Theor Appl Genet (1986) 72:256–263

Individual and group selection with competition

A. J. Wright *

Department of Statistics, North Carolina State University, Raleigh, NC 27695-8203, USA

Received October 10, 1985; Accepted November 28, 1985
Communicated by P. M. A. Tigerstedt

Summary. The response of a randomly mating population which is expected to follow selection of phenotypic units, comprising individuals or groups whose members have an arbitrary degree of relatedness, was formulated using a model which included additive and dominance competition effects. The derivation involved three steps. Twenty-two quadratic components were defined, six describing individual (direct) and neighbor (associate) effects, and 16 describing direct by associate interactions for different loci, for single loci with different alleles, and for identical alleles. Six covariances between pairs of individual phenotypes and three of individuals with their offspring were defined according to whether or not their direct or associate genotypes are common, and expressed in terms of the quadratic components. Finally, variances of selection units of different types and their covariance with their offspring were expressed as compounds of these individual covariances. Explicit formulations for mass, clonal and full-sib selection show that without constraints on the quadratic components, and hence on the magnitude and type of competition operative, no predictions as to the relative efficiencies of these three methods can be made.

Key words: Inter-plant competition – Covariances of relatives – Mass selection – Full-sib selection – Clonal selection

Introduction

Inter-plant competition can have a major influence on the efficiency of selection procedures when the units under selection, which may be genotypes, families, varieties or other groups, have to be assessed under different competitive influences from those which prevail in the conditions for which the selected material is required. An individual selection unit may experience competition arising both among member plants of the unit and from neighboring plants belonging to different units. These two problems are distinct, and the second has been approached largely through the development of suitable experimental designs and analyses.

The problem of competition within selection units was examined in a series of papers by Griffing (1967, 1968a, 1969, 1976a, b, 1977). He used an additive model which included direct and associate genotype effects to examine the selection of individuals, of randomly constructed groups, and ordered groups such as families and clones when response is evaluated in terms of the performance of their random-bred offspring. Gallais (1976) also applied an additive genetic model to the problem of estimation of general combining ability but included direct by associate interactions between like and between unlike alleles. In this paper, a similar model which includes dominance interactions will be used.

Griffing initially developed his analysis in terms of a single gene model (1967, 1968a) but later (1968b) generalized it in terms of the covariances of relatives to accommodate an arbitrary number of genes. Although the analysis can be modified to deal with other mating systems, the present investigation, like Griffing's will deal specifically with the case of a large randomly outcrossing population and the necessary covariances among relatives will be derived using the very direct and general method of the probability of identity by descent of alleles (Malecot 1949).

The expectation of selection response

The expected permanent response to selection using a particular selection unit x can be expressed as

$$R_{xy} = i\, 2\, C_{xy}/(V_x + \sigma^2_{e(x)})^{1/2},$$

* Present address: c/o Plant Breeding Institute, Trumpington, Cambridge CB2 2LQ, UK

where $\sigma^2_{e(x)}$ is an error variance whose exact form depends on the type of selection, C_{xy} is the covariance of the selected units with their offspring in the system of culture under which response is measured, V_x is their genotypic variance, and i is the standardized selection differential. The response required in the present case is the difference in mean value between the offspring produced by random mating from the parental population before and after selection, when each offspring population is grown as a single mixed stand. The chief problem in the formulation of response is thus the derivation of C_{xy} and V_x in terms of a model of inter-plant competition.

Models and definitions

The complete description of the phenotype of one individual growing in competition with a second requires a much larger number of parameters than does that of an isolated individual. For a two-locus system, dominance and epistatic as well as additive terms have to be defined for the genotype of the individual itself (direct effects) and for that of its competitor (associate effects) and for direct by associate interactions. Competition takes place at the level of whole phenotypes rather than individual alleles, and the direct by associate effects include interactions of alleles at different loci as well as at the same locus. This complete specification is very unwieldy and some simplification is necessary before any comprehensible formulation can be achieved, and for this purpose, epistasis will be ignored.

The value of a member of a large population in random outcrossing equilibrium carrying alleles notated r and s at each locus when grown in competition with one other unrelated individual carrying alleles r′ and s′ can then be written as

$$\begin{aligned} X_{rs\cdot r's'} = \mu &+ \sum_l [d_{lAr} + d_{lAs} + d_{lDrs} + a_{lAr'} + a_{lAs'} + a_{lDr's'}] \\ &+ \sum_l \sum_k [da_{lAr\cdot kAr'} + da_{lAr\cdot kAs'} + da_{lAs\cdot kAr'} + da_{lAs\cdot kAs'} \\ &+ da_{lAr\cdot kDr's'} + da_{lAs\cdot kDr's'} + da_{lDrs\cdot kAr'} \\ &+ da_{lDrs\cdot kAs'} + da_{lDrs\cdot kDr's'}]. \end{aligned}$$

The mean μ is the average of all individuals when grown in a single mixed population, and all other terms are defined with respect to this population. Direct and associate effects are denoted by d and a, respectively, while their subscripts refer respectively to the locus, the type of effect (whether additive (A) or dominance (D)), and the allele(s) carrying the effect. Interaction effects are defined in a similar fashion, so that, for example, the term $da_{lAr\cdot kDr's'}$ is the interaction of the direct additive effect of allele r at locus l with an associate dominance interaction of alleles r′ and s′ at locus k (where l may or may not equal k). Summation is over all loci for direct and associate effects and, for direct by associate interactions, over all possible pairs of loci, including each locus with itself.

