families with rapidly growing seedlings were also found, and these differences appear not to be related to growth rate (C.D. NELSON, unpublished). Successful use of the *P. e. densa* germplasm in a breeding program would require a backcross breeding strategy, where genes for host reaction from *P. e. densa* are introgressed into fast-growing *P. e. elliottii* populations. The moderately high individual heritability estimates within *P. e. elliottii* should help to expedite this breeding process.

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Loss of Genetic Diversity Following Selection from Populations with a Family Structure

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Summary

Loss of genetic diversity for selection from populations of unrelated families was analytically formulated for a series of selection strategies. Two components are identified, one caused by selection and another by random drift. The total loss of genetic diversity increases as selection becomes more based on family information. Selection dominates the loss except in cases where significantly more within-family deviations are used, where random drift becomes more important. When heritability is higher and the members of families are more closely related, selection effect becomes stronger but drift effect becomes weaker. The total loss of diversity and selection effect become worse with large family number and size. Drift effect decays with small family number and large family size. The significance of controlling the loss of genetic diversity in breeding populations is discussed in both breeding and conservation biology aspects.

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Introduction

A breeding population underlies the core of a conventional breeding programme aiming at a directional change of the performances of species. One main concern to breeders is the analysis of the degree and nature of genetic diversity in breeding populations. Genetic diversity measures the gene frequency and pedigree composition and generally decreases with the regeneration and advancement of the breeding population. Changes in genetic diversity often occur in the wake of selection of the superior individuals and recombinations of the genotypes. It has been recognized that the loss of genetic diversity has impacts on the achievement of the high cumulated genetic gain over generations or the success of a breeding programme (DEMPFLE, 1975; GALLEGO and LOPEZ-FANJUL, 1983; TORO and PEREZ-ENCISO, 1990; QUINTON et al., 1992; WEI and LINDGREN, 1995), and this has led to the concept of diversity conservation in the breeding industry (e.g. NAMKOONG, 1984). However, few efforts have been made to solve this problem (ROBERTSON, 1961; BULMER, 1971; BURROWS, 1984; LINDGREN and MATHESON, 1986; KEIGHTLEY and HILL, 1987; LINDGREN et al., 1989; WRAY and THOMPSON, 1990; WEI and LINDGREN, 1991).

Many factors may influence the degree of the genetic diversity in a breeding programme. This study focuses on the effects of selection and random drift. Artificial selection is seen by breeders as the most powerful breeding operation in directionally changing the gene frequency and improving the genetic gain of a breeding population. It is also perceived, however, that selection is often combined with a drastic decrease in genetic diversity. Optimum index selection is a typical example in that genetic gain is maximized and genetic diversity is greatly reduced (WEI and LINDGREN, 1991; QUINTON et al., 1992; WEI and LINDGREN, 1995). Random drift is associated with the finiteness of population size, summarizing many random processes in the regeneration and adaptation to environmental conditions of a breeding population. Drift effect reduces genetic variation, increases coancestry or inbreeding, and is listed as one of the most important factors in controlling the loss of genetic diversity in small managed populations and in the conservation of rare species or populations (e.g. LACY, 1987; CHEVALET, 1988). We will develop formulations for predicting the respective effects of selection and drift on the loss of genetic diversity under selection from breeding populations with a family structure.

Assumptions and Models

It is assumed that a breeding population comprises a number (m) of unrelated families, each of equal size (s). Family members are genetically related by the coefficient of relatedness, r. The phenotypic value (x_{jk}) of the kth individual in the jth family of the character observed can be split into 2 independent components – family mean, x_j, distributed with zero mean and variance σ_{FP}^2, and within-family deviation, d_{jk}, distributed with zero mean and variance σ_{WP}^2. The total phenotypic variance will be $\sigma_P^2=\sigma_{FP}^2+\sigma_{WP}^2$. All gene effects are assumed to be additive. Let h^2 denote the heritability, the fraction of the total genetic variance to σ_P^2. The ratio of the phenotypic variance of family mean to the total phenotypic variance is

$K=[1+(s-1)t]/s=[1+(s-1)rh^2]/s$

where t is the intraclass correlation.

