solely on the estimations of their multimeric structure before carrying out a survey on clones from the field. The isozyme polymorphism has provided the useful information. Full-sib progeny from controlled crosses shows mendelian segregation for lap-1 and pgm-2 (most probably, this can be expected as well for aco-1). Got-3 segregates as well but is only exceptionally observed in the intraspecific *S. fragilis* progeny of family DxG. Est-1 and adh-2 (most probably also 6pg-1) have fixed heterozygous enzyme patterns and do not show homozygotes. The hybrids are difficult to identify since the more or less diagnostic enzymes ADH and β-EST exhibit 2 main patterns corresponding to either *S. alba* and *S. fragilis.* Most *S. fragilis*-like samples are homozygous or nearly fixed for the allele B in lap-1 which might be a good marker for calculating the fixation index and hierarchical F-statistics in clones from the field (TRIEST et al., 1998).

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References

ARAVANOPOULOS, F.: Inheritance of alcohol dehydrogenase and phosphoglucomutase in *Salix exigua* NUTT.. In: Recent advances in Poplar selection and Propagation techniques. Hann-Münden, Germany, 2 to 5 Oct. 1989, Hessian Forest Research Institute: 167–175 (1989). — ARAVANOPOULOS, F.: Dynamics of isoenzyme electrophoretic spectra in intraspecific families of *Salix eriocephala* MUHL. and *S. exigua* NUTT. and their implementation in willow breeding research. PhD dissertation, University of Toronto (1992). — ARAVANOPOULOS, F., ZSUFFA, L. and CHONG, K.: The genetic basis of enzymatic variation in *Salix exigua.* Hereditas **119**: 77–88 (1993). — BROCHMAN, C., SOLTIS, P. and SOLTIS, D.: Recurrent formation and polyphyly of Nordic polyploids in Draba (Brassicaceae). Amer. J. Bot. **79**: 673–688 (1992). — BRUNSFELD, S., SOLTIS, D. and SOLTIS, P.: Patterns of genetic variation in *Salix* section *Longifoliae (Salicaceae).* Amer. J. Bot. **78**: 855–869 (1991). — DE BONDT, R.: Role of genetic diversity and identity in replantations – Case study on *Salix* sp.. MSc. thesis, Vrije Universiteit Brussel, 82 p. (1996). — HAMRICK, J. L. and GODT, M. J.: Allozyme diversity in plant species. In: BROWN, A., CLEGG, M., KAHLER, A. and WEIR, S. (eds): Plant population genetics, breeding and genetic resources. 43–63. Sinauer, Sunderland, MA. (1989). — LOVELESS, M. and HAMRICK, J.: Genetic organization and evolutionary history in two North American species of Cirsium. Evolution **42**: 254–265 (1988). — MÜLLER-STARCK, G.: Genetic control and inheritance of isoenzymes in Poplars of the Tacamaha section and hybrids. Silv. Genet. **41**: 87–95 (1992). — NEI, M.: Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics **89**: 583–590 (1978). — PURDY, B. and BAYER, R.: Allozyme variation in the Athabasca sand dune endemic, *Salix silicola,* and the closely related widespread species, *S. alaxensis.* Syst. Bot. **20**: 179–190 (1995). — RAJORA, O. P.: Genetics of allozymes in *Populus deltoides* MARSH., *P. nigra* L., and *P. maximowiczii* HENRY. J. Hered. **81**: 301–308. — ROGERS, J.: Measures of genetic similarity and genetic distance. Studies in genetics. Univ. Texas Publ. 7213: 145–153 (1972). — SOLTIS, D. and SOLTIS, P.: Molecular data and the dynamic nature of polyploidy. Critical Reviews in Plant Sciences **12**: 243–273 (1993). — STRAUSS, S. H. and CONKLE, M. T.: Segregation, linkage, and diversity of allozymes in knobcone pine. Theor. Appl. Genet. **72**: 483–493. — SWOFFORD, D. and SELANDER, R.: BIOSYS-1: a Fortran program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Hered. **72**: 281–283 (1981). — TRIEST, L.: Electrophoretic polymorphism and divergence in *Najas marina* L. (*Najadaceae*): molecular markers for individuals, hybrids, cytodemes, lower taxa, ecodemes and conservation of genetic diversity. Aquat. Bot. **33**: 301–380 (1989). — TRIEST, L., DE GREEF, B., DE BONDT, R., VANDEN BOSSCHE, D., D'HAESELEER, M., VAN SLYCKEN, J. and COART, E.: Use of RAPD markers to estimate hybridization in *Salix alba* and *Salix fragilis.* Belg. J. Bot. **129**: 140–148 (1997). — TRIEST, L., DE GREEF, B., VERMEERSCH, S., VAN SLYCKEN, J., COART, E.: Genetic variation and putative hybridisation in *Salix alba* and *Salix fragilis:* Evidence from allozyme data. Plant Systematics and Evolution (accepted for publication 15.1.98).

A Model for Infusion of Unrelated Material into a Breeding Population

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Abstract

A consequence of selection in a closed breeding population is an increased level of relatedness. One remedy to this may be infusion of unrelated genetic material into the breeding population. A model is established to study such infusion assuming that new plus-trees equivalent with the old are available. The model uses group merit as the criterion for balancing genetic gain and relatedness measured by group coancestry. Infusion is optimized by finding the maximum group merit. The model involves variables such as average breeding value, structure (family number and size), heritability, relatedness (group coancestry) and its importance (penalty coefficient), and inbreeding. The most important determinant for infusion is the breeding value of the bred material followed by the relatedness between the selected families. An example with considerable similarities to the Swedish breeding program of Norway spruce and Scots pine was given. For establishing the first generation breeding population, it seems optimal to add about 20% to 25% new plus-tree selections rather than to make all selections in the progenies of the existing untested plus-trees. If the plus-trees were progeny tested, about 5% to 10% new selection seems desirable. For more advanced generations, the desire of infusion depends on progress in breeding value and accumulation of relatedness and inbreeding in the breeding population.

Key words: Diversity, inbreeding, relatedness, group coancestry, group merit, selection, breeding population.

