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ORIGINAL PAPER

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

II. Unequal distribution of testing effort

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Abstract This study compares population-wide positive assortative mating (PAM) with open-nucleus breeding with an elite and main population when more effort is allocated to parents of the elite. A companion study showed that PAM is advantageous when testing effort is independent of parental value. In the present study, unbalanced testing was imposed by varying the number of crosses or the number of genotypes per cross. These unbalanced alternatives are compared with PAM, where the testing effort was varied so that better parents were mated more frequently. More effort allocated to parents of higher rank increased the additive effect and the additive variance and only slightly altered the group coancestry and inbreeding in the breeding population (BP) compared with completely balanced scenarios. Of particular interest to the breeder, large enhancement of the additive variance in the BP contributed to higher gains in the production population (PP). These simulations demonstrate that population-wide PAM leads to higher genetic gains compared with open-nucleus alternatives at any desired target level of diversity in the PP. This is true for both balanced (part I) and unbalanced distribution of testing effort (part II).

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Introduction

This is the second part of a simulation study comparing open-nucleus breeding and population-wide positive assortative mating (PAM) in long-term forest tree breeding based on recurrent selection for general combining ability. Part I illustrated comparisons under a relatively simple set of situations (Lstibůrek et al. 2004, this issue). In reality, breeding plans are often more complex (White et al. 1993; Danell 1995; McKeand and Bridgwater 1998; White et al. 1999; Li et al. 2000). These may combine both hierarchical structuring and sublining of the breeding population (BP). Hierarchical structuring means that a mating hierarchy is imposed on the BP, either at an individual level (PAM) or in groups (nucleus breeding). The main advantage of imposing a hierarchy for mating is the enhancement of additive variance in the BP, which can be utilized in the selected production population (PP) (Rosvall and Mullin 2003). Sublining means that a BP is divided into a number of subpopulations that are kept isolated and provide unrelated genotypes for the PP, e.g., a seed orchard, in each breeding cycle. In this way, inbreeding in the material deployed to forest plantations can be avoided (McKeand and Beineke 1980; Ruotsalainen and Lindgren 2000). "Multiple populations" is a related concept in forest tree breeding (Namkoong et al. 1988; White 1992), referring to a set of populations managed for different breeding objectives (Burdon and Namkoong 1983).

In the first part of this study, it was demonstrated quantitatively that population-wide PAM is superior to open-nucleus breeding for a variety of selection alternatives (unrestricted to restricted selection) when the distribution of testing effort across the recruitment population is balanced (Lstibůrek et al. 2004, this issue). In this second part, more complex situations are evaluated, where the distribution of testing effort is not balanced. It has often been suggested to direct more effort on higher-ranking parents in the BP (e.g., Cotterill 1989). Focusing more resources on the elite part of a BP (nucleus tier) can be done in a number of ways (Smith 1988; White 1992).

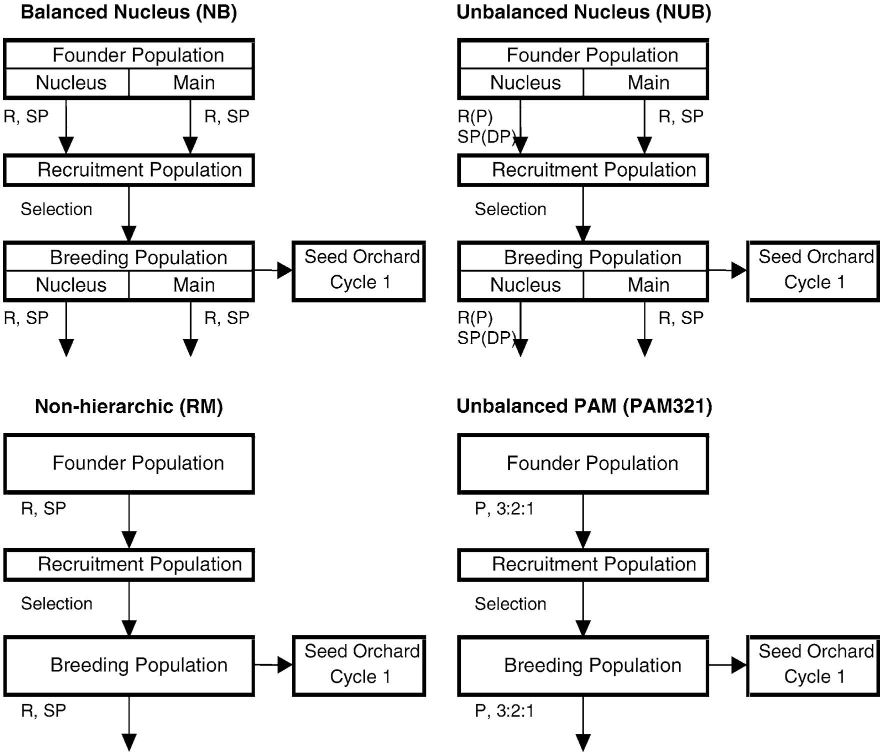

Fig. 1 Breeding alternatives compared in this study. Mating was either random (*R*) or positive assortative (*P*) and either single-pair (*SP*), double-pair (*DP*), or 3:2:1 design

One way is to apply less expensive open pollination to regenerate the main tier and to reallocate financial resources to advance the nucleus tier by means of control crosses. More parental combinations or more progenies per parent can be made in the nucleus tier compared with the main tier. In addition, parents can be individually ranked by their values in the nucleus before mating takes place (Cotterill et al. 1989; Hagedorn 1991; White et al. 1999; Mikola 2002).

