DOI: 10.1534/genetics.105.041723

Positive Assortative Mating With Family Size as a Function of Predicted Parental Breeding Values

M. Lstibůrek,*,[1] T. J. Mullin,*,[2] T. F. C. Mackay,[†] D. Huber[‡] and B. Li*

**Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, North Carolina 27695, [†]Department of Genetics, North Carolina State University, Raleigh, North Carolina 27695 and [‡]School of Forest Resources and Conservation, University of Florida, Gainesville, Florida 32611*

Manuscript received February 7, 2005
Accepted for publication May 31, 2005

ABSTRACT

While other investigations have described benefits of positive assortative mating (PAM) for forest tree breeding, the allocation of resources among mates in these studies was either equal or varied, using schemes corresponding only to parental rank (*i.e.*, more resources invested in higher-ranking parents). In this simulation study, family sizes were proportional to predicted midparent BLUP values. The distribution of midparent BLUP values was standardized by a constant, which was varied to study the range of distributions of family size. Redistributing progenies from lower- to higher-ranking families to a point where an equal number of progenies were still selected out of each family to the next generation caused minimal change in group coancestry and inbreeding in the breeding population (BP), while the additive genetic response and variance in the BP were both greatly enhanced. This generated additional genetic gains for forest plantations by selecting more superior genotypes from the BP (compared to PAM with equal family sizes) for production of improved regeneration materials. These conclusions were verified for a range of heritability under a polygenic model and under a mixed-inheritance model with a QTL contributing to the trait variation.

EARLIER studies by computer simulation have demonstrated that positive assortative mating (PAM) applied in a long-term forest tree breeding program has the potential to generate extra genetic improvement in forest plantations (*e.g.*, dissertations by Mahalovich 1990; Rosvall 1999). This is due to the enhancement of the additive genetic response and variance in the breeding population (BP), enabling the selection of more extreme genotypes from the BP. These genotypes can be established in orchards to produce seeds for production of reforestation nursery stock or alternatively can be vegetatively propagated and directly planted as clones. When both genetic gain and diversity are considered in a single selection criterion, PAM does not much alter the effective population size compared with that achieved under random mating, but increases the average inbreeding in the BP as a consequence of mating among more related individuals (Rosvall and Mullin 2003).

Ideally, the contribution of individuals in the BP to the next generation should correlate with their breeding values (Lindgren 1986). Various weighting schemes have been proposed to assign mating frequencies to individuals in the BP. These are built on different assumptions about the distribution of breeding values and the function used to assign the corresponding mating frequencies (Kang and Namkoong 1988; Kang 1989; Wei and Lindgren 1995). Two approaches for controlling parental contributions during PAM were investigated by Rosvall *et al.* (2003), using a stochastic model of a forest-tree breeding program. In the first approach, balanced mating (each individual involved in an equal number of combinations) was followed by unbalanced selection (more progenies selected from higher-ranking families and fewer from lower-ranking families). In the second, unbalanced mating (individuals of higher rank mated more frequently than lower-ranking trees) was followed by balanced within-family selection. Even though the second approach led to less additive genetic response in the BP, this was overcompensated by a larger expansion of additive variance, resulting in greater genetic gains from the very best genotypes deployed in plantations. In the unbalanced mating scheme, individuals in the BP were ranked by breeding value and subdivided into three distinct hierarchical groups of equal size. The number of mating combinations per individual within a group varied among groups: more in the best group and fewer in the lowest-ranking group.

Optimization of genetic contributions has received considerable attention among quantitative geneticists

[1]*Present address:* Faculty of Forestry and Environment, Czech University of Agriculture, Kamýcká 1176, Praha 6-Suchdol, 165 21, Czech Republic.

[2]*Corresponding author:* Department of Forestry and Environmental Resources, North Carolina State University, Box 8002, Raleigh, NC 27695-8002. E-mail: tim_mullin@ncsu.edu

and breeders. Algorithms have been developed to optimize genetic contributions in individual generations with the goal to maximize genetic response in the breeding population over a total target number of generations. The optimization problem is often constrained by the intended rate of inbreeding. Grundy *et al.* (1998) subdivide these approaches as *a priori* (on the basis of deterministic predictions) and *a posteriori* (dynamic selection algorithms) schemes. The latter could be used to optimize contributions with respect to only the next generation (Meuwissen 1997) or to multiple generations (Woolliams and Thompson 1994). Tactical mate selection then integrates the theory of genetic contributions with technical, logical, and cost factors (Shepherd and Kinghorn 1998).

Forest trees are characterized by long generation intervals. The particular breeding program that provided the basis for the breeding strategy illustrated in this study is that for Norway spruce [*Picea abies* (L.) Karst.] in Sweden (Karlson and Rosvall 1993; Danell 1995). The current generation turnover time in this program is ~30 years. Further, only a selected subset of trees in the BP (*i.e.*, not the whole population) in each generation contribute to new forest plantations. Seed orchards are established with a mixture of several trees selected across multiple breeding populations in given geographical area. Seeds harvested from these orchards are used for current reforestation. Apart from immediate reforestation needs is the long-term management of the BP, where the goal is to achieve a sustainable supply of improved genetic material under uncertain economic and environmental conditions in both the short and the long term. The management of the BP in this particular program was therefore designed to minimize the reduction of gene diversity (or equivalently, effective population size). This is achieved by equal contribution of all individuals in the BP to future generations. A balanced mating scheme followed by balanced within-family selection is a key characteristic of the program. Clonal replication of progeny tests is used to enhance genetic progress in the BP from within-family selection. To enhance the selection response for current and future reforestation needs, Rosvall and Mullin (2003) proposed the incorporation of PAM. The purpose is to enhance the additive variance in the BP, which provides additional genetic gain when selecting the seed orchard, since only a few genotypes from the BP contribute to the orchard.

In earlier investigations (Rosvall *et al.* 2003; Lstibůrek *et al.* 2004), parental contributions did not follow the actual distributional patterns of their predicted breeding values. The number of mating combinations assigned to each individual followed its rank, rather than its predicted breeding value, which imposed an unrealistic assumption that the correlation between rank and breeding value was one. Furthermore, the number of combinations was constant within each hierarchical group, such that the highest-ranking individual was involved in the same number of combinations as the lowest-ranking member of the same group.

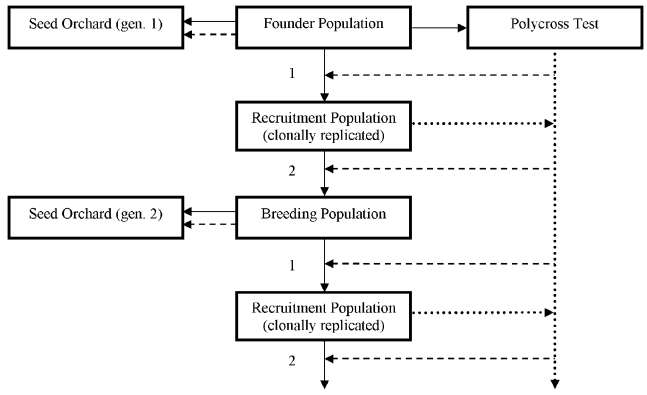

Figure 1.—Schematic of the conceptual breeding strategy, where the symbols are: 1, positive assortative mating and 2, selection. The addition of information on relatives for genetic evaluation is depicted by dotted lines, while dashed lines designate the use of predicted BLUP values. Only the first two generations are depicted; subsequent generations follow an identical plan.