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Introduction

Genetically inferior material is generally undesirable for breeding purposes. In order to obtain maximum genetic gain, it is a common practice that individuals are selected on the criterion of predicted breeding value alone, resulting in use of a few superior genotypes which are often closely related. This leads to an elevated level of relatedness (WEI, 1995) and an increased rate of inbreeding (QUINTON and SMITH, 1995; WRAY and GODDARD, 1994; LEITCH *et al.,* 1994; SMITH and QUINTON, 1993) in the selected population. Accumulation of inbreeding leads to reduction of future genetic gain through both reduction of additive variance and inbreeding depression (WRAY and GODDARD, 1994). An efficient way to reduce the potential inbreeding is to reduce the relatedness among parents (LINDGREN and MULLIN, 1997; ZHENG *et al.,* 1997). Nevertheless, a reduction in relatedness also comes together with an increase in genetic diversity (Effective population size). The breeding objective should therefore be finding an optimal balance between the genetic value and the relatedness of the selected (breeding) population.

To achieve this goal, attention has usually been paid to improvements of selection methods and mating designs for the breeding population (BP). Selection can be made on breeding value either with a restriction imposed on parental contribution to the selected population or with an adjustment of the breeding value on relatedness (coancestry in parents or potential inbreeding in offspring) (ZHENG *et al.,* 1997; LINDGREN and MULLIN, 1997; BALLOU and LACY, 1995; BRISBANE and GIBSON, 1995; WEI, 1995; ASKEW and BURROWS, 1983). In addition to these methods, the purpose of maintaining diversity and controlling relatedness can also be realized by infusing unrelated genetic material into the BP. By infusion, genes not available from the bred material at advanced generations are introduced from external material. The advantage of this is not only the maintenance of diversity but also potential improvement of genetic gain. For example, in the progenies of crossed plus-tree families, theoretically there are still half number of the families averaged under the population mean (equivalent to plus-tree average), it may be wise to use the plus-tree parents (or select new plus-trees) to replace progenies who are below the population mean if they are to be used for the next generation BP.

The idea of infusion of new unrelated material for maintaining overall genetic diversity has resulted in developments of breeding strategies using various ways of structuring the breeding population such as MPBS (Multiple population breeding strategy), Sub-lining, Nucleus breeding, Elites breeding or use of materials related to their breeding value (NAMKOONG *et al.,* 1988; COTTERILL *et al.,* 1989; WHITE, 1992; KANOWSKI, 1993; ERIKSSON *et al.,* 1993). The main principle used in these strategies is that whilst making use of few superior genotypes to obtain high genetic gain, the overall level of relatedness and the genetic diversity is maintained by exchange of unrelated genetic resources between/among substructured populations or population strata. However, implementation of such breeding strategies as MPBS involves complicated managerial and sound financial resources (BARNES *et al.,* 1995). A simpler and cheaper way for practical application may be to reuse the old plus-trees or to select new plus-trees for the BP. However, this infusion of unimproved material may not always be beneficial, it could cause loss of genetic gain. The infusion therefore needs to be optimized by balancing the genetic gain and relatedness. This requires us to quantify the optimal amount of infusion so that the BP gives the maximum performance combining both aspects of breeding (genetic gain) and conservation (maintenance of variability).

A first step to address this problem is to define an appropriate measure to quantify the genetic relatedness of the BP. This measure can then be incorporated mathematically with the genetic value into a single evaluation criterion, which can be maximized. This criterion can be used to evaluate a population as a whole as far as conservation of genetic diversity/variability (control of relatedness) is concerned. The infusion of new genetic material into a population is equivalent to pooling two populations together. The infusion changes population composition and hence its performance as a whole. The objective of this study is to define an evaluation criterion as a measurement for group performance, and based on this criterion to develop a dynamic model to describe and monitor the changes in gain and relatedness caused by infusion. We will demonstrate the application of the model to a relevant practical breeding program and the use of a search algorithm for optimizing the process of infusion. We will also investigate a number of factors such as breeding value, heritability, coancestry and inbreeding that have influences on the model.

Theoretical Development

Group merit as evaluation criterion

The inbreeding of an individual is a consequence of mating between parents who are related to each other by ancestry (MALÉCOT, 1948; FALCONER and MACKAY, 1996). In a breeding population, all individuals are prospective parents under the assumption of random mating. Genetic relatedness between a pair of individuals determines the level of inbreeding of their progeny. This relatedness can be conveniently measured by coancestry (θ_{ij}), the probability that two homologous genes taken at random one from each of the two individuals are identical by descent (IBD) (MALÉCOT, 1948; FALCONER and MACKAY, 1996). Average relatedness of the population is then measured by group (population) coancestry (Θ), the probability that two genes taken at random with replacement from the population are IBD (COCKERHAM, 1967). Group coancestry is calculated as the average of all possible pair-wise coancestries including selfs and reciprocals.

$$\Theta = \frac{1}{n^2}\sum_{i=1}^{n}\sum_{j=1}^{n}\theta_{ij} \qquad (1)$$

The genetic diversity of the breeding population can be expressed in terms of relatedness by Status Number N_S (LINDGREN *et al.,* 1996, 1997; WEI *et al.,* 1997). The Status Number is associated with the group coancestry as:

$$N_s = \frac{1}{2\Theta} \qquad (2)$$

It can be seen as the effective population size describing the status of relatedness in a population.

A criterion that combines genetic value (hence genetic gain) and relatedness (hence diversity) can be used for balancing the two contrast factors, we call it group merit. It measures the performance of a group (or population) as a whole. Similar terms 'population merit' (LINDGREN and MULLIN, 1997) and 'benefit' (ZHENG *et al.,* 1997) were used for this as a selection criterion. We define the group merit (M) as group genetic value G (average genetic value of population members) minus the group coancestry (Θ) times a penalty coefficient (c).

$$M = G - c\Theta \qquad (3)$$

In this formulation, the genetic gain and relatedness is balanced by the size of the penalty coefficient, which controls to

what degree relatedness will be considered. It can be used as a measure for the purposes of either gain improvement or diversity conservation or both.

To illustrate the use of the criteria for a specific population, we assume a population composed of m families. The group genetic value of the population is calculated as the mean of its all members:

$$G = \bar{g} = \frac{1}{n}\sum_{k=1}^{m}\sum_{i=1}^{s_k} g_{ki} \qquad (4)$$

where n is the number of individuals, g_{ki} is the genetic value of the ith individual of kth family and s_k the size of kth family. The group coancestry is formed from three types of relatedness, self coancestry, sib coancestry (within-family) and non-sib coancestry (between-family):

$$\Theta = \frac{1}{n^2}\sum_{k=1}^{m}[\tfrac{1}{2}s_k(1+F_k) + s_k(s_k-1)\theta_{w_k}] + \frac{1}{n^2}\sum_{k=1}^{m}\sum_{l=1,k\neq l}^{m}(s_k s_l \theta_{b_{k,l}}) \qquad (5)$$

where s_k and s_l are sizes of family k and l respectively. F_k and θ_{w_k} are respectively the inbreeding coefficient and the sib coancestry, $\theta_{b_{k,l}}$ is the non-sib coancestry between families k and l.

