

O. Rosvall · T. J. Mullin

Positive assortative mating with selection restrictions on group coancestry enhances gain while conserving genetic diversity in long-term forest tree breeding

Received: 12 September 2002 / Accepted: 13 February 2003 / Published online: 8 July 2003
© Springer-Verlag 2003

Abstract Selection and mating principles in a closed breeding population (BP) were studied by computer simulation. The BP was advanced, either by random assortment of mates (RAM), or by positive assortative mating (PAM). Selection was done with high precision using clonal testing. Selection considered both genetic gain and gene diversity by “group-merit selection”, i.e. selection for breeding value weighted by group coancestry of the selected individuals. A range of weights on group coancestry was applied during selection to vary parent contributions and thereby adjust the balance between gain and diversity. This resulted in a series of scenarios with low to high effective population sizes measured by status effective number. Production populations (PP) were selected only for gain, as a subset of the BP. PAM improved gain in the PP substantially, by increasing the additive variance (i.e. the gain potential) of the BP. This effect was more pronounced under restricted selection when parent contributions to the next generation were more balanced with within-family selection as the extreme, i.e. when a higher status effective number was maintained in the BP. In that case, the additional gain over the BP mean for the clone PP and seed PPs was 32 and 84% higher, respectively, for PAM than for RAM in generation 5. PAM did not reduce gene diversity of the BP but increased inbreeding, and in that way caused a departure from Hardy-Weinberg equilibrium. The effect of inbreeding was eliminated by recombination during the production of seed orchard progeny. Also, for a given level of inbreeding in the seed orchard progeny or in a

mixture of genotypes selected for clonal deployment, gain was higher for PAM than for RAM. After including inbreeding depression in the simulation, inbreeding was counteracted by selection, and the enhancement of PAM on production population gain was slightly reduced. In the presence of inbreeding depression the greatest PP gain was achieved at still higher levels of status effective number, i.e. when more gene diversity was conserved in the BP. Thus, the combination of precise selection and PAM resulted in close to maximal short-term PP gain, while conserving maximal gene diversity in the BP.

Keywords Breeding population · Effective population size · Genetic gain · Inbreeding depression · Positive assortative mating

Introduction

The design of a breeding programme must reconcile the trade-off between gains achieved in the short term and those possible in the longer term (Danell 1993a; Lindgren and Mullin 1997; Meuwissen 1997; Grundy et al. 1998; Kerr et al. 1998). In a breeding population (BP) of constant size, without substructure and with unrelated founders, an emphasis on within-family with little or no among-family selection will maximise the long term response to selection (Dempfle 1975; Villanueva and Woolliams 1997). In the long run, gene diversity is also maximised by within-family selection and by equal parental contributions (Ballou and Lacy 1995; Lindgren et al. 1996). On the other hand, the greatest short-term genetic improvement is achieved when intensive family selection is applied in addition to selection within families. This greater exploitation of the additive genetic variance involves a loss of founder contributions, an increase in relatedness, and thus accelerates the loss of gene diversity, i.e. effective population size, reducing long-term breeding potential.

Genetically improved reforestation material is commonly derived from production populations (PP) such as

Communicated by O. Savolainen

O. Rosvall (✉)
The Forestry Research Institute of Sweden (SkogForsk),
Box 3, Sävar, 918 21, Sweden
e-mail: Ola.Rosvall@skogforsk.se
Tel.: +46-90-150950
Fax: +46-90-150960

T. J. Mullin
Department of Forestry, North Carolina State University,
Box 8002, Raleigh, NC 27695-8002, USA

seed orchards or clonal mixtures, usually being selected as subsets of a larger BP. At this stage, family selection within the BP can be applied without compromising short-term gain for conservation of genetic diversity in the BP (Burdon 1986). It is the population mean in combination with the within-population genetic variance that determines the potential to select a subset of outstanding individuals to serve as orchard parents or as ortets for clonal deployment. A long-term breeding strategy might therefore, in addition to average genetic improvement and gene diversity, also consider the apparent genetic variance of the BP.

Effect of selection and mating on genetic variance

During the first rounds of selection, among-family variance is reduced as a consequence of the selected parents being more alike, the “*Bulmer effect*” (Bulmer 1971, 1980; Falconer and Mackay 1996). This is a temporary reduction caused primarily by gametic phase or linkage disequilibrium and is counteracted by free recombination at meiosis (Mendelian sampling), and a balance is reached after a few generations. The magnitude of the decrease in variance due to selection depends on the initial narrow-sense heritability, selection accuracy and intensity (among others Bulmer 1971; Mueller and James 1983b; Wray and Hill 1989; Gomez-Raya and Burnside 1990). Consequently, under strong selection, there will be a substantial decrease both in BP response over the first generations and in the additional gain available from PPs. There is also a decrease in variance due to random assortment of mates (Falconer and Mackay 1996). When each selected tree is paired once with a random mate, the among-family additive variance in the next generation (variance of mid-parent values) is halved as compared to the total genetic variance of the selected parents. Positive assortative mating (PAM) has the opposite effect, enhancing among-family variance as a consequence primarily of gametic phase disequilibrium (Fisher 1918; Wright 1921; see also Jorjani 1995a, 1997b, c) and, if combined with selection, has the potential to raise the population mean.

The effect of PAM on response to selection has been proposed theoretically, and demonstrated both empirically and by simulation in a number of studies, as reviewed by Jorjani (1995b). However, these findings have, on occasion, been challenged by selection experiments. In his review Jorjani (1995b) concluded that the main inconsistency may be explained by “unconscious” assortative mating within small, selected lines of the control population that were erroneously thought to be mating at random.

PAM has been suggested as a means to enhance gain also in forest tree breeding (e.g. Cotterill 1984; Foster 1986, 1993; Cotterill et al. 1989) and was studied by computer simulation by Mahalovich (1990) and King and Johnson (1993). The reported effects for selection under PAM vary from about 5 to 50%. Selection following

PAM seems to be even more effective for a multi-trait index (Gianola 1982; Tallis and Leppard 1988). However, it is obvious that the effect of PAM depends very much on the specific conditions of the studies. In addition, variation in parent contribution at selection and accompanying different loss of effective size among alternative strategies makes it difficult to interpret the improvements due strictly to PAM.

As indicated by Smith and Hammond (1987), a combination of restricted parent contributions and high selection accuracy offers a potential for PAM to increase variance that has not yet been fully investigated. Furthermore, in tree breeding, studies of selection and PAM would be more relevant if they also focused on a selected PP, in addition to the behaviour over the entire BP. Finally, to be fair, any comparisons should be done at the same level of gene diversity or inbreeding (Lindgren 1986; Quinton et al. 1992). The objective of this study was to examine how selection and mating in a closed BP could combine gain and maintenance of high among-family genetic variance, while creating potential for large short-term gains in intensively selected PPs.

Materials and methods

Mating the breeding population and testing the candidates

Monte Carlo simulation was used to compare alternative mating and selection schemes. Our study is based generally on the Swedish Norway spruce breeding strategy, which is characterised by restricted selection, using primarily within-family selection, high selection intensity and selection precision increased by clonal replication (Danell 1991a, 1993b; Karlsson and Rosvall 1993; Rosvall et al. 1998). In all simulated scenarios 48 trees of a single BP were crossed to generate 24 full-sib families with 100 offspring per family, each clonally replicated with ten ramets. Random assortment of mates (RAM) involved random pairing of individuals in the BP, excluding the possibility of selfing. For positive assortative mating (PAM), the pairs were assigned in order of breeding values estimated from clone means. The term “random mating”, i.e. an equal chance for any individual to mate with any other individual, *including* the individual with itself, is used here only in a theoretical context. The simulation was carried out for five cycles of breeding and selection from generation 0 to 5, both considering and ignoring inbreeding depression.

Selection of the breeding and production populations

Selection of the 48 trees to the breeding population from the 2,400 tested clones was restricted by their relatedness in a set of parallel scenarios to vary parent contributions and generate a wide range of effective population sizes. The method of “group-merit selection” (GMS) (Lindgren and Mullin 1997) was used to vary relatedness to various degrees. The selection criterion used in GMS is: $B_{\omega} = \bar{G}_{\omega} - cT_{\omega}$, where B_{ω} is the “group-merit” of the selected sub-set ω ; \bar{G}_{ω} is the average of the breeding values of ω ; T_{ω} is the “group coancestry” (Cockerham 1967); and c is a weighting factor converting the group coancestry to the same scale as the breeding values. Breeding values were calculated as a combined-index (CI) where family and individual (clone mean) values were weighted by their respective heritabilities (as reviewed by Baker 1986). An iterative search algorithm was used to find the set of individuals that maximised the selection criterion function. By varying c from 0 to ∞ (approximated in the simulations by 1.0×10^7), sets of

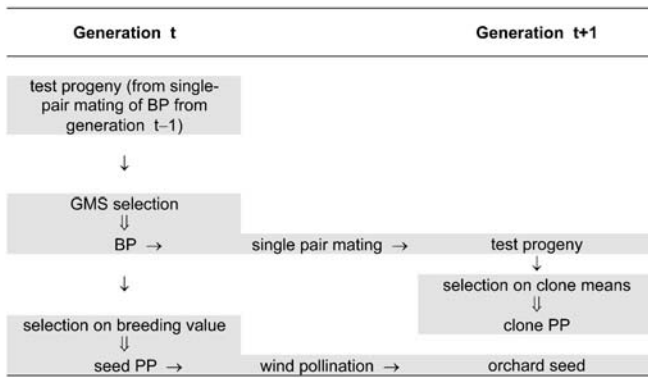


Fig. 1 Selection of the breeding (BP) and production populations (seed PP and clone PP)

selected individuals were identified that represented different levels of relatedness, as expressed by group coancestry (T_w) and status effective number ($N_s = 1/2T$), which is a measure of effective population size (Lindgren and Kang 1997).