Similar options of resource reallocation are available when the BP is not managed in distinct hierarchical layers, but rather parental assortment is done on a population-wide basis. In theory, it is expected that the optimum contribution of parents to the next generation is linearly related to their respective breeding values (Wei and Lindgren 1995). Similarly, one might expect that the optimum resource allocation is related to parental breeding values and, since the distribution of these values is continuous, so might be the resource allocation. An effort to study more matings among better parents was done by Rosvall et al. (2003), but in their study the effect of resources is not separated from the effect of selection.

The objective of this study was to compare population-wide PAM with open-nucleus breeding under unbalanced distribution of testing effort, with more resources allocated to parents of higher rank. In the first part of this study, it was demonstrated that open-nucleus breeding does not provide any additional genetic benefit beyond that achieved by allocating the mates into two distinct hierarchical layers (assortment in a group sense). Thus, the hypothesis under the unbalanced set of conditions was that the population-wide assortment of mates would again provide more gain in the PP compared with the open-nucleus breeding.

Materials and methods

The simulation in this study was 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. The breeding simulation software “POPSIM” developed by Mullin and Park (1995) was modified to model an open-nucleus breeding system with two hierarchical levels (nucleus and main tiers). Main model structures and assumptions are described in our earlier study dealing with the balanced distribution of testing effort (Lstibůrek et al. 2004, this issue). Figure 1 presents the main breeding alternatives compared in this study.

Each alternative started by generating 48 unrelated, non-inbred founders. In each breeding cycle, a BP was selected from a clonally replicated recruitment population (progenies of parents from the previous breeding cycle) by group-merit selection, combining average breeding value and group coancestry into a single selection criterion (Lindgren and Mullin 1997). Different scenarios were run for each breeding alternative, using a wide range of weights on group coancestry to produce results across a range of effective population sizes. In each breeding cycle, six top-ranking genotypes were selected from the BP to contribute to a PP (seed orchard). Breeding alternatives differed in the hierarchical structuring of the BP as follows.

Balanced nucleus

Founder and BP were divided into two tiers: nucleus and main. The nucleus was composed of the 16 top-ranked parents in the BP (a third of the total BP). Mating within tiers was random. Single-pair mating was used with eight crosses made among nucleus tier parents and 16 crosses among main tier parents. A total of 100 genotypes (seedlings) were generated for each parental combination. Thus, there were 800 progenies in nucleus-tier families and 1,600 progenies in main-tier families. This alternative was identical to the balanced nucleus (NB) alternative in the first part of this study and was used here as a basis for comparisons.

Unbalanced nucleus

At unbalanced nucleus alternatives (NUB), the nucleus was composed of the 16 top-ranked parents (as in the NB alternative). Three options for concentrating more effort on nucleus parents were evaluated.

Unbalanced nucleus with double-pair mating

Unbalanced nucleus with double pair mating (NDP) means that double-pair random mating was performed in the nucleus tier (16 crosses) and single-pair random mating in the main tier (16 crosses). The size of all families in the recruitment population was 75 genotypes, giving a total of 2,400 genotypes in the recruitment population.

Unbalanced nucleus with bigger families

Unbalanced nucleus with bigger families (NBF) means that single-pair mating was applied at random in both tiers (eight crosses in nucleus, 16 crosses in main tier) with larger families generated in the nucleus and smaller families in the main tier: 150/75 (2×); 200/50 (4×) and 250/25 (10×); giving a total of 1,200/1,200; 1,600/800 and 2,000/400 genotypes in the nucleus/main families.

Unbalanced nucleus with positive assortment of mates

At unbalanced nucleus with positive assortment of mates (NPAM), the nucleus parents were sorted by breeding values before mating took place. Main tier parents were mated randomly. Double-pair mating was used in the nucleus tier (16 crosses) and single-pair mating in the main tier (16 crosses). A total of 75 seedlings were generated for each family, resulting in total of 2,400 genotypes in the recruitment population.

Non-hierarchic random mating

This alternative functioned as a baseline [identical to the random mating (RM) alternative in the first part of this study]; the founder and BP were not subdivided into tiers (no hierarchical structure), and assignment of mates was at random. Single-pair mating resulted in a total of 24 crosses. Each family had a uniform size of 100 genotypes, giving a total of 2,400 genotypes in the recruitment population.

Unbalanced population-wide positive assortative mating

In this alternative, population-wide PAM was modified to distribute more effort to higher-ranking parents and less to lower-ranking parents. In this modified PAM alternative, parents were first ranked by their breeding (combined-index) values. The top third of the parents were then each involved in three crosses, the middle third in two crosses, and the lowest third of parents in one cross—PAM 3:2:1 (PAM321) design (Ruotsalainen and Lindgren 2001; Rosvall et al. 2003). Thus, there were, in total, 48 crosses. A total of 50 genotypes were generated per each family, resulting in 2,400 genotypes in the recruitment population. The like-with-like mating design was optimized such that the phenotypic correlation of mates was maximized (Fig. 2).

