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ORIGINAL PAPER

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# Open-nucleus breeding strategies compared with population-wide positive assortative mating

## I. Equal distribution of testing effort

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**Abstract** Positive assortative mating (PAM) can enhance the additive genetic variance in a breeding population (BP). This increases the potential for gains in the production population (PP, selected subset of the BP) for recurrent selection programs in forest trees. The assortment of mates can be either: (1) by individual tree rank across the whole BP (PAM), or (2) trees of similar rank can be merged into larger hierarchical groups and then mated randomly within group ("open"-nucleus breeding, NB). The objective of this study was to compare PAM and NB in quantitative terms. The NB simulation model assumed two tiers (nucleus, main) with unrestricted migration between the tiers. Clonal tests were used to predict breeding values and test resources per mate were kept constant for all mates. Both gain and diversity were combined into a single selection criterion, "group-merit selection." Alternatives were compared over five breeding cycles by considering genetic gain and diversity in a selected PP established in a seed orchard. The assortment of mates in both alternatives enhanced additive variance and increased the additive effect in the BP, leading to additional gain in the PP. Gains generated under PAM always exceeded gains under NB. Thus, the main message from this study is that PAM in both the short- and long-term results in more gain at any target level of diversity in the PP (the breeder's target) than is achieved by the NB alternative. The optimum size of the nucleus varies with the desired level of seed orchard diversity. At lower target diversity, smaller nucleus sizes are favorable, while larger sizes result in more gain when seed orchard diversity is considered more important.

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## Introduction

Two basic forms of mating can be described in terms of the correlation between phenotypic values of mated individuals. One is random mating (RM), where the expected correlation is zero, and the other is non-RM, where the correlation differs from zero. When the correlation is positive, mating is positive assortative, and when the correlation is negative, mating is negative assortative (Crow and Kimura 1970; Jorjani 1995). The advantage of positive assortative mating (PAM) for practical breeding is the potential for expansion of the additive variance (Breese 1956). This expansion is mainly influenced by the phenotypic correlation of mates, the narrow-sense heritability and the effective number of loci affecting a trait of interest (Lynch and Walsh 1998). The actual benefit of assortative mating for practical breeding programs under selection is complex to evaluate. Computer simulation can be used to combine simultaneously quantitative models with other important factors. For example, Rosvall and Mullin (2003) evaluated the effect of PAM in long-term forest tree breeding programs. They found a large expansion of additive variance, which was attributable to the effects of PAM and restricted among-family selection. The increased additive variance enhanced gains in deployed genetic material (forest plantations) derived from a selected seed orchard production population (PP), while conserving genetic diversity in the breeding population (BP).

Nucleus breeding (NB) can be described as a form of PAM where selected individuals are allocated into a few distinct hierarchical levels (tiers) prior to mating within tiers. The nucleus tier (also known as the elite population) is the uppermost tier and can either be closed (no gene flow into the nucleus) or open [the gene pool in the nucleus is periodically enriched by migration from lower tier(s) or external populations]. Allocation to the different tiers is done after ranking individuals for breeding values, so it can lead to an expansion of additive variance. The concept of NB was originally developed and used in animal breeding programs. The first open-NB schemes for sheep were developed in the mid 1960s in Australia and New Zealand. The concept became popular in these two countries in the late 1960s and the 1970s. A detailed review of the development is provided by del-Bosque González (1989) and Roden (1994).

A number of simulation models have been developed to investigate the optimum tier structure under NB schemes. James (1977) introduced the first general open-NB model. Genetic progress was expressed deterministically as a function of selection differentials, migration rates and genetic lag between tiers. Among the main findings was that a constant equilibrium in genetic differentiation between tiers and annual gain is achieved after repeated cycles of selection. At the equilibrium, the rate of gain in both tiers is equal and depends only on selection and migration. James (1977) concluded that migration in an open-nucleus system reduces the rate of inbreeding to approximately one half of that in a closed-nucleus system (when the size of nucleus is small). James (1978) derived a simple formula for effective population size with an open-NB system and Hopkins and James (1978) introduced a modified model for overlapping generations. All of these models assumed constant genetic variances. Later, Mueller and James (1983) improved the model and showed that the rate of genetic gain could be overestimated if the loss of variance due to selection (Bulmer 1971) was not considered. Shepherd (1991) and Shepherd and Kinghorn (1992) investigated schemes with multiple-tiers and proposed examining NB schemes as “structured” assortative mating. They concluded that additional genetic gain was generated with the addition of extra tiers in the open-nucleus system due to the introduction of additional between-tier assortative mating. Roden (1995) compared three alternative schemes and found that the mean annual gain was highest and the rate of inbreeding lowest with the open-nucleus system.