In all scenarios, two PPs of six clones were selected, one for seed production (seed PP) being the highest-ranking subset of the BP, and the other as a mix of test-progeny genotypes selected for clonal deployment (clone PP) (Fig. 1). Selection of the seed PPs was based solely on breeding value, without further consideration of the gene diversity or inbreeding in the subset, thus no additional restrictions were applied, beyond those used for GMS selection of the BP itself. Selection of the clone PP was based on clone means, also without considering gene diversity or inbreeding. Note that the clone mix was selected from the test progeny of the current BP, and are thus the same generation as the seeds collected from the seed PP (Fig. 1).

Simulation model

Population advancement was simulated by POPSIM, a stochastic simulation software application based on a quantitative infinitesimal model (Mullin and 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 and 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 $N(\mu, V_A)$. The initial population mean (μ) and variance (V_{A0}) 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 $N(0, 0.5 V_{A0} (1 - F_{fm}))$, where F_{fm} is the average of F_f and F_m , which are the inbreeding coefficients of the female parent and male parents, respectively, obtained from pedigree analysis. The dominance effects for full sibs were sampled from a normal family distribution with variance equal to $N(0, 0.75 V_D (1 - F_{fm}))$, (the within-family portion of dominance variance) and with a family mean dominance effect sampled from $N(0, 0.25 V_D)$, where V_D was set to 25, thus being $0.25 V_A$. Environmental effects were sampled from $N(0, V_E)$, where V_E was set to 375 resulting in narrow-sense heritability $h^2 = 0.2$.

Inbreeding depression was simulated by reducing the individual dominance effect by $b F_{fm} \sqrt{V_P}$, the regression of inbreeding depression on the inbreeding coefficient of 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). The coefficient b was set to -4.4752 , to generate 1.0% inbreeding depression per 0.01 increase in F at additive variance

coefficient 0.1, which was considered appropriate for Norway spruce considering both growth and fitness characters (Eriksson et al. 1973; Andersson et al. 1974; Skrøppa 1996) and other tree species (Griffin and Lindgren 1985; Griffin and Cotterill 1988; Durel et al. 1996; Williams and Savolainen 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.

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 $G \times E$ interaction), with no variances associated with cloning (i.e. no C -effects). The stochastic variation in expected genetic effects and variances of a single scenario was described by the coefficient of variation (CV%) for results from 100 simulation iterations of a given scenario.

Comparisons at the same level of gene diversity

Group coancestry (T) is the probability that two homologous genes sampled randomly from a population are *identical* by descent (Cockerham 1967). Minimising T in a closed BP will minimise the random loss of alleles by genetic drift (Ballou and Lacy 1995) and maximise the proportional gene diversity in generation t ($GD_t/GD_0 = 1 - T$), where GD_0 is considered 1.0 in the source population of unrelated, non-inbred genotypes (Lacy 1995). Gene diversity is the probability that genes are *not* identical by descent and is equal to the expected heterozygosity after random mating (Nei 1973). Proportional GD describes the decay in GD due to increased relationship, and is independent of initial gene frequencies at a locus. Minimising group coancestry will also maximise conventional measures of effective population size, such as variance effective size (N_{eV}) (Crow and Kimura 1970), founder genome equivalents (FGE) (Lacy 1995), and, by definition, status effective number $N_s = 1/2T$ (Lindgren et al. 1996), but will not maximise inbreeding effective size (N_{eI}).

An increase in the inbreeding coefficient (F) reduces heterozygosity in proportion $(1-F)$, and may reduce tree performance due to inbreeding depression (Williams and Savolainen 1996). Since the group coancestry of the parents becomes the expected inbreeding coefficient of their progeny under panmictic mating, T or N_s are also important diversity parameters for trees selected for seed orchards (Lindgren and Mullin 1998). If selfing in a seed orchard is assumed not to produce viable offspring it is the average pair-wise coancestry ($\bar{\theta}$) for the N seed PP parent trees that becomes the expected inbreeding of the progeny (Falconer and Mackay 1996).

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 (Cockerham 1967; Nei 1977; Caballero 1994; Wang 1997a). Wright's F_{IS} parameter is negative, zero and positive with avoidance of close inbreeding, random mating and close inbreeding, respectively.

The PAM effect was defined as either the absolute or relative difference between PAM and RAM. It was of special interest to compare gain after five cycles of breeding and selection, at the maximum diversity obtained by within-family selection [corresponding to effective population size $N_{eV} = 96 - 1 = 95$ (Falconer and Mackay 1996)], with that obtained by GMS at an intermediate level of diversity. Here, $N_s = 8$ ($T = 0.0625$) was chosen as an "intermediate" diversity target, corresponding to $N_{eV} = 47$, near the minimum acceptable threshold ($N_{eV} = 50$) under the Swedish breeding strategy (Danell 1993b). In contrast, "minimum"- and "maximum"-diversity targets corresponded to the lowest and highest N_s obtainable after five cycles of breeding, respectively.

Results

Effective population size

In early generations, greater weight on group coancestry (T) generally maintained higher status effective number (N_s), but with less additive response (A) in the BP (Fig. 2a). After one cycle of breeding and selection, the additive variance (V_A) of the 48 new BP members was reduced from the initial level of 100 to 36 when selection was unrestricted among families (no weight on T), and to 80 when selection was balanced within families (infinite weight on T). The greater V_A at higher BP N_s led to relatively more gain from subsequent selection of PPs, resulting in PP gain that was much the same over the entire range of BP N_s (Fig. 2a). The larger gain of the clone PP compared to the seed PP is due to the tested clones being one generation more advanced and selected less restrictively, increasing additive gain, and a dominance effect (D) varying between 4.6 and 6.8, independent of the breeding cycle and BP N_s .

In later generations, the greatest gains were obtained at intermediate levels of BP N_s (Fig. 2b). At low BP N_s , there was a decline in the additive mean response of the BP, and less PP gain due to lower BP variance from both more-intense family selection and higher rate of inbreeding (Fig. 2d). At high BP N_s , the lower gain did not result from a decline in response but from greater restriction on relatedness, i.e. less intense family selection. The weight on T and the BP N_s giving the greatest gain increased in subsequent generations and tended to be higher for the PPs than for the BP. A variety of population parameters after five generations at the intermediate-diversity target level (BP $N_s = 8.0$) are given in Table 1.

Effects of PAM compared to RAM

Putting a high weight on T under PAM increased V_A substantially, after an initial decline in the first generation due to selection (Figs. 2a and b). The effect was greater the higher the weight on T. The increase of V_A by PAM continued throughout all five generations, while V_A for

Fig. 2 Additive variance (V_A) in the BP, and genetic effects for the BP, seed PP (A) and clone PP (A + D) after (a) 1 and (b) 5 generations, and the corresponding inbreeding coefficients (F) after (c) 1 and (d) 5 generations, assuming no inbreeding depression. The comparison is shown over a range of diversity (BP N_s) resulting from different weights on group coancestry (T) when advancing the BP