We consider a generalized selection model (WEI and LINDGREN, 1994)

$$I_{jk}=(1-\beta)d_{jk}+\beta x_j, \qquad (1)$$

which describes the relationship between conventional selection methods (FALCONER, 1989; WEI and LINDGREN, 1991) and approximates optimal selection in some circumstances (WEI and LINDGREN, 1994). The factor β expresses the weight given to family performance ($0\leq\beta\leq1$). A value of β corresponds to a specific selection alternative. Thus, the choice of β (and selection intensity) will decide the outcome of the selection including genetic diversity preserved in the selected group. An alternative with a β maximizing genetic gain is defined as optimal index selection (LUSH, 1947; BURROWS, 1984; FALCONER, 1989). It should be mentioned, however, that the value of β corresponding to optimal index selection can not be chosen by breeders but is a function of heritability (h^2) and sib type (r),

$\beta=(1-K)[1+(s-1)r]/\{[1+(s-1)r](1-2K)+sK\}$.

The variance of the index is σ_I^2. The fraction of the variance which can be "explained" by variance of family mean is

$$V=\beta^2\sigma_{FP}^2/[\beta^2\sigma_{FP}^2+(1-\beta)^2\sigma_{WP}^2]=\beta^2K/[\beta^2K+(1-\beta)^2(1-K)],\ (0\leq V\leq1). \qquad (2)$$

A number of the n top-ranking individuals based on I_{jk} will be truncated. From the jth family the number of selections is denoted by n_j. The total selected proportion $P=n/(ms)$ of the initial population. Effective family number following selection is given by ROBERTSON (1961),

$$N_e=n^2/\sum n_j^2=n^2/[mE(n_j^2)], \qquad (3)$$

where $E(n_j^2)$ is the expectation of n_j^2. Clearly, the effective family number, before selection, is equal to m, the initial family number. The definition can be used to measure the genetic diversity preserved in the selected group, as suggested by ASKEW and EL-KASSABY (1993). Thus, the absolute loss of genetic diversity is

$$LA=m-N_e, \qquad (4)$$

and the relative loss is expressed in the form

$$LR=(m-N_e)/m. \qquad (5)$$

In the present situation, the loss of genetic diversity following selection will be explained by 2 forces – pure selection effect, and the interaction effect of selection and drift caused by finite population size (simplified with drift effect). The drift effect retrogresses as population size increases. This could, in practice, be separated comparing an ideal population of the same family structure that avoids sampling error.

Predictions of Diversity Loss

To efficiently use gene resources and to conserve genetic diversity for the improvement of a species, a breeder should have knowledge about the effects of selection and random drift before planning the breeding programme. The problem is to formulate the effective family number (3) following selection. Thus, we proceed in analogy with Burrows (1984) and Wei and Lindgren (1996).

We assume that U_j represents the probable number of individuals in the jth family being selected. Thus they sum to a random variable and are distributed over integers 0, 1, ..., s. The first and second moments of U_j are obtained by Wei and Lindgren (1996)

$$E(U_j) = sP, \qquad (6)$$

and

$$E(U_j^2) = s(s-1)P^2/N_r(V,P) + E(U_j) = s(s-1)P^2/N_r(V,P) + sP, \qquad (7)$$

where $N_r(V, P)$ is the relative effective family number under selection from a population of infinitely large family number and size (Wei and Lindgren, 1991). Let $f(x)$ denote the frequency function of family means and $p(x)$ the portion of the selected individuals from a family with the mean value x, then

$$N_r(V,P) = P^2/\int[p(x)]^2 f(x)dx, \quad 0 \leq N_r(V,P) \leq 1.$$

As $V \to 0$, $N_r(V, P) \to 1$; as $V \to 1$, $N_r(V, P) \to P$. To obtain $N_r(V, P)$, numerical computation is needed (for details see Burrows, 1984 and Wei and Lindgren, 1991). Burrows (1984) tabulated $N_r(V, P)$ with 5 decimals for V=0.1(0.1)0.9 and P=0.01(0.01)0.3(0.02)0.5. However, Burrows' table is not dense enough for reliable linear interpolation. An extended table with the same decimals for V=0.01(0.01)1 and P=0.01(0.01)0.5 was presented by Wei (1995). This table would provide very good interpolation of $N_r(V, P)$ for most practical operations. A relation between $N_r(V, P)$ and $N_r(V, 1-P)$ could be applied to the situations with $P > 0.5$ (Burrows, 1984).