The NB concept was introduced into forestry by Cotterill (1989) and incorporated into breeding plans for radiata pine (*Pinus radiata* D. Don) in Australia (White et al. 1999) and bluegum eucalypt (*Eucalyptus globulus* Labill.) in Portugal (Cotterill et al. 1989). Cotterill et al. (1989) and Cotterill (1989) summarized some advantages of NB over classic schemes in tree improvement, including the potential gains in the nucleus population as a result of concentrating elite breeding individuals in the nucleus, so that the majority of investment is on outstanding genetic material, and the versatility of the nucleus in terms of the potential transfer of selections from outside the breeding program. The latter concept fits neatly within the structure of breeding cooperatives in forestry, where NB has been considered in Finland (Mikola 2002), the Southeastern United States (White et al. 1993; McKeand and Bridgwater 1998), Denmark (Wellendorf et al. 1994) and South Africa (Hagedorn 1991).

Few simulation studies have investigated the NB concept specifically in forest trees. Most of these have focused on the BP as the primary target, rather than the PP (e.g., seed orchard). Mahalovich and Bridgwater (1989) investigated the advantage of an elite population for forest tree breeding and found that gains in the random-mating elite population exceeded those in the main population by 4–45% over 12 generations. In an alternate scenario, the elite population was periodically enriched by replacing the poorest trees with the best trees from the main population to offset inbreeding in the nucleus. Inbreeding was reduced, but gain in the elite population was not greater than without enrichment. This was explained as due to low narrow-sense heritability; and progeny testing of replacements was suggested. King and Johnson (1993) compared an open-nucleus scheme with four other mating schemes. Making additional crosses among elite genotypes in each generation offered more potential for genetic gain, but the effective population size was reduced as more selections shared the same parents.

Kinghorn et al. (2000) suggested that assortment across the whole BP (PAM) could be genetically more efficient than the open-nucleus system. It therefore seems interesting to compare in detail a two-tiered open-nucleus system with PAM across the whole BP (where each parental cross comprises a distinct hierarchical level). The aim of the current study was to quantitatively compare open-NB to population-wide PAM in a long-term program with recurrent selection for general combining ability in forest trees. Situations with a balanced distribution of testing resources are considered in this paper; and more complex scenarios follow in a companion paper (part II, this issue). Under balanced testing efforts, the hypothesis is that open-NB leads to a lower expansion of additive variance in the BP and thus to lower genetic gains in the PP than is the case with population-wide PAM.

## Materials and methods

Three breeding alternatives were compared in this study (Fig. 1). Under NB, the BP was structured into two distinct tiers, the nucleus (elite) and main (base). Under the population-wide PAM and non-hierarchic RM alternatives, the BP was not divided into tiers. In PAM, parental assortment was done at the individual-tree level and applied across the entire BP. Mates were paired at random in the RM alternative. RM in this study means that mates were randomized, but duplicate and self-crosses were excluded.

A discrete-generation model was developed for stochastic simulation of an open-NB system relevant for forest trees. Each scenario (unique set of input parameters) was replicated by 800 independent runs (iterations). Parameter means across all iterations were calculated for each scenario and presented along with 95% confidence