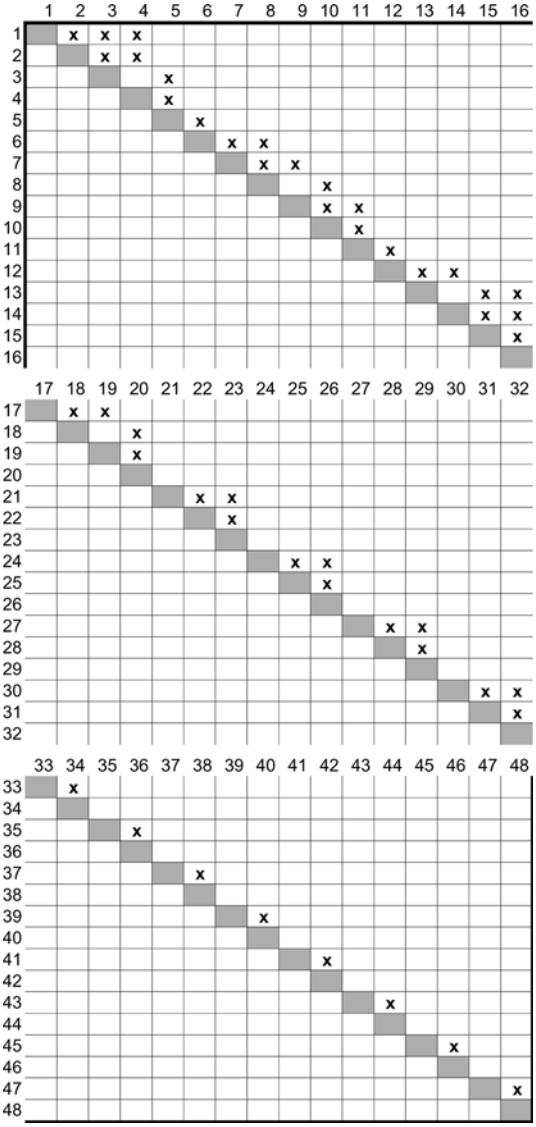

Fig. 2 3:2:1 mating design. Parents are denoted by their rank. Top ranking third of parents (*1–16*) were each involved in three crosses; middle ranking third of parents (*17–32*) in two crosses; the lowest ranking third of parents (*33–48*) in one cross

All test genotypes (seedlings) were clonally replicated by ten ramets, resulting in total testing effort (size of recruitment population) of 24,000 test plants in each breeding alternative. The simulation was conducted for five cycles of selection and breeding. Each simulation scenario was replicated by 800 iterations.

Results

More crosses in the nucleus

Figure 3 shows the average additive effect (A), additive variance (V_A) and average inbreeding coefficient (F) in the BP after five breeding cycles for unbalanced nucleus (NDP, NPAM), the PAM321, the PAM, and the RM alternative.