The effects are constrained in the usual way such that

$$\begin{aligned} \sum p_r d_{lAr} = \sum p_{r'} a_{lAr'} &= \sum p_r p_s d_{lDrs} = \sum p_{r'} p_{s'} a_{lDr's'} \\ &= \sum p_r p_{r'} da_{lAr\cdot kAr'} = \sum p_r p_{r'} p_{s'} da_{lAr\cdot kDr's'} \\ &= \sum p_r p_s p_{r'} da_{lDrs\cdot kAr'} = \sum p_r p_s p_{r'} p_{s'} da_{lDrs\cdot kDr's'} = 0 \end{aligned}$$

for summation of subscripts r, r′, s or s′ where p_r is the population frequency of the r^{th} allele. However, it is necessary to note that the sums of subsets of interactions which involve identical alleles (homoallelic interactions) are not necessarily zero. These are interactions caused when alleles or pairs of alleles at a locus are carried by both direct and associate genotpyes, and because they can occur with different frequencies in different types of groups, they can lead to difference in the mean phentoypes of these groups (Gallais 1976). For future use, the following sum is defined

$$\begin{aligned} \mu^*_l = &E(da_{lAr\cdot lAr}) + E(da_{lAr\cdot lDrs}) + E(da_{lDrs\cdot lAr}) \\ &+ E(da_{lDrs\cdot lDrs'}). \end{aligned}$$

Quadratic functions of the effects are defined as

$$2E(d^2_{lAr}) = \sigma^2_{d_{Al}}, \quad 2E(a^2_{lAr'}) = \sigma^2_{a_{Al}}, \quad 2E(d_{lAr}\, a_{lAr}) = \sigma_{d_{Al}\cdot a_{Al}},$$
$$E(d^2_{lDrs}) = \sigma^2_{d_{Dl}}, \quad E(a^2_{lDr's'}) = \sigma^2_{a_{Dl}}, \quad E(d_{lDrs}\, a_{lsDrs}) = \sigma_{d_{Dl}\cdot a_{Dl}},$$
$$4E(da^2_{lAr\cdot kAr'}) = \sigma^2_{da_{AlAk}}, \quad 2E(da^2_{lAr\cdot kDr's'}) = \sigma^2_{da_{AlDk}},$$
$$2E(da^2_{lDrs\cdot kAr'}) = \sigma^2_{da_{DlAk}}, \quad E(da^2_{lDrs\cdot kDr's'}) = \sigma^2_{da_{DlDk}}.$$

The total variance or covariance of direct and associate terms is obtained by summation over loci, for example,

$$\sum_l (\sigma^2_{dAl}) = \sigma^2_{dA}.$$

In the case of direct by associate interactions, summation is used to separate variances due to interactions of effects of the same or different loci. A dash suffix is applied to the former and the now unnecessary da suffixes dropped:

$$\sum_l \sum_{k(?)l} (\sigma^2_{da_{AlAk}}) = \sigma^2_{AA} \quad \text{and} \quad \sum_l (\sigma^2_{da_{AlAl}}) = \sigma^2_{AA'}.$$

Further definitions are necessary to allow different variances for interactions of additive or dominance effects at a single locus when common alleles are involved (homoallelic interactions):

$$4\sum_l E\{[da_{lAr\cdot lAr} - E(da_{lAr\cdot lAr})]^2\} = \sigma^2_{AA^*},$$
$$2\sum_l E\{[da_{lAr\cdot lDrs} - E(da_{lAr\cdot lDrs})]^2\} = \sigma^2_{AD^*},$$
$$2\sum_l E\{[da_{lDrs\cdot lAr} - E(da_{lDrs\cdot lAr})]^2\} = \sigma^2_{DA^*},$$
$$\sum_l E\{[da_{lDrs\cdot lDrs'} - E(da_{lDrs\cdot lDrs'})]^2\} = \sigma^2_{DD^*},$$
$$\sum_l E\{[da_{lDrs\cdot lDrs} - E(da_{lDrs\cdot lDrs})]^2\} = \sigma^2_{DD^{**}},$$

and the products:

$$2\sum_l E\{d_{lAr}[da_{lAr\cdot lAr} - E(da_{lAr\cdot lAr})]\} = \sigma_{dA\cdot AA^*},$$
$$2\sum_l E\{a_{lAr}[da_{lAr\cdot lAr} - E(da_{lAr\cdot lAr})]\} = \sigma_{aA\cdot AA^*}.$$

It will be seen later that the final pair of covariances is of importance in the formulation of selection responses, but for simplicity, similar covariances among dominance effects will be neglected, as will any possible covariances between homoallelic and heteroallelic interactions.