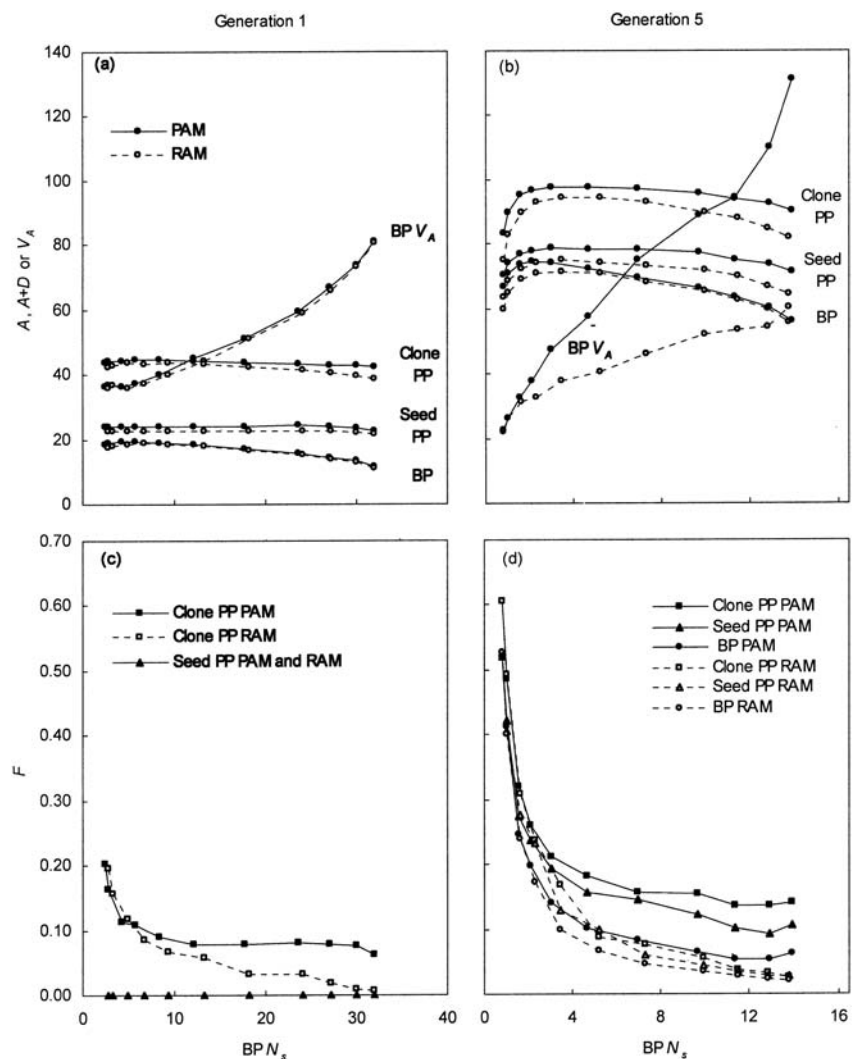


Table 1 Genetic parameters in the BP, seed PP and clone PP after five generations, for RAM and PAM at the intermediate-diversity target ($N_s = 8.0$ in the BP at generation 5) with and without accounting for inbreeding depression in the simulation. The coefficient of variation (CV%) describes the deviation from the

expected mean likely to occur by chance in a single iteration of the simulated program. The parameters are status effective number (N_s), additive variance (V_A), additive effect (A), dominance variance (V_D), dominance effect (D) and inbreeding coefficient (F)

Parameter	BP				Seed PP				Clone PP			
	RAM		PAM		RAM		PAM		RAM		PAM	
	Mean	CV%	Mean	CV%	Mean	CV%	Mean	CV%	Mean	CV%	Mean	CV%
No inbreeding depression												
N_s	8.0	6	8.0	7	2.0	19	1.8	26	3.0	16	2.4	29
V_A	47.4	27	77.3	38								
A	67.8	4	68.3	4	73.0	6	77.2	7	86.1	5	91.3	6
V_D	20.9	21	20.4	25								
D	4.9	23	4.8	19					6.3	31	5.5	40
F	0.04	31	0.07	35	0.06	88	0.13	88	0.06	71	0.14	67
With inbreeding depression												
N_s	8.0	6	8.0	7	2.1	20	2.2	20	3.1	17	2.9	18
V_A	46.2	27	68.1	31								
A	66.5	4	66.0	4	71.3	6	73.3	6	84.2	5	85.6	6
V_D	23.8	26	28.2	34								
D	2.3	51	1.6	77					2.7	78	1.9	135
F	0.02	20	0.03	31	0.02	54	0.03	68	0.03	29	0.04	38

Table 2 Genetic parameters under PAM, with their relative value expressed as a percentage of that under RAM in parentheses, for generations 1 through 5 for the intermediate- and maximum-diversity targets ($N_s = 8.0$ and 13.8 in the BP at generation 5,

respectively), assuming no inbreeding depression. The parameters are status effective number (N_s), additive variance (V_A), additive effect (A), dominance effect (D) and inbreeding coefficient (F)

Generation	BP				Seed PP			Clone PP		
	N_s	A	V_A	F	N_s	A^a	F	N_s	$A+D^a$	F
Intermediate-diversity level										
1	19.9 (101)	17 (102)	55 (104)	0.00	2.0 (96)	7 (119)	0.00	3.1 (80)	27 (105)	0.08 (190)
2	14.4 (101)	30 (100)	62 (122)	0.03 (193)	2.0 (93)	8 (144)	0.08 (192)	2.8 (81)	28 (111)	0.10 (235)
3	11.3 (99)	43 (101)	66 (138)	0.04 (188)	1.9 (89)	8 (136)	0.09 (207)	2.6 (80)	28 (110)	0.11 (268)
4	9.4 (100)	56 (101)	71 (151)	0.06 (183)	1.9 (91)	9 (164)	0.11 (279)	2.4 (76)	28 (112)	0.12 (201)
5	8.0 (100)	68 (101)	77 (163)	0.07 (165)	1.8 (89)	9 (171)	0.13 (220)	2.4 (79)	28 (115)	0.14 (216)
Maximum-diversity level										
1	32.0 (100)	11 (103)	81 (101)	0.00	4.2 (101)	11 (107)	0.00	3.4 (88)	31 (111)	0.06 (1007)
2	24.0 (100)	23 (101)	91 (131)	0.03 (441)	3.6 (94)	12 (126)	0.05 (862)	2.9 (72)	32 (121)	0.08 (663)
3	19.3 (100)	34 (101)	106 (168)	0.04 (353)	3.3 (90)	14 (159)	0.07 (549)	2.6 (72)	33 (122)	0.08 (529)
4	16.2 (101)	45 (100)	118 (188)	0.05 (287)	3.1 (87)	15 (177)	0.07 (497)	2.5 (66)	34 (128)	0.12 (431)
5	13.9 (101)	56 (100)	131 (218)	0.06 (301)	2.9 (84)	16 (184)	0.11 (383)	2.5 (70)	34 (132)	0.14 (536)

^a PP – BP

RAM continued to decrease, although more slowly after the large drop in generation one and with less differentiation with respect to BP N_s (Table 2, Fig. 2b). The difference in BP V_A between PAM and RAM became more pronounced from generations 2 through 5, (from 22 to 63% at BP $N_s = 8.0$, and from 31 to 118% at BP $N_s = 13.8$).

Compared to RAM, PAM increased the BP additive mean up to 6% in early generations, and up to 12% in later generations, but only when BP N_s was low (Figs. 2a and b). Concomitant with the largest increase in BP V_A (maximum-diversity level), the additional gain over the BP mean for the seed PP and clone PP was increased by

PAM for generation one to five by 7 to 84% and 11 to 32%, respectively (Figs. 2a and b, Table 2).

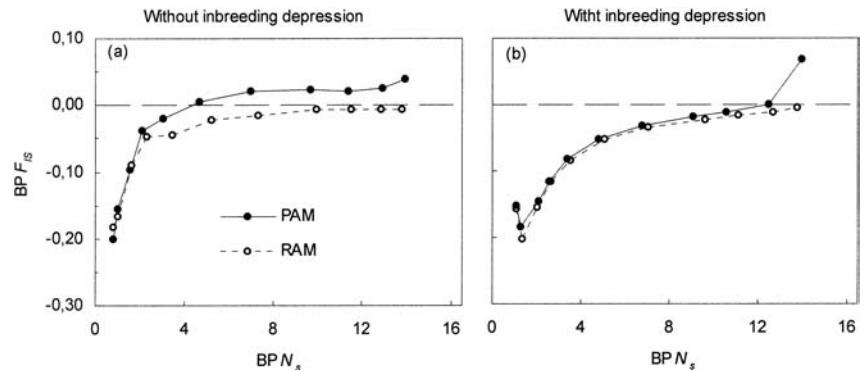
If the maximum-diversity level is given up for the intermediate level (BP N_s declining from 13.8 to 8.0), the accumulated response within the BP under PAM was initially 45.7% higher, but decreased to 21.2 over the generations (Table 3). The differences were similar for the BP under RAM. However, the corresponding increase in total genetic gain from the clone PP obtained under PAM was only 4.0 to 7.2% (generation 1 to 5), which was about half as large an increase as produced under RAM (Table 3).

For a given weight on T in selection, the BP N_s differed very little between PAM and RAM, but within-

Table 3 Differences in % over generations in total gain, between the maximum- (N_s 13.8) and intermediate-diversity target (N_s 8.0) for the BP, seed PP and clone PP. Results are presented both with and without inbreeding depression in the simulation

Generation	RAM			PAM		
	BP	Seed PP	Clone PP	BP	Seed PP	Clone PP
No inbreeding depression						
1	45.7	3.7	9.0	44.2	5.5	4.0
2	31.3	9.8	11.3	30.0	8.4	4.8
3	25.8	14.2	11.6	25.8	6.5	5.6
4	22.9	13.6	12.2	23.6	7.6	5.9
5	21.2	13.3	12.8	22.0	7.9	7.2
With inbreeding depression						
1	44.2	3.8	7.1	42.2	5.8	4.4
2	29.0	8.8	8.9	26.4	7.0	3.9
3	23.6	11.8	9.4	21.4	5.3	4.9
4	20.6	11.4	8.1	20.0	6.7	4.9
5	18.9	11.4	8.7	18.6	7.9	4.5

Fig. 3 F_{IS} in the BP after 5 generations for PAM and RAM, (a) assuming no inbreeding depression and (b) accounting for inbreeding depression in the simulation. The comparison is shown over a range of diversity (BP N_s) resulting from different weights on group coancestry (T) when advancing the BP



family selection (maximum-diversity target) under PAM increased N_s slightly in later generations (Table 2). Thus, the maximum possible BP N_s after five generations was higher under PAM. This is explained by increased F_{IS} at medium and high levels of BP N_s under PAM, while decreasing under RAM from the expected value of zero under truly random mating (Fig. 3a). For unrestricted selection, the exclusion of selfing made F_{IS} negative for both mating systems.

