COMPLEMENTING INBREEDING COEFFICIENT INFORMATION WITH STATUS NUMBER: IMPLICATIONS FOR STRUCTURING BREEDING POPULATIONS

L. D. GEA,

New Zealand Forest Research Institute Limited,
Private Bag 3020, Rotorua, New Zealand

D. LINDGREN,

Department of Forest Genetics and Plant Physiology,
Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden

C. J. A. SHELBOURNE,

New Zealand Forest Research Institute Limited,
Private Bag 3020, Rotorua, New Zealand

and T. MULLIN

Genesis Forest Science Canada Inc., 203–215 Côte de la Montagne C.P. 64,
Succursale Haute-Ville, Québec, QC G1R 4M8, Canada

ABSTRACT

Using stochastic simulations, the effects of size of unrelated groups, mating designs, and selection strategies were investigated to address the issue of assuring long-term genetic gains. The parameters analysed were status number (N_S), inbreeding coefficient (F), and genetic gain for two heritabilities (0.05 and 0.2).

Under a fixed-resource scenario, unrelated and non-inbred founders were clustered into variable group sizes (from 12 to 128), with 0.5 to 5.5 crosses per parent. Also considered were phenotypic selection and combined index selection, with and without restrictions on the number of individuals selected per family.

Breeding schemes with small, disconnected groups were slightly more efficient in preserving status number through a large number of generations than breeding schemes with large groups, but medium- to large-size groups showed larger expected gains. Inbreeding in small groups may become so severe as to cause fertility problems and considerably reduce the efficiency of selection for additive gene effects. Hence, using very small groups would probably not provide a sustainable long-term breeding strategy. Nevertheless, small groups may form a critical component of breeding strategies that employ marker-assisted selection, since the maintenance of marker-QTL associations would be facilitated in these small populations.

Substantial extra gain resulted from restricted combined index selection if more crosses per parent were made. Gain almost doubled during the first four generations with the increase from 0.5 to 1.5 crosses per parent. Constraints on the number of individuals selected per family severely curtailed gain, especially early on at low heritability and with one or fewer crosses per parent.

Small groups could be the means of delivering rapid gains through a concentration of breeding resources combined with a reasonably short breeding cycle, but small groups by themselves will probably not constitute a sustainable long-term breeding strategy.

INTRODUCTION

An important reason for assuring long-term gains in tree breeding is to guarantee future access to combinations of unrelated genotypes for inter-crossing in production populations. This can be achieved by arranging the breeding population in unrelated groups.

The increase in inbreeding within the groups during successive generations of recurrent selection is potentially a major problem in long-term breeding programmes. It can be delayed by restricting selection to within families, and by equal and symmetric representation of all parents and founders in mating schemes. Balanced mating designs are thus more advantageous than unbalanced ones for maximising effective population size and minimising allele losses rather than for immediate efficiency in realising genetic gains (Dempfle 1975; Kang & Namkoong 1979; van Buijtenen & Burdon 1990). Selecting predominantly within families is necessary for maintaining effective population size in the breeding population, even if this disregards family information and in each generation operates on only half the additive variance of the base population (Burdon 1988).

Selection that allows the offspring of different parents to be differentially selected may erode diversity drastically (e.g., Wei & Lindgren 1995). Methods proposed to delay such loss of genetic diversity within the unrelated groups are aggressive use of inbreeding (Lindgren & Gregorius 1976), use of small and essentially unrelated breeding groups, and equal representation for different families (Wei & Lindgren 1995). Choosing population replacements so that families (or rather parents) are equally represented reduces diversity as little as possible (Dempfle 1975).

Van Buijtenen & Burdon (1990) studied the expected efficiencies of alternative mating designs within those groups, for obtaining genetic gains from "forwards" selection in advanced generations, and Burdon & van Buijtenen (1990) also explored the differences in gain between mating designs for estimating breeding values for reselection of parents. They found that numerous crosses per parent, while increasing costs, added little to expected gain from forwards selection, unless specific combining ability (SCA) was substantial. However, with small numbers of crosses, selection of sufficient unrelated individuals could be expected to entail much-reduced gains. Burdon (1988) emphasised the risk of losing or wasting the genes of a parent if each parent was committed to only a single pair-cross. This argument favoured some sort of double-pair mating despite the fact that it showed no clear advantage in expected gains (from forwards selection) from increased numbers of crosses (van Buijtenen & Burdon 1990).

In this paper we address the effects that different group sizes, mating designs, and selection strategies have on status number (N_S), inbreeding coefficient (F), and genetic gain and analyse the implications for structuring breeding populations, assuming two different levels of heritability. Since traditional concepts of effective population size have some rather awkward properties when used for characterising the state of populations, N_S would provide useful information for many purposes (Lindgren *et al.* 1996), mainly for when the breeding population is divided into unrelated groups which have zero gene exchange and F alone is an insufficient descriptor for population changes in gene frequency and status. N_S, F, and genetic gain were calculated with POPSIM 2.3.00, a computer program that stochastically simulates changes in the genetic structure of managed tree populations (Mullin & Park 1995).

METHODS
Details of Model and Settings of the Simulations

The initial plus-tree selection was referred to as generation 0, and the expected breeding value of these unrelated trees was set, by convention, to zero (with stochastic variation), with coefficients of inbreeding (F) and co-ancestry (*f*) also set to zero. These trees, which comprise the founders of the breeding population, were mated according to a specified design and generated progenies whose genetic structure depends on the mating design. From these progenies, new trees were selected to form the parents of the next cycle of the breeding population through the following 10 simulated generations.

Two complementary studies were made. For the first study, which was on the effects of group size on genetic gain, F, and N_S after 10 generations of breeding, a simple double-pair-cross mating design (DPM) was chosen for group sizes of 12, 32, 64, and 128 parents, and the selection of trees was made according to combined among- and within-family index selection which involved predicting the breeding value of each tree and using these predictions as the basis of selection. The predicted breeding value is based on the phenotype of the tree and the mean performance of its sibs, weighted according to heritability of within-family effects and heritability (or repeatability) of sib-family effects respectively. Thus, the weighting will depend not only on individual heritability but also on family size.