Covariances of neighbors

In the absence of pairwise or higher-order interactions among plants with respect to the competitive effects they jointly exert on others, variances of individuals or groups will consist of combinations of expressions involving an individual with each of its neighbors. As a basic unit for these derivations, the between two members of a group, each of which have only one neighbor (Table 1). The coefficients are obtained by considering the probabilities of identity by descent (*ibd*) of individual alleles or pairs chosen from the eight which constitute the phenotypes of the two individuals through their own direct genotypes and the associate genotypes of their neighbors. These alleles can be regarded as those carried at one locus or two different loci, according to the type of effect being considered. The probability of *ibd* of single alleles chosen from random members of a group, their coancestry, is defined as θ, and that of a pair of alleles at a locus as δ. Without inbreeding, as assumed here, there can be no identity between the pair of alleles at a locus within a genotype.

Six different covariances can be envisaged, depending on whether or not the two individuals have a common genotype for the direct or associate components of the phenotype. For the covariance between the phenotypes of the same individual when grown with different neighbors, the direct effect is common (C_d), while for two individuals with a common neighbor, the associate effect is common (C_a). In the case of the covariance of a phenotype with itself, then both effects are common (C_{da}). For example, it will be seen later that only covariances of types C_d and C_{da} can contribute to the variance of individuals since in that case, the direct effect must always be common. Alternatively, the direct genotype of one individual may be common with the associate genotype of the other ($C_{d'}$), or both

Table 1. Allelic identities and quadratic components contributing to the covariance of two group members, $X_{rs \cdot r's'}$ and $X_{pq \cdot p'q'}$ [a]

Quadratic component	Covariance with allelic identities					
	rs = pq, r's' = p'q'	rs = p'q', r's' = pq	rs = pq	r's' = p'q'	rs = p'q' or r's' = pq	Nil
	(C_{da})	($C_{d'a'}$)	(C_d)	(C_a)	($C_{d'}$)	(C)
σ^2_{dA}	1	2θ	1	2θ	2θ	2θ
σ^2_{dD}	1	δ	1	δ	δ	δ
σ^2_{aA}	1	2θ	2θ	1	2θ	2θ
σ^2_{aD}	1	δ	δ	1	δ	δ
$\sigma^2_{dA \cdot aA}$	4θ	2	4θ	4θ	$1+2\theta$	4θ
$\sigma^2_{dD \cdot aD}$	2δ	2	2δ	2δ	$1+\delta$	2δ
σ^2_{AA}	1	$4\theta^2$	2θ	2θ	$4\theta^2$	$4\theta^2$
$\sigma^2_{AA'}$	α	$4\theta^2\alpha$	$2\theta\alpha$	$2\theta\alpha$	$4\theta^2\alpha$	$4\theta^2\alpha$
$\sigma^2_{AA^*}$	θ	$4\theta^3$	$2\theta^2$	$2\theta^2$	$4\theta^3$	$4\theta^3$
σ^2_{AD}	1	$2\theta\delta$	δ	2θ	$2\theta\delta$	$2\theta\delta$
$\sigma^2_{AD'}$	β	$2\theta\delta\beta$	$\delta\beta$	$2\theta\beta$	$2\theta\delta\beta$	$2\theta\delta\beta$
$\sigma^2_{AD^*}$	2θ	$4\theta^2\delta$	$2\theta\delta$	$4\theta^2$	$4\theta^2\delta$	$4\theta^2\delta$
σ^2_{DA}	1	$2\theta\delta$	2θ	δ	$2\theta\delta$	$2\theta\delta$
$\sigma^2_{DA'}$	β	$2\theta\delta\beta$	$2\theta\beta$	$\delta\beta$	$2\theta\delta\beta$	$2\theta\delta\beta$
$\sigma^2_{DA^*}$	2θ	$4\theta^2\delta$	$4\theta^2$	$2\theta\delta$	$4\theta^2\delta$	$4\theta^2\delta$
σ^2_{DD}	1	δ^2	δ	δ	δ^2	δ^2
$\sigma^2_{DD'}$	Γ	$\delta^2\Gamma$	$\delta\Gamma$	$\delta\Gamma$	$\delta^2\Gamma$	δ^2
$\sigma^2_{DD^*}$	π	$\delta^2\pi$	$\delta\pi$	$\delta\pi$	$\delta^2\pi$	$\delta^2\pi$
$\sigma^2_{DD^{**}}$	δ	δ^3	δ^2	δ^2	δ^3	δ^3
$\sigma^2_{dA \cdot AA^*}$	4θ	4θ	4θ	$8\theta^2$	$2\theta(1+2\theta)$	$8\theta^2$
$\sigma^2_{aA \cdot AA^*}$	4θ	4θ	$8\theta^2$	4θ	$2\theta(1+2\theta)$	$8\theta^2$

[a] Note: (1) multiple identity requirements are written in a single expression: for example, rs = pq indicates r = p and s = q or r = q and s = p; (2) in the case of σ^2_{AA}, σ^2_{AD}, σ^2_{DA}, and σ^2_{DD}, allele pairs rs and pq, and r's' and p'q' are assumed to come from different loci, whereas for all other interaction components, all eight alleles are at the same locus; (3) $\alpha = (1-\theta)$, $\beta = (1-2\theta)$, $\Gamma = (1-4\theta+\delta)$, $\pi = 2(2\theta-\delta)$

these reciprocal genotypic identities may coexist ($C_{d'a'}$). (The intuitively apparent reciprocal identity $C_{a'}$ need not be considered, as this is identical to $C_{d'}$). The final covariance, C, is that for two members of the group for which no genotypes are common. The identity of alleles for direct or associate genotypes which are not common depends on their probability of identity by descent and hence on the type of group considered.