The objective of this study was to dynamically control parental contributions, allowing the importance assigned to each mate to be guided by a linear function of predicted BLUP values. In this study, we quantify the effect of this approach on genetic response and diversity in the BP and on the actual benefit to forest plantations derived from the BP. We also test the sensitivity of the approach with respect to a single major-gene locus contributing to variation in the quantitative trait of interest. In this study, we stress situations where parental contributions are balanced and where genetic progress is constrained by fixed resources for testing, as these are of greatest practical interest to forest tree breeders.

METHODS

The computer simulation program "POPSIM" (Mullin and Park 1995) was modified as described below. The situation modeled represents a single breeding population managed over 12 discrete (non-overlapping) generations (Figure 1). The strategy is based on the actual breeding program implemented for Norway spruce in Sweden (discussed above), although some of the components were modified or eliminated to provide general recommendations over a wider range of forest tree breeding programs. In many such programs, the genetic component of observed variation in a quantitative trait is attributable primarily to additive gene action, and the basic breeding strategy employed is based on "recurrent selection for general combining ability" (Namkoong *et al.* 1988).

Genetic model: A single quantitative trait was described by the genetic model for a population of

diploid, monoecious individuals, with an initial population mean of 100. The trait was influenced by a large number of loci, segregating independently, each with a small effect (polygenic model). In the polygenic model, the phenotypic value (P) of each individual was composed of an independent additive polygenic (A_P) component and an environmental deviation (E), such that $P = A_P + E$. Correspondingly, the phenotypic variance (V_P) was $V_P = V_{A_P} + V_E$. The V_{A_P} was adjusted for individual sets of simulation scenarios such that initial narrow-sense heritability h^2 was 0.1, 0.3, or 0.5, while initial V_P remained constant at 500 (Rosvall *et al.* 1999).

Founder population: Forty-eight founder genotypes were sampled randomly from a population of unrelated, noninbred individuals. The additive effect was sampled from Normal(0, V_{A_P}) and the environmental deviation was sampled from Normal(100, V_E). Each founder was progeny tested with a pollen mix (polycross test). To generate this test, each founder was mated at random to a common pool of 20 unique unrelated, noninbred individuals (representing the mixture of tester pollen). These individuals were sampled from the same distribution of effects as that of the founder population. One hundred fifty polycross-test progenies were generated for each founder. The additive effect for each test progeny was randomly sampled from Normal(a_{FS}, $0.5V_{A_P}$), where a_{FS} is the midparent additive effect. The environmental effect for each progeny genotype was drawn randomly from Normal(100, V_E). The best linear unbiased prediction (BLUP) value of each founder was then calculated from the test, using the animal model (Mrode 1996; Lynch and Walsh 1998) implemented in the ASReml software package (Gilmour *et al.* 2002). In this totally balanced case of unrelated founders, the initial breeding values could be as well calculated as simple deviations from family means. In later generations (following the introduction of imbalance), founders must also be included in the genetic evaluation. Therefore, to simplify programming, we incorporated generalized BLUP analysis from the initial generation. In all situations prior to the BLUP analysis, ASReml was used to estimate variances from the supplied phenotypic and pedigree data.

Assortment of mates: Founders were sorted by BLUP values and mated in a single-pair mating scheme (total number of families $N_f = 24$) to generate progenies that are selection candidates for the breeding population in the next generation. For example, the founder with the highest BLUP value, 1, was mated with founder 2 having the second-highest BLUP value; the next mating was between founders 3 and 4, etc.; and eventually the last mating was between 23 and 24, *i.e.*, between the second-lowest and the lowest-ranking founders, respectively. Thus, every tree was involved in only one mating. This form of assortment was performed among selected individuals in later generations prior to mating.

TABLE 1

Description of individual simulation scenarios (1–10)

Scenario	V_f/V_{fmax}	Note
	Variance of family sizes	
1	0	Equal family size[a]
2	2×10^{-5}	
3	1×10^{-3}	↓
4	2×10^{-3}	
5	1×10^{-2}	Imbalance
6	1.25×10^{-2}	
7	2×10^{-2}	↓
8	5×10^{-2}	
9	3×10^{-1}	
10	1	Maximum V_f[b]

The particular values of V_f/V_{fmax} simulated were selected experimentally to cover the entire range of variation in family size. Each scenario corresponds to a specified variance in family sizes (V_f) relative to the maximum possible variance in family sizes (V_{fmax}). The total number of progenies (N_{RP}) was 720 in all scenarios. The distribution of family sizes was varied, bounded by two extremes:

[a] Size of each family was 30 (N_{RP}/N_f).

[b] Size of top-ranking family was 720 (N_{RP}), and size of remaining families was 0.

Derivation of family sizes: The number of full-sib progenies in each family (family size) was determined as a linear function of the midparent BLUP value (average of parental BLUP values). Midparent BLUP values were standardized to the arithmetic mean a_A. Following this standardization, all negative values were converted to zero and all positive values were converted to a relative scale. Family sizes were then determined as a product of the recruitment population size N_{RP} (total number of test progenies within each generation, equal to 720) and these relative values. The average family size was equal to 30, *i.e.*, 720 progeny genotypes/24 families. The variance in family sizes (V_f) can have two extremes: (1) all family sizes are equal to 30 ($V_f = 0$), and (2) all progenies (720) are generated in the top-ranking family, and all remaining families have family size zero ($V_{fmax} = 20,700$). The desired proportion of variance in family sizes relative to the maximum variance V_f/V_{fmax} is then bounded within the interval [0, 1]. This desired proportion was specified as a simulation input parameter and was varied in individual simulation scenarios to cover the entire interval (Table 1). Parameter a_A was then determined iteratively from V_f/V_{fmax} within each generation, according to the actual distribution of midparent BLUP values.

Generation of recruitment progenies: The additive effect of each progeny was randomly sampled from Normal(a_{FS}, $0.5V_{A_P}(1 - 0.5(F_f + F_m))$), where F_f and F_m are inbreeding coefficients of female and male parents, respectively. Each progeny genotype was replicated by eight clonal copies (ramets), where the environmental effect for each ramet was drawn randomly from

Normal(100, V_E). A constant testing environment was assumed throughout all generations, and the cause of all variability among ramets was assumed to be environmental.