Different from U_j, the n_j represents the sampled number of selections. They are constrained to sum to n and are distributed over integers 0, 1, ..., $min(s, n)$. Apparently it is not appropriate to directly employ $E(U_j^2)$ as a determination of $E(n_j^2)$. However, for purposes of approximation, we could assume that

$$E(n_j^2) = WE(U_j^2), \qquad (8)$$

where W will be obtained using limiting cases $V \to 0$ and $V \to 1$ as follows.

Selection effect

A breeding population can be viewed as an ideal population in that family means and within-family deviations are exactly equal to the respective expected values of order statistics. Therefore, the change of effective family number is exclusively caused by selection force (without drift effect). It is further assumed that, when selection is exclusively based on family means (β=1) or within-family deviations (β=0), the selected number, n, will be seen as the multiples of family size or number. Selection with β=1 indicates between-family selection while selection with β=0 leads to no loss in diversity (Wei and Lindgren, 1991). Therefore, it is easy to obtain

$$E(n_j^2) = s^2P, \text{ as } V \to 1 \text{ or } N_r(V,P) \to P, \text{ and} \qquad (9)$$

$$E(n_j^2) = s^2P^2, \text{ as } V=0 \text{ or } N_r(V,P)=1. \qquad (10)$$

Substitution of (8) and (9) or (10) into (3) will give a value to W at $N_r(V, P)=P$ or 1. A linear relationship between W and $N_r(V, P)$, which passes through the limiting points, produces

$$W = [sP-N_r(V,P)+1]/(sP-P+1). \qquad (11)$$

Therefore

$$N_e = msPN_r(V,P)(sP-P+1)/\{[sP-N_r(V,P)+1][sP-P+N_r(V,P)]\}. \qquad (12)$$

In selection with a relatively high intensity, we may have n smaller than m or s, or both. In this case, it can be seen that the possible candidates are confined to the n top-ranking families or family members. Allowing for these restrictions, a general form approximating effective family number is given in the form (Wei, 1995)

$$N_e = msPP_1N_r(V,P,P_1,P_2)/\{W'[sPP_1-P+P_1N_r(V,P,P_1,P_2)]\} \qquad (13)$$

with

$$W' = P_1[sP+P_2-N_r(V,P,P_1,P_2)]/(sPP_1+P_1P_2-P),$$

where P_1=1 (or P_2=1) if $n>s$ (or m); $P_1=n/s$ (or $P_2=n/m$) if $n \leq s$ (or m) and $N_r(V, P, P_1, P_2)$ is the relative effective family number under restricted selection from a population of infinitely large family number and size (Wei, 1995). With $n>s$ and $n>m$, (13) reduces to (12).

Selection with drift effect

When drift effect is considered, (9) still holds because of no drift effect present with the extreme case β=1, but selection with β=0 is equivalent to random selection without respect to pedigree even though based on within-family deviations (1). Hence, the relevant hypergeometric sampling moments produce

$$E(n_j^2) = s^2P(m+msP-mP-1)/(ms-1), \text{ as } V=0 \text{ or } N_r(V,P)=1. \qquad (14)$$

In the same way as in the last section, we obtained

$$W = 1+(1-s)[N_r(V,P)-P]/[(ms-1)(sP-P+1)] \qquad (15)$$

and

$$N_e = msPN_r(V,P)(ms-1)(sP-P+1)/\{[sP-P+N_r(V,P)][ms^2P+ms+N_r(V,P)-msP-sN_r(V,P)-1]\}. \qquad (16)$$

Taking the situation with $n<m$ or s into account, a general form approximating effective family number is given by Wei (1995),

$$N_e = msPP_1N_r(V,P,P_1,P_2)/\{P_2W'[sPP_1-P+P_1N_r(V,P,P_1,P_2)]\} \qquad (17)$$

with

$$W' = 1/P_2+\{[P_1N_r(V,P,P_1,P_2)\text{-}P)]/(P_1P_2\text{-}P)\}\{sP_1(smP_1P_2+mP_1P_2\text{-}mP\text{-}P_1)/[(msP_1P_2\text{-}1)(sPP_1+P_1P_2\text{-}P)]\text{-}1/P_2\}$$

where P_1=1 (or P_2=1) if $n>s$ (or m); $P_1=n/s$ (or $P_2=n/m$) if $n\leq s$ (or m). With $n>s$ and $n>m$, (17) reduces to (16).