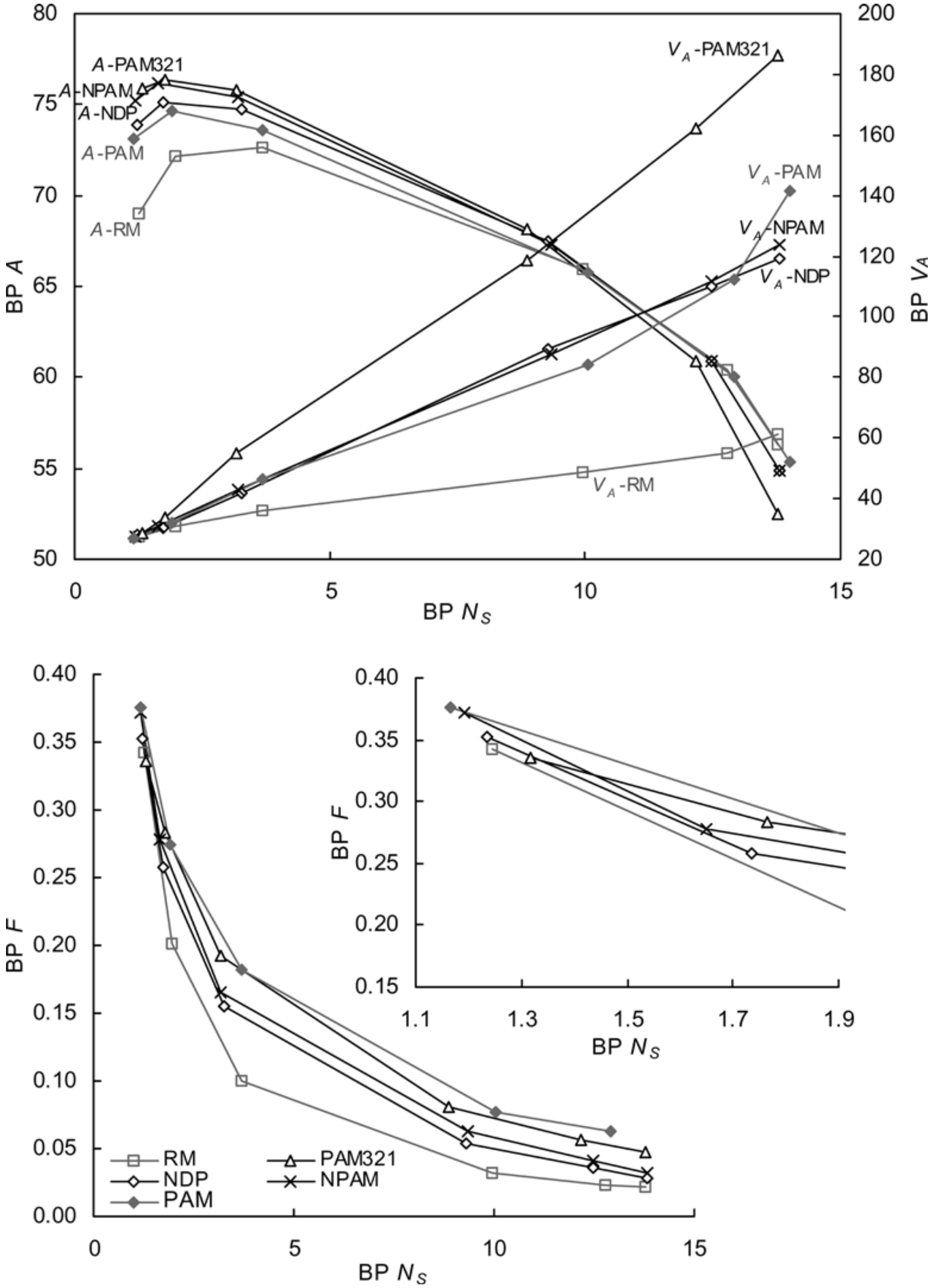

Fig. 3 *Upper figure* shows average additive effect (*A*) and additive variance (V_A) in the breeding population (BP) after five breeding cycles for a set of scenarios with variable weight on group coancestry in the selection criterion resulting in different BP status numbers (N_S). *Lower figure* shows corresponding average inbreeding coefficient (*F*) in BP. The *small figure* shows the upper left corner of the diagram at higher resolution. The lines connect scenarios for nonhierarchic random mating (RM), unbalanced nucleus with double-pair mating (NDP), unbalanced nucleus with positive assortment of mates (NPAM), positive assortative mating (PAM), and unbalanced population-wide positive assortative mating (PAM321). *Light lines* depict comparison alternatives from the first part of this study (I. Equal distribution of testing effort)

The values for status number (N_S) on the *x*-axis vary from low at low weight on group coancestry in selecting the BP (low N_S resulting from unbalanced selection scenarios) to high at high weight (high N_S resulting from balanced selection scenarios). In all alternatives, the maximum BP *A* was found in the lower end of the BP N_S range and the minimum at the maximum BP N_S (balanced within-family selection). BP *A* at the lower end of the BP N_S range was greatest under the PAM321 alternative, followed by the nucleus and RM alternatives. In this range of BP N_S, NPAM generated more gain than the corresponding alternative with random mating in the nucleus, NDP. When the weighting on group coancestry resulted in BP N_S approximately equal to 10, all alternatives achieved similar BP *A*. With greater restriction on diversity, the ranking of alternatives was inverted compared with ranks under low BP N_S, but the range among alternatives was smaller. There was negligible enhancement of BP V_A due to parental assortment at low BP N_S. The difference in BP V_A among alternatives increased with higher weight on group coancestry (higher BP N_S). Maximum enhancement of BP V_A was obtained by the PAM321 alternative. The two nucleus alternatives (NDP, NPAM) were similar to each other. When there was