Selection: After generation of the recruitment population, input files for the ASReml software were updated (to include information on all individuals in the pedigree, including founders, their polycross progenies, and all selection candidates in all generations). ASReml was then run to predict BLUP values of selection candidates (current recruitment population). Group-merit selection (Lindgren and Mullin 1997) was then performed to select the next-generation breeding population from the recruitment population. The selection algorithm maximized iteratively the population merit: $B_\omega = \bar{g}_\omega - c\Theta_\omega$, where B_ω is the group merit of a selected set ω; $\bar{g}_\omega$ is the average BLUP value of the set; Θ_ω is the group coancestry of the set; and c is a weighting constant. Group coancestry is the average of all pairwise coancestries, including self-coancestry and reciprocals. It is the probability that two genes taken at random from the gene pool, with replacement, are identical by descent (Cockerham 1967). The weighting constant was set to a very large value, forcing the group-merit selection algorithm to minimize group coancestry of the selected set of trees (next-generation BP). Under the majority of scenarios, this is equivalent to selecting exactly two individuals (with the highest BLUP values) from each full-sib family (balanced within-family selection). At a higher degree of imbalance (when some family sizes are less than two), the algorithm would select additional individuals within the available families (some families contributing more than two), while minimizing the group coancestry of the selected group.

Production population: Genetically improved planting stock is commonly derived from a production population, such as a seed orchard, selected as a subset of the breeding population. The six trees with highest BLUP values irrespective of their coancestry were selected for the production population. The purpose was to test the ability of the breeding population to support a production population (the breeder's target) and to determine the proportional gene diversity of these best clones.

Mixed-inheritance model: Additional simulation scenarios were run using a "mixed-inheritance" model. The purpose of this model was to investigate whether the main conclusions of this study would be significantly altered by the presence of a single, biallelic, major-gene locus, contributing up to 10% of the additive genetic variance in the quantitative trait. The simulation was implemented as described by Gomez-Raya and Klemetsdal (1999). The phenotypic value (P) was composed of three independent components $P = A_M + A_P + E$, where A_M is the additive effect of a major gene, A_P is the additive effect due to a large number of polygenic loci, each with a small effect (polygenic background), and E is the residual deviation. The phenotypic variance (V_P) can be expressed as $V_P = V_{A_M} + V_{A_P} + V_E$, where V_{A_M} and V_{A_P} are the additive variances (referring to the base unselected population) due to the major-gene component ($V_{A_M} = 2p(1-p)\alpha^2$) and the polygene component, respectively (p is the initial gene frequency of allele M_1 at the major-gene locus). The effect of a major gene (α) was calculated as $\alpha = \sqrt{\lambda h^2 V_P / 2p(1-p)}$, where λ is the proportion of the additive variance explained by the major-gene component [$\lambda = V_{A_M}/(V_{A_M} + V_{A_P})$], and h^2 is the narrow-sense heritability [$h^2 = (V_{A_M} + V_{A_P})/V_P$]. Simulation scenarios were run at $\lambda = 0.1$, where it was assumed that λ was constant through all generations. V_{A_P} was calculated as $V_{A_P} = h^2 V_P - V_{A_M}$. To generate the founder population, alleles at the major-gene locus were sampled randomly from the allelic pool with a frequency of the M_1 allele $p = 0.1$. The additive effect of the major gene was then α for M_1M_1 and $-\alpha$ for M_2M_2 genotypes. To generate progenies, alleles at the major-gene locus were sampled from parental genotypes with the probability 0.5.

Simulation and evaluation of results: The process described above was repeated over 12 generations for each simulation scenario. Each scenario (unique variance in family sizes, presented in Table 1) was replicated by 250 independent runs (iterations). Parametric means across all iterations were calculated for each scenario along with 95% confidence intervals. The random number generator used in this simulation was "MRG32k3a" (L'Ecuyer *et al.* 2002). Parametric means for each scenario (average additive response, variance, and inbreeding) were plotted as a function of the resulting group coancestry in both the breeding and production populations.

RESULTS AND DISCUSSION

In this study, the redistribution of test resources among families by varying their sizes under fixed total test resources magnified the effect of PAM, which by itself provides a large enhancement of $V_{A(BP)}$, particularly under low-selection-intensity scenarios (Baker 1973; De Lange 1974; Jorjani 1995; Rosvall and Mullin 2003). The enhancement of $V_{A(BP)}$ observed in this study exceeds the magnitude reported earlier under unbalanced mating schemes (Rosvall *et al.* 2003; Lstibůrek *et al.* 2004). This conclusion holds under infinitesimal model assumptions, as well as under the mixed-inheritance model with a single major-gene locus, contributing 10% of the additive genetic variance.

Simulation showed that the use of clonal replication in progeny testing was the primary factor giving rise to more accurate assessment of breeding values, facilitating high within-family selection differentials and a stronger effect by PAM on expansion of additive variance. The effect of clonal testing was more important