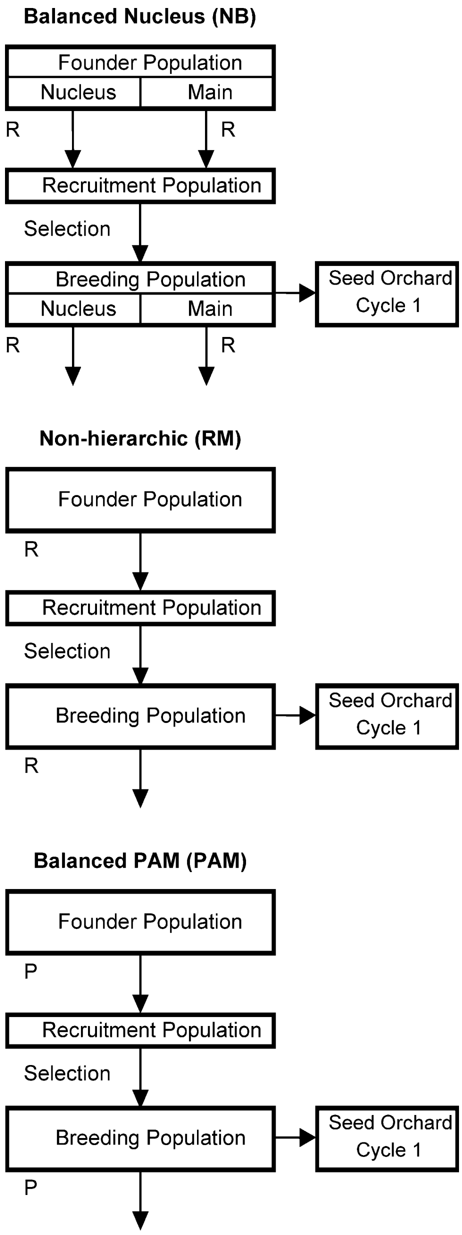

**Fig. 1** Breeding alternatives compared in this study. Mating was either random (*R*) or positive assortative (*P*) as indicated below the population box

intervals (CI). Generation intervals were assumed to be constant in all scenarios.

The breeding simulation software "POPSIM", developed by Mullin and Park (1995), served as the basis for the stochastic simulation. The model structures and parameters were initially those used by Rosvall et al. (1999) to model the current Norway spruce [*Picea abies* (L.) Karst.] breeding program in Sweden, which features the use of clonal testing, although much of their study is relevant to a broader range of species and programs. Both Mullin and Park (1995) and Rosvall et al. (1999) discuss underlying assumptions of the simulation model, the majority of which are relevant to this study.

A founder population of 48 unrelated, non-inbred trees ($N$=48) was constructed by random sampling from normal distributions of genetic and environmental effects. A single polygenic trait in a diploid organism was assumed (although this trait may be a complex index of many observations). The trait was under the influence of a large number of autosomal loci, each with a small effect (infinitesimal model). Initial variance components were set to approximate growth traits in conifer species according to Rosvall et al. (1999): additive variance ($V_A$)=100, dominance variance ($V_D$)=25 and environmental variance ($V_E$)=375 (giving $h^2$=0.2) with a phenotypic mean = 100. In the NB alternative, the nucleus was initialized by sampling $N_N$ best phenotypes from the founder population. The remaining trees ($48-N_N$) were allocated to the main tier. The nucleus size was varied by increments of eight trees ($N_N$=8, 16, 24, ...). Single-pair RM was used within both tiers to generate a recruitment population of 24 full-sib families, $N_N/2$ of which were generated in the nucleus. A total testing effort of 2,400 seedlings (genotypes) was assumed to be distributed uniformly in the recruitment population, i.e., equal family size. Each seedling was clonally replicated by ten ramets. Clonal replication of genetic tests is current practice for Norway spruce in Sweden (Karlsson and Rosvall 1993) and has been recommended for applications in other tree breeding programs (e.g., Danusevicius and Lindgren 2002; Isik et al. 2003).

The phenotypic value of each tree was the sum of independent additive, dominance and environmental effects. Epistatic interactions and maternal effects were not considered. The mean additive effect for each full-sib family $a_{FS}$ was calculated as the mid-parent additive effect. The additive effect for each offspring within each family was then generated by random sampling from *Normal* $\{a_{FS},\ 0.5V_A\ [1-0.5(F_f+F_m)]\}$, accounting for the expected reduction of within-family additive variance due to inbreeding of the female $F_f$ and male $F_m$ parents, respectively. The mean dominance effect for each full-sib family $d_{FS}$ was drawn randomly from *Normal* $(0,\ 0.25V_D)$. The dominance effect for each offspring within each family was then generated by random sampling from *Normal* $\{d_{FS},\ 0.75V_D\ [1-0.5(F_f+F_m)]\}$. Inbreeding depression was not considered. The environmental effect for a clonal copy (ramet) of each genotype within each family was drawn randomly from *Normal* $(0,\ V_E)$; and it was assumed that there was no additional source of variation associated with clonal replication. Genotype-environment covariance and interaction were not considered. Natural selection, migration (closed BP) and mutation were further assumed absent.

