SELECTION IN REFERENCE TO BIOLOGICAL GROUPS. VI. USE OF EXTREME FORMS OF NONRANDOM GROUPS TO INCREASE SELECTION EFFICIENCY

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ABSTRACT

The strategy of using non-random groups to increase the efficiency of truncation selection is discussed. The present study, which considers extreme forms of non-random groups, complements a previous study involving full-sib groups. It is shown that of the two kinds of non-randomness, i.e. that due to homozygosity or that due to homogeneity (as represented by cloning), the latter is the most effective. This suggests that with those plant crops in which intense competition among plants exists, use of clonal propagation to produce non-random groups should be investigated.

IN the previous study of this series (GRIFFING 1976), use of non-random (full-sib) groups was explored as a technique to increase the efficiency of truncation selection operating with regard to populations of groups within which individuals may interact. In general, it was found that individual and group selection methods change gene frequency more efficiently with full-sib than with random group structure.

Use of full-sib groups is possible in most forms of plants and animals and hence is a readily available technique. However, in some plant species it is also possible to construct more extreme forms of non-random groups. The present study considers the use of these fascinating possibilities.

In some plant species clonal propagation of a single organism is possible. Clearly, then, use of genetically identical propagules to form groups represents a method of constructing non-random groups with maximum homogeneity. In the arguments to follow it is assumed that the act of propagation does not appreciably alter the genotypic value of the propagule relative to the parent plant from which it is derived.

It is also possible in some plant species to extract isogenic diploids from heterozygous parents by doubling haploid forms which arise from gametophytic tissue. For example, in maize an ingenious use of genetic stocks has been devised to make this technique of practical importance (CHASE 1952, 1974). More recently, techniques have been developed that show promise of making the doubled-haploid procedure even more powerful (see KASHA 1974 for general review). Therefore, the possibility exists of converting a random-mating, hetero-

zygous population into a population of homozygous genotypes. This homozygous material can then be used to form non-random groups.

The present study assumes that the basic population undergoing selection initially exists in equilibrium under random mating. The objective of the selection procedure is to change the mean of the population of random groups generated by such a base population. However, the mode of attack is to use extreme non-random rather than random groups as a framework within which selection operates. It will be shown that such a strategy results in increasing the efficiency of selection.

POPULATION SPECIFICATION

The conceptual population of primary interest is assumed to be in equilibrium under random mating. The genotypic array is generated by an arbitrary number, m, of alleles at a single autosomal locus, i.e.

$$\sum_i \sum_j p_i p_j (A_i A_j).$$

Random groups of size n are obtained from an n-way combinatorial product involving this array. A typical random group may be represented by the following n-tuple.

$$(A_{i_1} A_{j_1}, \ldots, A_{i_n} A_{j_n}).$$

Assuming only additive effects, the gene model for $A_{i_1} A_{j_1}$, as expressed in this group and measured as a deviation from the population mean, is

$$_{i_1 j_1} d_{i_2 j_2, \ldots, i_n j_n} = ({}_d\alpha_{i_1} + {}_d\alpha_{j_1}) + \sum_{t=2}^{n} ({}_a\alpha_{i_t} + {}_a\alpha_{j_t}),$$

where

$({}_d\alpha_{i_1} + {}_d\alpha_{j_1})$ = direct additive effects of the genotype $A_{i_1} A_{j_1}$;

and

$({}_a\alpha_{i_t} + {}_a\alpha_{j_t})$ = associate additive effects of the t^{th} genotype as measured on $A_{i_1} A_{j_1}$.

These genotypic values, as defined with regard to random groups, constitute the universal set of genotypic values required in the following discussions.

Associated with this model are the genotypic variance components,

$$_{dd}\sigma^2_A = 2\Sigma p_i ({}_d\alpha_i)^2,$$

$$_{aa}\sigma^2_A = 2\Sigma p_i ({}_a\alpha_i)^2,$$

and the covariance component,

$$_{da}\sigma_A = 2\Sigma p_i ({}_d\alpha_i)({}_a\alpha_i).$$

For further elaboration of the conceptual framework see GRIFFING (1967). It should be noted that the term "random group" refers to the group formed at random from the *random-mating* base population as described above.