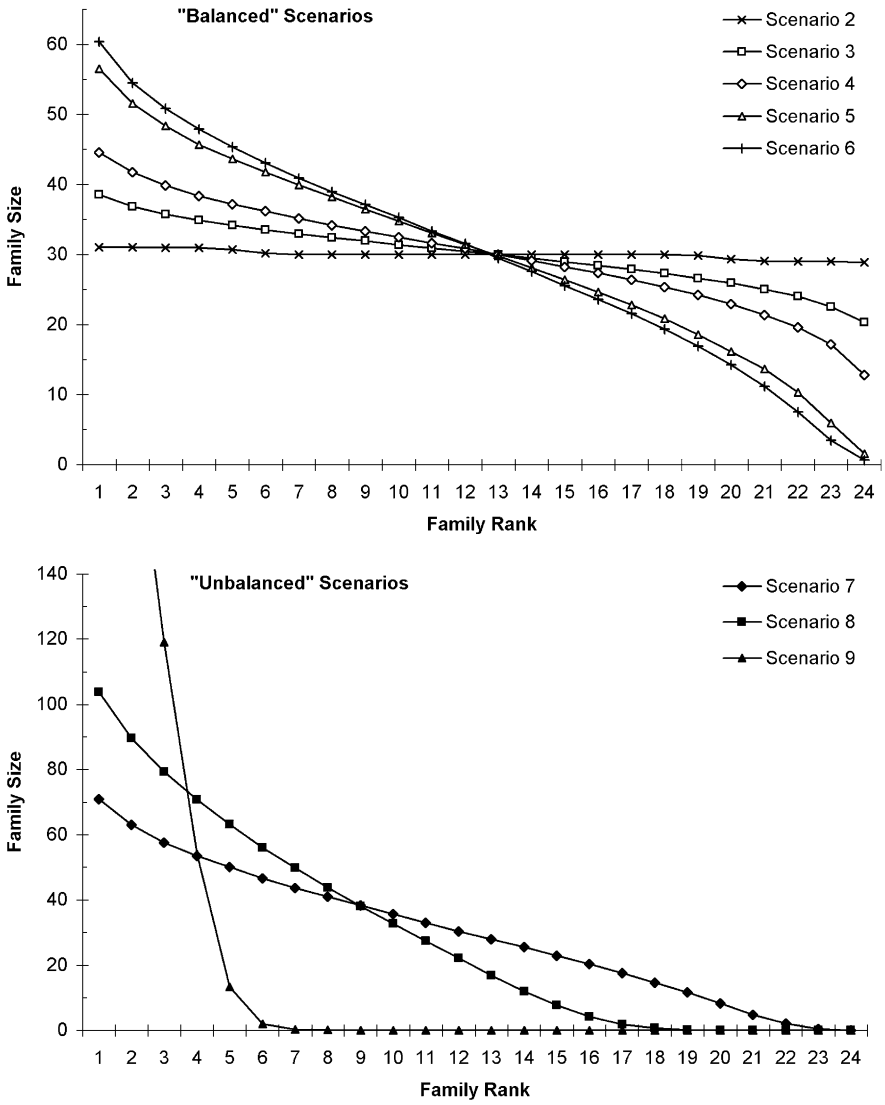

FIGURE 2.—Distribution of family sizes in generation 5. Individual lines were drawn for each scenario (1–10) presented in Table 1. The *x*-axis shows the rank of each family; families are sorted by mid-parent BLUP value from the left (highest rank) to the right (lowest rank). Each line connects family sizes within an individual simulation scenario, averaged over 250 iterations. Scenario 8 had an average size of family 2 of 196.9 and of family 1 of 334.1 (outside the scale of the figure). $h^2 = 0.3$, and $\lambda = 0$.

than the inclusion of the multigeneration relationship data set to the genetic evaluation by BLUP. This supports the benefits of clonal assessment in progeny testing for forest tree breeding programs described by other authors (*e.g.*, SHAW and HOOD 1985; RUSSELL and LOO-DINKINS 1993; MULLIN and PARK 1994; DANUSEVICIUS and LINDGREN 2002; ISIK *et al.* 2003).

The average distribution of family sizes in the fifth generation for scenarios 1–10 (as presented in Table 1) is depicted in Figure 2. This general trend in the distribution of family sizes was also observed in earlier and later generations. For clarity in further discussion, scenarios 1–6 are referred to as "balanced" and all remaining scenarios (7–10) as "unbalanced." The term "balance" in this context refers to balanced within-family selection (equal number of individuals selected from each family), as opposed to balanced distribution of test resources. This distinction between the balanced and unbalanced sets of scenarios is not completely accurate, because scenarios were evaluated across multiple independent simulation iterations, where each was unique in terms of the actual distribution of parental BLUP values. Balanced within-family selection was facilitated by a high weighting on group coancestry during selection.

The reallocation of test effort among families had a significant effect on the BP. Θ_{BP} increased as a result of redistributing more progenies to higher-ranking families (Figures 3–5). The marginal increase in Θ_{BP} under balanced scenarios ($0.021 \leq \Theta_{BP} \leq 0.024$ in generation 3, $0.035 \leq \Theta_{BP} \leq 0.046$ in generation 6, and $0.062 \leq \Theta_{BP} \leq 0.092$ in generation 12) agrees with the finding of ROSVALL *et al.* (2003) that keeping equal parent contributions by means of balanced mating and selection maintained the lowest Θ_{BP}. After this point was exceeded (typically in scenario 7), some parents did not contribute to the next generation (*i.e.*, family size equal to 0), which resulted in more progenies being selected from the fewer remaining families and consequently in a more rapid increase of Θ_{BP}. Even in these unbalanced

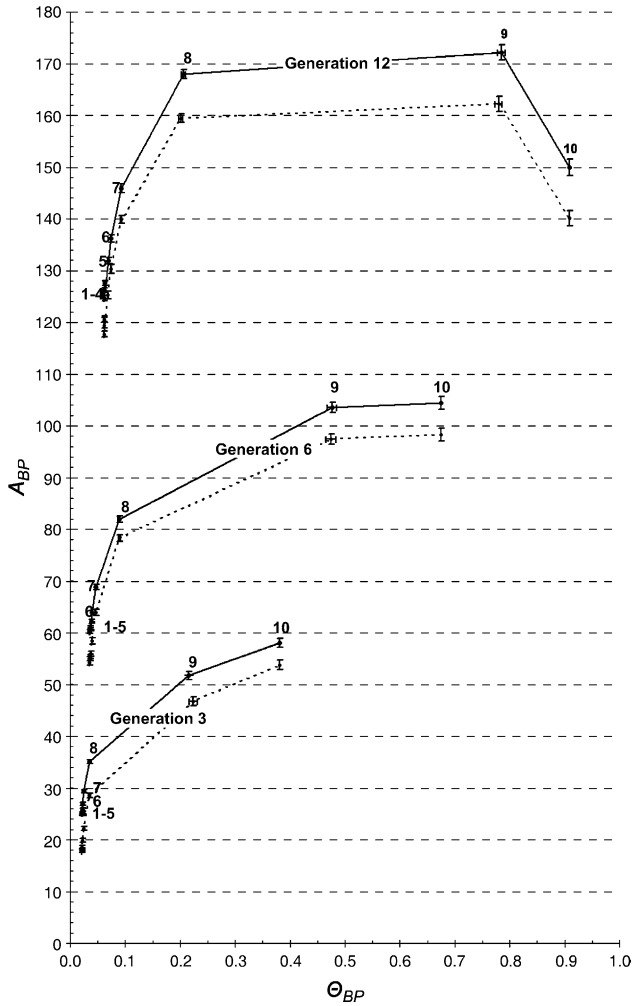

FIGURE 3.—Average additive effect (A_{BP}) and group coancestry Θ_{BP} in breeding population (BP) in generations 3, 6, and 12. Lines connect individual scenarios described in Table 1, such that the variation in family sizes V_f increases (in individual scenarios) from the left to the right in the graph. The number of each scenario is presented at each point. Initial values of $h^2 = 0.3$ and $\lambda = 0$ are shown. Identical scenarios but with $\lambda = 0.1$ are represented by dotted lines. Confidence intervals at the 95% level are presented around each average of 250 simulation iterations.