The breeding value of each progeny genotype was predicted using the combined index of individual clonal mean and family mean (average of clonal means within a family). The general approach for combined index calculation was presented by Baker (1986, pp 110–111). Relatedness was described by "group coancestry", $\Theta$, a concept introduced by Cockerham (1967). Group coancestry is the average of all pairwise coancestries, including

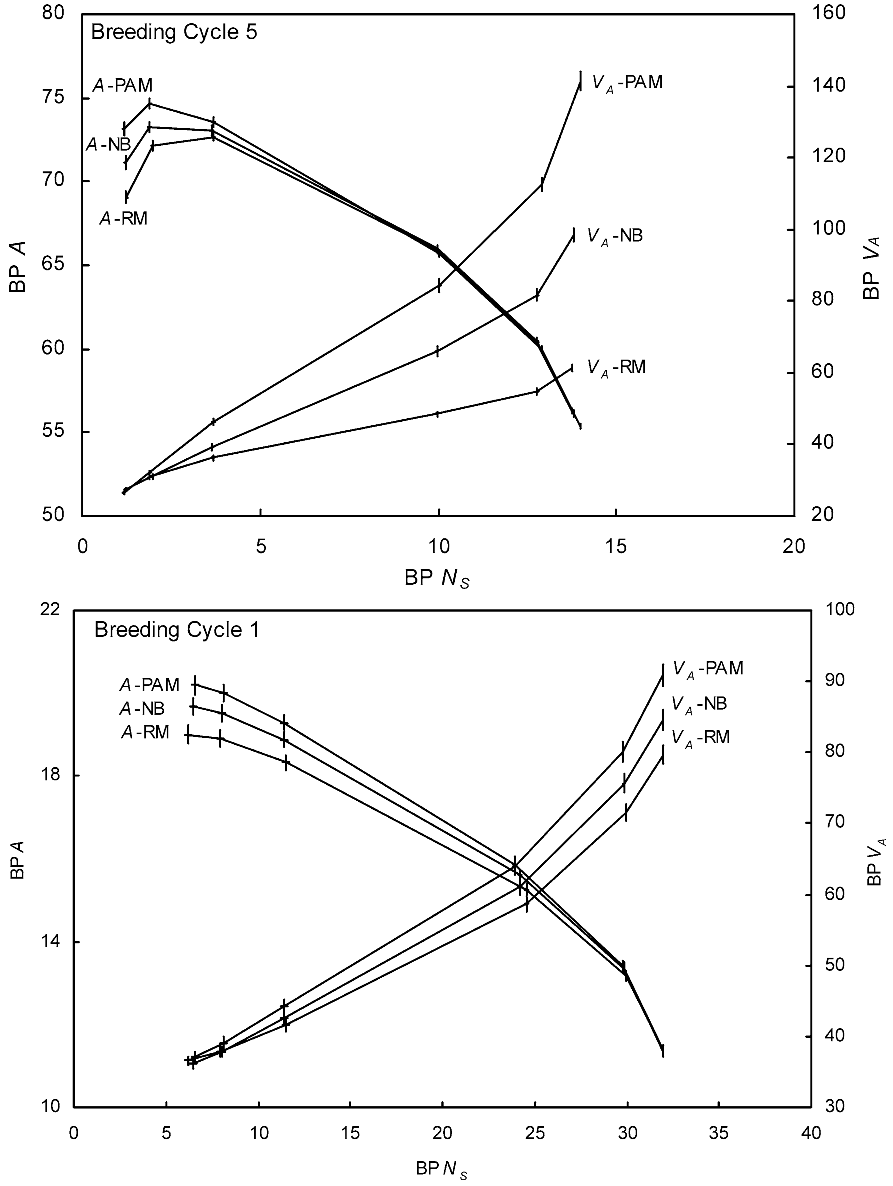

**Fig. 2** Average additive effect $A$ and additive variance $V_A$ in the BP after one and five breeding cycles for a set of scenarios with variable weight on group coancestry in the selection criterion, resulting in different BP status numbers ($N_S$). The three lines connect scenarios for: non-hierarchic RM, NB with nucleus size $N_N$=16 and PAM. CI (95%) for BP $A$, $V_A$ and $N_S$ are based on 800 iterations of the simulation

self-coancestry and reciprocals. It is the probability that two genes taken at random from the gene pool, with replacement, are identical by descent. Status number, $N_S$, is a measure of effective population size: it is the census size of an equivalent population composed of unrelated, non-inbred individuals, where the probability to draw two genes identical by descent is the same as for the population under study (Lindgren et al. 1996). Status number was calculated from group coancestry ($N_S$=1/2Θ).