In the study of the effects of mating design and selection strategies on gain, F, and N_S, disconnected groups ranging from 12 to 128 trees were selected. The selection of trees was made according to two methods: (i) phenotypic selection or mass selection (P), and (ii) combined index selection (CI). Simulations were done either without any restriction on the numbers of trees selected per full-sib family or with the restriction of one or two selections per full-sib family (but no restriction on the number of selections per half-sib family).

Cumulative status number was defined as the sum of N_S over all the groups, and relative status number (N_R) was defined as the N_S of the group divided by the number of individuals in the group.

Eight different balanced-symmetric designs (with the same number of crosses for each parent) were considered (Table 1). The mating designs were characterised primarily by the number of crosses per parent.

All simulations were repeated with 100 replicate runs per set of conditions to obtain reliable prediction.

TABLE 1–Summary of assumed population parameters

• Group size	12 to 128
• Offspring per cross	10 to 200
• Total offspring per parent	100
• Number of generations	10
• Additive genetic variance σ^2_A	1
• Dominance and epistatic variance σ^2_D; σ^2_I	0
• Environmental variance σ^2_E	19 and 4
• Narrow sense heritability $h^2 = \dfrac{\sigma^2_A}{\sigma^2_A + \sigma^2_E}$	0.05 and 0.2

RESULTS

Mating designs considered are presented in Fig. 1. The results of the first simulation study (in terms of gain, F, and N_R) for a heritability of 0.2, 10 generations, double pair-cross mating (DPM) designs, and different group sizes are shown in Table 2 and Fig. 2, 3, 4, and 5.

Results for the second simulation study, which involved heritabilities of 0.2 and 0.05 for all the one-cross-per-parent designs (DPC, DPF, PFM, DD3) and the other designs after 10 generations, are given in Table 3. The results from these mating designs (Fig. 6, 7, 8, and 9)
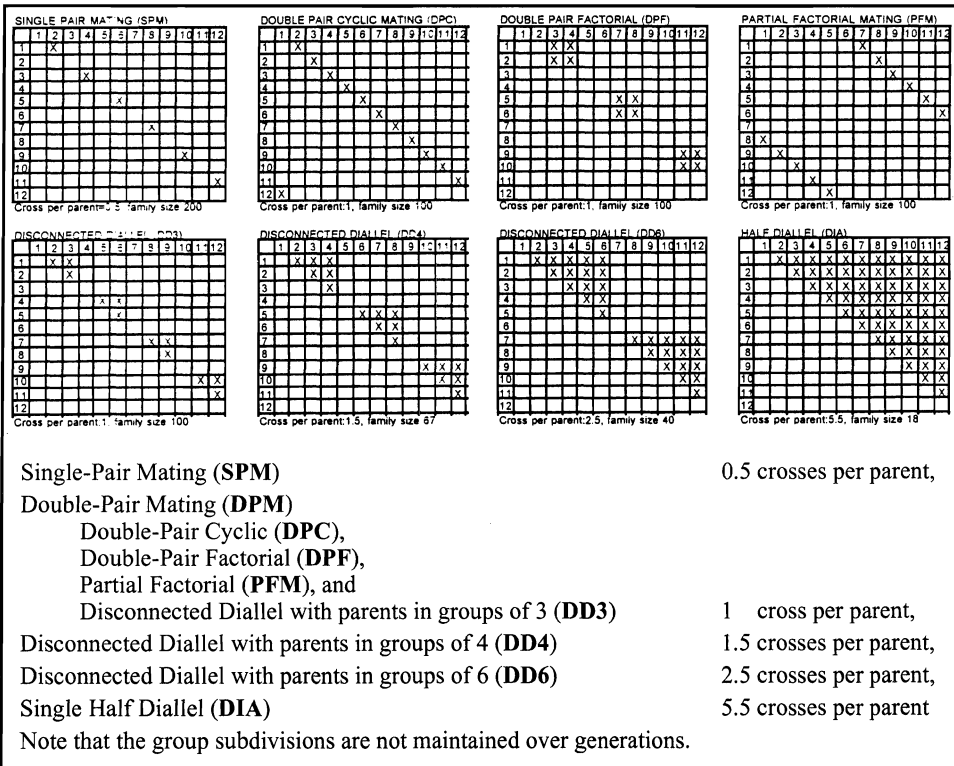

Single-Pair Mating (**SPM**)	0.5 crosses per parent,
Double-Pair Mating (**DPM**)	
Double-Pair Cyclic (**DPC**),	
Double-Pair Factorial (**DPF**),	
Partial Factorial (**PFM**), and	
Disconnected Diallel with parents in groups of 3 (**DD3**)	1 cross per parent,
Disconnected Diallel with parents in groups of 4 (**DD4**)	1.5 crosses per parent,
Disconnected Diallel with parents in groups of 6 (**DD6**)	2.5 crosses per parent,
Single Half Diallel (**DIA**)	5.5 crosses per parent

Note that the group subdivisions are not maintained over generations.

FIG. 1–Mating designs (for a group size of 12 parents)

were pooled for ease of interpretation, because there were no differences evident amongst them (see below).

Status Number (N_S)