The coefficients for the interaction variance of each type requires some explanation. The model given above is for an individual and a neighbor to which it is unrelated. With a related neighbor, the additive by additive effects would have a probability θ of being homoallelic, the remaining $(1-\theta)$ being heteroallelic. The similar probabilities for additive by dominance and dominance by additive effects are 2θ and $(1-2\theta)$, and those for dominance by dominance are δ, $2(2\theta-\delta)$, and $(1-4\theta+\delta)$, being the probabilities that an individual and its neighbor have exactly 2, 1 or no identical alleles at a locus.

Genotypic variances

Before considering the derivation of formulations of particular variances, it is important to distinguish clearly between the neighborhood size, m, which is the number of plants which are sufficiently close to exert a competitive influence on the phenotype of any particular individual, and the total group size, n. The value of m has to be assumed constant for all n group members, and so ignores any edge effects which are likely with field plots. It also assumes that there is a finite neighborhood whose members all have an equal opportunity to influence the yield of the central plant, whereas in practice, their influence will be dependent on distance. The parameter m must therefore be taken to represent some effective neighborhood size.

The value of an individual is the average of the various phenotypes produced when competing with each of the m neighbors which are random members of the group, and its variance is the mean of the m^2 terms arising from the square of this compound. Of these, m are the variances of phenotypic values and so have expectations equal to C_{da}, while each of the remaining $m\,m_1$ (where $m_i = m - i$) is the covariance of the phenotypes of one individual with two different neighbors, equal to C_d. The variance, excluding error terms, is therefore

$$V_{(1,n,m)} = [C_{da} + m_1 C_d]/m\,,$$

denoting the variance of individuals grown in groups of size n with a neighborhood of m, and replacing the notation V_x used in the response equation above. It is evident that this variance is dependent on m but not on n.

Using similar reasoning to that above, the composition of the variance of groups of size n is the mean of $(n\,m)^2$ terms which (provided that $n > 0$, $m > 0$) can be written as

$$V_{(n,n,m)} = [C_{da} + C_{d'a'} + m_1 (C_d + C_a + 2C_{d'}) + (n_4 m + 2)\,C]/n\,m\,.$$

This observed variance includes a contribution from the variance among genotypes within the group, so that

$$V_{(n,n,m)} = V_{b(n,m)} + V_{w(n,m)}/n\,,$$

where $V_{b(n,m)}$ is the true group variance.

The variance of individuals measured around the mean of their group can be obtained from the above two variances since

$$V_{w(n,m)} = n(V_{(1,n,m)} - V_{(n,n,m)})/n_1 = [n_1 C_{da} + n_1 m_1 C_d - C_{d'a'} - m_1 (C_a + 2C_{d'}) - (n_4 m + 2)\,C]/n_1 m\,.$$

This within-group variance is due to the usual genotypic variance among the members of any group other than a clone. However, there is an additional contribution due to the unequal distribution of homoallelic interactions to different phenotypes. When an individual has one allele in common with its neighbor, the contribution of homoallelic interactions to its phenotype is μ_l^*, and if it is assumed that

$$E(da_{lDrs} \cdot a_{lDrs}) = 2\,E(da_{lDrs} \cdot a_{lDrs'})\,,$$

then the contribution with both alleles common is $2\mu_l^*$. Since the probability of identity for both alleles is δ, for just one is $2(2\theta-\delta)$ and for none is $(1-4\theta+\delta)$, then the variance arising from one locus is $[4\theta(1-4\theta) + 2\delta]\,\mu_l^{*2}$. Hence, this term is zero for random groups as well as for clones. It can be summed over independent loci, but its contribution to the variance of

Table 2. Coefficients of direct and associate variances and covariances in individual and between and within group variances

	Individuals	Groups	Within groups
σ^2_{dA}	1	$\frac{(1+2n_1\theta)}{n}$	$(1-2\theta)$
σ^2_{dD}	1	$\frac{(1+n_1\delta)}{n}$	$(1-\delta)$
σ^2_{aA}	$\frac{(1+2m_1\theta)}{m}$	$\frac{(1+2n_1\theta)}{n}$	$\frac{(n-m)(1-2\theta)}{n_1 m}$
σ^2_{aD}	$\frac{(1+m_1\delta)}{m}$	$\frac{(1+n_1\delta)}{n}$	$\frac{(n-m)(1-\delta)}{n_1 m}$
$\sigma^2_{dA\cdot aA}$	4θ	$\frac{2(1+2n_1\theta)}{n}$	$\frac{2(2\theta-1)}{n_1}$
$\sigma_{dD\cdot aD}$	2δ	$\frac{2(1+n_1\delta)}{n}$	$\frac{2(\delta-1)}{n_1}$