CONSEQUENCES OF SELECTION WITH NON-RANDOM GROUPS

Use of isogenic extraction technique to form inbred groups

Assume that it is possible to extract a conceptual population of isogenic genotypes in the absence of forces changing gene frequency. In this case, the random-mating population is converted into the following array,

$$\sum_i p_i(A_iA_i).$$

The term "inbred group" refers to groups formed at random from the n-way combinatorial product involving the inbred array. A typical group may be represented by the following n-tuple,

$$(A_{i_1}A_{i_1}, A_{i_2}A_{i_2}, \ldots, A_{i_n}A_{i_n}).$$

The genotypic value of $A_{i_1}A_{i_1}$ in this group, in terms of the additive gene model for random groups, is

$${}_{i_1i_1}d_{i_2i_2}, \ldots, {}_{i_ni_n} = (2)({}_d\alpha_{i_1}) + (2)\sum_{t=2}^{n}({}_a\alpha_{i_t}).$$

Individual selection:

The selection value of $A_{i_1}A_{i_1}$ averaged over all groups is defined to be

$$w_{i_1i_1} = 1 + (\bar{\imath}/\sigma)_I[2({}_d\alpha_{i_1})].$$

Since the genotype, $A_{i_1}A_{i_1}$, produces only A_{i_1} gametes, the total selected gametic array is

$$\Sigma p_{i_1}(w_{i_1i_1})(A_{i_1}) = \Sigma p^1_{i_1}(A_{i_1}),$$

where,

$$p^1_{i_1} = (p_{i_1})\{1 + (\bar{\imath}/\sigma)_I[2({}_d\alpha_{i_1})]\}.$$

Hence, the change in gene frequency is

$${}_{II}\Delta p_i = (\bar{\imath}/\sigma)_I(p_{i_1})[2({}_d\alpha_{i_1})],$$

and the change in the population mean of *random* groups (generated by the random-mating base population) of size n is then

$$= \Sigma p^1_{i_1}p^1_{j_1}p^1_{i_2}p^1_{j_2}\ldots p^1_{i_n}p^1_{j_n}({}_{i_1j_1}d_{i_2j_2}, \ldots, {}_{i_nj_n})$$
$$\simeq (2)(\bar{\imath}/\sigma)_I\{{}_{dd}\sigma^2_A + (n-1)\,{}_{da}\sigma_A\}.$$

Group selection:

Group selection procedure, which either accepts or rejects an entire group as the unit of selection, results in the following selection value to be associated with $A_{i_1}A_{i_1}$,

$$w_{i_1i_1} = 1 + (\bar{\imath}/\sigma)_G(2/n)\{{}_d\alpha_{i_1} + (n-1)\,{}_a\alpha_{i_1}\}.$$

This form of selection produces the following change in gene frequency.

$${}_{IG}\Delta p_{i_1} = (2/n)(\bar{\imath}/\sigma)_G(p_{i_1})\{{}_d\alpha_{i_1} + (n-1)\,{}_a\alpha_{i_1}\}.$$

In this case the change in the population mean of *random* groups of size n becomes

$$\Delta\mu \simeq (2/n)(\bar{\imath}/\sigma)_G\{_{dd}\sigma_A^2 + 2(n-1)_{da}\sigma_A + (n-1)^2{}_{aa}\sigma_A^2\}.$$

Use of clonal propagation to form clonal groups

Clonal groups of size n are obtained from the random-mating base population in such a manner that members of the same group are propagules of the same genotype. A typical group can be represented by the n-tuple.

$$(A_iA_j, A_iA_j, \ldots, A_iA_j).$$

Assuming the additive random group model, the genotypic value of any member of such a group can be represented as

$${}_{ij}d_{ij}, \ldots, {}_{ij} = ({}_d\alpha_i + {}_d\alpha_j) + (n-1)({}_a\alpha_i + {}_a\alpha_j).$$