For different group sizes

N_R under conservative strategies (with restriction to one individual selected per pair-cross) was better preserved by small groups (Fig. 2). However, this difference became perceptible only in the later generations. After 10 generations small groups (12) gave a N_R of 0.18 while a population of 128 parents had a N_R of 0.17. If more individuals in any one pair-cross could be selected, the overall N_S declined faster and was then preserved much better with small groups (Table 2 and Fig. 2). With no restrictions on the number of individuals selected per cross, almost 90% of the N_S of the small group was lost in one generation (and nearly 80% for a large group). Under this extreme scenario the advantage of small group size was greatest. N_S essentially levelled off at around generation 3 under no restriction on the number of individuals selected per cross, and around generation 8 for two individuals selected per pair-cross, while with a conservative strategy N_S was expected to level off even later (Fig. 2).
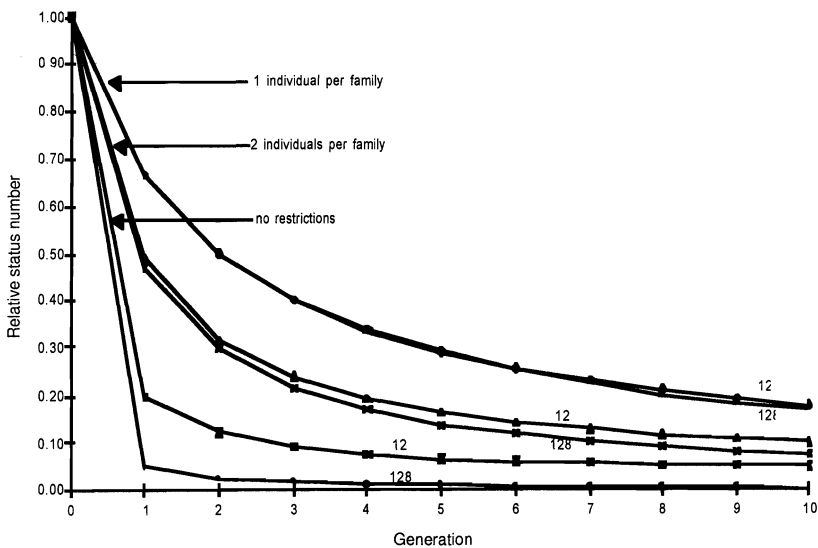

FIG. 2–N_R at successive generations for two group sizes (12 and 128) and three selection strategies, with a DPM design and heritability 0.2.

Higher levels of gain per unit decline of N_S loss were obtained with a conservative within-family selection strategy, but to reach the same level of gain this strategy would take more generations to achieve (Fig. 3).

For different mating designs

Within-family selection with one individual chosen per full-sib cross (under various DPM schemes) (Table 3C and Fig. 2) maintained the highest N_S. Even so, the N_S dropped

TABLE 2–N_R, F, and cumulative gains for 10 generations of breeding with DPM, using different group sizes and selection strategies.

Gener-ation	1 individual per family				2 individuals per family				No restrictions			
	12	32	64	128	12	32	64	128	12	32	64	128
(A) Relative status numbers (N_R)												
0	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
1	0.67	0.67	0.67	0.67	0.49	0.48	0.47	0.47	0.20	0.11	0.07	0.05
2	0.50	0.50	0.50	0.50	0.32	0.30	0.30	0.30	0.12	0.06	0.03	0.02
3	0.40	0.40	0.40	0.40	0.24	0.22	0.22	0.22	0.09	0.04	0.02	0.02
4	0.34	0.33	0.33	0.33	0.19	0.17	0.17	0.17	0.08	0.03	0.02	0.01
5	0.29	0.29	0.29	0.29	0.16	0.14	0.14	0.14	0.07	0.03	0.02	0.01
6	0.26	0.25	0.25	0.25	0.14	0.12	0.12	0.12	0.06	0.02	0.01	0.01
7	0.23	0.23	0.22	0.22	0.13	0.11	0.10	0.10	0.06	0.02	0.01	0.01
8	0.21	0.20	0.20	0.20	0.12	0.10	0.09	0.09	0.05	0.02	0.01	0.01
9	0.19	0.19	0.18	0.18	0.11	0.09	0.08	0.08	0.05	0.02	0.01	0.01
10	0.18	0.17	0.17	0.17	0.10	0.08	0.08	0.07	0.05	0.02	0.01	0.01
(B) Coefficients of inbreeding (F)												
0	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
2	0.023	0.008	0.003	0.002	0.053	0.018	0.008	0.006	0.203	0.146	0.129	0.099
3	0.047	0.016	0.008	0.004	0.099	0.040	0.018	0.010	0.334	0.272	0.246	0.194
4	0.067	0.026	0.012	0.006	0.150	0.060	0.030	0.016	0.450	0.365	0.352	0.278
5	0.089	0.031	0.015	0.008	0.190	0.075	0.038	0.020	0.540	0.464	0.435	0.359
6	0.106	0.039	0.020	0.010	0.230	0.096	0.050	0.026	0.620	0.549	0.510	0.441
7	0.127	0.047	0.023	0.012	0.270	0.111	0.057	0.030	0.686	0.619	0.581	0.509
8	0.144	0.055	0.027	0.014	0.300	0.128	0.067	0.035	0.741	0.675	0.637	0.556
9	0.163	0.062	0.031	0.016	0.330	0.147	0.076	0.040	0.783	0.726	0.685	0.608
10	0.182	0.069	0.035	0.018	0.370	0.163	0.086	0.044	0.823	0.769	0.725	0.648
(C) Cumulative gains												
0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1	0.59	0.62	0.60	0.58	1.02	1.10	1.10	1.09	1.43	1.62	1.79	1.84
2	1.18	1.21	1.19	1.17	1.94	2.06	2.07	2.06	2.52	2.82	3.10	3.14
3	1.74	1.77	1.78	1.76	2.80	2.99	3.02	3.00	3.48	3.92	4.39	4.46
4	2.31	2.36	2.38	2.36	3.64	3.89	3.97	3.96	4.38	5.00	5.57	5.67
5	2.85	2.93	2.95	2.96	4.44	4.80	4.90	4.91	5.14	5.98	6.56	6.82
6	3.41	3.49	3.55	3.55	5.24	5.68	5.85	5.85	5.83	6.90	7.51	7.92
7	3.94	4.06	4.12	4.13	5.99	6.54	6.76	6.79	6.45	7.67	8.36	8.80
8	4.48	4.64	4.70	4.72	6.72	7.43	7.68	7.73	6.97	8.35	9.12	9.60
9	5.02	5.20	5.27	5.31	7.42	8.29	8.59	8.65	7.43	8.97	9.83	10.40
10	5.51	5.77	5.85	5.89	8.08	9.12	9.49	9.58	7.81	9.50	10.49	11.00

to approximately 40% of the original value in three generations, with the largest decrease occurring in the first generation. N_S values also declined more rapidly with mating designs

TABLE 3–N_R, F, and cumulative gain after 10 generations of breeding for different mating designs and selection strategies for a group size of 12 and two heritabilities.