Table 3. Coefficients of direct by associate interaction variances and covariances in individual and between and within group variances [a]

	Individuals	Groups	Within groups
σ^2_{AA}	$(1+2m_1\theta)$	$[1+4m_1\theta+4(n_2m+1)\theta^2]$	$(1-2\theta)[n_1+2(n_2m+1)\theta]$
$\sigma^2_{AA'}$	$\alpha(1+2m_1\theta)$	$\alpha[1+4m_1\theta+4(n_2m+1)\theta^2]$	$\alpha(1-2\theta)[n_1+2(n_2m+1)\theta]$
$\sigma^2_{AA^*}$	$\theta(1+2m_1\theta)$	$\theta[1+4m_1\theta+4(n_2m+1)\theta^2]$	$\theta(1-2\theta)[n_1+2(n_2m+1)\theta]$
σ^2_{AD}	$(1+m_1\delta)$	$[1+m_1(\delta+2\theta)+2(n_2m+1)\theta\delta]$	$[n_1+n_1m_1\delta-2m_1\theta-2(n_2m+1)\theta\delta]$
$\sigma^2_{AD'}$	$\beta(1+m_1\delta)$	$\beta[1+m_1(\delta+2\theta)+2(n_2m+1)\theta\delta]$	$\beta[n_1+n_1m_1\delta-2m_1\theta-2(n_2m+1)\theta\delta]$
$\sigma^2_{AD^*}$	$2\theta(1+m_1\delta)$	$2\theta[1+m_1(\delta+2\theta)+2(n_2m+1)\theta\delta]$	$2\theta[n_1+n_1m_1\delta-2m_1\theta-2(n_2m+1)\theta\delta]$
σ^2_{DA}	$(1+2m_1\theta)$	$[1+m_1(\delta+2\theta)+2(n_2m+1)\theta\delta]$	$[n_1+2n_1m_1\theta-m_1\delta-2(n_2m+1)\theta\delta]$
$\sigma^2_{DA'}$	$\beta(1+2m_1\theta)$	$\beta[1+m_1(\delta+2\theta)+2(n_2m+1)\theta\delta]$	$\beta[n_1+2n_1m_1\theta-m_1\delta-2(n_2m+1)\theta\delta]$
$\sigma^2_{DA^*}$	$2\theta(1+2m_1\theta)$	$2\theta[1+m_1(\delta+2\theta)+2(n_2m+1)\theta\delta]$	$2\theta[n_1+2n_1m_1\theta-m_1\delta-2(n_2m+1)\theta\delta]$
σ^2_{DD}	$(1+m_1\delta)$	$[1+2m_1\delta+(n_2m+1)\delta^2]$	$(1-\delta)[n_1+(n_2m+1)\delta]$
$\sigma^2_{DD'}$	$\Gamma(1+m_1\delta)$	$\Gamma[1+2m_1\delta+(n_2m+1)\delta^2]$	$\Gamma(1-\delta)[n_1+(n_2m+1)\delta]$
$\sigma^2_{DD^*}$	$\pi(1+m_1\delta)$	$\pi[1+2m_1\delta+(n_2m+1)\delta^2]$	$\pi(1-\delta)[n_1+(n_2m+1)\delta]$
$\sigma^2_{DD^{**}}$	$\delta(1+m_1\delta)$	$\delta[1+2m_1\delta+(n_2m+1)\delta^2]$	$\delta(1-\delta)[n_1+(n_2m+1)\delta]$
$\sigma_{dA\cdot AA^*}$	4θ	$8m\theta(1+n_2\theta)$	$4\theta[n-2m(1+n_2\theta)]$
$\sigma_{aA\cdot AA^*}$	$4\theta(1+2m_1\theta)$	$8m\theta(1+n_2\theta)$	$4\theta(1-2\theta)(n-2m)$
$\sum_l \mu_l^{*2}$	$[4\theta(1-4\theta)+2\delta]$	$[4\theta(1-4\theta)+2\delta]$	$[4\theta(1-4\theta)+2\delta]$

[a] For ease of representation, all individual, group, and within-group variances have been multiplied by m, nm and n_1m, respectively. Also, $\alpha=(1-\theta)$, $\beta=(1-2\theta)$, $\Gamma=(1-4\theta+\delta)$, $\pi=2(2\theta-\delta)$

individuals will be reduced according to the number of neighbors over which averaging takes place. It enters the observed variance of group means as a further source of sampling variance.

The complete expressions in terms of all quadratic components for individual and between- and within-group variances are given in Tables 2 and 3.