Group-merit selection (Lindgren and Mullin 1997) considering both breeding value and relatedness was applied to select 48 progeny genotypes to form the next cycle of the BP. The algorithm utilized in this model maximized iteratively the population merit: $B_\omega = \bar{g}_\omega - c\ \Theta_\omega$, where $B_\omega$ is the group merit of a selected set ω, $\bar{g}_\omega$ is the average breeding value of the set, $\Theta_\omega$ is the group coancestry of the set and $c$ is a weighting constant. The weighting constant was varied between zero, the extreme when only breeding value was considered, and infinity (approximated by $1.0\times10^7$), when only group coancestry was considered in selecting among families. In this way it was possible to study a wide range of alternatives varying from low to high restrictions on relatedness. Trees in the selected BP were then ranked by their respective breeding values (combined index). The top-ranking selections were allocated to the nucleus tier and the remaining members formed the main tier.

Group coancestry between the nucleus and main tier, $\Theta_{NM}$, was calculated in each cycle to express the average relatedness of trees in the nucleus tier with those in the main tier. Since trees were not duplicated, this was equal to the average of all pairwise coancestries between the two tiers.

In each cycle, the six genotypes with the highest breeding values were selected from the BP to contribute to a PP (seed orchard). Group coancestry was not considered as a selection criterion in selecting the orchard. This was done to test the ability of the BP to support seed orchards and determine what gene diversity these best clones could carry. The number of genotypes used in the orchard (six) is somewhat arbitrary (Rosvall et al. 1999); and it is assumed that other sources (adjacent BPs) of selected genotypes would contribute to any given seed orchard.

Selection and breeding were repeated, as described above, for five generations. The NB alternative was compared with PAM and RM alternatives, using the same BP size (48), and under the same testing effort. Positive assortative mating in the PAM alternative was done such that all trees in the BP were sorted according to their combined-index values before mating.

## Results

The main effect of selection and selection restrictions on the BP structure is demonstrated for the three mating alternatives in Fig. 2. The values for BP $N_S$ vary from low at low weight on group coancestry in selecting the BP (low $N_S$ resulting from unbalanced selection scenarios) to high at a high weight (high $N_S$ resulting from balanced selection scenarios). A nucleus size of 16 is used for the results presented in the figures unless otherwise specified. Both the population-wide assortment of mates (PAM) and the assortment in a group sense (NB) resulted in changes in the average additive effect ($A$), $V_A$ and average inbreeding coefficient ($F$) in the BP (Fig. 3). The average dominance effect and the dominance variance in the BP were not significantly altered by any parental assortment.

Breeding population $A$ was enhanced by the positive assortment of mates (NB, PAM) compared with RM when the BP was selected with a low weight on group coancestry, resulting in a low BP $N_S$ (Fig. 2). The difference is more pronounced in the later breeding cycles (see graph corresponding to breeding cycle 5 in Fig. 2). Compared with RM, the PAM alternative resulted in the greatest enhancement in BP $A$, followed by the NB alternative. With higher weight on group coancestry (higher BP $N_S$), there were no differences in BP $A$ among the three alternatives.

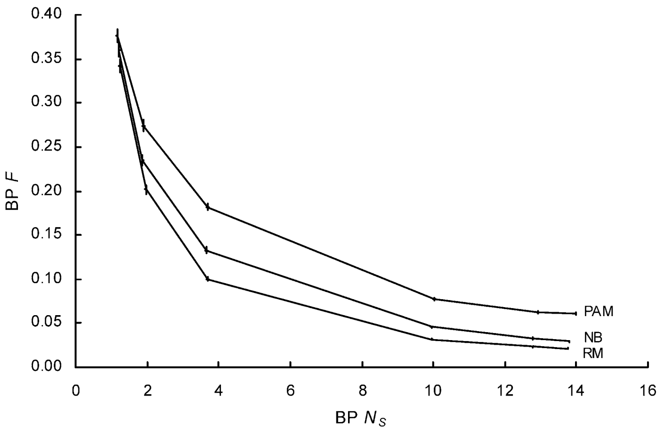

**Fig. 3** Average inbreeding coefficient ($F$) in the BP after five breeding cycles for a set of scenarios with variable weight on group coancestry in the selection criterion, resulting in different BP status numbers ($N_S$). The three lines connect scenarios for: non-hierarchic RM, NB with nucleus size $N_N$=16 and PAM. CI (95%) for BP $F$ and $N_S$ are plotted based on 800 iterations of the simulation