Individual selection:

With individual selection operating within clonal groups, the selection value of A_iA_j is

$$w_{ij} = 1 + (\bar{\imath}/\sigma)_I\{({}_d\alpha_i + {}_d\alpha_j) + (n-1)({}_a\alpha_i + {}_a\alpha_j)\},$$

which results in the gene frequency change,

$${}_{GI}\Delta p_i = (\bar{\imath}/\sigma)_I(p_i)\{{}_d\alpha_i + (n-1)_a\alpha_i)\},$$

which, in turn, produces the following change in the population mean of *random* groups of size n,

$$\Delta\mu \simeq (\bar{\imath}/\sigma)_I\{_{dd}\sigma_A^2 + 2(n-1)_{da}\sigma_A + (n-1)^2{}_{aa}\sigma_A^2\}.$$

Group selection:

Since all members of the group have the same genotype, the results of group selection are identical to those for individual selection except that $\bar{\imath}$ and σ now relate to distributions of group means.

Use of clonal propagation of isogenic material to form inbred-clonal groups

With this form of group structure, both kinds of non-randomness are brought together. Thus groups of size n are formed from the base inbred population in such a way that all members of a group are propagules of the same isogenic genotype. A typical group has the following n-tuple representation,

$$(A_iA_i, A_iA_i, \ldots, A_iA_i).$$

The genotypic value of any member of the groups is associated with the model,

$${}_{ii}d_{ii}, \ldots, {}_{ii} = 2\{{}_d\alpha_i + (n-1)({}_a\alpha_i)\}.$$

Individual selection:

When individual selection operates within inbred-clonal groups, the selection value of A_iA_i is

$$w_{ii} = 1 + (\bar{\imath}/\sigma)_I\{2[{}_d\alpha_i + (n-1)_a\alpha_i]\}.$$

The change in gene frequency becomes

$$_{IGI}\Delta p_i = (\bar{\imath}/\sigma)_I(p_i)\{2[_d\alpha_i+(n-1)_a\alpha_i]\},$$

and the change in the population mean of random groups of size n is

$$\Delta\mu \simeq (2)(\bar{\imath}/\sigma)_I\{_{dd}\sigma_A^2+2(n-1)_{da}\sigma_A+(n-1)^2{}_{aa}\sigma_A\}.$$

Group selection:

Since members of the group are genetically identical, the results of group selection are similar to those for individual selection except that $\bar{\imath}$ and σ relate to group mean distributions.

RELATIVE EFFICIENCES OF GROUP SELECTION WHEN OPERATING ON NON-RANDOM *versus* RANDOM GROUPS

In this section the efficiency of group selection operating on non-random groups is determined relative to group selection operating on random groups. This requires forming the ratios of gene frequency changes in which the change due to random group selection is the denominator.

Table 1 presents the necessary gene frequency changes. The results for random and full-sib groups are obtained from the companion paper (GRIFFING 1976). Assuming that the selection differential is the same for all forms of selection, the changes in gene frequency differ in only two respects: (i) coefficients for the quantity $[_d\alpha_i + (n-1)_a\alpha_i]$, and (ii) composition of the standard deviations of means.

It is apparent from the efficiency ratios provided in Table 2 that selection among non-random groups is more efficient than selection among random groups.