Eq. (17) explains the total effect of selection and drift and thence the total loss of genetic diversity (4) while the difference between (13) and (17) is exclusively caused by the drift effect because of small population size.

Results and Discussion

Some numerical results are given in order to draw general conclusions. The total phenotypic variance is assumed to be one. For a range of situations, the relative loss of genetic diversity was compiled in *table 1*. Phenotypic and optimal index selection were used to examine the effects of family number and size. Full-sib families (r=0.5) with heritability =0.25 were considered. *Figures 1* and *2* demonstrate the absolute values of the respective diversity losses against family number and size when the number of selections is kept constant (n=20). *Figure 3* indicates the situations with both the total population size (ms=10000) and selected number constant (n=40).

Selection strategy and diversity loss

A selection strategy is expressed as the degree of the utilization of family information, β (1) or the fraction of the variance of family performance, V (2). As expected, by increasing β and therefore V, the total loss of genetic diversity and selection effect increase and drift effects decrease (*Table 1*). Two extreme cases are associated with β=0 or 1. When β=0 (V=0), selection is equivalent to complete random selection without respect to pedigree even though based on within-family deviations, and the loss of genetic diversity is exclusively caused by random drift. When β=1 (V=1), selection is totally based on the pedigree or the performances of families of population and there is no drift effect (*Table 1*). Usually, breeders prefer methods producing high genetic gain, like family selection, optimal index selection and selection based on BLP or BLUP of breeding values that are associated with the intense use of family information (HAZEL, 1943; LUSH, 1947; WHITE and HODGE, 1988; FALCONER, 1989). Obviously, the price is high if genetic diversity is of any value. Selection strategies mainly based on within-family deviation are seen as promising alter-

Table 1. — Predicted relative losses of genetic diversity due to selection (*LRs*) and drift (*LRd*) under different selection strategies from different breeding populations.

	m=10								m=20							
	s=20				s=40				s=20				s=40			
	P=.1		P=.2		P=.1		P=.2		P=.1		P=.2		P=.1		P=.2	
β*	*LRs*	*LRd*	*LRs*	*LRd*	*LRs*	*LRd*	*LRs*	*LRd*	*LRs*	*LRd*	*LRs*	*LRd*	*LRs*	*LRd*	*LRs*	*LRd*
r=0.25 h^2=0.1																
1.0	.9000	.0000	.8000	.0000	.9000	.0000	.8000	.0000	.9000	.0000	.8000	.0000	.9000	.0000	.8000	.0000
#	.7786	.0087	.6344	.0116	.7956	.0040	.6563	.0051	.7786	.0091	.6344	.0122	.7956	.0042	.6563	.0054
2/3	.4904	.0689	.3454	.0573	.3836	.0599	.2651	.0407	.4904	.0720	.3454	.0600	.3836	.0629	.2651	.0427
0.5	.2128	.1774	.1331	.1111	.1412	.1226	.0904	.0668	.2128	.1846	.1331	.1162	.1412	.1282	.0904	.0701
1/3	.0654	.2526	.0385	.1404	.0400	.1550	.0249	.0782	.0654	.2622	.0385	.1467	.0400	.1620	.0249	.0821
0.0	.0000	.2893	.0000	.1532	.0000	.1688	.0000	.0828	.0000	.3000	.0000	.1600	.0000	.1763	.0000	.0869
r=0.25 h^2=0.25																
1.0	.9000	.0000	.8000	.0000	.9000	.0000	.8000	.0000	.9000	.0000	.8000	.0000	.9000	.0000	.8000	.0000
#	.7349	.0142	.5838	.0172	.7404	.0077	.5922	.0087	.7349	.0149	.5838	.0181	.7404	.0081	.5922	.0092
2/3	.5795	.0443	.4253	.0414	.5142	.0352	.3724	.0277	.5795	.0464	.4253	.0434	.5142	.0370	.3724	.0292
0.5	.2895	.1429	.1869	.0958	.2268	.0980	.1491	.0573	.2895	.1488	.1869	.1003	.2268	.1026	.1491	.0602
1/3	.0968	.2357	.0577	.1341	.0699	.1450	.0438	.0748	.0968	.2447	.0577	.1402	.0699	.1516	.0438	.0785
0.0	.0000	.2893	.0000	.1532	.0000	.1688	.0000	.0828	.0000	.3000	.0000	.1600	.0000	.1763	.0000	.0869
r=0.5 h^2=0.1																
1.0	.9000	.0000	.8000	.0000	.9000	.0000	.8000	.0000	.9000	.0000	.8000	.0000	.9000	.0000	.8000	.0000
#	.8617	.0017	.7423	.0028	.8658	.0008	.7485	.0013	.8617	.0018	.7423	.0030	.8658	.0009	.7485	.0014
2/3	.5541	.0508	.4018	.0458	.4780	.0414	.3415	.0312	.5541	.0532	.4018	.0480	.4780	.0435	.3415	.0328
0.5	.2654	.1534	.1696	.1006	.1998	.1055	.1302	.0603	.2654	.1597	.1696	.1053	.1998	.1104	.1302	.0633
1/3	.0863	.2412	.0513	.1362	.0599	.1483	.0375	.0759	.0863	.2505	.0513	.1423	.0599	.1550	.0375	.0797
0.0	.0000	.2893	.0000	.1532	.0000	.1688	.0000	.0828	.0000	.3000	.0000	.1600	.0000	.1763	.0000	.0869
r=0.5 h^2=0.25																
1.0	.9000	.0000	.8000	.0000	.9000	.0000	.8000	.0000	.9000	.0000	.8000	.0000	.9000	.0000	.8000	.0000
#	.8424	.0029	.7155	.0046	.8440	.0016	.7182	.0024	.8424	.0031	.7155	.0048	.8440	.0017	.7182	.0025
2/3	.6681	.0252	.5121	.0270	.6338	.0183	.4818	.0170	.6681	.0264	.5121	.0283	.6338	.0192	.4818	.0179
0.5	.3929	.1017	.2651	.0756	.3431	.0689	.2340	.0449	.3929	.1061	.2651	.0792	.3431	.0722	.2340	.0471
1/3	.1490	.2086	.0908	.1238	.1202	.1290	.0765	.0691	.1490	.2168	.0908	.1294	.1202	.1349	.0765	.0726
0.0	.0000	.2893	.0000	.1532	.0000	.1688	.0000	.0828	.0000	.3000	.0000	.1600	.0000	.1763	.0000	.0869