Mating design	$h^2 = 0.2$					$h^2 = 0.05$				
	SPM	DP*	DD4	DD6	DIA	SPM	DP*	DD4	DD6	DIA
No. crosses per parent	0.5	1	1.5	2.5	5.5	0.5	1	1.5	2.5	5.5
Family size	200	100	67	40	18	200	100	67	40	18
(A) Status number (N_S)										
Phenotypic selection	1.07	1.08	1.13	1.11	1.16	1.27	1.24	1.27	1.28	1.29
Comb. index (unrestricted)	0.58	0.58	0.59	0.61	0.67	0.57	0.57	0.58	0.60	0.68
Comb. index 2 per full-sib	2.14	1.19	1.02	0.91	0.88	2.14	1.19	1.06	0.99	0.97
Comb. index 1 per full-sib		2.14	1.57	1.24	1.06		2.14	1.60	1.32	1.18
(B) Coefficients of inbreeding (F)										
Phenotypic selection	0.430	0.420	0.400	0.400	0.380	0.350	0.350	0.340	0.340	0.330
Comb. index (unrestricted)	0.820	0.820	0.800	0.770	0.700	0.840	0.830	0.810	0.780	0.690
Comb. index 2 per full-sib	0.180	0.370	0.440	0.500	0.520	0.180	0.370	0.420	0.490	0.460
Comb. index 1 per full-sib		0.180	0.270	0.350	0.420		0.180	0.260	0.330	0.370
(C) Cumulative gain										
Phenotypic selection	7.20	7.73	7.98	7.95	7.96	3.84	4.40	4.47	4.39	4.30
Comb. index (unrestricted)	7.22	7.91	8.08	8.00	7.93	4.74	5.57	5.23	5.13	4.90
Comb. index 2 per full-sib	5.29	8.08	8.73	8.87	8.76	2.51	5.51	5.83	5.84	5.57
Comb. index 1 per full-sib		5.51	7.51	8.23	8.64		2.68	4.52	5.28	5.45

* DP represents an average for the one-cross-per-parent mating designs, DPC, DPF, PFM, and DD3. Note that there are no restrictions on the number of individuals within half-sib.

involving more crosses per parent (Fig.4). The four DPM mating systems (DPC, DPF, PFM, DD3) were very similar for N_S (Fig. 5).

Inbreeding Coefficient (F)

For different group sizes

Group size was an important factor for delaying inbreeding. A selection strategy based on keeping no more than two individuals per pair-cross under a large group would have a significantly smaller F than the conservative strategy of one individual per pair-cross (Fig. 6).
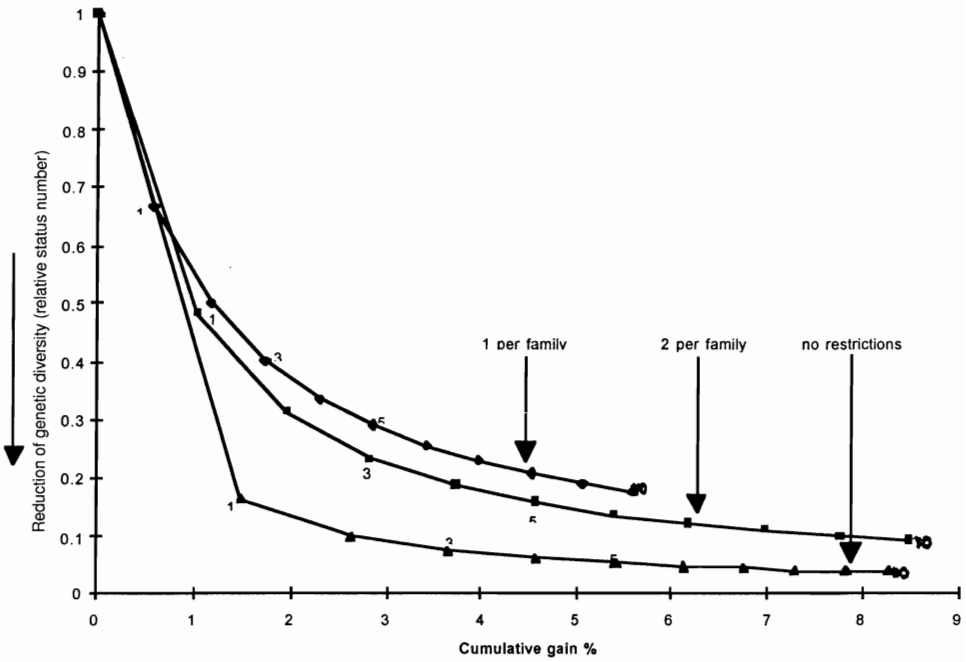
FIG. 3–N_R in relation to cumulative genetic gain over successive generations for different
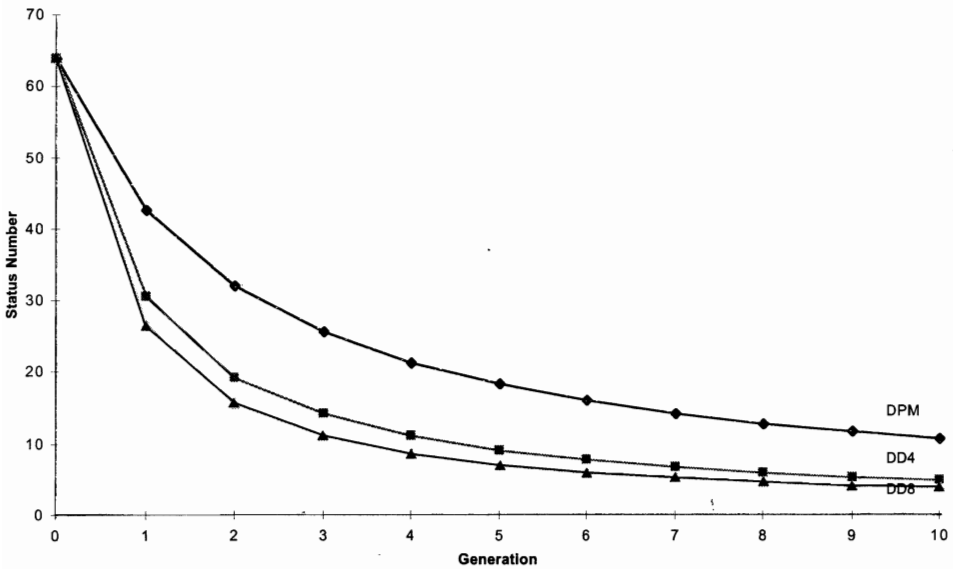selection strategies with DPM design and heritability 0.2.