If all families are of the same type (e.g. full sib or half sib families) and if they are equally related and equally inbred, the group coancestry is simplified as:

$$\Theta = \frac{1}{2n}(1+F) + \frac{s-1}{n}\theta_w + \frac{m-1}{m}\theta_b \qquad (6)$$

where F, s, θ_w and θ_b are respectively the average inbreeding coefficient, the family size, the sib coancestry and the non-sib coancestry. The corresponding effective population size (status number) is obtained as:

$$N_s = \frac{n}{1+F+2(s-1)\theta_w + 2(n-s)\theta_b} \qquad (7)$$

When all families are non-inbred ($F=0$) and unrelated ($\theta_b=0$), the group coancestry and the status number become:

$$\Theta = \frac{1}{2n} + \frac{s-1}{n}\theta_w \qquad (8)$$

$$N_s = \frac{n}{1+2(s-1)\theta_w} \qquad (9)$$

Note that (8) is identical to the average pairwise coancestry discussed by ASKEW and BURROWS (1984, eq. 17). The corresponding Status Number is equivalent to the variance effective population size based on variance of change in gene frequency for neutral alleles (COCKERHAM, 1969). Note that for population with no family structure, the group coancestry is calculated as:

$$\Theta = \frac{1}{2n}(1+F) + \frac{n-1}{n}\theta \qquad (10)$$

where θ is the average coancestry of a pair of individuals (excluding self coancestry). Note that (10) is identical to COCKERHAM's definition of group coancestry for a group with itself (COCKERHAM, 1967, 1969; WEIR, 1989, 1990).

The calculations of θ_w, θ_b and F can be respectively obtained with the following equations:

$$\theta_w = \frac{1}{4}(\theta_{pp} + 2\theta_{pq} + \theta_{qq}) \qquad (11)$$

$$F_k = \theta_{pq} \text{ and } F = \frac{1}{m}\sum_{k}^{m} F_k \qquad (12)$$

$$\theta_b = \frac{1}{4}(\theta_{p_1p_2} + \theta_{p_1q_2} + \theta_{q_1p_2} + \theta_{q_1q_2}) \qquad (13)$$

where p and q are parents of a family, p_1, p_2 and q_1, q_2 are parents of two families respectively. If all parents are unrelated and non-inbred, the inbreeding coefficient of a family is 0, θ_w is 0.25 for full sibs and 0.125 for half sibs, θ_b is 0.

Infusion of new material (pooling two populations)

Here the infusion is referred to that genetic material unrelated to a population is introgressed into the population. The infusion process is equivalent to pooling two populations together. The population size, the family number, the average genetic value, the inbreeding coefficient, and the group coancestry are denoted n_1, m_1, F_1, G_1 and Θ_1 for the first population and n_2, m_2, F_2, G_2 and Θ_2 for the second. The following parameters can be calculated for the pooled population:

Population size: $N = N_1 + N_2$

Group genetic value:

Group coancestry:

$$G = \frac{n_1 G_1 + n_2 G_2}{N} \qquad (14)$$

$$\Theta = \frac{1}{N^2}(n_1^2\Theta_1 + n_2^2\Theta_2 + 2\sum_{i=1}^{n_1}\sum_{j=1}^{n_2}\theta_{1_i 2_j}) \qquad (15)$$

where $\theta_{1_i 2_j}$ is the coancestry between the ith individual of population 1 and the jth one of population 2. It is assumed that there is no relatedness between the two populations ($\theta_{1_i 2_j}=0$).

When both populations have an ideal structure (i.e. same family size, equal relatedness and inbreeding). Substituting (6) for both populations into (15), the group coancestry of the pooled population is as below:

$$\Theta = \frac{1}{2N}(1+\frac{n_1F_1+n_2F_2}{N}) + \frac{n_1(n_1-m_1)\theta_{w_1} + n_1^2(m_1-1)\theta_{b_1}}{N^2 m_1} + \frac{n_2(n_2-m_2)\theta_{w_2} + n_2^2(m_2-1)\theta_{b_2}}{N^2 m_2} \qquad (16)$$

This can be rewritten as:

$$\Theta = \Theta_0(1+\overline{F} - 2\overline{\theta_w}) + \frac{1}{m_1}r_1^2\theta_{d_1} + \frac{1}{m_2}r_2^2\theta_{d_2} + r_1^2\theta_{b_1} + r_2^2\theta_{b_2} \qquad (17)$$

where $\Theta_0 = \frac{1}{2N}$, $r_1 = \frac{n_1}{N}$, $r_2 = \frac{n_2}{N}$, $\overline{F} = r_1F_1 + r_2F_2$, $\overline{\theta}_w = r_1\theta_{w_1} + r_2\theta_{w_2}$, $\theta_{d_1} = \theta_{w_1} - \theta_{b_1}$, and $\theta_{d_2} = \theta_{w_2} - \theta_{b_2}$. Θ_0 can be considered as the group coancestry of a reference (or founder) population with the same size of the pooled one but in which members are unrelated and non-inbred. $\overline{F}$ and $\overline{\theta}_w$ are respectively the weighted mean of inbreeding coefficient and mean sib-coancestry of the pooled population, and θ_{d_1}, θ_{d_2} are respectively the differences between sib relatedness and non-sib relatedness for the two populations, which indicate the distribution of relatedness in the two populations before

pooling together. When the two populations have no family structure, (17) reduces to:

$$\Theta = \Theta_0(1+\overline{F}) + \frac{m_1 - 1}{m_1} r_1^2 \theta_{b_1} + \frac{m_2 - 1}{m_2} r_2^2 \theta_{b_2} \qquad (18)$$

The group merit of the pooled population is obtained by substituting (14) and (16) to (3).