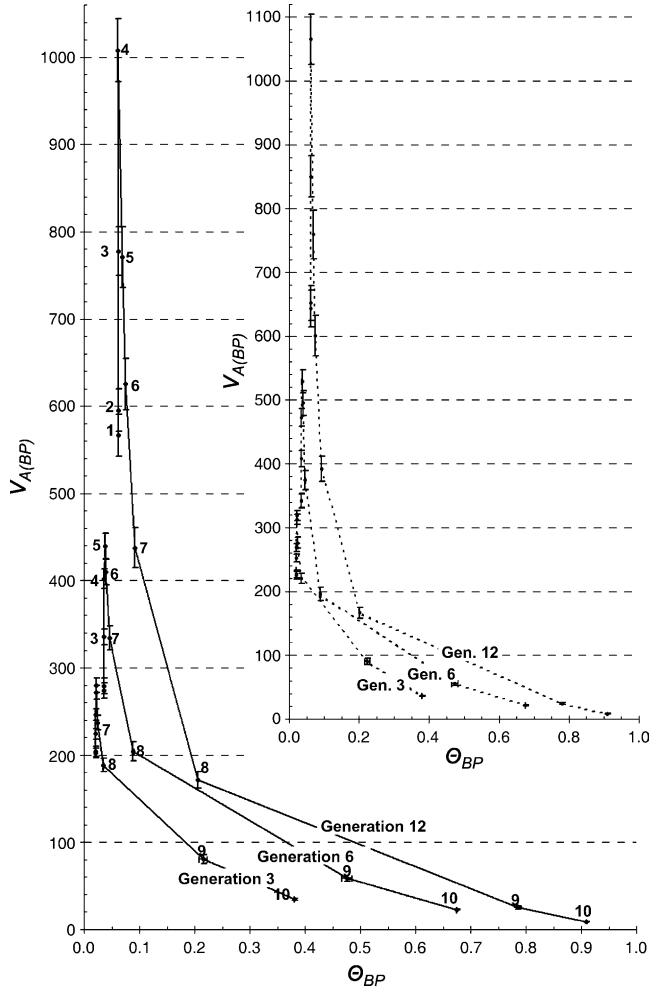

FIGURE 4.—Additive variance $V_{A(BP)}$ and group coancestry Θ_{BP} in breeding populations (BP) in generations 3, 6, and 12. Lines connect individual scenarios described in Table 1, such that the variation in family sizes V_f increases (in individual scenarios) from the left to the right in the graph. The number of each scenario is presented at each point. Initial values of $h^2 = 0.3$ and $\lambda = 0$ are shown. Identical scenarios but with $\lambda = 0.1$ are represented by dotted lines in the top part. Confidence intervals at the 95% level are presented around each average of 250 simulation iterations.

scenarios, Θ_{BP} was minimized during the group-merit selection. Balanced scenarios also resulted in a much lower increase in Θ_{BP} at generation shifts, compared to more imbalanced scenarios. Θ_{BP} was not significantly altered when a mixed-inheritance model was considered (Figures 3 and 4, dotted lines).

The average additive effect in the BP (A_{BP}) increased under balanced scenarios ($25.0 \leq A_{BP} \leq 26.9$ in generation 3, $60.2 \leq A_{BP} \leq 63.9$ in generation 6, and $124.6 \leq A_{BP} \leq 136.2$ in generation 12) and even more under unbalanced scenarios (Figure 3). The general increase in genetic response due to PAM is expected from the theory, because PAM induces gametic-phase disequilibrium, *i.e.*, expands additive variance (the among-family component), which creates opportunities for additional genetic response to selection (*e.g.*, CROW 1986). In this model, the added unbalance induces a positive correlation between the expected family value and corresponding family size. Thus, higher selection differentials are achieved within families of higher expected (midparent additive) values. This induces further expansion of additive variance in generations that follow, but also more efficient conversion of variance into genetic gains. Interestingly, A_{BP} in earlier generations under unbalanced scenarios reached, and potentially exceeded, gains in later generations generated under more balanced scenarios. Thus, for example, in the fourth generation, $A_{BP} = 69.98$ (scenario 9), exceeding A_{BP} in the sixth generation ($A_{BP} = 69.1654$ in scenario 6). This, of course, assumes complete absence

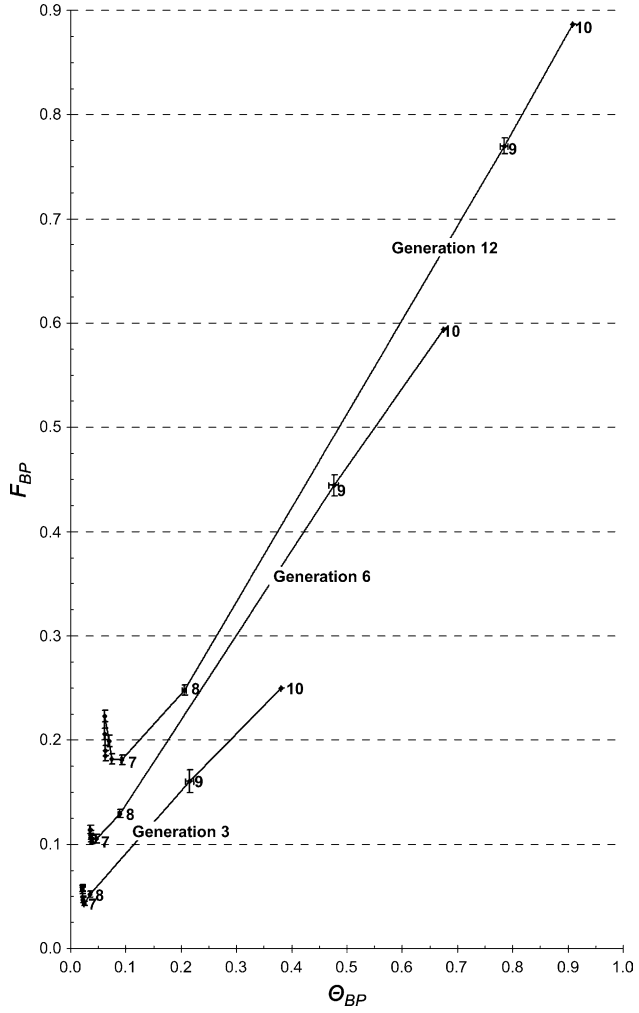

FIGURE 5.—Average inbreeding coefficient $F_{(BP)}$ and group coancestry Θ_{BP} in breeding populations in generations 3, 6, and 12. Lines connect individual scenarios described in Table 1, such that the variation in family sizes V_f increases (in individual scenarios) from the left to the right in the graph. The number of each scenario is presented at each point. Initial values of $h^2 = 0.3$ and $\lambda = 0$ are shown. Confidence intervals at the 95% level are presented around each average of 250 simulation iterations.

of inbreeding depression, which could adversely affect the additive response under unbalanced scenarios, depending upon the distribution and magnitude of the depression (WILLIAMS and SAVOLAINEN 1996). Since generation intervals in forest trees are measured in decades, results for generations 3–6 are of greatest practical importance. Results for generation 12 are presented primarily from academic interest and should be interpreted with caution.