PAM reduced the seed PP N_s to 89 and 84% of that obtained under RAM at the intermediate- and maximum-diversity targets, respectively, in generation five (Table 2). This translates to a potential increase in inbreeding of the seed PP progeny (F_{prog}) by up to 0.03 units of F (data not shown). However, when compared at the same levels of seed PP N_s , i.e. the same inbreeding in the progeny following random mating in the orchard, the additive mean for the seed PP was higher under PAM than it was under RAM (Fig. 4a). If selfs are assumed to be non-viable, the expected inbreeding of the seed PP progeny was slightly lower under PAM than for RAM (Table 4). Compared at the same level of inbreeding, the clone PP gain under PAM was superior to RAM, except at the lowest levels of inbreeding (Fig. 5a).

Under PAM, more matings took place between related trees, which increased F (Fig. 2d, Table 2). For the BP at the intermediate-diversity target, F was increased by PAM with 93–65% to 0.03–0.07 over the generations. In

comparison, at the maximum-diversity target, BP F was slightly lower, even though the relative increase by PAM was higher (Table 2). Since there were no restrictions on relatedness or inbreeding for selection of high-ranking trees to PPs, these trees were even more inbred, especially under PAM (Figs. 2c and d). At the maximum-diversity target, F under PAM in generation 5 for the seed PP and the one-generation-older clone PP was 0.11 and 0.14, respectively, an increase of 0.08 and 0.12 units above the level of RAM was obtained, respectively (Fig. 2d, Table 2).

The coefficient of variation among simulation runs (CV%) at generation five for a variety of population parameters at the intermediate-diversity target level (BP $N_s = 8.0$) are given in Table 1. The CV for the BP additive genetic effects was 4% for both RAM and PAM, while genetic variances and dominance effects were more variable with CVs in the range of 20 to 40%. F in the PPs showed even greater variation, 70 to 90%. N_s was more variable in the seed PP than in the BP, with CVs 19 to 26% and 6 to 7%, respectively. Similar CVs were observed for parameters under the maximum diversity scheme (BP $N_s = 13.8$); except for N_s whose CV was less than 1% in the BP and 8 to 11% in the seed PP (data not shown).

Fig. 4 Seed PP additive gain (A) for PAM and RAM compared at the same seed PP N_s , after 1 and 5 generations (a) assuming no inbreeding depression and (b) accounting for inbreeding depression in the simulation. The comparison is shown over a range of diversity (seed PP N_s) resulting from different weights on group coancestry (T) when advancing the BP

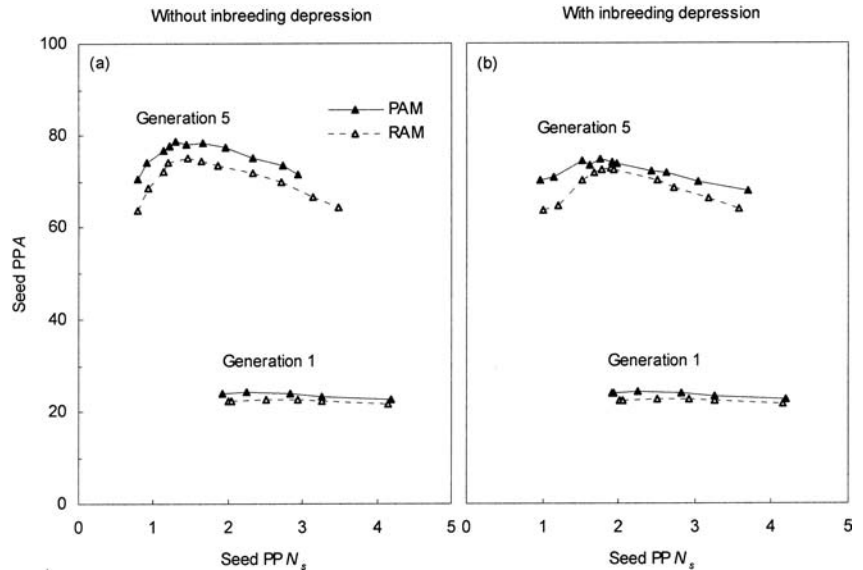


Table 4 Expected inbreeding in seed PP (F) and seed PP progeny (F_{prog}) in generation 5, under RAM and PAM at intermediate- and maximum-diversity levels in the BP ($N_s = 8.0$ and 13.8 , respectively, at generation 5), with and without both inbreeding depression and selfing in the seed orchard. The comparison is made at the same seed PP $N_s = 2.00$ for the intermediate-diversity target, and at the highest N_s found for the maximum-diversity target level

Seed PP and seed PP-progent parameters	No inbreeding depression		Inbreeding depression	
	RAM	PAM	RAM	PAM
Intermediate-diversity level				
Seed PP N_s	2.00		2.00	
Seed PP F	0.057	0.120	0.024	0.035
F_{prog} with selfing ^a	0.250	0.250	0.250	0.250
F_{prog} no selfing ^b	0.194	0.188	0.198	0.197
Maximum-diversity level				
Seed PP N_s	2.93		3.57	
Seed PP F	0.031	0.107	0.010	0.017
F_{prog} with selfing ^a	0.171	0.171	0.140	0.140
F_{prog} no selfing ^b	0.102	0.094	0.067	0.066

^a F_{prog} with selfing = group coancestry (T) of the six parents

^b F_{prog} no selfing = average pair-wise coancestry (θ) of the six parents

Simulated inbreeding depression

In the presence of inbreeding depression, the enhancement of V_A by PAM was slightly reduced (Fig. 6a compared to Fig. 2b, Table 1). In general for both RAM and PAM, the additive mean of the BP was reduced by 1 to 2% and the gain of the PPs by 5 to 7% at the intermediate- and maximum-diversity levels, with the higher figures for PAM in generation five. This was caused partly by lower selection precision due to greater dominance variance (Table 1). For low BP N_s scenarios causing high F , the genotype mean of the clone PP was much depressed and inbreeding reached levels in later generations at which all extra gain from the clone PP was lost (Fig. 6a).

The effect of PAM over RAM on PP gain was reduced by about two thirds and one half for the seed PP and clone PP, respectively, compared to the case with no inbreeding depression at both intermediate and high levels of N_s in the BP (Fig. 6a compared to 2b). However, when examined at the same level of PP N_s and F , PAM

maintained its advantage over RAM for both types of PPs (Figs. 4b and 5b).

The chance of selecting highly inbred trees was reduced in the presence of inbreeding depression, and F was much decreased in both the BP and PPs, especially from the high levels of inbreeding caused by PAM in simulations without inbreeding depression (Figs. 2d and 6b, Table 1). The enhancement of F_{IS} by PAM also disappeared (Fig. 3b). The BP F for the maximum-diversity target scenario was an exception, since no selection against inbreeding can take place when a BP is advanced entirely by within-family selection under the assumption of equal inbreeding depression for sibs of a family considered in the simulation. Selection against inbred offspring also reduced the variation in F among replicate runs, while inbreeding depression increased dominance variance and its variation among runs (Table 1).