Covariances of parent and offspring

The influence of an offspring phenotype extends throughout the neighborhood in which it grows, and so response has to be measured in terms of the total value of this neighborhood. As all members of the neighborhood other than the offspring of interest are supposed to be random, unrelated genotypes, their direct and associate effects, as well as all direct by associate interactions, have no covariance with the parental phenotype and can be omitted. The expected value of any member of the neighborhood is the mean of its phenotypes when in competition in turn with each other member. After deletion of all zero terms, the value of the entire neighborhood, including the offspring carrying alleles r and s at locus l, is therefore

$$E(Y_{rs})=(m+1)\mu+\sum_l [d_{lAr}+d_{lAs}+d_{lDrs}+a_{lAr}+a_{lAs}+a_{lDrs}].$$

For the group of offspring with a common parent from which they received allele r, allele s is random and

$$E(Y_r)=(m+1)\mu+\sum_l [d_{lAr}+a_{lAr}].$$

In addition to the usual covariance of parent and offspring, it is now necessary to consider covariances of one group member with the offspring of another. Such covariances are analogous with the six different types of covariance established for the parents themselves, but now only three types need be defined. Using a dash suffix to denote covariances of parents and offspring, these are C'_d, the covariance of an offspring with its parental phenotype, C'_a, the covariance of an offspring with a neigbor of its parent, and C', the covariance of an offspring with a member of the parental group which is neither the parent nor one of its neighbors. According to the models for $X_{rs\cdot r's'}$ and Y_r, these three covariances have the following composition in terms of quadratic components:

	C'_d	C'_a	C'
σ^2_{dA}	1/2	θ	θ
σ^2_{aA}	θ	1/2	θ
$\sigma_{dA\cdot aA}$	$(1+2\theta)/2$	$(1+2\theta)/2$	2θ
$\sigma_{dA\cdot AA^*}$	θ	θ	$2\theta^2$
$\sigma_{aA\cdot AA^*}$	θ	θ	$2\theta^2$

Replacing the term C_{xy} with a similar notation to that used earlier for variances, the covariances of individual parent and offspring, of a group of parents with their offspring, and the covariance within groups, are

$$C_{(1,n,m)} = C'_d,$$

$$C_{(n,n,m)} = (C'_d + C'_a + n_2 C)/n, \quad \text{and}$$

$$C_{w(n,m)} = n\,[C_{(1,n,m)} - C_{(n,n,m)}]/n_1 = (n_1 C'_d - C'_a - n_2 C')/n_1,$$

respectively.

In terms of their quadratic components, these covariances can be expanded as

$$C_{(1,n,m)} = \tfrac{1}{2}[\sigma^2_{dA} + (1+2\theta)\,\sigma_{dA\cdot aA} + 2\theta\,\sigma^2_{aA} + 2\theta\,(\sigma_{dA\cdot AA^*} + \sigma_{aA\cdot AA^*})],$$

$$C_{(n,n,m)} = [(1+2n_1\theta)(\sigma^2_{dA} + 2\,\sigma_{dA\cdot aA} + \sigma^2_{aA}) + 4\theta(1+n_2\theta)(\sigma_{dA\cdot AA^*} + \sigma_{aA\cdot AA^*})]/2n,$$

$$C_{w(n)} = (1-2\theta)\,[n_1\sigma^2_{dA} + n_2\,\sigma_{dA\cdot aA} - \sigma^2_{aA} + 2n_2\theta(\sigma_{dA\cdot AA^*} + \sigma_{aA\cdot AA^*})]/2n_1.$$

The terms $\sigma_{dA\cdot AA^*}$ and $\sigma_{aA\cdot AA^*}$ always have identical coefficients in these covariances and can be pooled as $\sigma_{A\cdot AA^*} = \sigma_{dA\cdot AA^*} + \sigma_{aA\cdot AA^*}$. Unlike the parental variances, the parent-offspring covariances are independent of the neighborhood size.

The magnitude of response

Exact comparisons of expected selection responses for different methods are complicated as they depend on many parameters, including the direct, associate, and interaction variances and covariances, for both additive and dominance effects, the error variance both within and between plots (groups), and n, m, θ and δ. The expectations of three important methods, namely mass (M), full-sib family (F), and clonal (C) selection, are given in Table 4. These expressions allow some of the general properties of the different methods to be recognized.

As shown by Griffing (1967), a negative correlation between additive direct and associate effects reduces the gain from group selection, but can lead to negative response from individual selection. Since associate effects cannot be used by individual selection, large associate variances, like dominance and error variances, favor the use of groups. The effect of a negative dominance correlation between direct and associate effects is simply to reduce the overall dominance variance and therefore to favor individual selection. Interaction is seen to be detrimental to all types of selection, but has the smaller effect with individual selection, particularly when a large neighborhood allows adequate sampling of interactions, and this is a factor which could have a major influence on comparisons between the two types of selection.