FIG. 4–N_S over successive generations for different mating designs and no more than one
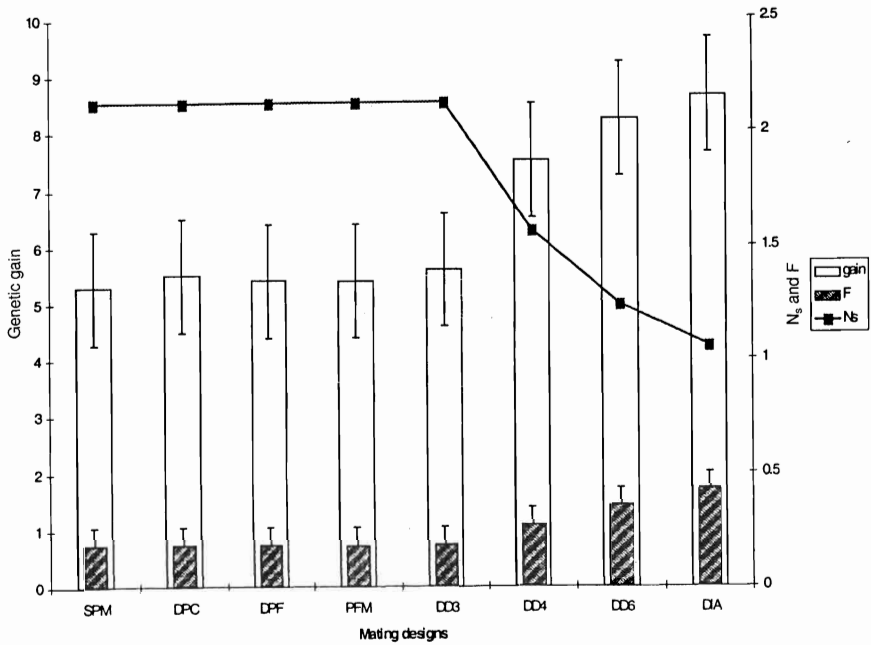individual selected per pair-cross.

FIG. 5—Genetic gain, F, and aggregated N_S at generation 10 for different mating designs; one individual selected per pair-cross (when feasible) and a group size of 12.
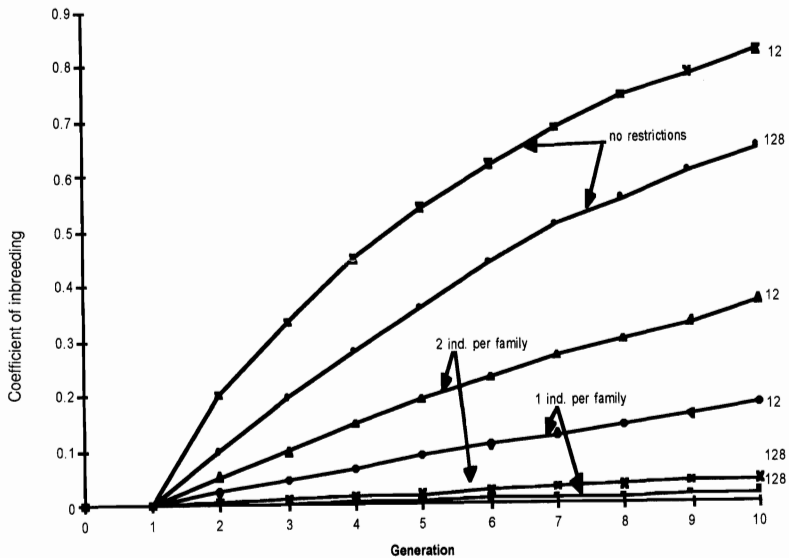

FIG. 6—F over successive generations for two group sizes (12 and 128), three selection strategies, and DPM design.

F became extremely high with no restrictions on the number of individuals per family. If such a strategy was applied the level of F exceeded 0.2 after only four generations of breeding, for all group sizes.

F quickly reached 0.2 in the smallest group. However, for group sizes larger than 64, F was still negligible after 10 generations (Table 2B) even with up to two individuals kept per pair-cross.

For different mating designs

The three mating systems (DPC, DPF, DD3) were very similar for F (Fig. 5). N_S and F for the single-pair mating design (SPM) were similar to those for one cross per parent. F was also higher for mating designs with more crosses per parent (Fig. 7). F in the SPM and DPM systems seemed to build up more slowly, which could be expected since selection was distributed more evenly among pair-crosses than for random selection, especially with the restrictions applied. Both F and N_S were quite similar for the same selection scenarios (Table 3B and C) at different heritabilities.

Expected Genetic Gain

For different group sizes

Expected breeding-population gain (Fig. 8) increased with group size, especially in later generations. There was little difference in gain for the first two generations if restrictions were imposed on selection. Gain for the 12-parent group with no restriction in the number of individuals kept per cross slowed down around generation 5. This "plateauing" in gain for the smaller group under an aggressive selection strategy coincided with high F values, but without actually invoking inbreeding depression.