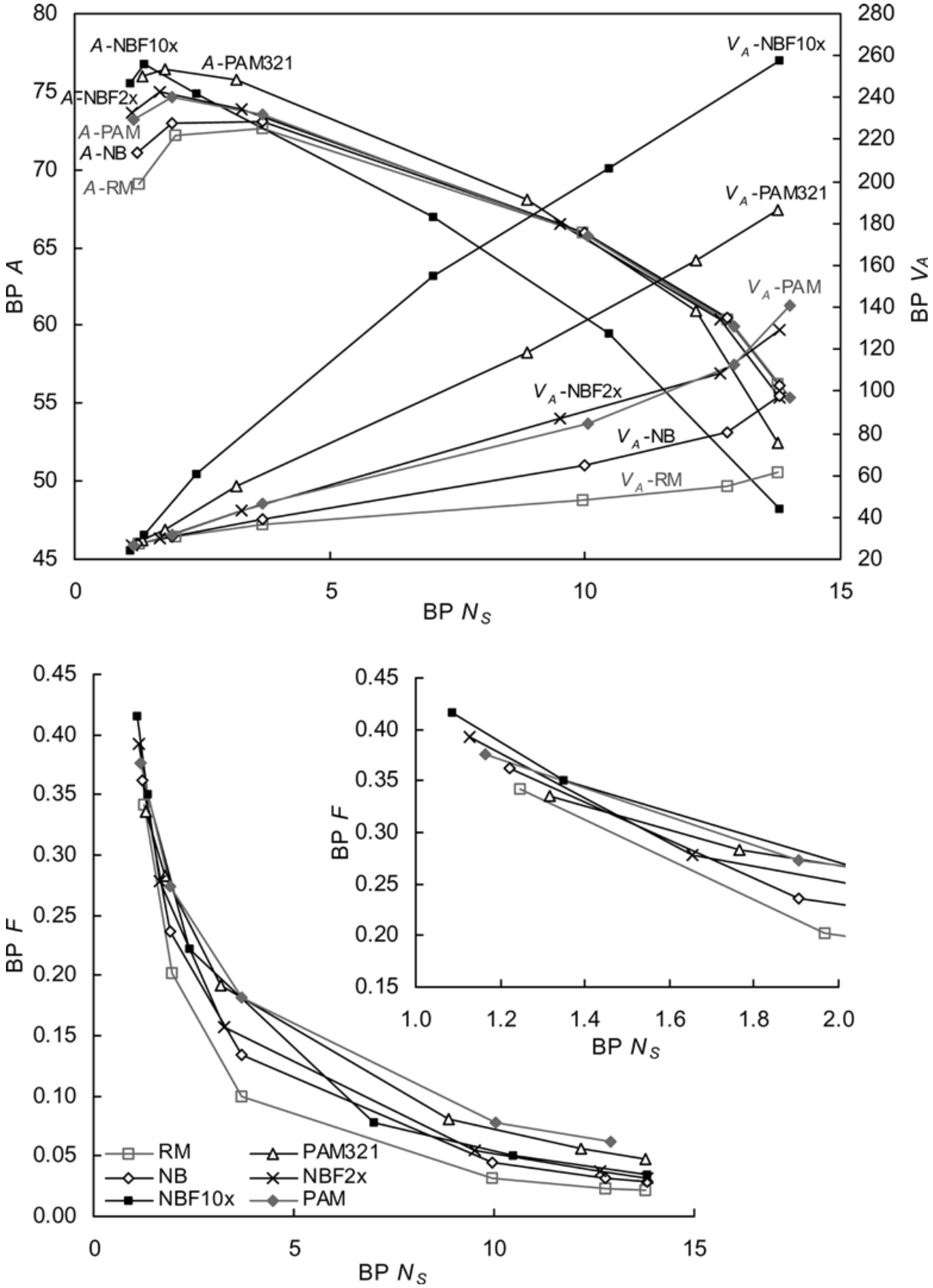

Fig. 4 *Upper figure* shows A and V_A in the BP after five breeding cycles for a set of scenarios with variable weight on group coancestry in the selection criterion resulting in different BP N_S. *Lower figure* shows corresponding average F in BP. The *small figure* shows the upper left corner of the diagram at higher resolution. The lines connect scenarios for RM, balanced nucleus (NB), unbalanced nucleus with two times (NBF2×) and ten times (NBF10×) bigger families in nucleus, PAM, and PAM321. *Light lines* depict comparison alternatives from the first part of this study (I. Equal distribution of testing effort)

low or no weight on group coancestry (low BP N_S), nucleus alternatives resulted in the greatest BP F, followed by RM and PAM321 alternatives. With greater weights (higher BP N_S), the PAM321 alternative resulted in the greatest BP F followed by the nucleus and RM alternatives.

Larger families in the nucleus

Increasing family sizes in the nucleus can also lead to enhancement of A and V_A in the BP. An NBF (two times and ten times more genotypes per family in the nucleus compared with the main tier) is compared with NB, PAM321, PAM and RM alternatives in Fig. 4.

When there was low or no weight on group coancestry (low BP N_S), larger family sizes in the nucleus resulted in greater A in the BP. Similar to alternatives with larger numbers of crosses in the nucleus (Fig. 3), scenarios with larger family sizes in the nucleus also resulted in approximately the same A in BP at N_S close to ten. The exception was when family size in the nucleus greatly exceeded the family size in the main tier (A-NBF10×). This extreme alternative achieved the least additive

