main population in each cycle were based on the rank

order of the 48 trees, without considering from which population the parents originated. The nucleus is thus "open", with the possibility for transfer in both directions.

The degree of imbalance in the UM mating design, i.e., the number of crosses exchanged between high- and low-ranking trees, will determine the size of the nucleus. When two crosses are exchanged under the 2:1:0 mating scheme, the 4 highest-ranking trees constitute the open nucleus, while the total breeding population is reduced to 44 (i.e., the four lowest-ranking trees are not crossed). In this way, ranking and mating was a second step of selection. If 12 crosses are exchanged, the overall breeding population will be reduced to 24 trees, all in the nucleus population and each mated two times. In this case, the 2:1:0 mating scheme is almost identical to a balanced DPM scheme for a total population of 24 trees and 24 crosses, and allowing two instead of one selection per family. With all 12 crosses exchanged for the 3:2:1 mating scheme, half of the population contributed three gametes and the other half contributed one, and the breeding population was maintained at size 48, making this strategy less extreme.

When unbalanced selection through GMS is used, the degree of variation in contributions is determined by the weight placed on group coancestry. Compared to UM schemes, US using GMS can result in more variation in parent contributions, including no contribution and there are no limits on the number of selections per parent or family (as an example, see ANDERSSON *et al.* 1999, Tables 2 and 3). However, the BP was always kept at the size of 48. Thus, for US under GMS, the nucleus can become more related, i.e. lower  $N_s$ , than under the more restricted balanced within-family selection of UM.

### Breeding population selection response

In general, the observed response to PAM in the BP is in agreement with expectation (e.g., SMITH & HAMMOND 1987; FERNANDO & GIANOLA 1986; SHEPHERD & KINGHORN 1994; JORJANI *et al.* 1997b, c; ROSVALL & MULLIN 2003). The enhanced variance by PAM can only be transformed to a response in the BP itself by a component of family selection, i.e. unequal parent contributions. Therefore the BP  $A$  is only enhanced under low  $N_s$  scenarios (as discussed by ROSVALL & MULLIN 2003).

In most cases, US produced the greatest gain in the BP, but very aggressive UM with the 2:1:0 mating design was superior at lower BP  $N_s$ , due to higher selection intensity when a lower number of individuals

were breeding out of a constant total tested population (2 400). For a given size of the recruitment population, there are an optimum number of individuals to be selected for breeding the new generation to achieve maximum gain at a given level of diversity, i.e., optimal selection intensity (VILLANUEVA & WOOLLIAMS 1997; MEUWISSEN 1997; KERR *et al.* 1998). Based on the results from the 2:1:0 scheme, the only scheme where a decrease in the number of breeding individuals was allowed, the optimal breeding population size seems to be closer to 24 than 48 for the recruitment population, test precision and five generations studied.

The GMS method used in our US strategies is a dynamic selection rule, given the selection candidates available and the target group coancestry, while the UM strategies use a static selection rule which has to be optimised beforehand (see VILLANUEVA & WOOLLIAMS 1997; MEUWISSEN & SONESSON 1998). Thus, with equal selection intensity at any BP  $N_s$ , GMS would result in the greatest BP response and diversity use efficiency (LINDGREN & MULLIN 1997; ROSVALL & ANDERSSON 1999). However, to achieve maximum gain in the long term, the weight on group coancestry has to be changed successively over generations (ROSVALL & ANDERSSON 1999). This will apply also if the UM strategy is optimised (which was not the case for our study).

The greater response for SPM and 2:1:0, compared to DPM and 3:2:1 at medium to high  $N_s$ , is primarily due to higher selection intensity. When selection is completely within families, 2 selected out of 100 for SPM and 2:1:0, compared to 1 of 50 from DPM and 3:2:1 (standardised selection differential  $i = 2.3279$  and 2.2491, respectively) causes 3.5 % greater response. This difference in  $i$  between mating schemes is not maintained at lower BP  $N_s$ , since selection is then not restricted to within families.