With inbreeding depression N_s of the seed PP after five generations was increased under PAM (Fig. 4b compared to 4a, Table 2), reducing the potential inbreeding depression in orchard progeny, seen for the maximum-

Fig. 5 Clone PP total gain ($A+D$) under RAM and PAM, compared at the same clone PP F after 1 and 5 generations (a) assuming no inbreeding depression and (b) accounting for inbreeding depression in the simulation. The comparison is shown over a range of inbreeding (clone PP F) resulting from different weights on group coancestry (T) when advancing the BP

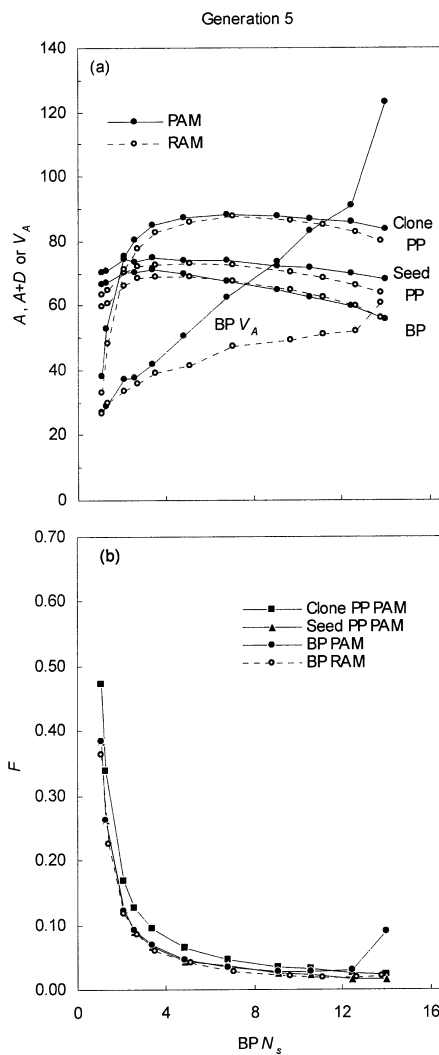
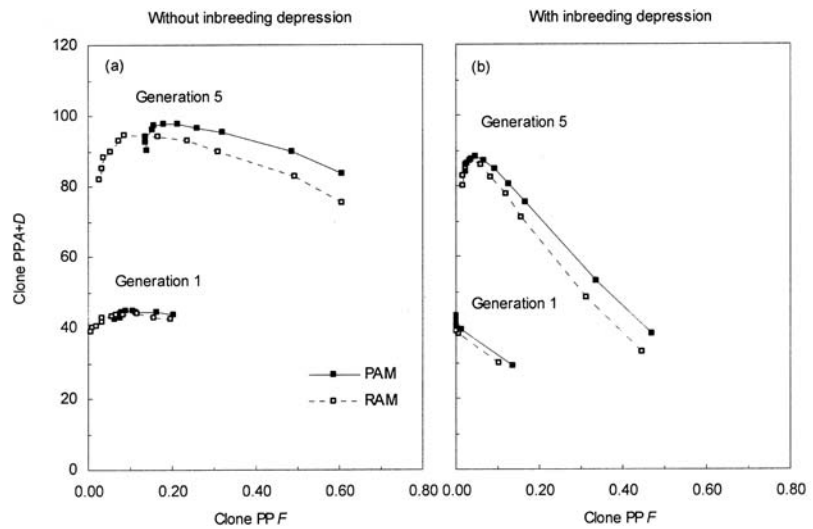


Fig. 6 (a) Additive variance (V_A) in the BP and genetic effects for the BP, seed PP (A) and clone PP ($A+D$) after 5 generations for simulations including inbreeding depression, and (b) corresponding inbreeding coefficient (F) for those scenarios with PAM. The comparison is given over a range of diversity ($BP N_s$), resulting from different weights on group coancestry (T) when advancing the BP

diversity level in Table 4. As expected, the substantial reduction in F for a seed PP at a given $BP N_s$ had much less effect in reducing the inbreeding of the seed PP progeny (Table 4).

Inbreeding depression increased the level of $BP N_s$ giving maximum PP gain, especially for the clone mix (Fig. 6a compared to Fig. 2b) and the maximum for PP gain became very flat. Therefore, the additional increase in clone PP total genetic gain, when the maximum-diversity level was given up for the intermediate-diversity level, was lower with inbreeding depression and varied between 3.9 and 4.9% over generations (Table 3).

Discussion

Breeding population mean and variance

Most studies of PAM have been either for selected populations with unrestricted parent contributions or unselected populations (Jorjani 1995b; Jorjani et al. 1997a). In this simulation study, exploring the full range of possible parent contributions and the resulting range of effective population size gave an informative demonstration of the effects of PAM. In addition, comparisons of populations were most meaningful at the same N_s , having the same proportional gene diversity and the same decay in expected heterozygosity due to drift, relative to the common source population (Lacy 1995; Lindgren et al. 1996; Lindgren and Kang 1997), and thus the same reduction in genic variance (*in sensu* Bulmer 1976), i.e. potential genetic variance.

The key result of this study is the maintenance of the enhanced additive variance by PAM, when relatedness is strongly restricted during selection. With equal or near-equal parent contributions resulting from within-family selection at the extreme, PAM more than compensated for the decrease in variance due to both selection (Bulmer 1971) and random assortment of mates (Falconer and Mackay 1996). These results are consistent with the

theory and earlier findings that the enhancing effect of PAM on variance is largest in unselected populations where no family selection counteracts the gametic phase disequilibrium (e.g. Bulmer 1976; Jorjani et al. 1997b; Mueller and James 1983a; Verrier et al. 1989). Consequently, greater genetic gain could be obtained from subsets of the BP selected as PPs, producing a more favourable trade-off between short-term gain and conservation of gene diversity.

This effect of PAM in maintaining a large variance in the BP under restricted selection excludes a concurrent selection response in the BP additive mean. The enhanced variance can only be transformed to a response in the BP itself by a component of family selection, i.e. unequal parent contributions, achieved here by GMS with lower weights on group coancestry. If the enhanced variance is used to advance the BP in this way, the increased response in the BP is also converted into gain in the PPs, but to a lesser degree and at the cost of lost gene diversity and increased inbreeding. Consequently, under PAM with highly restricted parent contributions, more PP gain is produced, and with more efficient use of both genetic variance and diversity.

Other studies that have been focused on the response to selection in a breeding population under PAM (e.g. Smith and Hammond 1987; Shepherd and Kinghorn 1994) have reported that the effect of PAM on the BP additive mean increases when selection includes information from relatives, i.e. combined-index selection or selection on BLUP breeding values. This is consistent with our finding of a greater PAM effect in the BP for no weight on T, compared with a lower PAM effect for intermediate and high weights, where the former corresponds to unrestricted combined-index selection. In general, high heritability and high selected proportion (low selection intensity) are two prerequisites for strong relative response effects of PAM compared to RAM (e.g. Fernando and Gianola 1986; Smith and Hammond 1987; Shepherd and Kinghorn 1994; Jorjani 1995b). Clonal testing, although influenced by non-additive variance, is highly efficient in increasing test precision to predict breeding values (e.g. Rosvall et al. 1998) and can be seen as increasing narrow-sense heritability, in this case from 0.2 to approximately 0.9. Thus, the small relative increase, in the BP additive mean under unrestricted selection, not more than 12%, is due rather to the low selected proportion (0.02), while larger relative effects of PAM are expected at higher selected proportions (0.5–0.9). However, effects of PAM, similar to those found in our study under intensive selection and high heritability/test precision, have been reported by Shepherd and Kinghorn (1994) for unrestricted selection when accounting for deviation from normality in breeding values, as was simulated by the stochastic model used here.

The expansion of the additive variance by PAM is primarily due to gametic phase disequilibrium (Bulmer 1971, 1986; Falconer and Mackay 1996). Both selection and PAM can also cause a departure from H-W equilibrium, acting to decrease and increase, respectively, the

additive variance (Bulmer 1976, 1980; Mueller and James 1983a; Verrier et al. 1989; Jorjani et al. 1997b, c). If the numbers of parents or loci are large, departures from H-W equilibrium are negligible (Bulmer 1980; Mueller and James 1983a). However, if the population is small, drift and an increase in homozygosity at the expense of heterozygotes, lead together to a net reduction of the within-family variance (Crow and Felsenstein 1968; Bulmer 1976; Verrier et al. 1989; Wang 1996; and see also Jorjani 1995a and Jorjani 1997b, c), as occurred under the unrestricted selection scenarios.

Theoretically, under the infinitesimal model, the increase in additive variance by PAM has no upper limit for gametic phase disequilibrium among an infinite number of loci (Wright 1921; Bulmer 1980; Jorjani 1997b), while inbreeding can at most double the variance (Falconer and Mackay 1996). However, the benefits of PAM in the long term are limited if the number of loci controlling the selection trait is small. After the initial increase in variance due to gametic phase disequilibrium, the additive variance will then decrease due to fixation of favourable alleles (Jorjani et al. 1997c). PAM cannot increase the limit of selection response, but this limit can be reached in fewer generations.

Bulmer (1980) considered a trait determined by a large number of loci without epistasis, and showed that PAM does not affect the distribution of dominance or environmental effects. It is commonly accepted that, for practical purposes, one can assume that dominance variance is unchanged by PAM (e.g. Crow and Kimura 1970; Vetta 1976; Falconer and Mackay 1996), although Jorjani et al. (1998) claimed that with a small population size and a large number of loci, the dominance variance increases in the long term.

Breeding population structure

Increased inbreeding is a potential drawback of PAM (e.g. McBride and Robertson 1963; Shepherd and Kinghorn 1994). In our scenarios more uniform parent contributions enhanced BP N_s and decreased F for both PAM and RAM. Concomitantly, PAM by itself increased F over the whole range of N_s compared to RAM, although PAM had almost no effect on BP N_s , as indicated by a higher F_{IS} . This occurs since mating along the rank order takes place more frequently among related trees causing a “lining effect” (Falconer and Mackay 1996), shown as a departure from H-W equilibrium. The lining effect occurs in a way that does not split the BP into higher and lower performing parts, as there is a continuous migration of trees up the ranking, in response to the precise selection of individuals within families and the continuous re-establishment of within-family variance. When T is subdivided into within- and among-individual components, the lining effect is reflected as an increase in self-coancestry, $0.5(1+F)$, and a decrease in average pair-wise coancestry, $\bar{\theta}$. For our most restricted selection scheme under PAM,

the net effect of reducing $\bar{\theta}$ and increasing F was a slight increase in BP N_s . In this case, more gene diversity was conserved in the BP, as is commonly reported for populations structured by sublining (Lindgren et al. 1996; Gea et al. 1997; McKeand and Bridgewater 1998). More important is that the positive difference between F and $\bar{\theta}$, as seen under PAM, indicates that more unrelated trees can be selected for seed production and that less inbreeding will occur after out-crossing in seed orchards.