TABLE 1

Gene frequency changes from random and non-random group selection

	Standard deviation of mean
Random group:	
$_{RG}\Delta p_i = (\bar{\imath}/\sigma)_G(p_i)(1/n)[_d\alpha_i+(n-1)_a\alpha_i]$	$\sigma_{RG} = \{(1/n)A+(1/n)B\}^{1/2}$
Inbred group:	
$_{IG}\Delta p_i = (\bar{\imath}/\sigma)_G(p_i)(2/n)[_d\alpha_i+(n-1)_a\alpha_i]$	$\sigma_{IG} = \{(2/n)A+(1/n)B\}^{1/2}$
Full-sib group:	
$_{FSG}\Delta p_i = (\bar{\imath}/\sigma)_G(p_i)\left(\frac{n+1}{2n}\right)[_d\alpha_i+(n-1)_a\alpha_i]$	$\sigma_{FSG} = \{\left(\frac{n+1}{2n}\right)A+(1/n)B\}^{1/2}$
Clonal group:	
$_{CG}\Delta p_i = (\bar{\imath}/\sigma)_G(p_i)[_d\alpha_i+(n-1)_a\alpha_i]$	$\sigma_{CG} = \{A+(1/n)B\}^{1/2}$
Inbred-clonal group:	
$_{ICG}\Delta p_i = (\bar{\imath}/\sigma)_G(p_i)(2)[_d\alpha_i+(n-1)_a\alpha_i]$	$\sigma_{ICG} = \{(2)A+(1/n)B\}^{1/2}$
Where: $A = [_{dd}\sigma_A{}^2+2(n-1)_{da}\sigma_A+(n-1)^2{}_{aa}\sigma_A{}^2]$ (summed over all loci)	$B = [\sigma_E{}^2+(n-1)_E\sigma_E]$

TABLE 2

Efficiencies of non-random relative to random group selection

	If $A \neq 0, B \cong 0$	If $A=B$	If $B>>A$
Random group	$\frac{{}_{RG}\Delta p_i}{{}_{RG}\Delta p_i} = 1$	1	1
Inbred group	$\frac{{}_{IG}\Delta p_i}{{}_{RG}\Delta p_i} = \sqrt{2}$	$(2/3)\sqrt{6}$	2
Full-sib group	$\frac{{}_{FSG}\Delta p_i}{{}_{RG}\Delta p_i} = (1/2)\sqrt{2(n+1)}$	$\left(\frac{n+1}{n+3}\right)\sqrt{n+3}$	$\frac{n+1}{2}$
Clonal group	$\frac{{}_{CG}\Delta p_i}{{}_{RG}\Delta p_i} = \sqrt{n}$	$n\sqrt{\frac{2}{n+1}}$	n
Inbred-clonal group	$\frac{{}_{ICG}\Delta p_i}{{}_{RG}\Delta p_i} = \sqrt{2n}$	$2n\sqrt{\frac{2}{2n+1}}$	$2n$
Where: $A = [{}_{dd}\sigma_A{}^2 + 2(n-1){}_{da}\sigma_A + (n-1)^2{}_{aa}\sigma_A{}^2]$ (summed over all loci)		$B = [\sigma_E{}^2 + (n-1){}_E\sigma_E]$	

Moreover, three of the four relative efficiencies are functions of n. Also, if

$A = [{}_{dd}\sigma_A^2 + 2(n-1){}_{da}\sigma_A + (n-1)^2{}_{aa}\sigma_A^2]$, where the components are summed over all loci,

$B = [\sigma_E^2 + (n-1){}_E\sigma_E]$,

and if the concept of heritability is generalized so that,

(i) $A \neq 0$ and $B \cong 0$ implies high heritability,
(ii) $A = B$ implies moderate heritability, and
(iii) $B >> A$ implies low heritability,

then one can argue that the advantage in the use of non-random groups is greatest with low heritability.

Tables 3 and 4 demonstrate which form of non-randomness is relatively the most important for the cases of high and low heritabilities, respectively. It is clear that "homogeneity" is increasingly the most important form of non-randomness as the group size, n, increases.

In these considerations, no attempt has been made to evaluate the effect due to the extension of time required to form non-random groups in order to complete a selection cycle. Such evaluation depends on the techniques involved and the species used. Extension of cycle time would, of course, reduce the relative advantage of the use of non-random groups.