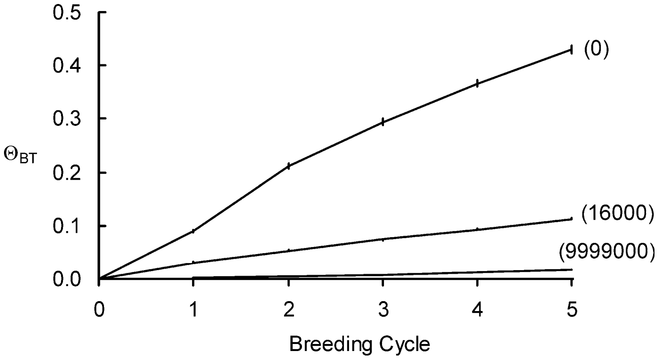

**Fig. 4** Development of between-group coancestry ($\Theta_{BT}$) over five breeding cycles in the NB alternative. The result of three scenarios with different weights (given in parentheses) on group coancestry while selecting the BP are illustrated. The nucleus size $N_N$=16. CI (95%) for $\Theta_{BT}$ are based on 800 iterations of the simulation

Breeding population $V_A$ was reduced in the subsequent breeding cycles under the RM alternative (compare $V_A$ −RM in breeding cycles 1 and 5 in Fig. 2), while PAM and NB continuously enhanced BP $V_A$ in all breeding cycles, with the largest enhancement under more balanced selection scenarios (high BP $N_S$). The maximum enhancement again was observed under the PAM alternative, with the open-nucleus alternative resulting in values approximately intermediate to those of the RM and PAM alternatives.

The PAM alternative resulted in the highest BP $F$ of the three alternatives, while the RM alternative resulted in the lowest BP $F$ (Fig. 3).

Group coancestry between the nucleus and main tier in the NB alternative expressed accumulated relatedness between the tiers as a result of recurrent selection and breeding (Fig. 4). Low weight on group coancestry when selecting the BP resulted in higher group coancestry between tiers.

The most important results of this study are presented in Fig. 5, where the additive effect of the selected seed orchard, i.e., genetic gain (PP $A$) in the first and fifth cycles, is plotted against the PP $N_S$ (census number = 6). The greatest PP $A$ of the three alternatives was achieved with the PAM alternative. NB resulted in a PP $A$ intermediate between the RM and PAM alternatives. The position of a maximum value for PP $A$ suggests that restricted selection provides the greatest gain in a long run.

The effect of varying the size of the nucleus in the NB alternative on PP $A$ in the fifth cycle seed orchard at low and high PP $N_S$ respectively is shown in Fig. 6. Nucleus sizes of zero and 48 correspond to the nonhierarchical, randomly mated population “RM” with no population subdivision; and results for both cases are therefore equivalent. Smaller nucleus sizes were more favorable when lower levels of seed orchard diversity were accepted, while larger sizes resulted in greater cumulative gains when diversity was considered important.

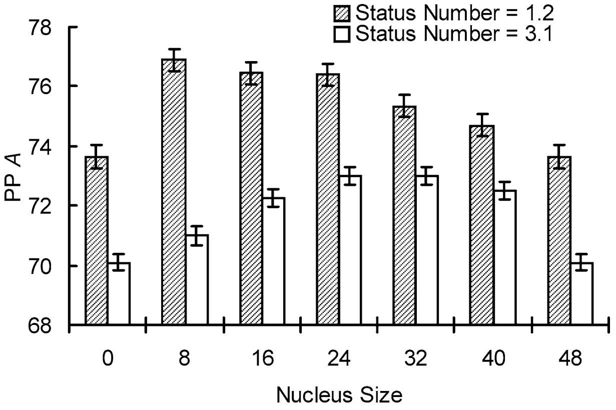

**Fig. 6** Average additive effect *A* in the seed orchard (PP) established after five breeding cycles at variable nucleus sizes in the NB alternative interpolated at lower (1.2) and higher (3.1) PP status numbers, corresponding to low and high weight on group coancestry in selecting the BP. CI (95%) for PP *A* are based on 800 iterations of the simulation

## Discussion

The simulation is based on the infinitesimal model for genetic variation in a quantitative trait that considers genetic sampling and the effects of selection and inbreeding on genetic variance. This model is suitable for showing generally applicable principles relevant to the majority of growth traits in conifer species (for references, see Mullin and Park 1995; Andersson 1999; Rosvall 1999). A BP of 48 individuals has been shown to be reasonable for studying the sustainable effect of assortative mating relevant to long-term forest tree breeding (Rosvall and Mullin 2003). Simulation iterations may be thought of as independent replicates of the same breeding program. Conclusions were drawn across these replicates. This study provides generally applicable recommendations under balanced, albeit somewhat ideal, conditions. Under some circumstances, operational constraints in a real breeding program may present difficulties to complete all desired assortative mating. In these cases, the advantage of such mating would be somewhat reduced according to the mating success rate.