Part of the solution to the built-in conflict between genetic gain in the short and long term can be met by structuring of the BP. Both a hierarchical structure and sublining of the BP will keep selection intensity high, control loss of gene diversity, and reducing inbreeding in production populations (Burdon et al. 1977; Danell 1993a; Williams et al. 1995). PAM with selection restrictions has similarities to both sublining and open-nucleus breeding (van Buijtenen 1976; Burdon and Namkoong 1983; Cotterill et al. 1989; White 1993; Shepherd and Kinghorn 1994; Williams and Hamrick 1996). Through departures from H-W equilibrium, all these breeding strategies are expected to increase total genetic variance and inbreeding, but decrease overall group coancestry and thus conserve more gene diversity. Genetic variance within a single subline or the nucleus will, however, become lower, decreasing the response to selection.

A major benefit of sublining is the option to select unrelated clones for seed production. The drawbacks are greater inbreeding in tested genotypes and slower progress in the BP (Smith and Quinton 1993; Gea et al. 1997; McKeand and Bridgewater 1998; Rosvall et al. 1998). Relatedness and inbreeding within an intensively managed nucleus increases rapidly if it is small, reducing both BP progress and PP gain (James 1977, 1978; Roden 1995). In an open nucleus, this is counteracted by periodic infusion of less-related trees from the main line. In this respect, PAM as applied here can be seen as a form of an open-nucleus breeding strategy (Shepherd and Kinghorn 1994).

Realised production population gain

The inclusion of inbreeding depression in the simulation helped to quantify the trade-off between increased gain from co-selected high-performing relatives and the loss in gain due to expression of the genetic load. Inbreeding depression affects genetic gain directly by reducing tree performance in commercial forest stands and indirectly through increased dominance variance, which makes prediction of additive effects, i.e. breeding values by clonal testing, less precise. Lower selection precision will reduce the rate of progress for the BP additive mean, and lower correlation between mates for additive effects will lessen the enhancement of BP additive variance by PAM. In addition, reproductive traits are affected and depressed

trees may lose fertility, decreasing seed orchard productivity (Lindgren and Gregorius 1976; Williams and Savolainen 1996).

For clonal testing and deployment of tested clone mixtures, it is the F of the clones that determines the inbreeding depression; clone performance was adjusted in the simulation at the assumed rate of inbreeding depression. Although slightly more inbred, and consequently more depressed, the clone mix under PAM was always superior to that under RAM, and this also holds true when compared at the same inbreeding coefficient.

The advantage in absolute terms of PAM over RAM seed PP gain when accounting for inbreeding depression will depend on how the matings are arranged. The additive effects presented here for the seed PPs are potential effects (without inbreeding depression), which can only be realised as gain in their progeny if the seed-PP selections are crossed with unrelated trees (from different sublines). If this is not the case, and the parents are related and/or if selfing produces viable progeny, the comparison of the seed PP progeny additive effect under PAM and RAM at the same level of seed PP N_s as in Fig. 4 (resulting in equal F and the same amount of inbreeding depression in the seed PP progeny under random mating), will still show the relative ranking for the progeny performance, PAM being superior to RAM. However, the "lining effect" (greater F_{IS} = higher F and lower $\bar{\theta}$ for the same N_s) under PAM (reached in scenarios when inbreeding depression was not accounted for), resulted in lower inbreeding in the progeny for PAM than for RAM at the same N_s . Therefore, if selfing is avoided or does not produce viable offspring the realised additive net gain of PAM (Fig. 4a) would be slightly greater than for RAM. Low viability of selfs is expected for Norway spruce (Koski 1973) and in many other species, according to Williams and Savolainen (1996). When inbreeding depression was included in the simulation (resulting in selection against inbreeding), F and F_{IS} were similar for PAM and RAM, and the relative difference at equal seed PP N_s (Fig. 4b) would apply similarly to seed PPs with or without selfing.

The results applied to the Swedish and other breeding programs

In a previous study of the Swedish Norway spruce breeding strategy, the within-family clonal selection option under RAM was shown to be sustainable, robust and efficient for ten generations, combining high genetic gain with gene conservation (Rosvall et al. 1998). Within-family selection leads to the lowest loss of BP gene diversity resulting from only genetic drift (Ballou and Lacy 1995). As shown here, under the same conditions PAM can improve genetic gain in production populations with no further loss of gene diversity from the BP.

In addition, by introducing a degree of family-selection and accepting a decrease in BP N_s , after five generations, from 13.8 to 8.0, the PP gain reached a level

very close to the observed maximum, although this additional gain is rather small and varied between 4 and 8% over five generations. The increase for BP T is from 0.036 to 0.062, which corresponds to a reduction in proportional gene diversity from 0.96 in the pure-drift scenario to 0.94, and a reduction in potential genetic variance with 4%. Thus under PAM, virtually all potential gain can be obtained at a fairly low cost in terms of loss of gene diversity and genetic variance. However, the increased inbreeding in seed orchard progeny (F_{prog} assuming no selfing is 0.19–0.20) is most harmful, and must be managed in the Swedish strategy by out-crossing among multiple sub-populations. The high rate of inbreeding will also cause problems in managing the breeding population and for clonal testing. Therefore, it might be questioned if the small additional gain obtained by imbalanced parent contributions is worth exploiting since the corresponding F_{prog} stays at 0.07–0.09 at the maximum-diversity level.

In the simulation of the Swedish program, the precise selection by clonal testing is largely responsible for the high gain under balanced parent contributions at high BP N_s . Efficient exploitation of within-family variance is without any cost in reduced variance, since the within-family variance is re-established by recombination. Owing to the high selection precision, the full effect of PAM on variance will in addition be reached within a few generations, as was also shown by Shepherd and Kinghorn (1994). In contrast, for situations with low heritability or low selection precision, progress from within-family selection is less and relatively more is gained from unbalanced parental contributions (Rosvall and Andersson 1999). However, if family variance is exploited there are large losses in both among-family variance (Bulmer 1971; Mueller and James 1983b; Wray and Hill 1989; Gomez-Raya and Burnside 1990) and within-family variance (Verrier et al. 1989, 1990, 1991).

Most breeding programs do not use clonal testing to improve selection precision. Still, these results are applicable to any strategy where individual trees are selected efficiently for breeding value, either by progeny testing or by phenotypic selection for characters with a high narrow-sense heritability. However, PAM cannot increase BP-variance in strategies where selection precision is improved by information from relatives, resulting in co-selection of sibs, i.e. family-selection. Therefore, no more complicated mating systems than single-pair mating are needed since it can achieve maximum efficiency for forward selection with minimum effort in tree-breeding populations (van Buijtenen and Burdon 1990; Kerr 1998). Breeding strategies with factorial or diallel mating systems using family-individual indexes (CI) or individual-BLUP breeding values for forward selection are not suitable for increasing BP variance unless the crosses are used for progeny testing and backward selection, even though these strategies will gain from the positive effect of PAM on BP-gain. Double-pair mating has some advantages to single-pair mating when considering inbreeding depression (Rosvall et al., in press 2003).

Limitations and options for future improvements of the simulation model

Mate allocation

While the assortment of mates has no effect on the group coancestry of their offspring, it has a substantial impact on inbreeding. In this study, pair-wise coancestry was not considered in mate allocation, except to avoid selfing. When accounting for inbreeding depression, highly inbred families had a lower probability to contribute to the breeding population since clonal testing was applied. Thus, some matings were done that could be predicted to perform poorly. In a real breeding situation, mating of highly related trees would generally be avoided, reducing the rate at which inbreeding increases in early generations. If selection is applied to a finite population without regard to family origin, avoidance of full- and half-sib mating will result in slightly lower inbreeding in the very long run, while selecting equally from each family will eventually result in higher inbreeding (e.g. Caballero 1994; Wang 1997b). Avoidance of mating relatives might also reduce the assortative effect of PAM, since similar trees tend to be related, i.e. the correlation between breeding values of the mates might be reduced, although the reduction seems to be small (Rosvall et al., in press 2003).