The above points emphasize that genetic response is influenced by the interaction of many factors, including selection intensity, accuracy of selection index, the current genetic variance and gene diversity, all of which will change over generations at different rates for the alternative strategies. A fair comparison between breeding strategies should account also for these differences in addition to comparisons at the same  $N_s$ .

#### Enhancement of variance by PAM and superior PP-gain

A key finding of this study is the greater expansion of variance from UM over US strategies under PAM at a given BP  $N_s$  that can result in greater gain in selected PPs. This superior PP gain is realised despite the mean

of the BP being *lower* than that achieved by US strategies! The equal number of selected trees from all families under UM maintained a fairly uniform distribution of parental contributions within the selected population, even when contributions from the poorest parents were totally excluded in the 2:1:0 scheme. For 2:1:0, the counteracting effect of PAM on the reduction in variance caused by selection, the "Bulmer effect" (BULMER 1971), was efficient to the point where 5 pairs of crosses had been exchanged, i.e., with more than 38 of the 48 trees used for breeding, while for 3:2:1, the variance was enhanced up to all 12 crosses was exchanged. This is consistent with earlier suggestions that PAM is only able to counteract the Bulmer effect if family selection is weak (SMITH & HAMMOND 1987; JORJANI *et al.* 1997b, c; ROSVALL & MULLIN 2003).

The expansion of the additive variance by PAM is primarily due to gametic phase (linkage) disequilibrium (BULMER 1971 1976; FALCONER & MACKAY 1996; JORJANI *et al.* 1997b). Departure from H-W proportions by PAM should also have an increasing effect on  $V_A$ ; however, the influence was weak at the levels of  $F$  reached here. Theoretically, the increase in additive variance by PAM has no upper limit for linkage disequilibrium among an infinite number of loci (WRIGHT 1921; BULMER 1980; JORJANI *et al.* 1997b), while inbreeding can at most double the variance (FALCONER & MACKAY 1996).

#### Breeding population structure affects seed orchard and clone mix inbreeding

Unequal parent contributions when advancing the BP will increase both  $\Theta$  and  $F$ . The non-random mating system by PAM increases the chance that mates are related and PAM itself will only increase  $F$ , thus maintaining the same  $\Theta$  (and same  $N_s$ ) as RAM. By this departure from H-W proportions, the increase in  $F$ , i.e. self-coancestry  $0,5(1+F)$ , at a given  $\Theta$  under PAM corresponds to a decrease in pair-wise coancestry ( $\bar{\theta}$ ), resulting in a positive  $F_{IS}$ . The effects of PAM on  $\bar{\theta}$  and  $F$  can be understood as a "lining effect" (FALCONER & MACKAY 1996). The altered structure of the breeding population under PAM will affect the net gain from production populations in a manner similar to sublining, where the build-up of inbreeding within sublines can be released at any time by out-crossing among sublines (VAN BUIJTENEN 1976; BURDON *et al.* 1977, VAN BUIJTENEN & LOWE 1979; BURDON & NAMKOONG 1983).

If selfs are not viable and do not contribute to the commercial seed crop, a reasonable assumption for

Norway spruce (KOSKI 1973), and many other species according to WILLIAMS & SAVOLAINEN (1996) nor contribute to the yield from the forest stand (LINDGREN & GREGORIUS 1976; LESICA & ALLENDORF 1992), then  $\bar{\theta}$  of the parents becomes  $F$  of the progeny. By this assumption of no effects from self-pollination in a seed orchard, the result also becomes independent of the number of selected parent clones. In this case, at any given  $\Theta$  (or BP  $N_s$ ) there will be slightly less inbreeding and inbreeding depression in the progeny of parents derived from a strategy that uses PAM as a mating system. However, the variation in  $F$  among the various mating designs at a particular BP  $N_s$  was too small to observe any substantial differences in progeny inbreeding.  $F$  was only reduced by 0.005 to 0.01 units in the progeny.