Numeric Example

Infusion of plus-trees

To demonstrate the application of the infusion model, an example with considerable similarities to the planned Swedish breeding program of Norway spruce and Scots pine (DANELL, 1993; WILHELMSSON and ANDERSSON, 1993; KARLSSON and ROSVALL, 1993) was given. The double pair mating design in the Swedish breeding program was simplified to a single pair mating design. It is assumed that selection of new plus-trees is possible and the new plus-trees will be equivalent to the old untested plus-trees (we regard this as a realistic assumption for a considerable part of the current Sweden). The new plus-trees will be put together with the bred material selected from progenies of the old plus-trees to form the next generation BP. Hereafter we will refer population 1 to the new plus-trees and 2 to the bred material. The new plus-trees are assumed to be unrelated and non-inbred ($\Theta_1 = \frac{1}{2n_1}$) and its expected genetic value (G_1) is set to zero. The group coancestry (eq. 16) and the group genetic value (eq. 14) are simplified to:

$$\Theta = \frac{1}{2N} + \frac{n_2}{N^2}[(s_2 - 1)\theta_{w_2} + (n_2 - s_2)\theta_{b_2} + \frac{1}{2}F_2] \quad (19)$$

$$G = \frac{n_2}{N} G_2 \qquad (20)$$

Genetic value of the selected bred material

The strategy of the Swedish breeding program is to establish the BP as a number of sub-populations by selecting progenies from controlled crosses of plus-trees and restricting future selection to within-families (DANELL, 1993). We assume that each sub-population starts with 100 plus-trees and that they are regenerated by making 50 crosses (Single Pair Mating) and selecting two offspring from each of these unrelated full sib families of size 100 (5000 in total) without infusion of new material. The baseline is to select two members per family. When infusion is considered, the number of trees selected per family may be varied if it turns out to be more beneficial to select 1 or 0 (i.e. selection of new plus-trees is needed). The standardized normal distribution is used for estimation of selection intensity, when the selected families are not constant in size, the selection intensity is calculated as:

$$i_{(u_2+u_1)} = \frac{u_2}{u_2 + u_1} i_{u_2} + \frac{u_1}{u_2 + u_1} i_{u_1} \qquad (21)$$

where i_{u_2}, u_2, i_{u_1} and u_1 are the selection intensities and selected proportions for families of 2 and 1 respectively. The total expected genetic gain (in unit standard deviation) following a combined family and within-family selection can be decomposed into gains from family and within-family selections. Assuming normal distribution of both family means and individual values within families, the total gain is predicted with the following formulae, modified from LINDGREN and WERNER (1989) (The formulae can also be seen as modifications of expressions from WEI (1995) or FALCONER and MACKAY (1996)):

$$R_T = \alpha i_f + \beta i_w \qquad (22)$$

$$\alpha = \frac{0.5(1 + 1/S)}{\sqrt{0.5(1 + 1/S) + 1/(h^2 S)}} \qquad (23)$$

$$\beta = \frac{0.5(1 - 1/S)}{\sqrt{0.5(1 - 1/S) + 1/h^2}} \qquad (24)$$

where α and β are the weighting factors for between and within-family selection, i_f and i_w are the standardized selection differentials (selection intensity) of family and within-family selection, h^2 is the individual heritability, S is the family size prior to selection. Denoting the genetic value (breeding value of the bred material prior to selection) G_s, predicted genetic (breeding) value (G_2) of the selected bred material is then obtained as:

$$G_2 = G_s + R_T \qquad (25)$$

Substituting (25) to G_2 in (20) and then the value of Θ in (19) to (3), the group merit is calculated as:

$$M = \frac{1}{N}[n_2(G_s + R_T) - 0.5c] - \frac{cn_2}{N^2}[0.5F_2 + (s_2 - 1)\theta_{w_2} + (n_2 - s_2)\theta_{b_2}] \quad (26)$$

It is clear that the group merit of the pooled population is a function of several parameters describing the structure, genetic value and relatedness of the selected bred material.

Algorithm for optimal infusion

Other parameters chosen as baseline values for the model are: c = 20, $h^2 = 0.25$, $G_s = 0$, $\theta_w = 0.25$, $\theta_b = 0$ and $F = 0$. These values represent a standard situation that the old plus-trees are non-inbred and unrelated, and are not progeny tested (for progeny tested plus-trees, $G_s > 0$). Our purpose is to see whether the infusion is necessary and to find the optimal allocation of the new and the bred material in the BP. We have studied two scenarios in which different selection strategies are applied. In the first scenario, all the selected families were represented by 2 individuals. In the second scenario the selected families varied in size from 2 to 1 (i.e. two individuals were first selected from the best families followed by selecting 1 from the second top families). An iterative search algorithm was used to find the most favorable allocation in the BP of bred material and the new plus-trees, which gives the maximal group merit. To establish a BP with 100 members, the search algorithm used is given as follows:

1. Decide a value for the penalty coefficient.

2. Choose the selection number (d_2) of families (represented by 2 individuals), starting from 0 to the total number of available families (50).

3. Choose the selection number (d_1) of families (represented by 1 individual), starting from 0 to 50 – d_2 (Second scenario only).

4. Calculate the number (n_1) of new selections of plus-trees to be used in the BP by subtracting the number of bred trees from the BP size ($n_1 = 100 - d_2 - d_1$).

5. Compute the group genetic value (G), the group coancestry (Θ) and then the group merit (M) of the BP. If the group merit is larger than the previous one, record the number of new plus-trees and corresponding numbers of families for the bred material.

6. Repeat from step 3 until the selection number (d_1) reaches $50 - d_2$ (second scenario only).

7. Repeat from step 2 until the number (d_2) reaches the total number of families 50.

8. Repeat from step 1 by changing values of penalty coefficient.

The algorithm is repeated by change other baseline parameters.

Results

Infusion for the first generation BP

Results for the 2 scenarios were compared in *figure 1* and *2*. It is clear that the flexible restriction on family contribution (the size of selected families can be either 2 or 1) is always better than the fixed restriction (family size of 2). The flexible restriction size returned higher N_s, G and M than the fixed restriction did (*Fig. 2*). This indicates that the deployment of families in the BP can be linearly related to the family genetic value, which optimizes the group merit.

In the second scenario, the maximal group merit was found by comparing different combinations of number of families of the bred material and the new plus-trees. The number of new plus-trees increases with the penalty value and fixed at 60 when penalty goes up to 440 (*Table 1*). With lower penalty values, the selection number was much larger for selecting 2 than for selecting 1 within families, because the relatedness was less important so that superior families can contribute more to the BP. As the relatedness became important (increased penalty) the selection number of families with size 2 decreased and that of 1 increased meanwhile the number of new plus-trees also increased.