Inbreeding depression

Our model for inbreeding depression is approximate, as it ignores the effect of inbreeding on the genetic covariance associated with dominance and assumes negligible purging of the genetic load over a small number of generations of weak inbreeding. Nevertheless, this approach to simulating effects of inbreeding depression as directional dominance (Falconer and Mackay 1996) should give unbiased predictions for traits influenced by large numbers of loci under complete dominance (de Boer and van Arendonk 1992). Since inbreeding depression was assumed to be proportional to F , it was also equal for all sibs in a full-sib family, and varied only among families. In reality, inbreeding depression varies among sibs, despite their having the same expectation of F from the pedigree (Durel et al. 1996; Wu et al. 1998a, b). For populations under selection, this variation will also reduce the impact of inbreeding depression, as will natural selection (Lesica and Allendorf 1992; Meuwissen and Woolliams 1994). It might be possible that the slightly higher inbreeding by PAM (increased F_{IS}) may intensify the purging of detrimental genes in early generations, without the more negative long-term effects, reducing the inbreeding depression more than by RAM (Williams and Savolainen 1996).

Conclusion

PAM in combination with precise and restricted selection of relatives can substantially enhance the additive variance of the BP, resulting in extra short-term gain in the PP and increased long-term sustainability of both genetic gain and diversity. The effect of PAM compared to RAM was greater the more balanced were the parental contributions, increasing the optimal status effective number, N_s , of the BP to realise maximum PP gain. PAM increased inbreeding resulting in departure from H-W equilibrium, but the simultaneous decrease in pair-wise coancestry between trees decreased the level of inbreeding in their seed progeny. Consequently, the effect of PAM will be greatest when applied to a diversity conservative breeding program, such as that in Sweden. A general finding is that, if the objective is maximum genetic gain in a PP, N_s of the BP should be maintained at a higher level than if the response is to be maximised in the BP. This was observed under both PAM and RAM. If inbreeding depression is a major factor, an even higher BP N_s will give the greatest PP gain. Thus, under these conditions there is little conflict between short-term and long-term maximum genetic gain.

Acknowledgements This work was carried out when the authors were visiting scientists at the Department of Forest Genetics and Plant Physiology, SLU, Umeå, Sweden. We gratefully acknowledge support received from the Jacob Wallenberg Foundation and Föreningen Skogsträdsförädling. We also thank Dr. Dag Lindgren, Dr. Hossein Jorjani, Dr. Bailian Li, and one anonymous reviewer, for valuable and constructive contributions to the manuscript.

References

- Andersson E, Jansson R, Lindgren D (1974) Some results from second generation crossings involving inbreeding in Norway spruce (*Picea abies*). *Silvae Genet* 23:34–43
- Baker RJ (1986) Selection indices in plant breeding. CRC Press, Boca Raton, Florida, USA
- Ballou JD, Lacy RC (1995) Identifying genetically important individuals for management of genetic variation in pedigreed populations, Chap. 5. In: Ballou JD, Gilpin M, Foose TJ (eds) Population management for survival and recovery: analytical methods and strategies in small population conservation. Columbia University Press, New York, pp 76–111
- Borralho NMG (1994) Heterogeneous selfing rates and dominance effects in estimating heritabilities from open-pollinated progeny. *Can J For Res* 24:1079–1082
- Buijtenen van JP (1976) Mating designs. In: Proc IUFRO Joint meeting of genetic working parties on advanced generation breeding, Bordeaux, 14–18 June 1976. Institut national de la recherche agronomique, Cestas, France, pp 11–20
- Buijtenen van JP, Burdon RD (1990) Expected efficiencies of mating designs for advanced generation selection. *Can J For Res* 20:1648–1663
- Bulmer MG (1971) The effect of selection on genetic variability. *Am Natl* 105:201–211
- Bulmer MG (1976) The effect of selection on genetic variability: a simulation study. *Genet Res* 28:101–117
- Bulmer MG (1980) The mathematical theory of quantitative genetics. Clarendon Press, Oxford
- Burdon RD, Namkoong G (1983) Short note: multiple populations and sibilines. *Silvae Genet* 32:221–222
- Burdon RD, Shelbourne CJA, Wilcox MD (1977) Advanced selection strategies. In: Proc FAO IUFRO Third World Consultation on Forest Tree Breeding, Canberra, Australia, 21–26 March 1977, Vol. 2. CSIRO, Canberra, Australia, pp 1133–1147
- Caballero A (1994) Developments in prediction of effective population size. *Heredity* 73:657–679
- Cockerham CC (1967) Group inbreeding and coancestry. *Genetics* 56:89–104
- Cotterill PP (1984) A plan for breeding radiata pine. *Silvae Genet* 33:84–90
- Cotterill PP, Dean CA, Cameron J, Brindbergs M (1989) Nucleus breeding: a new strategy for rapid improvement under clonal forestry. In: Gibson GL, Griffin AR, Matheson AC (eds) Breeding tropical trees: population structure and genetic improvement strategies in clonal and seedling forestry: Proc Conf held in Pattaya, Thailand, 28 November to 3 December 1988, by IUFRO Working Parties S2.02-08 Tropical species provenances and breeding, and S2.02-09 Eucalypt provenances and breeding. Oxford Forestry Institute, Oxford, UK and Winrock International, Arlington, Virginia, pp 39–51
- Crow JF, Felsenstein J (1968) The effects of assortative mating on the genetic composition of a population. *Eugenics Quart* 15:85–97
- Crow JF, Kimura M (1970) An introduction to population genetics theory. Harper and Row, New York
- Danell Ö (1991a) Survey of past, current and future Swedish forest tree breeding. *Silvae Fenn* 25:241–247
- Danell Ö (1991b) Possible gains in initial stages of a national tree improvement programme using different techniques. For Tree Improv 23. Proc Nordic Tree Breeders Meeting, September 1990, Hørsholm, Denmark pp 11–30
- Danell Ö (1993a) Tree breeding strategy: are we too concerned conservationists but inefficient breeders. In: Lee SJ (ed) Progeny testing and breeding strategies: Proceedings of the Nordic Group of Tree Breeders, Edinburgh, 6–10 October 1993. Forestry Authority, Scotland, pp 80–94
- Danell Ö (1993b) Breeding programmes in Sweden. 1. General approach. In: Lee SJ (ed) Progeny testing and breeding strategies: Proceedings of the Nordic Group of Tree Breeders, Edinburgh, 6–10 Oct 1993. Forestry Authority, Scotland, pp 128 (i–v)
- de Boer IJM, van Arendonk JAM (1992) Prediction of additive and dominance effects in selected and unselected populations with inbreeding. *Theor Appl Genet* 84:451–459
- Dempfle L (1975) A note on increasing the limit of selection through selection within families. *Genet Res* 24:127–135
- Durel CE, Bertin P, Kremer A (1996) Relationship between inbreeding depression and inbreeding coefficient in maritime pine (*Pinus pinaster*). *Theor Appl Genet* 92:347–356
- Eriksson G, Schelander B, Åkebrand V (1973) Inbreeding depression in old experimental plantations of *Picea abies*. *Hereditas* 73:185–194
- Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics, 4th (edn). Longman, London and New York
- Fernando RL, Gianola G (1986) Effect of assortative mating on genetic change due to selection. *Theor Appl Genet* 72:395–404
- Fisher RA (1918) The correlation between relatives on the assumption of Mendelian inheritance. *Trans Roy Soc Edn* 52:399–433
- Foster GS (1986) Making clonal forestry pay: breeding and selection for extreme genotypes. In: Conference Proceedings IUFRO Joint Meeting of Working Parties on Breeding Theory, Progeny Testing, Seed Orchards, 13–17 October 1986, Williamsburg, Virginia, North Carolina State University – Industry Cooperative Tree Improvement Program, Raleigh, North Carolina, pp 582–590
- Foster GS (1993) Selection and breeding for extreme genotypes, chapter 5 Clonal forestry, vol. 1: genetics and biotechnology. In: Ahuja MR, Libby WJ (eds) Springer-Verlag, Berlin, pp 50–67