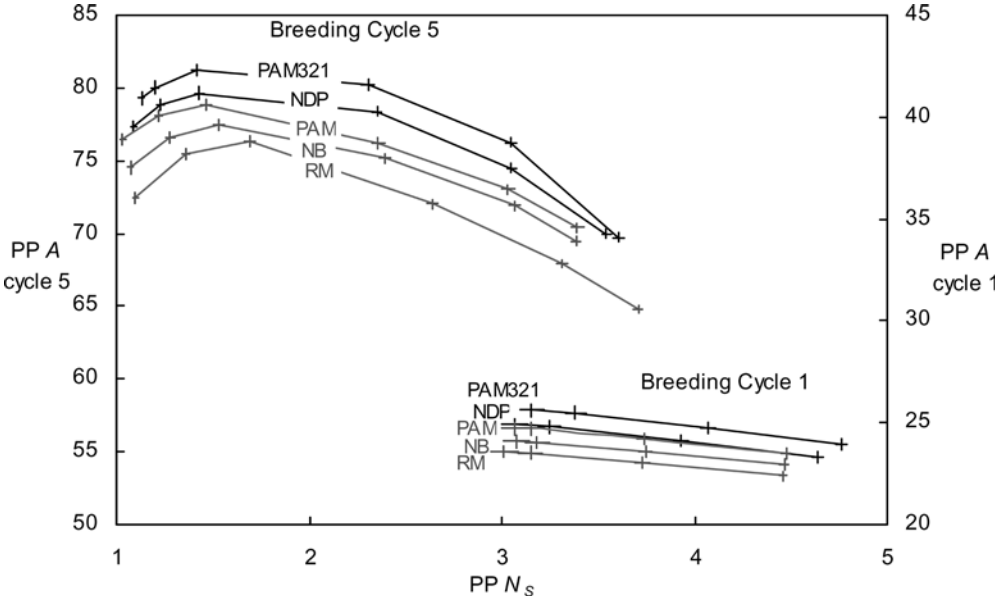

Fig. 5 *A* in the seed orchard (*PP*) established after one and five breeding cycles for a set of scenarios with variable weight on group coancestry in the selection criterion resulting in different PP N_S. The *lines* connect scenarios for RM, NB, NDP, PAM, and PAM321. *Light lines* depict comparison alternatives from the first part of this study (I. Equal distribution of testing effort). Confidence intervals of 95% for PP *A* and PP N_S are based on 800 iterations of the simulation

improvement of all the alternatives at the moderate to high BP N_S range. The ranking of nucleus alternatives in the high BP N_S range was again inverted, compared with ranks under low BP N_S. Greatest BP V_A enhancement was achieved with the NBF alternative with family sizes in the nucleus ten times that in the main tier. Other alternatives followed as indicated in Fig. 4. Nucleus alternatives produced the greatest BP *F* at lower BP N_S range, followed by the RM and PAM321 alternatives. The rank of alternatives under higher BP N_S changed (as in Fig. 3), with the PAM321 alternative producing the greatest BP *F*, followed by the NBF and RM alternatives.

Production population

Out of all the alternatives compared in this study, PAM321 produced the greatest genetic gain at any level of PP diversity (Figs. 5, 6, 7). Doubling the number of crosses in the nucleus tier substantially increased PP gain in all cycles at all levels of target diversity (Fig. 5).

Increasing family sizes in the nucleus also delivers more PP gain. Larger family sizes in the nucleus, compared with those in the main tier, are favorable at lower PP N_S, while more balanced conditions are favorable at higher diversity levels (Fig. 6). Vertical lines in Fig. 6 depict the space of solutions covering a range of unbalanced conditions.

Positive assortative mating in the nucleus further increases PP gain, but leads eventually to lower PP N_S in PP established in later cycles—at high weights on group coancestry when selecting the BP (Fig. 7).

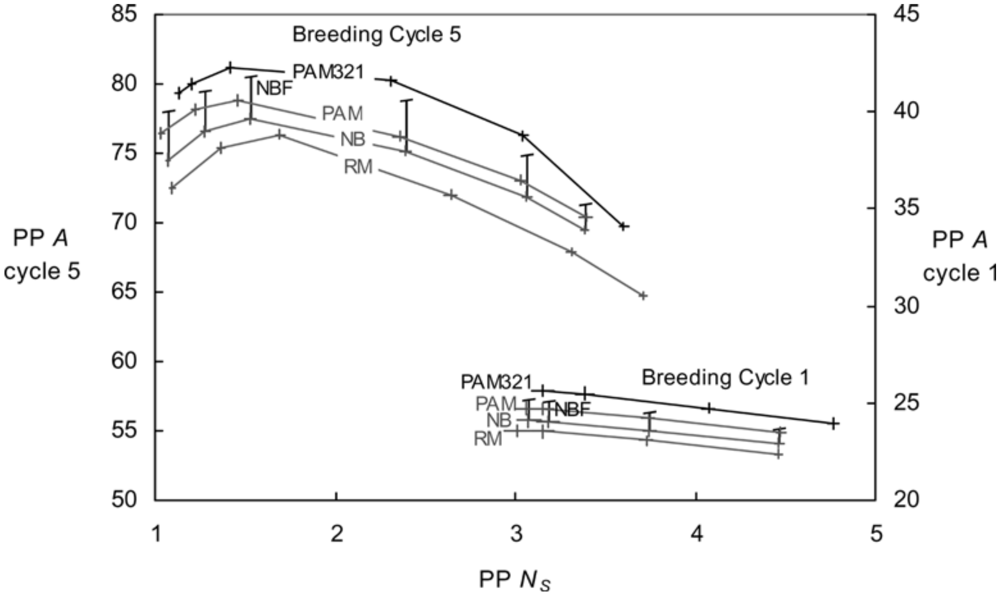

Fig. 6 *A* in the PP established after one and five breeding cycles for a set of scenarios with variable weight on group coancestry in the selection criterion resulting in different PP N_S. Alternatives compared in this figure are RM, NB, PAM, and PAM321. *Vertical lines* depict space of solutions for studied range of larger family sizes for nucleus families (*NBF*). *Light lines* depict comparison alternatives from the first part of this study (I. Equal distribution of testing effort). Confidence intervals of 95% for PP *A* and PP N_S are based on 800 iterations of the simulation