NUMERICAL EXAMPLE

In the previous study of this series and in the present one, use of certain kinds of non-random groups to improve balance and selection efficiency has been explored. The algebraic results are necessarily given in terms of parameter

TABLE 3

Relative importance of the two forms of non-randomness for the case of high heritability

		Degree of homogeneity	
		Random association	Homogeneous (clonal)
Degree of homozygosity	Non-inbred ($F=0$)	$\frac{{}_{RG}\Delta p_i}{{}_{RG}\Delta p_i} = 1$	$\frac{{}_{CG}\Delta p_i}{{}_{RG}\Delta p_i} \simeq \sqrt{n}$
	Inbred ($F=1$)	$\frac{{}_{IG}\Delta p_i}{{}_{RG}\Delta p_i} \simeq \sqrt{2}$	$\frac{{}_{ICG}\Delta p_i}{{}_{RG}\Delta p_i} \simeq \sqrt{2n}$

changes for one cycle of selection. It is useful to supplement these analyses with computer simulation studies that provide a comparison of selection methods over a history of several cycles of selection. To do this, the following completely additive genetic example involving groups of size 9 is used. The initial base population is generated by two equally frequent alleles with direct additive effects, ${}_d\alpha_1 = -1$ and ${}_d\alpha_2 = 1$, and associate additive effects, ${}_a\alpha_1 = 2$ and ${}_a\alpha_2 = -2$. A standardized selection differential, $\bar{i} = 2.0$, and a heritability value (on an individual basis) equal to 0.2 are used. When selection is based on groups, the heritability parameters of interest are $B \simeq (0.6)\ A$.

The plots of the population means over 25 cycles of individual selection are given in Figure 1 for R = random, F = full-sib, I = inbred, C = clonal, and IC = inbred-clonal group structures. Since the numerical example was designed to illustrate the incongruous situation of negative response to positive individual selection, it does so for the random groups and for the inbred groups. These are groups formed at random with either the random-mating or the inbred genotypic arrays as the base population. It is clear that with continued selection, fixation of the least desirable genotype will result. In the case of the particular numerical example presently considered, these undesirable change in population structure can be corrected by either (i) transferring the individual selection procedure to operate on non-random (full-sib, clonal or inbred-clonal) groups, or (ii) transferring the basis of selection from the individual to the group (see Figure 2).

When selection response curves are considered, the concept of efficiency can be measured in terms of the number of selection cycles required to shift the popu-

TABLE 4

Relative importance of the two forms of non-randomness for the case of low heritability

		Degree of homogeneity	
		Random association	Homogeneous (clonal)
Degree of homozygosity	Non-inbred ($F=0$)	$\frac{{}_{RG}\Delta p_i}{{}_{RG}\Delta p_i} = 1$	$\frac{{}_{CG}\Delta p_i}{{}_{RG}\Delta p_i} \simeq n$
	Inbred ($F=1$)	$\frac{{}_{IG}\Delta p_i}{{}_{RG}\Delta p_i} \simeq 2$	$\frac{{}_{ICG}\Delta p_i}{{}_{RG}\Delta p_i} \simeq 2n$