*) β=1.0, between-family selection; β=0.5, phenotypic selection; β=0.0 selection based on within-family deviations;

#) $\beta=(1\text{-}K)[1+(s\text{-}1)r]/\{[1+(s\text{-}1)r](1\text{-}2K)+sK\}$, optimum index selection, which maximizes genetic gain.

natives to conserve genetic diversity (Dempfle, 1975; Toro and Perez-Enciso, 1990; Wei and Lindgren, 1994, 1995). Yet drift effect is not small at all, particularly when population size is small and selection intensity is relatively strong.

Effects of heritability and sib type

An inspection of *table 1* reveals the influences of heritability (h^2) and sib type (r) on the loss of genetic diversity. Heritability and sib type decide β if optimal index selection is considered. However, comparison can be performed at different heritabilities and sib types for other cases where β may be considered at the same values (e.g. phenotypic selection). The total loss of genetic diversity, selection and drift component differ at different heritabilities and genetic relationships of family members except at $\beta=0$ and 1 (*Table 1*). As β increases from zero and decreases from one, the differences increase and reach maximum somewhere with intermediate β. As h^2 and/or r increases, selection effect increases and drift effect decreases. It also follows that selection is forced to use more family information when h^2 or r is high. Since the difference in the selection effect is larger than the drift effect, the total loss of genetic diversity changes in a similar way as the selection component. In other words, if h^2 or r is low (not close to zero), it is easier to conserve genetic diversity although the drift effect becomes worse. For example, it is easier to conserve genetic diversity with half sibs than full sibs (Wei and Lindgren, 1994, 1995).