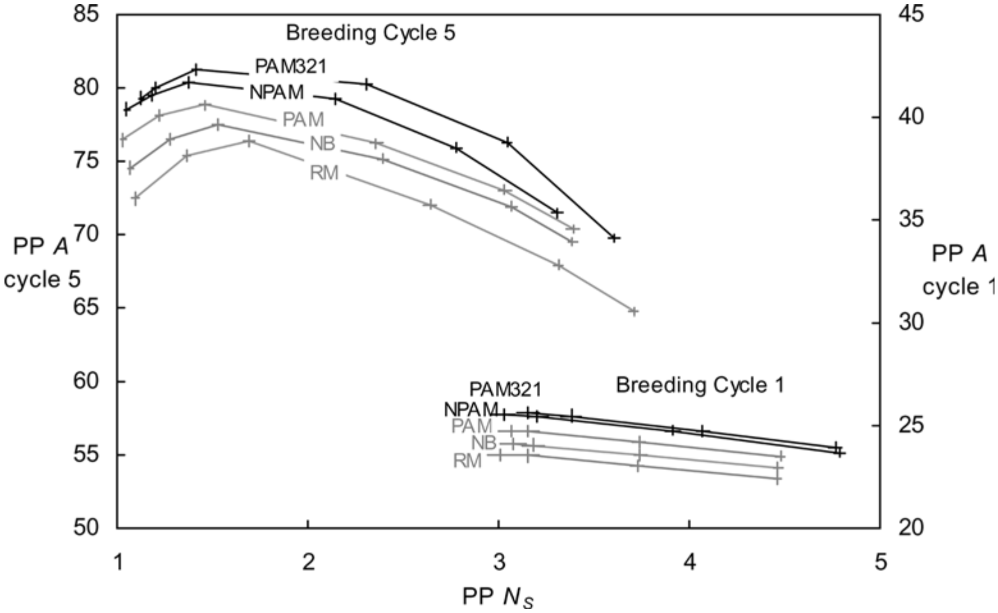

Fig. 7 A in the PP established after one and five breeding cycles for a set of scenarios with variable weight on group coancestry in the selection criterion resulting in different PP N_S. The lines connect scenarios for RM, NB, NPAM, PAM, and PAM321. *Light lines* depict comparison alternatives from the first part of this study (I. Equal distribution of testing effort). Confidence intervals of 95% for PP A and PP N_S are based on 800 iterations of the simulation

Discussion

This study demonstrates the advantage of allocating resources according to parental breeding values. This advantage generally supports suggestions made by Cotterill (1989) in the case of an open-nucleus breeding system and those by Rosvall et al. (2003) in the case of a population-wide PAM. This study quantitatively compares open-nucleus breeding with population-wide PAM at both balanced (Lstibůrek et al. 2004, this issue) and unbalanced distribution of testing effort (current study). The results support the genetic advantage of population-wide PAM over open-nucleus breeding under both situations.

Genetic advantage: breeding population

Generally, allocating more effort to better parents has the potential to enhance both A and V_A in the BP, which contributes to the beneficial effect of PAM per se described in this study and elsewhere (Jorjani 1995; Rosvall and Mullin 2003). By using group-merit selection to create a range of population effective sizes, it was shown that these conclusions are valid for a range of selection options that may occur under practical conditions.

When the desired level of genetic diversity is low (unbalanced selection scenarios), the allocation of more resources to the elite part of the BP produces additional gain in the BP. This is because unrestricted selection is made from a few superior parental combinations. Under this diversity objective, it is not worthwhile to spend resources on poor crosses that will not contribute to the next breeding cycle; it is more meaningful to reallocate these resources to better parental combinations (lower N_S, Figs. 3, 4). At higher target diversity levels (balanced selection scenarios), parental combinations are forced to contribute more equally to the next breeding cycle and allocating fewer resources to the poorer part of the BP can result in lower BP A. In this case, the reduction in gain is a consequence of unbalanced resource allocation (higher N_S, Figs. 3, 4). Under the circumstances in this study, a balance existed when N_S equaled about 10. At this point, BP A was constant for all alternatives unless the magnitude of imbalance was extreme (NBF10× in Fig. 4). In the PAM321 design, the allocation of resources to parents is closer to the expected optimum (more continuously distributed). This "close-to-optimum" distribution of effort produced gains exceeding those produced by all other alternatives at lower target levels of genetic diversity. Since less effort goes to the poorest part of BP in this design, BP A shrinks when the desired diversity is high. The results suggest that if BP gain is the target, then it would not be worthwhile to reallocate resources to better parents, but rather to distribute them equally. Under balanced selection strategies, it is the additional enhancement of BP V_A due to the unbalanced allocation of effort that is beneficial.

The peak BP V_A enhancement was reached under balanced within-family selection (maximum desired level of genetic diversity). Here, the unequal distribution of effort was combined with equal parental contributions to the next breeding cycle. The resulting recruitment population was more heterogeneous under unequal distribution of effort and when the selection scenarios were more balanced (high BP N_S); this further enhanced V_A of the selected BP in the next cycle.