Table 1. – Optimal numbers of selections of new plus trees (n_1) and families with size of 2 (d_2) and 1 (d_1) for the first generation BP for various penalty values (values used are: c = 20, $h^2 = 0.25$, $G_s = 0$, $\theta_w = 0.25$, $\theta_b = 0$ and $F = 0$).

c	n_1	d_2	d_1	N_s	Gain	Group merit
0	22	38	2	72.5	0.632	0.63
20	24	36	4	73.5	0.631	0.49
40	27	33	7	75.2	0.626	0.36
60	29	31	9	76.3	0.621	0.23
80	32	28	12	78.1	0.611	0.1
100	35	25	15	80	0.597	-0.03
200	48	12	28	89.3	0.501	-0.62
300	56	4	36	96.2	0.404	-1.16
400	59	1	39	99	0.354	-1.67
500	60	0	40	100	0.332	-2.17

The effects of genetic value (breeding value in this case) and heritability of the selected bred material were shown in *figure 3*. The number of new selections decreased with breeding value. There would be no new material needed if the breeding value was high enough (>=1.3), because the disadvantage of accumulated relatedness was compensated by the advantage of the high breeding value. A higher heritability resulted in a smaller number of new selections. With a heritability low enough (close to zero), almost half of the breeding population should use the fresh material. At the other extreme with heritability of 1, both curves merged together and about 10% of the BP should use the new selections.

The effect of family size of bred material prior to selection was generally similar to the effect of breeding value (*Fig. 4*), since a larger family size corresponds to a higher within-family selection intensity (hence a high breeding value). Regardless of the infusion of new material the BP will be regenerated by recruiting 100 new members from the progenies of 100 initial parents (50 crosses). If a larger number (>100) of initial parents were used, the need to replace bred material with new selections would be reduced (*Fig. 4*) due to increased selection intensity (therefore breeding value) and lowered level of relatedness (it is possible to select only 1 from some families in such case).

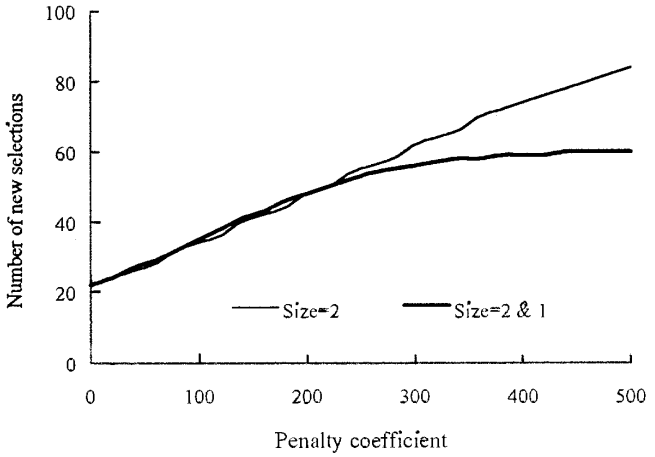

Figure 1. – Impact of penalty value on number of new selections when size of selected families is restricted to 2 or to 2 and 1.

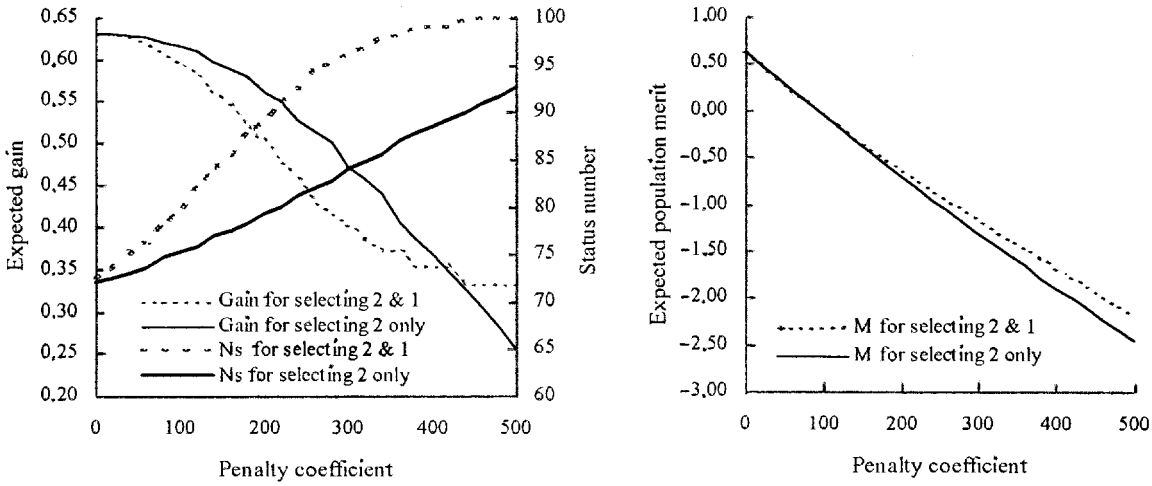

Figure 2. – Comparisons of G, N_s and M between selection of 2 and selection of 2 and 1 within families of bred material

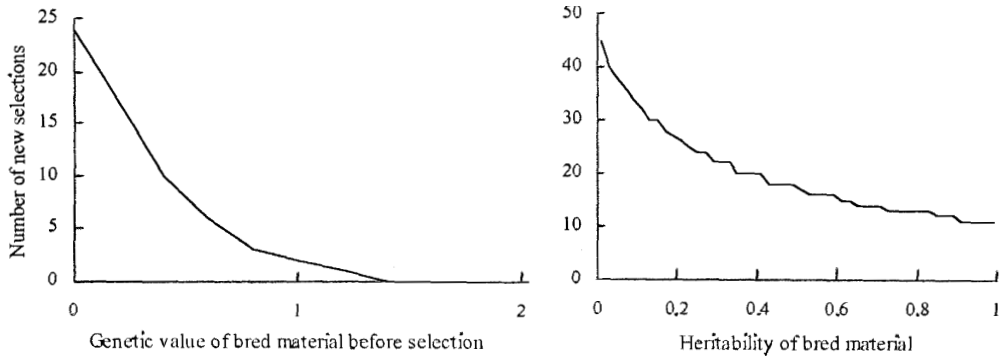

Figure 3. – Effect of initial genetic value and heritability of the bred material.