The advantage of population management schemes modeled in this study is that both gain and diversity are considered simultaneously when selecting the BP. Furthermore, the gene transfer between tiers is simply directed by the breeding value of available candidates in the recruitment population and the weight placed on group coancestry when the BP is selected. The population structure is optimized by maximizing genetic gain at any target level of diversity in the PP for any value of initial parameters. This is a powerful tool for comparing breeding alternatives.

Positive assortative mating enhanced the additive variance when a high weight was placed on group coancestry when selecting the BP (high BP $N_S$ resulting from more balanced selection scenarios) and increased the potential for gains in the PP. It has been described earlier that larger variance enhancement due to assortative mating is expected at lower selection intensities (Baker 1973; Lange and De Lange 1974; Jorjani 1995), since the enhancement in variation among families in the recruitment population is utilized when the BP is selected. The enhancement of additive variance due to PAM is greater compared with the effect of inbreeding, which may at most only double the additive variance in the absence of epistasis (Falconer and Mackay 1996; Lynch and Walsh 1998). PAM may cause greater expansion of additive variance, provided the number of loci is large (Crow and Felsenstein 1968). Assortative mating does not affect dominance and environmental variance, under the assumptions described by Crow (1986), and therefore the increased BP $V_A$ by PAM also increases heritability.

Under unbalanced selection scenarios (low BP $N_S$), most BP trees were selected within a limited number of superior crosses. The extra gain (*A*) in the BP by PAM

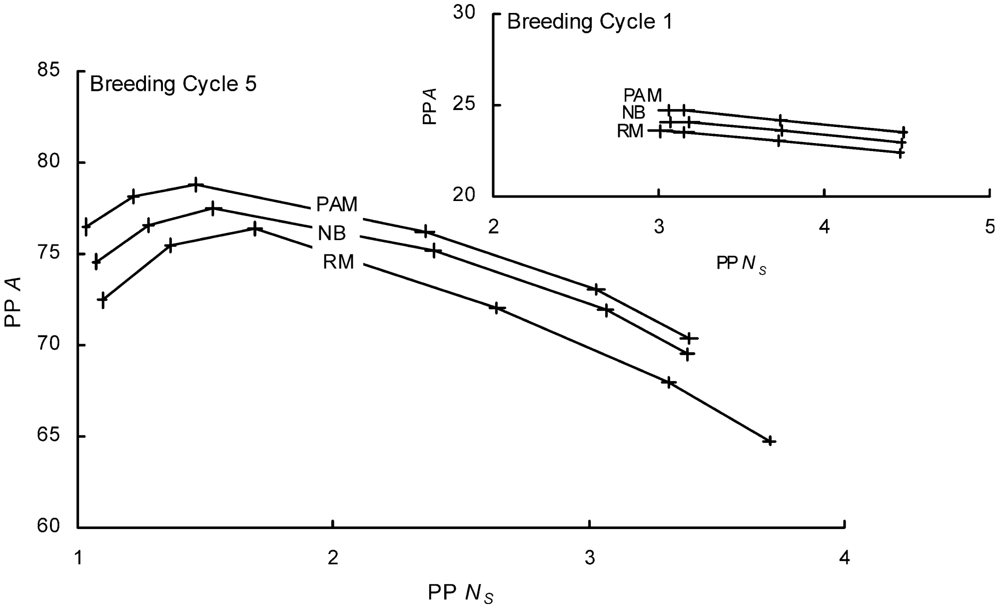

**Fig. 5** Average additive effect *A* in the seed orchard (PP) established after one and five breeding cycles for a set of scenarios with variable weight on group coancestry in the selection criterion, resulting in different PP status numbers ($N_S$). The three lines connect scenarios for: non-hierarchic RM, NB with nucleus size $N_N$=16 and PAM. CI (95%) for PP *A* and $N_S$ are based on 800 iterations of the simulation