Family number and size

Clearly increasing population size for selection is an efficient way to obtain high selection differential and genetic gain when the number of selected individuals is constant. The effect on genetic diversity could be predicted by (13) and (17). Although a larger family number leads to slightly higher genetic diversity in the selected population, it seems that the total loss of genetic diversity and the selection component linearly increases with family number. The losses increase in a small scale over small family sizes (*Figures 1* and *2*). Drift effect on the loss of genetic diversity occurs only when family size is finite. The effect significantly augments over small family numbers but reaches a stable value for large family numbers. Generally speaking, the loss slowly reduces with family size unless selection is close to between-family selection (like optimum index selection). However, very low family size may lead to low drift effect because selections are forced to dispersively distribute among many families. The extreme case is that, when $s=1$, there is no drift effect and selection is forced among families. Using phenotypic selection, optimum index selection or the selection strategy in between, the drift component is rather small in comparison with the total loss of genetic diversity and selection component if family number and size are not especially small (*Figures 1* and *2*). When heritability is low, large population size (both family number and size), combining a selection based on intense use of family information, is often used to improve genetic gain (Lush, 1947; Falconer, 1989). It is evident from this study, however, that a large proportion of genetic diversity representing many parental genes will be irreversibly lost.

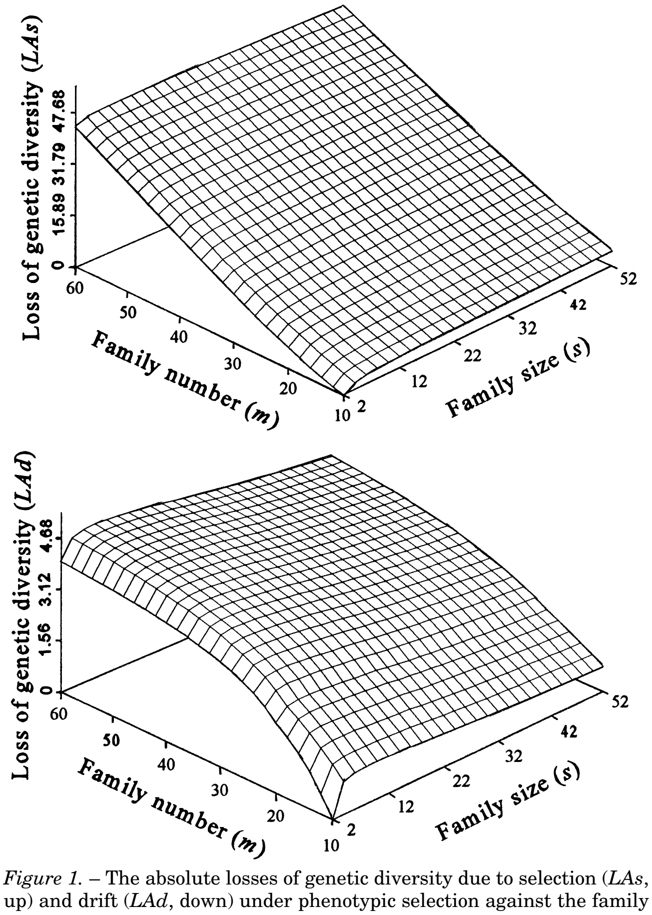

Figure 1. – The absolute losses of genetic diversity due to selection (*LAs*, up) and drift (*LAd*, down) under phenotypic selection against the family number (m) and size (s) when the selected number is kept constant (20). Full-sib families are assumed and heritability is set to 0.25.