The additional expansion of additive variance in the BP ($V_{A(BP)}$) due to the redistribution of family sizes was most pronounced under balanced scenarios (Figure 4). In generation 3, the maximum enhancement of $V_{A(BP)}$ was observed in scenario 5 [$V_{A(BP)} = 279.8$, compared with $V_{A(BP)} = 202.3$ in scenario 1]; the same was true also in generation 6 [$V_{A(BP)} = 439.7$, compared with $V_{A(BP)} = 273.8$ in scenario 1]; and eventually, maximum enhancement of $V_{A(BP)}$ in generation 12 was observed in scenario 4 [$V_{A(BP)} = 1007.9$, compared with $V_{A(BP)} = 566.7$ in scenario 1]. This suggests that the point of maximum enhancement shifts slowly to more balanced scenarios over multiple generations. Added imbalance (higher V_f in scenarios 7–10) caused a sharp reduction in $V_{A(BP)}$. In these unbalanced scenarios, some parents would not contribute to subsequent generations, and, therefore, the variation of expected family means sharply drops for each unit of increase in V_f (BULMER 1985). Larger variation in $V_{A(BP)}$ among individual simulation iterations (assessed by confidence intervals) was observed at lower values of Θ_{BP}, while greater run-to-run similarity was achieved at a higher Θ_{BP}.

There was a significant effect from the major gene on both A_{BP} and $V_{A(BP)}$ (Figures 3 and 4, dotted lines). A_{BP} was up to 10% lower (the difference was similar in all scenarios), while $V_{A(BP)}$ was up to 20% higher in the mixed-inheritance model. Higher $V_{A(BP)}$ is due to the presence of a segregating major-gene locus with an effect that is substantially higher than individual effects of remaining polygenic loci. Elevated $V_{A(BP)}$ under balanced scenarios is then due to the variation of allelic frequencies at this locus responding to selection and drift (FALCONER and MACKAY 1996). The probability of eventual fixation of the favorable allele was higher in scenarios with greater imbalance (Figure 5); thus the difference in $V_{A(BP)}$ due to the major gene locus almost disappeared with added unbalance. Since information on the major gene was not extracted (*e.g.*, by genetic marker analysis) and incorporated into the genetic evaluation (which may actually happen in real breeding programs, particularly for QTL associated with smaller effects), and since there was zero correlation between the additive value due to a major-gene locus and the corresponding value due to polygenic loci, there was no additional genetic response due to the presence of a major gene.

The average inbreeding in the BP (F_{BP}) in generations 1 (founder population) and 2 was equal to 0. Following the mating of individuals in the second-generation breeding population, F_{BP} reached a value of ~0.05 in the third generation under balanced scenarios and of up to 0.25 in scenario 10 (Figure 5). Values of F_{BP} in later generations varied from 0.18 to 0.88; however, F_{BP} under balanced scenarios was still within a much narrower interval (0.18–0.22). The increase in F_{BP} when progressing through generations was again more pronounced under imbalanced scenarios and minimal under balanced scenarios. An increase in F_{BP} when progressing through balanced scenarios (1–6) is a consequence of the assortment of mated individuals with no avoidance of mating among full-sibs, as performed in this study. The likelihood of mating among selected full-sibs depends to a certain extent on sizes of

higher- and lower-ranking families and the variation among the top two selections (full-sibs) from these families. Although F_{BP} was marginally higher in the mixed-inheritance model, the difference was not significant.

Narrow-sense heritability (h^2) is one of the main factors influencing the effectiveness of PAM (Falconer and Mackay 1996; Lynch and Walsh 1998) and its impact was further enhanced in this study by the use of clonal replication in progeny testing. Results described so far were obtained for scenarios where the initial value of h^2 was set to 0.3. The maximum observed enhancements of $V_{A(BP)}$ when $h^2 = 0.3$ were 138, 161, and 178% over that in the completely balanced scenario (scenario 1) in generations 3, 6, and 12, respectively. The corresponding maximum enhancements in generation 6 were 135% when $h^2 = 0.1$ and 177% when $h^2 = 0.5$. As for $V_{A(BP)}$, A_{BP} also increased with h^2 ($A_{BP} = 24.4$ when $h^2 = 0.1$, $A_{BP} = 60.9$ when $h^2 = 0.3$, and $A_{BP} = 89.6$ when $h^2 = 0.5$ in generation 6 of scenario 1). The increase in A_{BP} at the limit of balanced scenarios (scenario 6) was 104–106% of that in scenario 1 in the studied range of h^2. F_{BP} presented in Figure 5 was not significantly altered by lower ($h^2 = 0.1$) or higher ($h^2 = 0.5$) initial h^2 values.

Given that only the effect of PAM on the enhancement of $V_{A(BP)}$ would be of interest to the breeder, this variable-family-size approach would seem very straightforward. Nevertheless, this extra enhancement of variance in the BP influences the likelihood of mating among selected full-sibs, following the assortment of the BP. This may affect the F_{BP}, reducing the within-family portion of the additive variance and thus reducing the intensity of within-family selection and eventual reduction in additive response in the BP.

Similar to the BP, Θ_{PP} was only slightly influenced by variation in family sizes up to the limit of balanced scenarios (Figure 6). Θ_{PP} increased more progressively at higher levels of imbalance. The average additive effect (genetic gain) in the production population (PP) (A_{PP}) responded greatly to the increase in variance in family sizes. A_{PP} increased under balanced scenarios ($46.4 \leq A_{PP} \leq 51.0$ in generation 3, $84.6 \leq A_{PP} \leq 92.8$ in generation 6, and $157.3 \leq A_{PP} \leq 169.7$ in generation 12). Although higher values of A_{PP} were observed in scenarios 7–10, these are of less practical interest due to the rapid increase of Θ_{BP} and F_{BP}. At $h^2 = 0.1$ and generation 6, there were 9.3 and 12.8% additional A_{PP}'s, in scenarios 6 and 7, respectively (Figure 7). At $h^2 = 0.5$, the additional A_{PP}'s were 9.9 and 13.1%, in scenarios 6 and 7, respectively. Thus, for the entire range of h^2 studied, there were >9% extra A_{PP} in scenario 6 and >12% extra A_{PP} in scenario 7 in generation 6, due to the reallocation of testing effort in the BP, with minimal increase of Θ_{BP} and F_{BP}. These results hold also for the mixed-inheritance model (evaluated at $h^2 = 0.3$), where the advantage in A_{PP} due to the added imbalance was >11% in scenario 6 and >13% in scenario 7.