For different mating designs

The predicted gains for each mating design with one-cross-per-parent were similar (Fig. 5), although gain for the disconnected diallel design (DD3) was very marginally higher
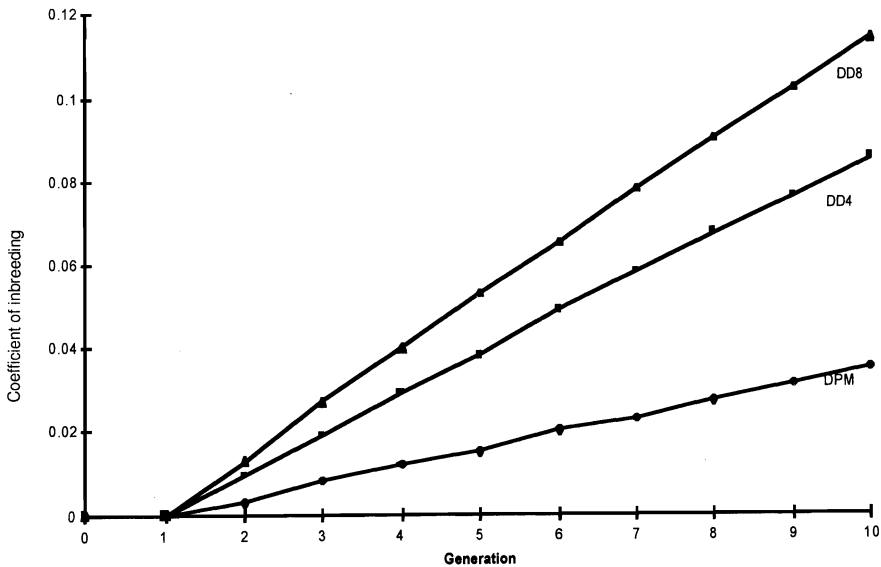

FIG. 7–F per generation for different mating designs and no more than one individual selected per pair-cross.
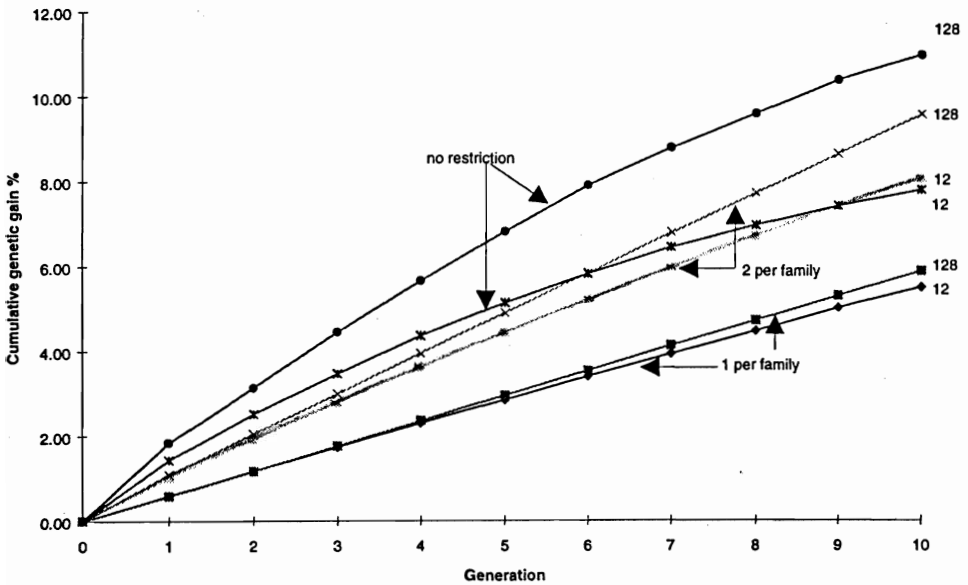
FIG. 8–Cumulative genetic gain by generation for two group sizes (12 and 128), three different
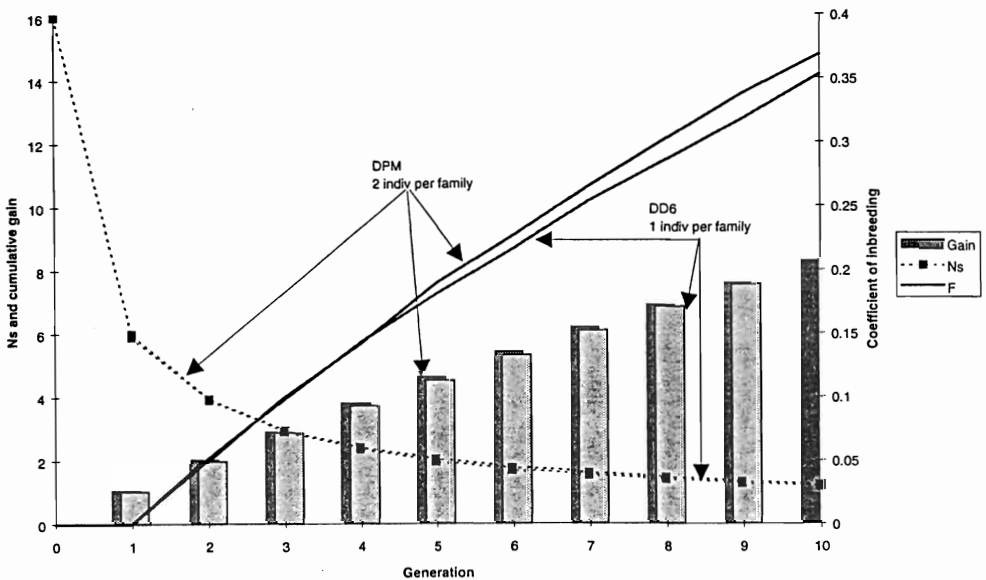selection strategies, and a DPM design.

FIG. 9–Cumulative genetic gain, F, and N_S for combinations of two different mating designs
and selection strategies and a group size of 12.

than for the other DPM designs; these gains are averaged in Table 3A. Substantial extra gain
resulted from restricted combined index selection (but less for unrestricted selection) if more
crosses per parent were made (Table 3); for instance, during the first four generations of

breeding gain almost doubled with the increase from 0.5 crosses per parent (SPM) to 1.5 crosses per parent (DD4). The extra gain was accompanied by more F and lower N_S, and the improvement in gain with increasing number of crosses per parent occurred up to 2.5 crosses (DD6) but not beyond (i.e., DIA).