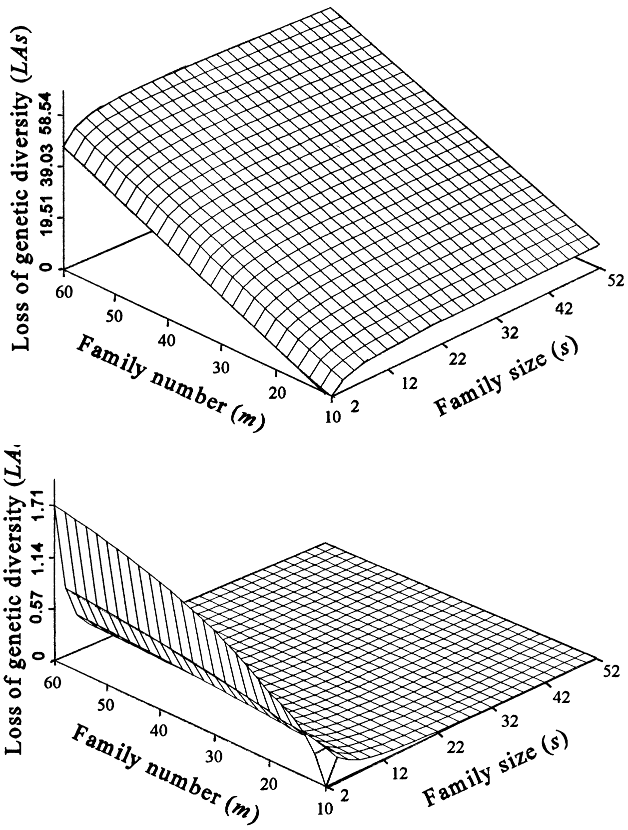

Figure 2. – The absolute losses of genetic diversity due to selection (*LAs*, up) and drift (*LAd*, down) under optimum index selection against the family number (m) and size (s) when the selected number is kept constant (20). Full-sib families are assumed and heritability is set to 0.25.

In practice, there is often a resource constraint on breeding operations. Therefore, it is impossible to infinitely increase population size. A common solution to this problem is to keep the total population size constant and to switch between family number and size. It is shown in *figure 3* that the total loss of genetic diversity and the 2 components increase with family number or decreases with family size. In general, increasing the family number is more efficient in gain than increasing the family size, particularly when heritability is low and selection uses more information about family performance than within-family deviations. Nevertheless, a population structure favouring gain is not efficient in controlling the loss of genetic diversity.

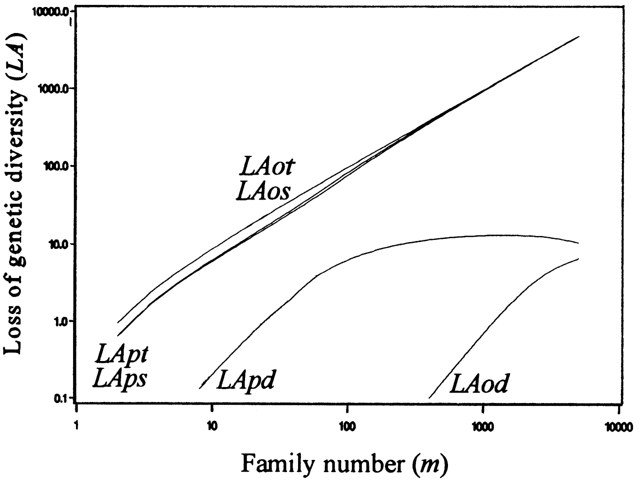

Figure 3. – Loss of genetic diversity against family number (*m*) given constant population size (*ms* = 10000) and selected number (40). Full-sib families are assumed and heritability is set to 0.25. The total loss, selection and drift effects are demonstrated for phenotypic selection (*LApt, LAps* and *LApd,* respectively) and optimum index selection (*LAot, LAos* and *LAod,* respectively). Note that the difference is not visible between *LAot* and *LAos,* and partly visible between *LApt* and *LAps.*

Optimization problems

Sufficient genetic diversity is necessary for both short-term and long-term breeding (WEI and LINDGREN, 1995). However, the conservation of genetic diversity contradicts the improvement of genetic gain. Genetic diversity will inevitably lose as long as gain is improved. In selective breeding, the problems of optimization are usually simplified to maximize gain (HAZEL, 1943; LUSH, 1947; ROBERTSON, 1957, 1970; FRANKHAM, 1977; FALCONER, 1989; WHITE and HODGE, 1988; GALLAIS, 1990). Obviously the conclusions obtained are one-sided. It would be preferable if both gain and genetic diversity are considered. Efforts have been made to identify methods that consider both aspects in an optimal manner (TORO and NIETO, 1984; TORO and PEREZ-ENCISO, 1990; LINDGREN et al., 1993; WEI and LINDGREN, 1994, 1995). It may be expected that, treating the problem in the same way as they did, optimal family number and size and selection intensity can be redefined (ROBERTSON, 1957, 1970; FRANKHAM, 1977). Furthermore, if the value of a certain amount of genetic diversity can be given on a scale compatible with the value of a certain value of gain (LINDGREN and WEI, 1994), the optimization problem could be solved in a much more comprehensive way, taking selection strategy, resources constraint, family number and size, selection intensity and conservation concerns into account.