Table 4. Coefficients of quadratic components in variances and covariances determining the expected responses to mass, clonal and full-sib selection

	Mass (M) ($\theta=0$, $\delta=0$)	Clonal (C) ($\theta=1/2$, $\delta=1$)	Full-sib (F) ($\theta=1/4$, $\delta=1/4$)
Covariance of selection units and offspring (C_{xy})			
σ^2_{dA}	1/2	1/2	(n + 1)/4 n
σ^2_{aA}	0	1/2	(n + 1)/4 n
$\sigma_{dA\cdot aA}$	1/2	1	(n + 1)/2 n
$\sigma_{A\cdot AA^*}$	0	1/2	(n + 2)/8 n
Variance of selection units (V_x)			
σ^2_{dA}	1	1	(n + 1)/2 n
σ^2_{dD}	1	1	(n + 3)/4 n
σ^2_{aA}	1/m	1	(n + 1)/2 n
σ^2_{aD}	1/m	1	(n + 3)/4 n
$\sigma_{dA\cdot aA}$	0	2	(n + 1)/n
$\sigma_{dD\cdot aD}$	0	2	(n + 3)/2 n
σ^2_{AA}	1/m	1	[(n + 2) m + 1]/4 nm
$\sigma^2_{AA'}$	1/m	1/2	3 [(n + 2) m + 1]/16 nm
$\sigma^2_{AA^*}$	0	1/2	[(n + 2) m + 1]/16 nm
σ^2_{AD}	1/m	1	[(n + 4) m + 3]/8 nm
$\sigma^2_{AD'}$	1/m	0	[(n + 4) m + 3]/16 nm
$\sigma^2_{AD^*}$	0	1	[(n + 4) m + 3]/16 nm
σ^2_{DA}	1/m	1	[(n + 4) m + 3]/8 nm
$\sigma^2_{DA'}$	1/m	0	[(n + 4) m + 3]/16 nm
$\sigma^2_{DA^*}$	0	1	[(n + 4) m + 3]/16 nm
σ^2_{DD}	1/m	1	[(n + 6) m + 9]/16 nm
$\sigma^2_{DD'}$	1/m	0	[(n + 6) m + 9]/64 nm
$\sigma^2_{DD^*}$	0	0	[(n + 6) m + 9]/32 nm
$\sigma^2_{DD^{**}}$	0	1	[(n + 6) m + 9]/64 nm
$\sigma_{A\cdot AA^*}$	0	2	(n + 2)/2 n
$\sum_l \mu_l^{*2}$	0	0	1/(2 nm)

Although the increased variance associated with highly related groups is an advantage in the presence of error variation, the choice of the optimum type of group is also seen to depend on several other variables. For large groups characterized by θ and δ, and ignoring any distinction between homo- and heteroallelic interactions, so that σ^2_{AA} is written for $(\sigma^2_{AA} + \sigma^2_{AA'} + \sigma^2_{AA^*})$ and similarly for other interactions, the response can be written in a form which appears very similar to that which is appropriate in the absence of competition:

$$R_{(\theta,\delta)} = i\,2\theta\,\sigma^2_A/[2\theta\,\sigma^2_A + \delta\,\sigma^2_D + (2\theta)^2\,\sigma^2_{AA} + 2\theta\,\delta(\sigma^2_{AD} + \sigma^2_{DA}) + \delta^2\,\sigma^2_{DD} + \sigma^2_\varepsilon]^{1/2},$$

where

$$\sigma^2_A = \sigma^2_{dA} + 2\,\sigma_{dA\cdot aA} + \sigma^2_{aA}$$

and

$$\sigma_D^2 = \sigma_{dD}^2 + 2\,\sigma_{dD\cdot aD} + \sigma_{aD}^2$$

are the additive and dominance variances of the summed direct and associate effects. The different types of interaction variance have coefficients identical to the analogous epistatic variances in the absence of competition, those for more highly related groups being larger as they permit less efficient sampling of different interactions by the group. All existing theory concerning the relative efficiencies of commonly used selection methods in the absence of competition therefore applies to this case when the appropriate substitutions are made.

If the homo- and heteroallelic interactions are distinguished, Tables 3 and 4 show that the less related groups are favored when the homoallelic effects have the larger variance and when their correlation with additive effects is negative. The term $\sum_l \mu_l^{*2}$ probably has little influence on group selection since n is usually large, but it could be significant in the case of within-family selection, particularly in systems of culture with a small neighborhood size. Further generalizations are difficult to make, and comparisons among methods can only be made for specific parameter values, but it is clear that combinations can exist which would allow all possible rankings of the expected gains from the three methods.

Discussion

Selection response always depends on the definition of the unit or units in which it is evaluated. The present discussion has been confined to the evaluation of the response of a single, large, unstructured offspring population, and the covariance governing response to selection among groups of any kind shown always to be a function only of the additive variance and covariance of direct, associate and interaction effects defined with respect to such a population. Predictions of selection response are often made using data from experiments in which full-sib families belonging to half-sib groups are grown in separate replicated plots. However, with competition, estimates of the additive genetic variance are inflated because $\mathrm{Cov}_{HS} = \frac{1}{4}\sigma_A^2 + \frac{1}{16}\sigma_{AA}^2$ where σ_{AA}^2 is the total allelic direct by associate variance. This covariance would be appropriate for the prediction of response measured on half-sib progenies of selections when grown in separate plots, but the direct by associate interaction component (σ_{AA}^2) is lost when these progenies are grown in a common mixed stand, as will usually be the case. This inflation of predicted gain is clearly analogous with that due to epistasis when response is defined for the distant descendants of selections (Griffing 1960).