compared with the RM alternative under these conditions was due to the higher values of these best crosses. The increased inbreeding in the BP by PAM (as more related trees have a tendency to be more closely ranked) had an adverse effect on gain by decreasing the within-family portion of additive variance. This loss was, however, greatly overcompensated by the increased additive effect and additive variance among families in BP (compare Figs. 2 and 3). Rosvall and Mullin (2003; Fig. 4) attempted to express the decline in the mean phenotype with increasing homozygosity in the population. When inbreeding depression was present, PAM still resulted in enhanced PP gains compared with a RM population (1% inbreeding depression per 0.01 increase in the inbreeding coefficient was considered in their model). However, modeling inbreeding depression by a simple reduction in the individual dominance effect and assuming that all trees with the same inbreeding coefficient are subjected to the same inbreeding depression seems the most unrealistic point in their infinitesimal simulation model (Rosvall 1999, p. 48). The biology underlying the inbreeding depression is much more complex (Williams and Savolainen 1996; Lynch and Walsh 1998) and no single recommendation can be generalized for numerous species under various management schemes. Under real situations, selection candidates that are highly inbred are likely avoided. When mates are ranked (PAM), some avoidance of crosses with close relatives can be applied, thus utilizing the advantage of increased phenotypic correlation of mates described in this study and at the same time reducing the negative impact of inbreeding on the mean phenotype in the recruitment and, consequently, the BP and PP.

Assortment of mates thus generated a potential for more PP gain due to the increased additive variance in the BP under more balanced selection scenarios and the increased additive effect in BP in more unbalanced selection scenarios (depending upon the weight applied to group coancestry when the BP was selected). The increased selection precision with clonal replication makes it possible to effectively explore the within-family portion of the additive variance (which is reproduced by genetic sampling in each new generation) under these balanced scenarios. The conserved among-family variance can then be exploited when selecting the PP. In this way, diversity is conserved in the BP, while PP gain is maintained at a high level. This beneficial effect of increased additive variance by assortative mating under restricted family selection was emphasized by Rosvall and Mullin (2003) for long-term forest tree breeding.

The key result of this study (presented in Fig. 5), that the assortment of mates in a group sense (open nucleus) is a less powerful version of the individual population-wide parental assortment, is in agreement with Kinghorn et al. (2000). Since there was no effect of NB on the BP or the PP, other than the one described for assortative mating, it can be concluded that open-NB would only provide genetic advantages under circumstances that favor population-wide assortative mating. However, under such circumstances, a population-wide assortment of mates would always provide more gain regardless of the target-level of production–population diversity. It can be noted from Fig. 5 that splitting the BP into just two hierarchical levels (open nucleus) has a large effect on the PP gain. The diminishing return from adding more and more tiers to the existing hierarchy was noted earlier by Shepherd (1991).

In this two-tier model, both gain and diversity in PP were influenced by the nucleus size. In a long-term perspective, smaller nucleus sizes (approximately 20% of the BP size) were more favorable (resulted in higher PP gain) when lower values of seed orchard diversity were accepted (low PP $N_S$). This was due to the increased correlation among mates within the small nucleus, which generated extra genetic response (increased $A$ in the selected PP). The optimum nucleus size increased to approximately 50–70% of the BP size when higher values of orchard diversity were the target (high PP $N_S$). The fact that relatively large nucleus sizes provided maximum PP long-term gain is a point to be noted for open-NB application in forest trees, where the financial investment is focused on relatively smaller nucleus sizes (White et al. 1999; Mikola 2002). In earlier animal-breeding studies, the optimum nucleus sizes were often underestimated due to some simplified assumptions in their models (e.g., genetic variance was assumed to be constant throughout breeding cycles). Later studies revealed that optimum nucleus sizes are larger, especially when the effects of inbreeding and selection on genetic variance are accounted for (Roden 1994).

In forest tree breeding, Rosvall et al. (2003) investigated PAM combined with an increased number of selections from the best BP members and found similarities to open-NB. The present study is the first in making a direct comparison of both approaches. Distributing the testing effort equally to BP members (as done in this study) is a simple approach to implementing such a scheme, but real-life breeding programs often propose a more complex allocation of effort. In the next part of this study (Lstibůrek et al. 2004, this issue), breeding alternatives are evaluated where more effort is concentrated on parents of higher rank (unequal distribution of testing effort).

## Conclusion

Applying population-wide PAM in the BP is more efficient in supporting the PP than is open-NB for any desired PP gene diversity. Both PAM and NB enhance the additive variance and the additive effect of the BP by mating closely ranked parents and thus the top clones used in the PP are improved compared with those used under unstructured breeding, but PAM is more effective. Larger nucleus sizes in the NB alternative result in higher PP gain when the desired level of PP diversity is high. Smaller nucleus sizes can be marginally more efficient when PP diversity is considered less important.

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