Implication on conservation biology

The conservation problem of genetic diversity in breeding populations is usually limited to the improved species themselves. In fact, genetic diversity in an improved species is likely to have a more profound significance in conservation biology although, for the species itself, there is no problem with the extinction of populations, races and species because of the loss of genetic diversity (LACY, 1987). For example, imagine a forest tree species naturally distributed over a vast range of areas. Due to a long period of evolution and adaptation to different environmental conditions, the species is characterized by a high degree of genetic diversity predominantly distributed among a series of stable but different ecological communities. If artificial regeneration using improved seeds is expected to replace natural regeneration (as found in many tree species), the loss of genetic diversity in the breeding population is probably a catastrophe to other rare populations or species co-existing in stands because the corresponding plantations with narrow genetic diversity result in different ecological conditions and may fail in environmental stress and biotic damage (LEDIG, 1992).

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The Mating System of Black Spruce in North-Central Alberta, Canada

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Summary

Mating system parameters for a lowland and an upland black spruce population were simultaneously estimated for the 1983, 1982 and 1981 seed years, and for bulked seed collections from the 1978 to 1976 seed years. Population multilocus outcrossing estimates increased from 0.62 in 1983, to 0.85 in 1978 to 1976. There were no significant differences in outcrossing estimates among populations, or between years, although there was a significant difference between the most recent (1983) and the oldest estimate (1978 to 1976).

Single-locus outcrossing estimates ranged from 0.326 to 1.03 with significant heterogeneity amongst loci in all 3 years in the lowland site, but with only the 1981 population showing significant heterogeneity in the upland site.

Correlation between stand density, assessed from fixed-area plots, and the multilocus outcrossing estimate from each plot was not significant in either population.

Three factors suggested population substructuring: (i) Means of single-locus estimates of outcrossing for each year were consistently lower than multilocus estimates. (ii) There was significant spatial heterogeneity of the outcross pollen pool. (iii) WRIGHT's Index of Fixation was higher than the inbreeding equilibrium coefficient.

Key words: Mating System, Outcrossing Rate, Population Substructuring, *Picea mariana*.

FDC: 165.4; 174.7 *Picea mariana*; (712.3).

Introduction

Black spruce (*Picea mariana* (MILL.) B.S.P.) is the most important pulpwood species in the Canadian boreal forest, due chiefly to the strength derived from its long fibres. It is widely used in reforestation from Manitoba to the Maritime Provinces (MORGENSTERN, 1975). It's importance in the pulp and paper industry has led to genetic improvement programs in many regions (NIENSTAEDT, 1984). Information from these studies indicates that black spruce is highly variable at the provenance level (PARK and FOWLER, 1983). Optimization of tree improvement strategies, however, requires information not only on the genetic variation present in the species, but also on those factors which affect the amount and organization of this variation. One such factor is the degree of outcrossing and selfing, i. e., the type of mating system (ALLARD, 1975). Knowledge of the proportion of selfed seed produced by a species is of practical importance as selfed progeny often exhibit marked inbreeding depression affecting many aspects of growth and survival (SORENSEN and MILES, 1982; YING, 1978). In addition, inbreeding violates a basic assumption of most tree breeding programs – that the parents of wind-pollinated progeny are unrelated. Violation of this assumption causes a bias in estimates of additive genetic variance, heritability and genetic gain (NAMKOONG, 1966; SQUILLACE, 1974).

The technique of gel electrophoresis, used in this study, is widely used to separate polymorphic allozymes of newly germinated tissues as genetic markers in mating system studies (PERRY and DANCIK, 1986; YU *et al.*, 1992).

The semi-serotinous cones of black spruce permit simultaneous collection of seed crops from different years and also allow one to examine variation in the mating system of viable seeds from different seed crops. Estimation of mating system parameters in current seed crops, i. e. soon after the actual mating event, can provide information on the contribution of the mating system to genetic variation in the population. Comparison of mating system parameters in different seeds crops could indicate differential survival of selfed and outcrossed seeds. If survival is random, one would expect mating system parameters to remain relatively constant from year to year, apart from fluctuations due to environmental effects, and assuming no significant temporal variation in selfing events themselves.

The only published reports on the mating system of black spruce have been from studies in central New Brunswick (BOYLE and MORGENSTERN, 1986) and in a seed orchard in Ontario (BARRETT *et al.*, 1987). In the present study mating system parameters were estimated from an isozyme analysis of seed from the 1983, 1982 and 1981 cone crops, plus a bulked seed collection from the 1978 to 1976 cone crops. Results of the isozyme study were also examined for variation in pollen pool allele frequencies, which can affect the amount of gene exchange in the population.

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