The PAM321 alternative resulted in lower BP F at lower BP N_S. This was because of a more conveniently structured recruitment population, with more evenly distributed values of superior crosses (selection was made from a greater number of parental combinations compared with nucleus or RM alternatives). Under more restricted selection (higher desired level of diversity), the PAM321 alternative resulted in the highest BP F over all alternatives. Here, the selection was made more evenly out of 48 crosses. The majority of these crosses were allocated among the top third of parents. Therefore, the group coancestry of selected trees was higher compared with alternatives where the distribution of parental contributions to the recruitment population was more balanced.

Genetic advantage: production population

Improved genetic material is delivered to forest plantations through the PP. Thus, the PP is the ultimate target for maximizing genetic gain. The consequences for practical breeding are given here, where the discussion focuses on the PP, which is a subset of top-ranking parents passing their genes through regeneration material to forest plantations. This is where the comparison of breeding alternatives is most relevant. Higher gene diversity in the BP gives more room for a more intensive selection sacrificing a larger share of the gene diversity when selections are made to the PP. Therefore, preservation of gene diversity in the BP will appear more important if the PP is considered than if progress in the BP is the only goal.

The PAM321 alternative produced the greatest gains at all target levels of diversity in the PP, in all breeding cycles. This alternative was superior due to the favorable balance between A, V_A, and F in BP. The PAM321 alternative is an easy scheme to implement, but there is probably a more optimum design where the allocation of effort is even more continuous and more adapted to the targets set. The advantage of 3:2:1 design as implemented in this study is that it clearly demonstrates the superiority of allocating more effort to better parents under population-wide PAM rather than spending more resources in just one tier, as in case of open-nucleus breeding. Our future research will investigate alternatives to PAM 3:2:1 design, with more continuous allocation of testing effort and where the degree of imbalance is controlled to a higher degree.

The nucleus breeding schemes with more resources spent on better parents resulted in additional PP gain compared with the NB alternative. Making more crosses in the nucleus compared with the main tier resulted in a wider pool of extreme candidates for the next cycle, which was reflected in larger genetic gains in seed orchards. PAM within the nucleus tier increased genetic gain in the seed orchard, but led eventually to a reduction of PP N_S in later cycles under balanced selection schemes. This occurred because the recruitment population became more heterogeneous and led to fewer families contributing to the PP. Increasing the family size in the nucleus generated a larger pool of extreme candidates for selection. It is not worthwhile to produce very large differences between family sizes in two tiers. An optimum in this study was where families in the nucleus were two to four times larger compared with the main tier (depending upon the target PP N_S).

Open-nucleus population in forest tree breeding?

Animal breeders first adopted the concept of nucleus breeding primarily as it offered a convenient way to cooperate. There are some practical factors that made nucleus breeding suitable for animal breeders in some countries (often rather small breeding organizations; the breeding stock mostly owned by private persons). Animal breeders are aware of some potential problems associated with nucleus breeding systems, and genotype-by-environment interaction is considered as the major problem (del-Bosque Gonzàlez 1989; Willis 1998).

The majority of the animal breeding-simulation studies have compared closed- versus open-nucleus breeding strategies (Roden 1994), as these were the alternatives considered under their practical circumstances. A direct comparison with animal breeding studies is hampered by key characteristics of animals, in particular, distinct sexes and low female reproductive rates. When compared with animals, the situation in forest tree breeding seems more practically suited to simultaneous evaluation of all candidates and the use of population-wide assortative mating, effects which can be further enhanced by the use of clonal replication in progeny testing.

In fact, nucleus schemes in animal breeding are considered more as an alternative to large-scale genetic evaluation, which entails detailed assessment of large populations, typically entire breeds (Bourdon 1997). Animals are evaluated objectively, utilizing all available information (BLUP analysis), which allows direct comparison of animals located in different herds or flocks. This leads to a larger pool of candidates for selection, which may in turn result in greater genetic progress.

The advantage of open nucleus breeding observed in this study is the potential for more gain in the PP due to the assortment in a group sense (when compared with the nonhierarchic RM population). However, when compared with population-wide PAM, the genetic advantage of open-nucleus for forest tree breeding seems less attractive.

In this study, the BP can be thought of as a single subline, and there might be a number of parallel sublines in a breeding program (Rosvall et al. 1999). There was no attempt in this study to evaluate all possible options of structuring BP, as the single-subline case demonstrates the main principle. The model could be tailored to a more specific case, if desired.

There might be some other advantages of open nucleus through factors not considered in this study. Functioning of breeding cooperatives or a shifting to smaller BP are examples of such factors that may favor the use of open-nucleus in forest tree breeding under specific conditions.

Conclusion

This study demonstrates that population-wide PAM provides more gain (short and long term) in the PP than open-nucleus breeding schemes. This is true for both balanced (Lstibůrek et al. 2004, this issue; first part of the study) and unbalanced distribution of effort (this paper; second part of the study). These results apply to any target level of genetic diversity in the PP. Unbalanced distribution of testing effort results in a substantial increase in genetic gain at any reasonable target value of diversity. Our proposal to forest tree breeders is to consider population-wide PAM with more effort concentrated in higher-ranking parents as a more powerful alternative to open-nucleus breeding schemes.

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