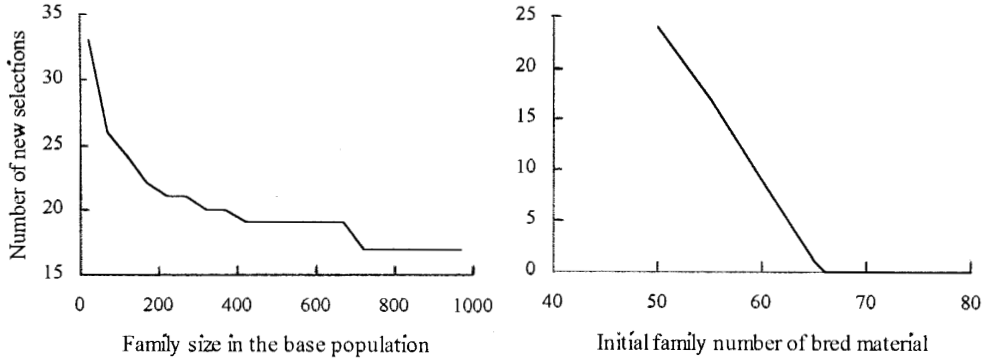

Figure 4. – Effects of initial family size and family number in the base population (progenies before selection).

Infusion at advanced generations

In advanced generations, the genetic value of the bred material increases and the levels of relatedness and inbreeding of the BP depends on what mating designs were used in the earlier generations. Increase of θ_b causes dramatic increase in the number of new selections, whereas the effects of θ_w and F is much smaller (*Fig. 5*). The inbreeding coefficient has very little influence compared to the relatedness. When other parameters are set to the baseline values, an increase of G_s to 1.3 results in no infusion (*Fig. 3*). An increase of θ_b from 0 to 0.25 gives rise of number of new selections from 20 to 83. The number of new selections increases from 24 to 32 and from 24 to 29 when θ_w increases from 0.25 to 1 and F from 0 to 1 respectively.

Discussion

The infusion model and the assumptions

One of the assumptions we made in the infusion model is that all individuals in the BP (selected bred material and new material) will equally mate with each other (random mating) and equally contribute to the next generation (no differences in reproductive output). This assumption has often been used when there are too many mating alternatives for theoretical studies (ASKEW and BURROWS, 1983). Assuming a constant number of successful number of gametes per parent the mating design has no effect on status number in a single generation shift (LINDGREN *et al.*, 1996) and it has negligible effect on gain in forward selection (ROSVALL, pers. comm.). We also assumed the normality of distributions of family means and the individual values within families. Result shows that for the first generation BP, even when the penalty is set to zero (note that the relatedness was considered by restricting family size to a maximum of 2), there is still about 20% new selections needed for maximal group merit. The reason for this is completely due to the variance of the family means.

Another assumption made in this study is that new plus-trees are available at no extra cost compared to selection from the progenies of the controlled crosses and reuse of the old plus-trees. At present the model developed does not consider any cost involved in selections. Cost for selection of new plus-trees may be compensated by the extra gain and diversity (N_s) obtained from the infusion. Furthermore, the new plus-trees may have the advantages of being young, higher probability to capture wider genetic variation and larger genetic base (since new selection can be made from new plantations and experimental stands, which are not available when the old

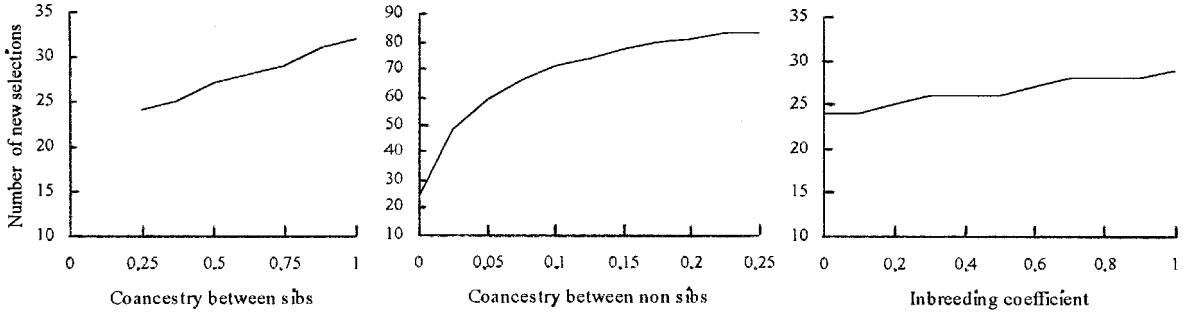

Figure 5. – Effects of sib coancestry, non-sib coancestry and inbreeding coefficient.

plus-trees were selected). An alternative to infusion of new material may be to start the breeding program with a larger number of initial parents (plus-trees). Our results show that for a BP of size 100, if number of initial parents increase to 132 (rather than 100 as planned), the number of new selections reduces to zero (*Fig. 4*). This suggests that it is generally safer if a breeding program starts with a larger number of plus-trees. Similar strategy was proposed by WEBER *et al.* (1989) that the risk of raising no good genotype is minimized if breeders make as many crosses as possible, consequently only a small number of progenies from each cross is needed.

Predictions of selection intensity and genetic gain

In the numeric example the prediction of selection intensity and hence genetic gain were approximated for finite number and size of families. The approximation slightly biased our estimation of selection intensity and the effect on the number of new selections determined by the algorithm is negligible. For within family selection exact values of selection intensity were used except when explicitly studying the effect of family size (LINDGREN and NILSSON, 1985). Our illustration of the infusion model has been focused on the selection for establishing first generation BP. If breeding objective is obtaining maximum genetic gain and if mating scheme was not managed for minimum inbreeding in offspring (relatedness between mates), the generation advancement would result in elevated levels of relatedness and inbreeding (e.g. positive assortative mating) together with the increased genetic value. However, how the increase of genetic value relates to the increase of relatedness and inbreeding was not given attention. Our model has shown that the number of new selections decreased substantially with increase of the average genetic value of the bred material (*Fig. 3*). If the initial parents (old plus-trees) are progeny-tested before entering the long-term breeding program, a positive G_s should be used, and consequently the number of new selections would be reduced. The demand for fresh material, with a given penalty value, is much depending on the amount of the genetic progress (G_s) that has achieved. If G_s is high enough after several generations the need for fresh selections may be virtually zero. For example, when the genetic (breeding) value of the bred material approaches to 1.3 with standard parameters, the number of new selections for maximal group merit comes to zero (*Fig. 3*). The model can be applied to any generation from the first generation onwards with an increased genetic value (G_s). It should be noted that both the relatedness and inbreeding increases at advanced generations if mating designs for the earlier generation were not chosen for avoiding these increases. It is of interest to further investigate the association of relatedness and inbreeding with the breeding value over a multiple generation breeding scheme.