Almost exactly the same values of N_S and F, and marginally higher gains, could be obtained with a strategy based on the same number of crosses as parents (DPM) and a maximum of two individuals selected per family as could be obtained with a mating design of 2.5 crosses per parent (DD6) and a maximum of one individual per family (Fig. 5). SPM was expected to produce slightly higher gain from within-family selection (as the selection intensity for the same selected proportion was higher) but less gain from between-family selection (as there were fewer families to select from), leaving almost no net difference (Fig. 5). Unrestricted combined index selection yielded relatively higher expected gains than phenotypic selection at both heritabilities but more so at low heritability (Table 3A).

Unrestricted combined index selection did not result in more gain, after 10 generations, than restricted combined index selection, unless the number of crosses per parent was one or less, or the selection was restricted to no more than one individual per full-sib family (Table 3). Thus, with these exceptions, it was possible to choose a strategy that after 10 generations of breeding would produce more expected gain than unrestricted combined index selection (Table 3A). The high genetic gains of unrestricted selection during the first generations (Table 2) were made at the cost of a reduced N_S and an increased F. When no restrictions were applied, the N_S dropped in two generations to less than a fifth of its initial value. This loss of N_S was also accompanied by a rapid increase in the F (to 0.2 in two generations for N = 12).

Constraints on the number of individuals selected per family severely curtailed gain, especially early on at low heritability and with one or fewer crosses per parent (Table 3A). For the low-heritability case and mating designs with the same number of crosses as parents, a 50% increase in gain after 10 generations was obtained by relaxing the constraint of equal representation of all families (one tree per pair-cross) to two or less individuals from the best pair-crosses. This scenario also carried a corresponding increase in the F level and a reduction in the N_S (Table 2). With mating designs that involved increasing crosses per parent (DD4, DD6, and DIA), the increase in gain progressively decreased. Because of the fixed-resources model used, gains from among-family selection increased but gains from within-family selection decreased as number of crosses per parent increased and number of individuals per family decreased, especially when the crosses per parent numbered more than 2.5.

Unrestricted phenotypic selection showed higher gains relative to the other alternatives at high heritability, but these were still inferior to those from combined index selection (Table 3A). Using family information thus becomes less important at higher heritabilities. Increasing the number of crosses per parent at both heritabilities did not increase gain proportionately, with gains appearing to plateau at 1.5 to 2.5 crosses per parent (Table 3A).

Phenotypic selection, and combined index selection restricted to a maximum of two selections per cross, resulted in similar values for N_S and F; only when more crosses per parent were used did phenotypic selection give higher N_S and lower F levels and gains (Table 3). Phenotypic selection resulted in less gain at the same N_S when heritability was low, but at the higher heritability the difference was small.

DISCUSSION
Group Size

Group size has the widest range of consequences, since it exerts influences in both the short-to-medium term (involving selection differential, inbreeding depression and the reduction of genetic variance within groups due to genetic drift) and the longer term (involving selection limits, and efficiency of selection).

Mahalovich & Bridgwater (1989) compared population variances for 20 generations, for subline (group) sizes ranging from 4 to 12, and showed that total expressed additive genetic variance for subline size 4 increased for 7 to 8 generations before slowly declining. They also showed that the additive genetic variance was reduced more rapidly in larger sublines. With the model assumptions (additive variance influenced by F) used here, the within-group additive variance for a group size of 12 will start declining after generation 10 with a conservative selection strategy, and levels off after generation 8 if no restrictions are applied to the number of individuals selected per family (Fig. 8). To prevent the decay of additive variance per generation, a conservative selection strategy (i.e., restricting the degree of among-family selection) is recommended, rather than an emphasis on population size. Mahalovich & Bridgwater (1989) argued that genetic variances summed over all groups decrease much more rapidly with larger groups; this will be true only when selection strategies are relaxed so that N_S is better preserved by small groups.

Breeding groups with fewer than 10 parents will be impossible to maintain for longer than a few generations without inbreeding, which may become so severe as to cause fertility problems and to hamper selection, depending on the level of genetic load in the species or the particular set of parents. Possible exceptions are species that have few lethal alleles and undergo inbreeding with minimal depression (Russell *et al.* 1996; Williams & Savolainen 1996). If inbreeding within the groups became severe, full-sib testing, clonal testing, and parental ranking would become less efficient for estimation of breeding values and less efficient for long-term breeding (unless unrelated tester material was used). Also, as the families within groups became related there would be less usable variation among them. Inbred breeding populations would also require large target numbers of offspring per cross because the probability of extinction for each group would be expected to be high. Theoretical advantages of highly inbred groups can include perfect assortative mating (with selfing), increased selection efficiency among groups, increased uniformity within groups (Williams & Savolainen 1996). Such groups may form a critical component of breeding strategies that employ marker-assisted selection, since the maintenance of marker-QTL associations would be facilitated in these small populations.

However, small groups will fail if, as Meuwissen & Woolliams (1994) described, they enter a "downward spiral of ever-decreasing fitness" as they reach high levels of inbreeding and low offspring survival and adult fecundity.

The N_S is a useful measure of the current state of genetic diversity in a breeding population and extends information given by inbreeding and co-ancestry coefficients. Although smaller groups raise ΔFs and lower gain within the groups, they allow higher N_S to be maintained. With very small groups, substantial cumulative effects on N_S will be seen only after a large number of generations. Breeding schemes with small groups are thus slightly more efficient in preserving N_S through a large number of generations than breeding systems with large

groups. Medium-to-large-size groups showed a comparatively small reduction in aggregated N_S over generations but showed larger increases in gain than small groups (Fig. 5).

Group size may also affect genetic gains by changes in selection intensity. The most important source of gain is the exploitation of effective number by intensive among-family selection. A higher N_S in the breeding population might mean that it can be exploited harder when transferring the gain to the production population.

Mating Designs and Selection Strategy

In these simulations, unrestricted combined among-cross and individual index selection always resulted in higher expected genetic gain than phenotypic selection and combined index selection with restriction on the number of individuals selected per family, agreeing with other findings reported (e.g., Falconer 1981; Namkoong *et al.* 1988; Pswarayi & Barnes 1994). However, combined index selection with no restrictions was *less* effective than phenotypic selection in maintaining genetic diversity -N_S- (Table 3C), though combined index selection with restrictions was *more* effective than phenotypic selection in this function.