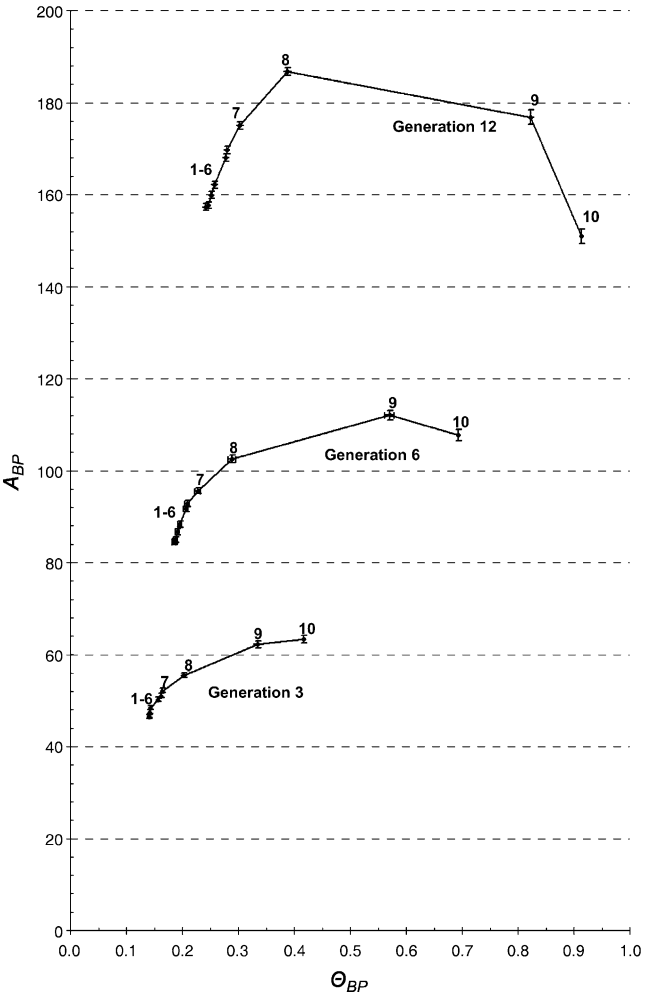

Figure 6.—Average additive effect A_{PP} and group coancestry Θ_{PP} in the production population (PP) in generations 3, 6, and 12. Lines connect individual scenarios described in Table 1, such that the variation in family sizes V_f increases (in individual scenarios) from the left to the right in the graph. The number of each scenario is presented at each point. Initial values of $h^2 = 0.3$ and $\lambda = 0$ are shown. Confidence intervals at the 95% level are presented around each average of 250 simulation iterations.

Alternatively, other forms of deployment of superior genetic material selected from BP could be considered (*e.g.*, deployment of full-sib families or clones). Our attempt, though, was to provide more general description of the accumulated additive response and the average relatedness among these best clones, without imposing assumptions on the actual form of their deployment. In reality, a number of breeding populations could contribute to any given production population (McKeand and Beineke 1980; Rosvall *et al.* 1999; Ruotsalainen and Lindgren 2000), resulting in a mixture of selections with a higher census number and with a lower level of relatedness than that presented in this study.

An additional comparison was performed with the unbalanced mating strategy with equal family sizes

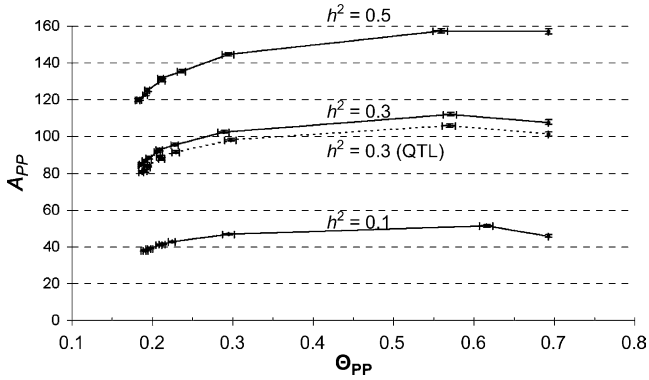

FIGURE 7.—Production population (PP) in generation 6. Average additive effect (A_{PP}) as a function of group coancestry (Θ_{PP}) is shown. Lines connect individual scenarios described in Table 1, and the variation in family sizes V_f increases (in individual scenarios) from the left to the right in the graph. The number identifying each scenario is presented at each point. Values of $h^2 = 0.1$, 0.3, and 0.5 at $\lambda = 0$ and $h^2 = 0.3$ at $\lambda = 0.1$ are shown. Confidence intervals at the 95% level are presented around each average of 250 simulation iterations.

(UM) proposed by ROSVALL *et al.* (2003). The variable-family-size approach presented in this study did not outperform the UM strategy. In the PP, both A_{PP} and Θ_{PP} were of a similar magnitude. We attribute this similarity primarily to a lower frequency of mating among selected full-sibs in the UM strategy (within the distinct hierarchical groups), as all families are of equal size, resulting in greater similarity among selected groups of full-sibs, and consequently greater dispersion of individuals, following their assortment. Thus, even though the enhancement of $V_{A(BP)}$ was more efficient using the variable-family-size approach and lower in the UM strategy, the lower F_{BP} in the latter led to a smaller reduction in the within-family portion of additive variance, resulting in ~4% extra additive response in the BP. On the other hand, the variable-family-size approach led to a lower value of Θ_{BP}, by retaining a larger share of lower-ranking individuals in the BP contributing to subsequent generations (Figure 2).

This study suggests that allocating resources during PAM according to midparent breeding values may greatly enhance genetic gains in forest plantations while causing a minimal increase of Θ_{BP} and F_{BP}. To reach a reasonable point of balance between Θ_{BP}, F_{BP}, and A_{PP} in the BP, we suggest minimizing the parameter a_A (*i.e.*, maximizing V_f) under a restriction where an equal number of progenies are selected from each family (balanced within-family selection; the size of the lowest-ranking family is at least two under single-pair mating). Reducing a_A below this limit would provide an additional boost of A_{PP}, but would also be accompanied by a much greater increase in Θ_{BP} and F_{BP} per unit of increase of A_{PP}. The findings of this study are of particular relevance to the breeding program of Norway spruce in Sweden, which is characterized by equal parental contributions. Reallocating available resources in this program as proposed would provide additional genetic gain for newly established forest plantations, but would not reduce the potential for sustainable production in the long term.

The group-merit selection method used in this study was constrained to maximize gene diversity in the BP, and genetic progress was primarily a consequence of strong within-family selection, facilitated by clonal replication of the recruitment population. Future research may demonstrate a larger genetic response per unit of gene diversity when this selection constraint on BP diversity is slightly relaxed (RODRÍGUEZ 2000).

We thank Dag Lindgren and Ola Rosvall for their valuable comments during the development of the study and Arthur Gilmour, Gary Hodge, and Salvador Gezan for their generous assistance with the ASReml software. We also thank the associate editor and two anonymous reviewers for their many recommendations and improvements to the article. We gratefully acknowledge financial support from the Föreningen Skogsträdsförädling (Swedish Tree Breeding Association), CellFor, and the North Carolina State University-Industry Cooperative Tree Improvement Program.

LITERATURE CITED

BAKER, R. J., 1973 Assortative mating and artificial selection. Heredity **31:** 231–238.

BULMER, M. G., 1985 *The Mathematical Theory of Quantitative Genetics.* Clarendon Press, Oxford.

COCKERHAM, C. C., 1967 Group inbreeding and coancestry. Genetics **56:** 89–104.

CROW, J. F., 1986 *Basic Concepts in Population, Quantitative, and Evolutionary Genetics.* W. H. Freeman, New York.