Penalty coefficient

The penalty coefficient c is the relative importance of the genetic relatedness in the assessment of the breeding progress. It can be considered as a mainly policy-decided factor, although there are biological reasons to avoid a very low value. It provides the flexibility that allows breeders to choose any value of penalty on coancestry to address their own problems regarding the balance between gain and relatedness. The magnitude of c expresses the significance of inbreeding (caused by relatedness among parents) and has to be leveled by experience. It can be any positive value, which expresses the extent of fear of relatedness in the BP. The group merit can be adopted for a specialized application for purposes of conservation when the c is given a significantly large value. It can also be a negative value which indicates the favor of relatedness, resulting in use of more related individuals, such as sibs from few families with the highest breeding values. If relatedness is significantly undesirable, the penalty coefficient has to be large and positive. It can be zero which implies that coancestry in parents and inbreeding in progeny are considered harm-free and therefore, the group merit is identical to its group genetic value. The influence of the penalty coefficient on the number of new selections and the compositions of the BP are shown in *figure 1* and *2* and *table 1*.

Inbreeding coefficient and coancestry

Since we assumed that the parents in the base population (plus-trees) be unrelated and non-inbred, the inbreeding would not occur for the first generation BP. Inbreeding occurs at advanced generations only when mating parents are related. An interesting finding is that the inbreeding coefficient of the bred material has little influence on the number of new selections (*Fig. 5*). This implies that families, which are highly inbred, may still be used in the BP as long as the families are superior in breeding value and the relatedness among them is low. This is in agreement with LINDGREN *et al.* (1996). In comparison, the genetic relatedness particularly the non-sib coancestry has a much stronger impact on the infusion in the case in which number of selections per family is not fixed. Tolerance of the group merit to the inbreeding coefficient (F) is substantially higher than to the non-sib coancestry (θ_b). This implies that the breeding strategies should be developed to avoid such relatedness in the BP. For a single BP the purpose for achieving high genetic gain and low level of inbreeding can therefore be realized by developing separated (unrelated) and inbred families (lines). This requires breeders to adopt appropriate mating designs in the recurrent selection strategies to keep the inbred families unrelated as much as possible.

Based on these results, BP can also be managed in separate sub populations to make use of inbred superior genotypes as long as the relatedness between the sub populations is kept at low level. This is in accordance with the principles of MPBS and Subline breeding strategies that have been practiced in many breeding programs (ZHENG, 1996; WHITE, 1992; KANOWSKI, 1993; BARNES and MULLIN, 1989). While the strategies provide ways for a better control of average inbreeding level and to maintain gene diversity, our concepts provides measures to monitor and to quantify the relatedness, gain and group performance in either the sub populations or the entire BP as a whole.

Application

Integration of gain and relatedness in breeding objective has recently been a major focus on many studies (ZHENG *et al.*, 1997; LINDGREN and MULLIN, 1997; MEUWISSEN, 1997; BRISBANE and GIBSON, 1995; QUINTON and SMITH, 1995; WEI, 1995; SMITH and QUINTON, 1993; WRAY and GODDARD, 1994; LEITCH *et al.*, 1994). We see the advantages of use of group evaluation criteria such as the group coancestry and group merit when the relatedness hence diversity is concerned, since these measures involves mostly a group (population) of individuals. Concepts and methods developed in this study can be used as a baseline for measuring relatedness (group coancestry), diversity (status number) and group merit for either single or pooled population. However, it should be borne in mind that the infusion model is a deterministic model and applicable to fixed populations (i.e. specific group of individuals with known pedigree). For random populations (i.e. sampling is involved) application of the model must be taken with caution, an additional error term should be estimated. Nonetheless, the group coancestry has been used to

estimate the gene diversity (expected heterozygosity) and population differentiation for random populations (COCKERHAM, 1967, 1969; WEIR, 1989, 1990).

In the Swedish breeding programs inclusion of plus-trees in BP for long term breeding is based on progeny testing, that probably corresponds to a raise of G_s by 1 standard deviation. It still seems recommendable to replace some 5% to 10% of planned selections with new plus-trees (*Fig. 3*). In programs without progeny testing a larger number of replacements is needed. In a more flexible case in which there were more than 50 (as used in this study) controlled crosses of plus-trees, for example 66 unrelated families (132 parents) (*Fig. 3*), it is unlikely that a need to replace bred material with the unimproved one would arise. However, the costs involved for large number of crosses would also be increased. This has to be balanced by consideration of cost-effective breeding.

We have demonstrated in this paper the application of the infusion model to a case in which the new plus-trees are to be selected and infused into the BP. It should be noted that the plus-trees have a simple structure that they are assumed non-inbred and unrelated. For more general and complicated situations, the material to be infused may also be structured bred material. Examples are programs with MPBS or Subline breeding strategies where exchange of material among structured BPs occurs. In these strategies, sub populations (lines) are maintained separately in order to reduce the relatedness among sub populations. Selected materials from different sub populations can then be inter-mated by exchange among them or putting into a composite breeding seedling orchard (BARNES *et al.,* 1995) to maintain the overall genetic diversity of the entire BP. However, how much such material exchange among sub populations is appropriate is still an open question. The infusion model is still applicable and the optimization algorithm presented in this paper can be used with little extension to find the optimal material exchange. In this case, the materials for exchange are both bred materials and their family structure must be considered.

For further studies, the model can be extended to a case in which the BP size is allowed to vary with a fixed number of trees of bred material. The infusion model and the iterative search algorithm can be extended for finding optimal deployment of families or clones in seed orchard or BP establishment, where maximal group merit is sought. If cost factor is considered the model can be extended to a cost-effective breeding model.