Choice of a selection strategy for a breeding population, will normally be strongly influenced by its ability to maintain genetic diversity in the long term as well as its capacity for realising high gains. The drop in N_S after unrestricted combined index selection is likely to be unacceptable, even after just a single generation, and using any mating design. Verrier *et al.* (1993) concluded that selection procedures that place less emphasis on family information would best meet long-term objectives of diversity (cf. Burdon 1988).

However, expected genetic gains may be unacceptably low for selection procedures that do not include an among-cross selection component, especially in low-heritability situations. It also seems to be impossible to avoid having the N_S decrease to something like one-third of its initial value after three rounds of selection, if the breeding programme is going to be reasonably effective in achieving gains. This is a good reason for using a large number of families as founders of the breeding population.

Van Buijtenen & Burdon (1990), addressing a single generation of breeding, asserted that SPM was an optimal mating design if all parents were equally represented, although some sort of double-pair mating design was seen to be preferable to avoid the risk of losing or wasting parents in the current round of crossing. In the scenario that we have addressed, however, SPM is an efficient way to preserve N_S but is sub-optimal for gain. Van Buijtenen & Burdon (1990) showed that under a fixed-resource scenario, in a single generation and without special restrictions on relatedness of selections, numerous crosses per parent (more than five) both raised costs and added little to expected genetic gain from forwards selection, unless SCA was substantial. However, in our study with an additive genetic model and fixed resources, an increase from 0.5 or 1 cross per parent (equivalent to within-family selection) to 2.5 crosses per parent (DD6) with use of restricted combined-index selection gave substantial increases in expected genetic gain. This accords with the stochastic simulation results of King & Johnson (1993) and deterministic simulation results of Gea & Shelbourne (1995). However, increasing the number of crosses per parent up to 2.5 does carry a penalty of increased F and reduced N_S.

If a minimal reduction of genetic diversity is required, however, families should be equally represented. Any selection scheme that is based exclusively on within-family

selection will produce low gains, but after some generations may result in a higher N_S than selection schemes that maximise immediate gain. Wei & Lindgren (1995) showed that genetic diversity was eroded quickly, even in a single generation, if selection allowed unequal representation of the progeny of different parents. In our study, gain increased substantially when restrictions were relaxed from no more than one individual per cross to up to two individuals per cross, while the N_S decreased from 6 to about 4 (for one-cross-per-parent design after 10 generations). It seems desirable to apply constraints but to make them flexible enough to permit some unequal representation of parents.

With conservative selection strategies, smaller group sizes raise F and lower gain but they lead to slightly higher aggregate N_S. Substantial cumulative effects of group size on N_S will emerge only with unrestricted selection (Lindgren *et al.* 1996).

The use of effective population size (N_e) as an index for monitoring genetic diversity has been proposed (King & Johnson 1993), but the drawbacks of this parameter for characterising genetic diversity (discussed by Lindgren *et al.* 1996) make it difficult to use in practice. N_S appears to be a more practical and efficient tool although its properties and limitations need to be understood.

Wider Implications of the Results

The basic concepts of quantitative genetics and the applicability of the genetic parameters used, including additive genetic variation, genetic correlations, and heritability, depend on a set of assumptions defined in the model. The detailed impact of possible violations of the most important assumptions of the models (infinitesimal model, initial co-ancestry (f) of zero, initial coefficient of inbreeding (F) of zero, selective neutrality, no mutation, genes shared in exact proportion to theoretical co-ancestry, and no linkage) have not been investigated.

It is probable when two or more assumptions are violated simultaneously that one gets the biggest impact. For instance, departures from neutrality, in conjunction with linkage and the presence of highly deleterious major genes, i.e., "hard load" (which could often reflect recent mutation) are likely to drag along whole linkage blocks, and calculated N_S and F could under-estimate the remaining diversity or genetic base.

N_S is not intended to replace any other measures but rather it is seen as complementary to existing measures and provides information for situations when the F and traditional measures of effective population size are less useful.

In an advanced breeding population strategy, small groups can be the means of delivering rapid gains through a concentration of breeding resources (testing, selection, and crosses and maybe cloning) combined with a reasonably short breeding cycle. Analysis of mating designs has shown that optimal gains are obtained with up to 2.5 crosses per parent and a less restricted selection strategy. Thus, small groups can take full advantage of this strategy and, in principle, provide individuals with high levels of gain, while a broad main breeding population can be managed with a more conservative and less expensive approach and fulfil the objectives of a long-term breeding strategy. Furthermore, small groups are slightly more efficient in preserving N_S through a large number of generations than large groups, but small groups by themselves will probably not constitute a sustainable long-term breeding strategy.

If small group breeding populations are kept closed (<20), minimising inbreeding depression within the group will be a guiding consideration. If F within the group becomes important, full-sib family information, clonal testing, and parental ranking will become less efficient for estimating breeding values for a long-term breeding population. As the families within the elites become related there will be less useful variation among them. One way of overcoming inbreeding will be by adopting an enrichment strategy whereby the elite are enriched every generation with genotypes from the main population to periodically reduce inbreeding levels and thus maintain gain (Bridgwater 1995).

Critical levels of N_S need yet to be determined, but the simulations presented here have shown that unrestricted selection will lose almost 90% of the genetic diversity in only one generation. On the other hand, within-family selection showed the highest levels of gain per unit loss of N_S, but will take longer to achieve a given level of gain.

Small groups can also be used as experimental populations in which high levels of inbreeding associated with high genetic gain can be managed, and accelerated breeding techniques implemented, without risking the success of long-term breeding population management.

Almost exactly the same N_S , F, and genetic gains can be obtained with a strategy based on the same number of crosses as parents (DPM) and a maximum of two individuals selected per cross as can be obtained with a mating design of 2.5 crosses per parent (DD6) and a maximum of one individual per cross. However, we would favour the second option because multiple crosses per parent will allow the capture of greater gains in the production population.

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