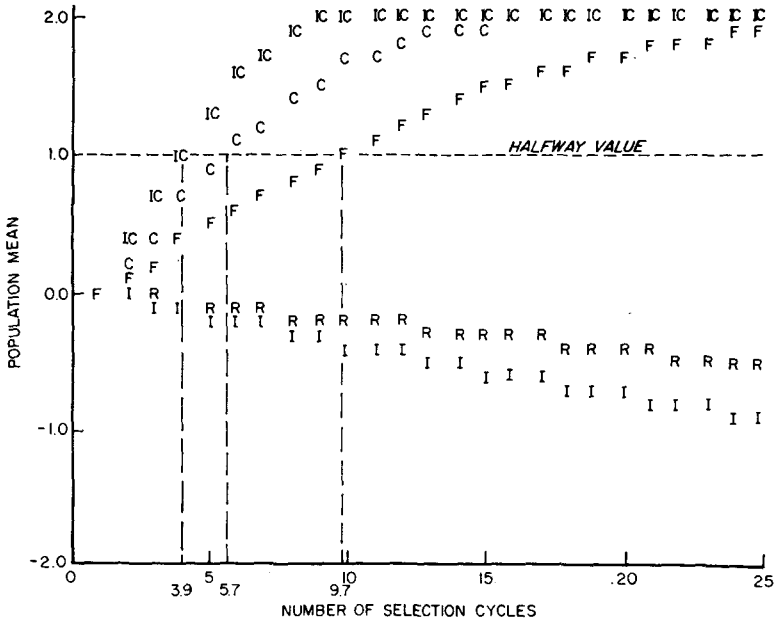

FIGURE 1.—Plot of computer run for 25 cycles of individual selection for R = random, F = full-sib, I = inbred, C = clonal, and IC = inbred-clonal group structures.

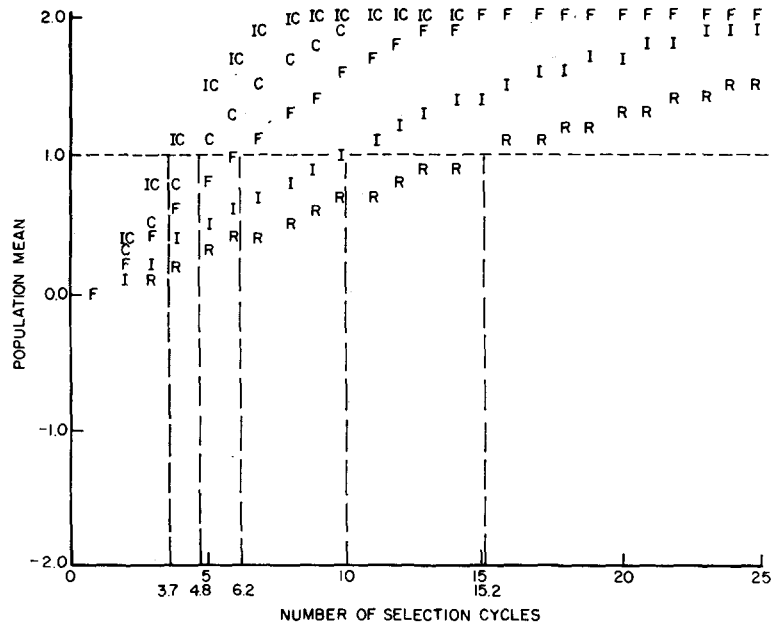

FIGURE 2.—Plot of computer run for 25 cycles of group selection for R = random, F = full-sib, I = inbred, C = clonal, and IC = inbred-clonal group structures.

lation mean halfway from its initial value to its limit. With this as a criterion, it is clear that use of non-random groups can greatly increase the efficiency of selection relative to that with random groups. For example, group selection with inbred-clonal groups achieves the halfway value in 3.7 generations, whereas it takes 15.2 generations to achieve the same value with random groups.

DISCUSSION

When selection operates within the framework of a biological model permitting interactions between individuals within groups, there are two kinds of problems that need consideration. The first is a qualitative one concerning the nature of the response to selection. Clearly a positive, or at least a non-negative, response to positive selection is desired. If competitive interactions exist, use of individual selection cannot guarantee such a desired response. However, there are other forms of selection which are "balanced" and do have this property.

The second problem has to do with the search for methods and strategies that will increase the efficiency of selection. It was shown (GRIFFING 1969) that the selection index yielded maximum genetic gain for the situation of random group structure. In the previous study (GRIFFING 1976) and the present one, the strategy of generating non-random groups in which selection operates has been employed. The results show that use of non-random groups can increase the effectiveness of selection. In particular, with those species in which clonal propagation is possible, enormous advantage may occur from the use of clonal groups. If the selection index approach is combined with the use of non-random groups, it is clear that extremely efficient selection methods, especially designed to accommodate genotypic interaction of any sort including the troublesome phenomenon of competition, can be obtained.

Finally, it should be noted that when non-additivities of various sorts are introduced into the model, the results are far more complicated. One complication is that the final population structure may differ in terms of fixation or equilibria of various kinds depending on which type of group selection operates. Further studies are required in this area.

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