The pattern of increase in  $F$  for the different populations with increasing contributions from high-performing parents differed between the US and UM strategies. In general for both strategies, the average inbreeding for the whole population increased gradually with reduced  $N_s$ . This was also the case for  $F$  in the group of six highest-ranking trees of the US strategies, while  $F$  for the UM strategies decreased as more crosses were made within the "open nucleus". Increasing the size of the nucleus in combination with the restricted selection of one or two per family created more opportunities to select high-ranking but less-related trees for the seed PP. This was seen as a stable seed PP  $N_s$  and decrease in  $F$  of the seed PP group after the first two pairs of crosses had been exchanged, in spite of the reduced BP  $N_s$  following the successively more unbalanced mating schemes.

### Inbreeding depression and net gain from production populations

The net gain of a clone PP is seen directly in the reported genotype value, which is derived from additive and dominance effects, both of which are affected by inbreeding depression and selection. For the rates of inbreeding arising here by changes to parent contributions, total net gain increased with increased inbreeding for the UM strategies, but under US inbreeding reached levels where inbreeding depression offset the additional gain from unequal parent contributions. Nevertheless, the net gain from the clone PP was always greater than the net gain from the seed progeny of a seed PP, also at the lowest BP  $N_s$  and highest  $F$ . The artificial selection of the clone PP acted against inbreeding depression.

The additive gain ( $A$ ) reported here for the seed PP parent trees (Figure 1a, c; Figure 3a, b and Figure 5a), i.e., breeding values, assumes that seed orchard progeny

are produced by controlled out-crossing of unrelated trees. In this case, neither the level of group coancestry nor the higher rate of inbreeding due to PAM will affect the progeny performance. Under these assumptions and within most of the range of parent contributions studied, the gain was greater as parent contributions became more unequal, i.e., when exploitation of the BP gene diversity was greater. This comparison indicated the clear superiority of PAM and UM strategies.

An important finding in this study concerned the differences among strategies in optimal BP  $N_s$  for maximum net genetic gain from a seed orchard when related trees are mated, and when accounting for the expected inbreeding depression in the orchard progeny (Figure 5b and c). Due to the different population structures, the net gain for seed PP progeny improved under UM strategies as contributions from better parents increased, while under US net gain declined. The difference was considerable at the low BP  $N_s$ , and the 3:2:1 strategy was consistently superior at the 1 % depression rate, while the 2:1:0 and 3:2:1 were equally superior at the 0.5 % depression rate. The advantage of the UM strategies is due to the higher  $N_s$  of its seed PP. Keeping in mind that 1 % inbreeding depression per 0.01 unit  $F$  is in the neighbourhood of an upper limit (WILLIAMS & SAVOLAINEN 1996), none of these UM strategies accumulated inbreeding to levels where inbreeding depression would offset the gain realised through greater utilisation of elite parents. Thus, for the number of breeding cycles considered, there was no trade-off between net gain and final BP  $N_s$  for the UM strategies.

In contrast, for strategies using US, there was an optimum BP  $N_s$  for maximum net gain and the optimum level varied depending on whether operational deployment was by seed (seed PP) or by clonal propagation (clone PP). The optimal BP  $N_s$  would be lowest if seed is produced by out-crossing seed parents from unrelated sublines. It would be intermediate if seed were produced by crossing related trees, assuming that natural selection eliminates depressed progeny, or if a selected clone mix is used, by which depressed clones are avoided. Finally, if inbreeding occurs, as in the progeny from parents of the same population, and there is no selection against depression, the optimum BP  $N_s$  would be close to its maximum to achieve the highest net gain. This contradicts what is commonly considered the optimum for short-term gain (DEMPFLE 1975; GEA *et al.* 1997), but these last two optima are especially sensitive to the assumptions of inbreeding depression. Hence, with an assumption of less severe inbreeding depression, it is reasonable that BP  $N_s$  for DPM+GMS could be reduced to half its maximum value without much decrease in response.