- Gea LD, Lindgren D, Shelbourne CJA, Mullin T (1997) Complementing inbreeding coefficient information with status number: implications for structuring breeding populations. *NZ J For Sci* 27:225–271
- Gianola D (1982) Assortative mating and the genetic correlation. *Theor Appl Genet* 62:225–231
- Griffin AR, Lindgren D (1985) Effect of inbreeding on production of filled seed in *Pinus radiata* – experimental results and a model of gene action. *Theor Appl Genet* 71:334–343
- Griffin AR, Cotterill PP (1988) Genetic variation in growth of outcrossed, selfed and open-pollinated progenies of *Eucalyptus regnans* and some implications for breeding strategy. *Silvae Genet* 37:124–131
- Grundy B, Luo ZW, Villanueva B, Woolliams JA (1998) The use of Mendelian indices to reduce the rate of inbreeding in selection programmes. *J Anim Breed Genet* 115:39–51
- Gomez-Raya L, Burnside EB (1990) The effect of repeated cycles of selection on genetic variance, heritability, and response. *Theor Appl Genet* 79: 568–574
- James JW (1977) Open nucleus breeding systems. *J Anim Prod* 24:287–305
- James JW (1978) Effective population size in open nucleus breeding schemes. *Acta Agric Scand* 28:387–392
- Jorjani H (1995a) Genetic studies of assortative mating in selected and unselected populations Publication No. 122, Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences, Uppsala, Sweden
- Jorjani H (1995b) Assortative mating and selection in populations of various sizes: a review of the literature. Publication No. 121, Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences, Uppsala, Sweden
- Jorjani H, Engström G, Strandberg E, Liljedahl L-E (1997a) Genetic studies of assortative mating – a simulation study. I. Characteristics of the control populations. *Acta Agric Scand, Sect A, Animal Sci* 47:65–73
- Jorjani H, Engström G, Strandberg E, Liljedahl L-E (1997b) Genetic studies of assortative mating – a simulation study. II. Assortative mating in unselected populations. *Acta Agric Scand, Sect A, Animal Sci* 47:74–81
- Jorjani H, Engström G, Strandberg E, Liljedahl L-E (1997c) Genetic studies of assortative mating – a simulation study. III. Assortative mating in selected populations. *Acta Agric Scand, Sect A, Animal Sci* 47:129–137
- Jorjani H, Engström G, Strandberg E, Liljedahl L-E (1998) Assortative mating and dominance variance. *Proc 6th World Congress on Genetics Applied to Livestock Production*, 11–16 January 1998, Armidale, NSW, Australia, pp 45–48
- Karlsson B, Rosvall O (1993) Breeding programmes in Sweden 3. Norway spruce. In: Lee SJ (ed) *Progeny testing and breeding strategies*. Proceedings of the Nordic Group of Tree Breeders, Edinburgh, 6–10 October 1993. Forestry Authority, Scotland, pp 135–141
- Kerr RJ (1998) Asymptotic rates of response from forest tree breeding strategies using best linear unbiased prediction. *Theor Appl Genet* 96:484–493
- Kerr RJ, Goddard ME, Jarvis SF (1998) Maximising genetic response in tree breeding with constraints on group coancestry. *Silvae Genet* 47:165–173
- King JN, Johnson GR (1993) Monte Carlo simulation models of breeding-population advancement. *Silvae Genet* 42:68–78
- Koski V (1973) On self-pollination, genetic load, and subsequent inbreeding in some coniferous. *Comm Inst For Fenn* 78:1–42
- Lacy RC (1995) Clarification of genetic terms and their use in the management of captive populations. *Zoo Biol* 14:565–578
- Lesica P, Allendorf FW (1992) Are small populations of plants worth preserving? *Conserv Biol* 6:135–139
- Lindgren D (1986) How should breeders respond to breeding values? In: Conference Proc IUFRO Joint Meeting of Working Parties on Breeding Theory, Progeny Testing, Seed Orchards, 13–17 October 1986, Williamsburg, Virginia, North Carolina State University – Industry Cooperative Tree Improvement Program, Raleigh, North Carolina, pp 361–371
- Lindgren D, Gregorius HR (1976) Inbreeding and coancestry. *Proc IUFRO Joint Meeting of Genetic Working Parties on Advanced Generation Breeding*, Bordeaux, 14–18 June 1976. Institut national de la recherche agronomique, Cestas, France, pp 49–72
- Lindgren D, Kang KS (1997) Status number – a useful tool for tree breeding. *Res Rep For Genet Res Inst Korea* 33:154–165
- Lindgren D, Mullin TJ (1997) Balancing gain and relatedness in selection. *Silvae Genet* 46:124–129
- Lindgren D, Mullin TJ (1998) Relatedness and status number in seed orchard crops. *Can J For Res* 28:276–283
- Lindgren D, Gea LD, Jefferson PA (1996) Loss of genetic diversity monitored by status number. *Silvae Genet*. 45:52–59
- Mahalovich MF (1990) Modelling positive assortative mating and elite populations in recurrent selection programs for general combining ability. PhD thesis, North Carolina State University, Raleigh, North Carolina
- McBride G, Robertson A (1963) Selection using assortative mating in *Drosophila melanogaster*. *Genet Res* 4:356–369
- McKeand SE, Bridgwater FE (1998) A strategy for the third breeding cycle of loblolly pine in southern U.S. *Silvae Genet* 47:223–234
- Meuwissen THE (1997) Maximizing the response of selection with a predefined rate of inbreeding. *J Anim Sci* 75:934–940
- Meuwissen THE, Woolliams JA (1994) Effective sizes of livestock populations to prevent a decline in fitness. *Theor Appl Genet* 89:1019–1026
- Mueller JP, James JW (1983a) Effect on linkage disequilibrium of selection for a quantitative character with epistasis. *Theor Appl Genet* 65:25–30
- Mueller JP, James JW (1983b) Effects of reduced variance due to selection in open nucleus breeding systems. *Aust J Agric Res* 34:53–62
- Mullin TJ, Park YS (1995) Stochastic simulation of population management strategies for tree breeding: a new decision support tool for personal computers. *Silvae Genet* 44:132–141
- Nei M (1973) Analysis of gene diversity in subdivided populations. *Proc Natl Acad Sci USA* 70:3321–3323
- Nei M (1977) *F*-statistics and analysis of gene diversity in subdivided populations. *Ann Human Genet* 41:225–233
- Quinton M, Smith C, Goddard ME (1992) Comparison of selection methods at the same level of inbreeding. *J Anim Sci* 70:1060–1067
- Roden JA (1995) Review of the theory of open nucleus breeding systems. *Anim Breed Abstr* 62:151–137
- Rosvall O, Andersson E (1999) Group-merit selection compared to conventional restricted selection for trade-offs between genetic gain and diversity. *For Genet* 6:11–24
- Rosvall O, Lindgren D, Mullin TJ (1998) Sustainability robustness and efficiency of a multi-generation breeding strategy based on within-family clonal selection. *Silvae Genet* 47:307–321
- Rosvall O, Mullin TJ, Lindgren D (2003) Controlling parent contributions during positive assortative mating and selection increases gain in long-term forest tree breeding (in press)
- Shepherd RK, Kinghorn BP (1994) A deterministic multitier model of assortative mating following selection. *Genet Sel Evol* 26:495–516
- Skrøppa T (1996) Diallel crosses in *Picea abies*. II. Performance and inbreeding depression of selfed families. *For Genet* 3:69–79
- Smith C, Quinton M (1993) The effect of selection in sublines and crossing on genetic response and inbreeding. *J Anim Sci* 71:2631–2638
- Smith SP, Hammond K (1987) Assortative mating and artificial selection: a second appraisal. *Genet Sel Evol* 19:181–196
- Tallis GM, Leppard P (1988) The joint effects of selection and assortative mating on multiple polygenic characters. *Theor Appl Genet* 75:278–281
- Verrier E, Colleau JJ, Folley JL (1989) Effect of mass selection on the within-family variance in finite populations. *Theor Appl Genet* 77:141–148

- Verrier E, Colleau JJ, Folley JL (1990) Predicting cumulative response to directional selection in finite panmictic populations. *Theor Appl Genet* 79:833–840
- Verrier E, Colleau JJ, Folley JL (1991) Methods for predicting response to selection in small populations under additive genetic models: a review. *Livest Prod Sci* 29:93–114
- Vetta A (1976) Dominance variance in Fisher's model of assortative mating. *Ann Hum Genet* 39:447–453
- Villanueva B, Wooliams JA (1997) Optimization of breeding programmes under index selection and constrained inbreeding. *Genet Res* 69:145–158
- Wang J (1996) Deviation from Hardy-Weinberg proportions in finite populations. *Genet Res* 68:249–257
- Wang J (1997a) Effective size and F -statistics of subdivided populations. I. Monoecious species with partial selfing. *Genetics* 146:1453–1463
- Wang J (1997b) Effect of excluding sib matings on inbreeding coefficient and effective size of finite diploid populations. *Biometrics* 53:1354–1365
- White T (1993) Advanced-generation breeding populations: size and structure. In: Resolving tropical forest resource concerns through tree improvement, gene conservation and domestication of new species. In: Proc IUFRO Conference S2.02-08, Breeding tropical trees, 9–18 October 1992, Cartagena and Cali, Columbia, pp 208–221
- Williams CG, Hamrick JL (1996) Elite populations for conifer breeding and gene conservation. *Can J For Res* 26:453–461
- Williams CG, Savolainen O (1996) Inbreeding depression in conifers: implications for breeding strategy. *For Sci* 42:102–117
- Williams CG, Hamrick JL, Lewis PO (1995) Multiple-population versus hierarchical conifer breeding programs: a comparison of genetic diversity levels. *Theor Appl Genet* 90:584–594
- Wray NR, Hill WG (1989) Asymptotic rates of response from index selection. *Anim Prod* 49:217–227
- Wright S (1921) Systems of mating. *Genetics* 6:111–178
- Wright S (1969) Evolution and the genetics of populations. Vol. 2, The theory of gene frequencies. The University of Chicago Press, Chicago, Illinois
- Wu HX, Matheson AC, Spencer D (1998a) Inbreeding in radiata pine. I. Effect of inbreeding on survival, growth and variance. *Theor Appl Genet* 97:1256–1268
- Wu HX, Matheson AC, Spencer D (1998b) Inbreeding in *Pinus radiata*. II. Time course of inbreeding depression and effect on growth curve. *NZJ For Sci* 28:123–139