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Literature

ASKEW, G. R. and BURROWS, P. M.: Minimum coancestry selection. I. A *Pinus taeda* population and its simulation. Silvae Genetica **32**: 125–131 (1983). — BALLOU, J. D. and LACY, R. C.: Identifying genetically important individuals for management of genetic variation in pedigreed populations. In: BALLOU, J. D., GILPIN, M. and FOOSE, T. J. (eds): Population management for survival and recovery. Columbia University Press, New York. pp. 76–111 (1995). — BARNES, R. D. and MULLIN, L. J.: The multiple population breeding strategy in Zimbabwe – Five year results. In: Breeding Tropical Trees: Population Structure and Genetic Improvement Strategies in Clonal and Seedling Forestry. [Proc. IUFRO Conference, Pattaya, Thailand, Nov. 1988]. (GIBSON, G. L., GRIFFIN, A. R. and MATHESON, A. C. eds). Oxford Forestry Institute, Oxford, United Kingdom and Winrock International, Arlington, Virginia, USA, (1989). — BARNES, R. D., WHITE, T., NYOKA, B. I., JOHN, S. and PSWARAYI, I. Z. P.: The composite breeding seedling orchard. pp. 285–288. CRC/IUFRO conference, Eucalypt plantations: Improving fibre and quality, Hobart, Australia. (1995). — BRISBANE J. R., GIBSON, J. P.: Balancing selection response and rate of inbreeding by including genetic relationships in selection decisions. Theor. Appl. Genet. **91**: 421–431 (1995). — COCKERHAM, C. C.: Group inbreeding and coancestry. Genetics **56**: 89–104 (1967). — COCKERHAM, C. C.: Variance of gene frequencies. Evolution **23**: 72–84 (1969). — COTTERILL, P. P., DEAN, C. A., CAMERON, J. and BRINDBERGS, M.: Nucleus breeding: A new strategy for rapid improvement under clonal forestry. In: Breeding Tropical Trees: Population Structure and Genetic Improvement Strategies in Clonal and Seedling Forestry. (Eds.) GIBSON, G. L., GRIFFIN, A. R. and MATHESON, A. C. pp. 175–186 (1989). — DANELL, Ö.: Breeding programs in Sweden. 1. General approach. In: Progeny testing and breeding strategies. Proceedings of the Nordic group of tree breeding. October 1993. 184 pp. Forestry commission, Edinburgh, Scotland (1993). — ERIKSSON, G., NAMKOONG, G. and ROBERDS, J. H.: Dynamic gene conservation for uncertain futures. For. Ecol. Man. **62**: 15–37 (1993). — FALCONER, D. S. and MACKAY, T. F. C.: Introduction to quantitative genetics. 4th ed. Longman, London and New York. 340 pp. (1996). — KANOWSKI, P.: Forest genetics and tree breeding. Plant Breeding Abstracts **63**(6): 717–726 (1993). — KARLSSON, B. and ROSVALL, O.: Breeding programs in Sweden. 3. Norway spruce. In: Progeny testing and breeding strategies. Proceedings of the Nordic group of tree breeding. October 1993. 184 pp. Forestry commission, Edinburgh, Scotland (1993). — LEITCH, H. W., SMITH, C., BURNSIDE, E. B. and QUINTON, M.: Genetic response and inbreeding with different selection methods and mating designs for Nucleus breeding programs of diary cattle. J. Dairy Sci. **77**: 1702–1718 (1994). — LINDGREN, D., GEA, L. D. and JEFFERSON, P. A.: Loss of genetic diversity monitored by status number. Silvae Genet. **45**: 52–59 (1996). — LINDGREN, D., GEA, L. D. and JEFFERSON, P. A.: Status number for monitoring genetic diversity. Forest Genetics **4**(2): 69–76 (1997). — LINDGREN, D. and MULLIN, T.: Balancing gain and relatedness in selection. Silvae Genetica. **46**(2–3): 124–129 (1997). — LINDGREN, D. and NILSSON, J.-E.: Calculation concerning selection intensity. Report 5. Dept. Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences (1985). — LINDGREN, D. and WERNER, M.: Gain generating efficiency of different Norway spruce seed orchard designs. In: STENER, L. G. and WERNER, M. (eds). Norway spruce's provenances, breeding and genetic conservation. Report 11. The Institute of Forest Improvement. Uppsala, Sweden (1989). — MALÈCOT, G.: Les Mathématiques de l'hérédité. Masson, Paris (1948). — MEUWISSEN, T. H. E.: Maximizing the response of selection with a predefined rate of inbreeding. J. Anim. Sci. **75**: 934–940. — NAMKOONG, G., KANG, H. C. and BROUARD, J. S.: Tree breeding: Principles and strategies. New York, USA, Springer-Verlag. 180 pp. (1988). — QUINTON, M. and SMITH, C.: Comparison of evaluation-selection systems for maximizing genetic response at the same level of inbreeding. J. Anim. Sci. **73**: 2208–2212 (1995). — SMITH, C. and QUINTON, M.: The effect of selection in sublines and crossing on genetic response and inbreeding. J. Anim. Sci. **71**: 2631–2638 (1993). — WEBER, W. E., QUALSET, C. O. and WRICKE, G.: Selection strategies for the improvement of autogamous species. In: BROWN, A. H. D., CLEGG, M. T., KAHLER, A. L. and WEIR, B. S. (eds.): Plant population genetics, breeding, and genetic resources. Sinauer Associates Inc. pp 299–316. Sunderland, Massachusetts (1989). — WEI, R.-P.: Predicting genetic diversity and optimizing selection in breeding programmes. Dissertation. Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences (1995). — WEI, R.-P., LINDGREN, D. and YEH, F. C.: Expected gain and status number following restricted individual and combined-index selection. Genome **40**: 1–8 (1997). — WEIR, B. S.: Sampling properties of gene diversity. In: BROWN, A. H. D., CLEGG, M. T., KAHLER, A. L. and WEIR, B. S. (eds.): Plant population genetics, breeding, and genetic resources. Sinauer Associates Inc. pp 23–42. Sunderland, Massachusetts (1989). — WEIR, B. S.: Genetic data analysis. Sinauer Associates Inc. Sunderland, Massachusetts. 377 pp. (1990). — WILHELMSSON, L. and ANDERSSON, B.: Breeding programs in Sweden. 2. Breeding of Scots pine (*Pinus sylvestris*) and Lodgepole pine (*Pinus contorta* ssp. *latifolia*). In: Progeny testing and breeding strategies. Proceedings of the Nordic group of tree breeding. October 1993. 184 pp. Forestry commission, Edinburgh, Scotland (1993). — WHITE, T.: Advance-generation breeding populations: Size and structure. In: Breeding tropical trees: resolving tropical forest resource concerns through tree improvement, gene conservation and domestication of new species. Proceedings of IUFRO meeting. Cartegena and Cali, Colombia, 9–18 Oct. 1992 (1992). — WRAY, N. R. and GODDARD, M. E.: Increasing long-term response to seletion. Genet. Sel. Evol. **26**: 431–451 (1994). — ZHENG, Y.-Q.: Genetic studies and improvement of *Pinus caribaea.* PhD thesis, Edinburgh University. 205 pp. (1996). — ZHENG, Y.-Q., LINDGREN, D., ROSVALL, O. and WESTIN, J.: Combining genetic gain and diversity by considering average coancestry in clonal selection of Norway spruce. Theor. Appl. Genet. **95**: 1312–1319 (1997).