### One or two crosses per parent?

Mating designs are used in tree breeding for a variety of purposes (BURDON & SHELBORNE 1971) for example: (1) to provide parameter estimates (genetic variance components) for breeding value and gain predictions; (2) to regenerate genetic variation for forward selection; and (3) progeny testing of selection candidates for backward selection. It appears that using an individual in more than 2 or 3 crosses will not substantially improve the efficiency of backward selection (JOHNSON 1998; BURDON & VAN BUIJTENEN 1990; LINDGREN 1977), and SPM can achieve maximum efficiency for forward selection with minimum effort (VAN BUIJTENEN & BURDON 1990; KERR 1998).

In this study, the focus was on forward selection, and clonal replication was used in place of progeny testing to improve selection precision (approximately equivalent to an increase in heritability of the selection unit) (BURDON & SHELBOURNE 1974; SHELBOURNE 1991; RUSSELL & LOO-DINKINS 1993). Thus, the higher selection intensity for family selection that results from making more crosses per parent was of less value. Rather, additional crosses were made at the expense of lower within-family selection intensity due to smaller family size and reduced total response, as was also found for selection on BLUP by KERR (1998).

Making more crosses exposed more dominance variance to selection, as reflected in a slightly larger  $D$  effect for DPM and 3:2:1 mating schemes. Since only 1/4 of the  $V_D$  is among families, more crosses are not expected to substantially improve opportunities to benefit from dominance effects through family selection, if  $V_D$  is of similar magnitude to that assumed here (ROSVALL *et al.* 1998). However, lower inbreeding in the two-cross strategies both decreased the mean and variance of inbreeding depression. With more crosses, inbreeding depression was more effectively counteracted by selection and as a consequence the increase in  $V_D$  was retarded.

Under inbreeding depression, the mating designs that averaged more crosses per parent reached the very highest seed PP  $N_s$  and the lowest  $F$  in orchard progeny. In these designs, selection of two half-sibs instead of two full-sibs can increase the contribution of better trees while producing less relatedness.

An additional advantage of two-cross designs is that mating designs can be connected, improving the estimation of genetic parameters and prediction of breeding values.

### Reduced inbreeding by mate selection without loss of PAM effects

The effects of PAM depend on the genetic correlation between breeding values of mates and deviation from mating in rank order might reduce the response. In another study (ROSVALL & MULLIN 2003), we applied SPM with PAM in strict rank order ( $1 \times 2$ ,  $3 \times 4$ , etc.). In the present study, the pairing order under SPM was slightly offset ( $1 \times 3$ ,  $2 \times 4$ , etc.), to facilitate the exchange of crosses under the 2:1:0 schemes in a way comparable to that required for the DPM and 3:2:1 schemes (Table 3). This offset from strict rank order resulted in a difference in response of no more than 1%, being larger with inbreeding depression and lower without. The most obvious difference was a less pronounced "lining effect" (10–50% lower  $F$  at a given BP  $N_s$ , i.e., lower  $F_{IS}$ ) for simulations under the assumption of no inbreeding depression, and thus more inbreeding in the progeny. This was especially true when selection was entirely within family. However, in the presence of inbreeding depression, the net gains for both the clone mix and orchard progeny were very similar to those when SPM was applied in strict rank order.

Consequently, the prevention of mating the most highly related trees would evidently not reduce the benefit of PAM on additive variance, selection response and net gain. Therefore, avoidance of mating relatives can be used effectively to lessen the disadvantage of large variation in  $F$  among population members when advancing the BP. In real life, uniform development of  $F$  throughout the breeding population will improve the precision of selection based on clonal testing. However, a more even distribution of inbreeding might reduce the efficiency of purging deleterious genes (HEDRICK 1994; WILLIAMS & SAVOLAINEN 1996; DUDASH *et al.* 1997; FU 1998, FU *et al.* 1998).

If the correlation between breeding values of mates becomes as low as for a combination of one round of SPM PAM and one of SPM RAM, most of the extra gain from PAM is lost (data not shown). PAM effects will be even weaker for mating designs where the best third of trees are mated to random partners or systematically to the intermediate or low ranking third (KING & JOHNSON 1993; other data not shown).