Griffing (1968a) recognized that the direct and associate effects of a genotype may depend on the type of group in which they are expressed. He allowed for this possibility by providing specific definitions of these parameters for different sizes of groups, although later (1976a, b, 1977), apparently made no such distinction when comparing genetically different selection units, such as clones and full-sib families. An analysis of selection methods for groups which are physical mixtures of a small number of genotypes, and in which the definition of the genotypic effects depends on the proportions of intra- and inter-genotypic competition, and hence on the mixture size, was made by Wright (1983). The present treatment follows that which Gallais (1976) applied to an additive genetic model.

The effects are defined explicitly for an unstructured random-bred population, and their modification for groups of different degrees of relatedness depends on the distinction between homoallelic and heteroallelic interactions. Whereas the direct effect of an allele expressed in a random group is d_{lAr}, in a non-random group it is effectively $d_{lAr} + \theta(a_{lAr} + da_{lAr\cdot lAr})$. Negative response can follow selection of individuals when grown in any type of group due to a negative value of the covariance $\sigma_{dA\cdot aA}$, and the possibility of a negative sum of the covariances $\sigma_{dA\cdot AA^*}$ and $\sigma_{aA\cdot AA^*}$ means that positive response to selection of whole groups is certain only when the groups are of the same kind as those in which response is measured. These results evidently differ from those of Griffing (1968a, 1976a, b) who recognized the possibility of negative response for groups of different sizes but concluded that high levels of relatedness, such as in clonal groups, could only be beneficial. The present analysis shows that, although response is likely to be increased according to the degree of group relatedness because of the consequent increase in variance, the risk of negative response is also increased.

Griffing (1976b) also considered the use of homozygous parental material, either as a product of inbreeding or the doubled haploid technique, but his analysis must be regarded as incomplete from a genetical viewpoint as it included only additive effects. The effect of homozygosity in this case was simply to double the additive variance components and increase response by a factor of between 2.5 and 2, depending on the magnitude of σ_ϵ^2, exactly as in the absence of competition. The treatment of selection of inbred parental material for the improvement of their outcrossed progeny under a more general genetic model is complex even in the absence of inter-plant competition because response is a function of the covariance of self- and half-sibs which depends on the dominance properties of individual loci (Cockerham and Matzinger 1985). In the presence of competition, covariances of this type for direct, associate and interaction effects would also occur.

The detection and estimation of the 22 components necessary even for this incomplete description of selection response in groups with different degrees of relatedness would require a complex and extensive experiment even for a single population in one system of culture. However, such a description is not necessary in a practical context as operational predictions of response for any type of selection can be obtained more simply by direct estimation of the regression of offspring on parent in the appropriate group regime. The

chief outcome of the detailed elaboration given here is to show the complexity of the relationship between selection and response and that accurate predictions of the relative efficiencies of the different selection methods in the presence of inter-plant competition cannot be made on purely theoretical grounds unsupported by data.

Acknowledgements. I wish to express my thanks to Drs. C. C. Cockerham and H. Tachida for helpful discussions during preparation of this manuscript.

Paper No. 10144 of the Journal Series of the North Carolina Agricultural Research Service, Raleigh, NC 27695-7601. This investigation was supported in part by NIH Research Grant No. GM 11546 from the National Institute of General Medical Sciences.

References

Cockerham CC, Matzinger DF (1985) Selection response based on selfed progenies. Crop Sci 25:483–488

Gallais A (1976) Effects of competition on means, variances and covariances in quantitative genetics with an application to general combining ability selection. Theor Appl Genet 47:189–195

Griffing B (1960) Theoretical consequences of truncation selection based on the individual phenotype. Aust J Biol Sci 13:307–343

Griffing B (1967) Selection in reference to biological groups. 1. Individual and group selection applied to populations of unordered groups. Aust J Biol Sci 20:127–139

Griffing B (1968a) Selection in reference to biological groups. 2. Consequences of selection in groups of one size when evaluated in groups of another size. Aust J Biol Sci 21: 1163–1170

Griffing B (1968b) Selection in reference to biological groups. 3. Generalised results of individual and group selection in terms of parent-offspring covariances. Aust J Biol Sci 21: 1173–1178

Griffing B (1969) Selection in reference to biological groups. 4. Application of selection index theory. Aust J Biol Sci 22:131–142

Griffing B (1976a) Selection in reference to biological groups. 5. Analysis of full-sib groups. Genetics 82:703–722

Griffing B (1976b) Selection in reference to biological groups. 6. Use of extreme forms of non-random groups to increase selection efficiency. Genetics 82:723–731

Griffing B (1977) Selection for populations of interacting genotypes. In: Proc Int Congr Quant Genet. Iowa State Univ Press, Ames, Iowa, pp 51–55

Malecot G (1948) Les mathematiques de l'heredite. Masson, Paris

Weir B, Cockerham CC (1977) Two-locus theory in quantitative genetics. In: Proc Int Congr Quant Genet. Iowa State University Press, Ames, Iowa, pp 56–60

Wright AJ (1983) The expected efficiencies of some methods of selection of components for intergenotypic mixtures. Theor Appl Genet 67:45–52