DANELL, Ö., 1995 Breeding programs in Sweden. 1. General approach. SkogForsk. Arbetsrapport **302:** 1–4.

DANUSEVICIUS, D., and D. LINDGREN, 2002 Efficiency of selection based on phenotype, clone and progeny testing in long-term breeding. Silvae Genet. **51:** 19–26.

DE LANGE, A. O., 1974 A simulation study of the effects of assortative mating on the response to selection. *Proceedings of the 1st World Congress on Genetics Applied to Livestock Production*, Vol. III, pp. 421–425. Editorial Garsi, Madrid.

FALCONER, D. S., and T. F. C. MACKAY, 1996 *Introduction to Quantitative Genetics.* Longman, Harlow, UK.

GILMOUR, A. R., B. J. GOGEL, B. R. CULLIS, S. J. WELHAM and R. THOMPSON, 2002 *ASReml User Guide Release 1.0.* VSN International, Hemel Hempstead, UK.

GOMEZ-RAYA, L., and G. KLEMETSDAL, 1999 Two-stage selection strategies utilizing marker-quantitative trait locus information and individual performance. J. Anim. Sci. **77:** 2008–2018.

GRUNDY, B., B. VILLANUEVA and J. A. WOOLLIAMS, 1998 Dynamic selection procedures for constrained inbreeding and their consequences for pedigree development. Genet. Res. **72:** 159–168.

ISIK, F., B. LI, J. FRAMPTON and B. GOLDFARB, 2003 Efficiency of seedlings and rooted cuttings for testing and selection in Pinus taeda. For. Sci. **50:** 44–53.

JORJANI, H., 1995 Genetic studies of assortative mating in selected and unselected populations. Ph.D. Thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden.

KANG, H., 1989 Inbreeding effective population size under some artificial selection schemes. II. Normal distribution of breeding values. For. Sci. **35:** 303–318.

KANG, H., and G. NAMKOONG, 1988 Inbreeding effective population size under some artificial selection schemes. I. Linear distribution of breeding values. Theor. Appl. Genet. **75:** 333–339.

KARLSON, B., and O. ROSVALL, 1993 Breeding programmes in Sweden 3. Norway spruce, pp. 135–141 in *Progeny Testing and*

Breeding Strategies: Proceedings of the Nordic Group of Tree Breeding, edited by S. J. Lee. Forestry Commission, Edinburgh.

L'Ecuyer, P., R. Simard, E. J. Chen and W. D. Kelton, 2002 An objected-oriented random-number package with many long streams and substreams. Oper. Res. **50:** 1073–1075.

Lindgren, D., 1986 How should breeders respond to breeding values? Proceedings of the IUFRO Conference Joint Meeting: Working Parties on Breeding Theory, Progeny Testing, Seed Orchards, North Carolina State University-Industry Cooperative Tree Improvement Program, Raleigh, NC, pp. 361–371.

Lindgren, D., and T. J. Mullin, 1997 Balancing gain and relatedness in selection. Silvae Genet. **46:** 124–129.

Lstibůrek, M., T. J. Mullin, D. Lindgren and O. Rosvall, 2004 Open-nucleus breeding strategies compared to population-wide positive assortative mating. II. Unequal distribution of testing effort. Theor. Appl. Genet. **109:** 1169–1177.

Lynch, M., and B. Walsh, 1998 *Genetics and Analysis of Quantitative Traits*. Sinauer Associates, Sunderland, MA.

Mahalovich, M. F., 1990 Modelling positive assortative mating and elite populations in recurrent selection programs for general combining ability. Ph.D. Thesis, North Carolina State University, Raleigh, NC.

McKeand, S., and F. Beineke, 1980 Sublining for half-sib breeding populations of forest trees. Silvae Genet. **29:** 14–17.

Meuwissen, T. H. E., 1997 Maximizing the response of selection with a predefined rate of inbreeding. J. Anim. Sci. **75:** 934–940.

Mrode, R. A., 1996 *Linear Models for the Prediction of Animal Breeding Values*. CAB International, Wallingford, Oxon, UK.

Mullin, T. J., and Y. S. Park, 1994 Genetic parameters and age to age correlations in clonally replicated test of black spruce. Can. J. For. Res. **24:** 2330–2341.

Mullin, T. J., and Y. S. Park, 1995 Stochastic simulation of population management strategies for tree breeding: a new decision-support tool for personal computers. Silvae Genet. **44:** 132–141.

Namkoong, G., H. C. Kang and J. S. Brouard, 1988 *Tree Breeding: Principles and Strategies* (Monographs on Theoretical and Applied Genetics 11). Springer-Verlag, New York.

Rodríguez, L. S., 2000 Balanced vs. slightly unbalanced selection. Heredity **84:** 685–691.

Rosvall, O., 1999 Enhancing gain from long-term forest tree breeding while conserving genetic diversity. Ph.D. Thesis, Swedish University of Agricultural Sciences, Umeå, Sweden.

Rosvall, O., and T. J. Mullin, 2003 Positive assortative mating with selection restrictions on group coancestry enhances gain while conserving genetic diversity in long-term forest tree breeding. Theor. Appl. Genet. **107:** 629–642.

Rosvall, O., D. Lindgren and T. J. Mullin, 1999 Sustainability robustness and efficiency of a multi-generation breeding strategy based on within-family clonal selection. Silvae Genet. **47:** 307–321.

Rosvall, O., T. J. Mullin and D. Lindgren, 2003 Controlling parent contributions during positive assortative mating and selection increases gain in long-term forest tree breeding. For. Genet. **10:** 35–53.

Ruotsalainen, S., and D. Lindgren, 2000 Stratified sublining: a new option for structuring breeding populations. Can. J. For. Res. **30:** 596–604.

Russell, J. H., and J. A. Loo-Dinkins, 1993 Distribution of testing effort in cloned genetic tests. Silvae Genet. **42:** 98–104.

Shaw, D. V., and J. V. Hood, 1985 Maximizing gain per effort by using clonal replicates in genetic tests. Theor. Appl. Genet. **71:** 392–399.

Shepherd, R. K., and B. P. Kinghorn, 1998 A tactical approach to the design of crossbreeding programs. Proceedings of the 6th World Congress on Genetics Applied to Livestock Production, Armidale, Australia, Vol. 25, pp. 431–438.

Wei, R.-P., and D. Lindgren, 1995 Optimal family contributions and a linear approximation. Theor. Popul. Biol. **48:** 318–332.

Williams, C. G., and O. Savolainen, 1996 Inbreeding depression in conifers: implications for breeding strategy. For. Sci. **42:** 102–117.

Woolliams, J. A., and R. Thompson, 1994 A theory of genetic contributions. Proceedings of the 5th World Congress on Genetics Applied to Livestock Production, Guelph, Ontario, Canada, Vol. 19, pp. 127–134.

Communicating editor: J. B. Walsh