### Effects of assumptions on choice of breeding strategy

These comparisons among breeding strategies make several assumptions regarding the simulation model, the choice of parameters, and how reforestation material will be produced. There are limitations in the possibili-

ties to simulate dominance effects and variances correctly in presence of inbreeding under an infinitesimal model (DE BOER & VAN ARENDONK 1992; MEUWISSEN *et al.* 1995); however, the inclusion of the regression of inbreeding depression on  $F$  will give similar genetic effects as more accurate models. The present model assumes all loci having a semi-dominance relationship and a constant dominance variance re-established in the regenerated progeny population in the absence of inbreeding and inbreeding depression (ROSVALL *et al.* 1998). Thus, in the absence of inbreeding depression,  $V_D$  in the BP was re-established and maintained at the initial level over the generations under scenarios, with equal parent contributions but reduced under the most unbalanced US scenarios due to inbreeding and selection, while PAM had no effect on  $V_D$ . This behaviour of the model for the effect of PAM is in agreement with established theory (e.g., FISHER 1918; CROW & FELSENSTEIN 1968; BULMER 1980; FALCONER & MACKAY 1996), although JORJANI *et al.* (1998) claimed that under PAM with a small population size and a large number of loci, the dominance variance will increase in the long term if not counteracted by selection.

Including inbreeding depression in the model increased the variation in dominance effects, and thus dominance variance, which reduced heritability and hence the additive response to selection.  $V_D$  became higher for PAM than RAM under the most balanced US scenarios and for all UM scenarios, with the largest increase for 2:1:0. This occurs because no selection can take place against inbreeding depression when selection is only within families. Since inbreeding depression was simulated to be proportional to  $F$ , and  $F$  is equal within a full-sib family, inbreeding depression was also identical among siblings, and the within-family ranking was not affected. Consequently, when selection was entirely within family, inbreeding depression did not change  $F$ ,  $N_e$ , or  $A$  of the BP, other than a change in  $F$  under PAM due to rank-order changes among families. Under conditions when some degree of among-family selection was permitted, such as under GMS and in the selection of PPs, the inclusion of inbreeding depression in the simulation substantially decreased  $F$ , since highly inbred trees were not selected.

Both the manner in which inbreeding depression was simulated and the rate of inbreeding depression, have an impact on the magnitude of net gain and the level of gene diversity at which maximum net gain is obtained. However, for all kinds of production populations, the same relative ranking of the UM and US approaches was maintained throughout the study; increasing contributions from better trees by UM was superior to increasing contribution by US.

There are many conceivable ways to vary parental contributions other than by the number of crosses as done here under the UM strategy. One alternative would be to generate more progeny for crosses between better trees and to allow more selections within these larger families. It would then be possible to retain some contribution from all parents, even under SPM, while varying the parental contribution during selection to proportions such as 3:2:1. The strategies of varied number of crosses and varied number of selections per cross can also be combined.

## CONCLUSION

For breeding populations managed with a variety of mating designs and selection strategies that allow higher contributions from better trees, positive assortative mating (PAM) substantially increased net gain in production populations selected from those breeding populations over that possible under random assortment of mates. The effect of PAM depends on the approach used to increase parent contributions, as this determines the distribution of genetic variance, inbreeding and coancestry in the population and how they develop over breeding cycles. PAM as mating system combined with increasing contributions from better parents by making more crosses among these trees and selecting equally from each family (UM) increased additive variance more than by making equal number of crosses per parent and selecting more from better families (US). While UM gave less accumulated additive gain in the breeding population, this was more than compensated by the larger expansion of additive variance, which led to greater net gain from production populations for both seed and vegetative propagation. This finding was independent of the level of inbreeding depression. The generally lower relatedness among the production population selections and lower rate of inbreeding made the UM designs with on average two crosses per parent superior to designs having one cross per parent, since progeny and clones were less inbred. The lower level of  $F$ , resulting from selection of half-sibs rather than full-sibs, is an advantage in breeding population management with clonal selection.

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