

PREDICTION FORMULAE FOR GENERAL COMBINING ABILITY
SELECTION METHODS UTILIZING ONE OR TWO
RANDOM-MATING POPULATIONS

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[Manuscript received July 16, 1962]

Summary

This study is the first of a series in which theoretical comparisons are made among various general combining ability and specific combining ability selection methods. The particular purpose of this study is to set out the prediction formulae for all possible general combining ability selection methods which can be generated by one or two base populations.

Prediction formulae are considered for various levels of genetic complexity; a single locus, two linked loci, and a generalized, genetic situation.

To extend the prediction process to include a general combining ability selection procedure involving two different base populations, it is necessary to extend the gene model and variance partitioning to accommodate the hybrid population, and to define certain covariances between similar elements in different populations.

When this is done, it is possible to predict the consequences of n cycles of selection followed by t generations of random mating without selection for each selection method. With the two-locus model it is possible to show how linkage and the additive \times additive component of epistasis (as well as the additive genetic variance) enter into the prediction formulae when selection is applied. It is also possible to show, on relaxation from selection, that the disturbances due to linkage and epistasis tend to disappear.

With the completely general genetic situation, it is demonstrated that the response to selection is a function of covariances among half-sibs. These parameters are defined either in a single population, or as a sum of cross-products involving two different populations, depending on the selection method involved.

I. INTRODUCTION

Ever since the reciprocal selection method was suggested (Comstock, Robinson, and Harvey 1949), considerable interest has been manifest in comparing it in various ways with other methods of selection. Such comparisons have been in theoretical terms (Comstock, Robinson, and Harvey 1949; Dickerson 1952; and Schnell 1961), and in terms of actual experiments (Bell, Moore, and Warren 1955; Rasmusson 1956; and Douglas *et al.* 1961).

The purpose of this study is to extend the theoretical comparisons to an entire set of closely related selection methods which range from recurrent selection involving a single population to reciprocal selection involving two base populations. In this paper prediction formulae are generalized for these selection methods. The following papers will compare the potentialities of the various selection methods.

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In order to completely specify a selection scheme, it is necessary to define, first, the method used to evaluate the breeding value of the individual and, second, the method of mating the selected individuals.

In this study, evaluation of the individual is based on its general combining ability (hereafter abbreviated to g.c.a.). However, the g.c.a. of an individual depends, not only on its own genetic constitution, but also on the genetic composition of the tester population. Hence, this aspect of selection methodology is discussed under the heading of testing systems.

That aspect of selection methodology, which specifies the way in which the selected individuals are mated, is discussed under the heading of mating systems.

II. SPECIFICATION OF SELECTION SCHEMES

In this paper, interest is confined to all possible g.c.a. selection methods which can be generated by one or two random-mating populations in equilibrium.

(a) Testing Systems

The g.c.a. of an individual is estimated as the average performance of the progeny which result when the individual is crossed with random members of the tester population. Clearly, the tester population may be the population itself in which selection is practised, or it may be a different population. Hence, with one or two populations, all possible tester systems are enumerated as follows:

Selected Populations	Tester Populations	
	${}_a\Pi_0$	${}_b\Pi_0$
${}_a\Pi_0$	T_{aa}	T_{ab}
${}_b\Pi_0$	T_{ba}	T_{bb}

In this representation, ${}_a\Pi_0$ and ${}_b\Pi_0$ are the original random-mating populations in equilibrium, and T_{ij} represents the testing system in which elements of ${}_i\Pi_0$ are tested with ${}_j\Pi_0$.

(b) Mating Systems

All possible mating systems derivable from the testing methods listed above are set out as follows:

	T_{aa}	T_{ab}	T_{ba}	T_{bb}
T_{aa}	${}_{aa}M_{aa}$	${}_{aa}M_{ab}$	${}_{aa}M_{ba}$	${}_{aa}M_{bb}$
T_{ab}		${}_{ab}M_{ab}$	${}_{ab}M_{ba}$	${}_{ab}M_{bb}$
T_{ba}			${}_{ba}M_{ba}$	${}_{ba}M_{bb}$
T_{bb}				${}_{bb}M_{bb}$

The symbol ${}_{ij}M_{kl}$ represents the mating of selected elements of the i th and k th populations. Thus, it is clear that ${}_{aa}M_{aa}$ and ${}_{bb}M_{bb}$ correspond to recurrent selection, when the evaluation of the individual is based on its g.c.a., and ${}_{ab}M_{ba}$ represents reciprocal selection.

A cycle of selection involving the mating system ${}_{ij}M_{kl}$ consists of the following sequences. Elements of the i th population are tested with the j th population, and at the same time, elements of the k th population are tested with the l th population. The selected individuals of ${}_i\Pi_0$ are mated to give a new population designated as ${}_i\Pi_1$. Similarly a new population ${}_k\Pi_1$ is derived. The next cycle of selection starts with these populations. The hybrid population, resulting from mating the selected elements of the i th and k th populations, may be derived from any cycle. The purpose of the selection scheme is to produce a high yielding hybrid population, ${}_{ik}\Pi_n$, either directly or through the isolation and crossing of inbreds in the selected i th and k th populations.

The specific objective of this study is to predict the gain in the mean of the hybrid population with each cycle of selection.

It should be pointed out that an exchange of genes does not occur between any of the populations. Thus, in the methods outlined above, selection operates only on the genetic variability within each selected population.

III. CONSEQUENCES OF SELECTION

(a) Selection among Genotypes Generated by Alleles at One Locus

(i) *Parameters of the Various Populations.*—This section is concerned with selection involving random-mating populations generated by an arbitrary number of alleles at one locus. The following sets out the necessary extensions of the usual gene model and partitioning of variance to accommodate the hybrid population. Let

$$\sum_{i=1}^m ({}_ap_i)({}_aA_i) = \text{gametic array for } {}_a\Pi_0,$$

and

$$\sum_{k=1}^n ({}_bp_k)({}_bA_k) = \text{gametic array for } {}_b\Pi_0.$$

Then

$$\sum_{ik} ({}_ap_i)({}_bp_k)({}_aA_i)({}_bA_k) = \text{zygotic array for } {}_{ab}\Pi_0.$$

Let a_{ik} represent the genotypic effect of $({}_aA_i)({}_bA_k)$ relative to an arbitrary origin. It is assumed that difference in effects between genotypes at the locus are identical in different populations. Then

$$a_{..} = \sum_{ik} ({}_ap_i)({}_bp_k)a_{ik} = \text{uncoded genotypic mean of } {}_{ab}\Pi_0.$$

The genotypic mean of $({}_aA_i)({}_bA_k)$, measured as a deviation from $a_{..}$, is defined as

$${}_{ab}d_{a_ib_k} = a_{ik} - a_{..}$$

The mean of these genotypic deviations is represented as

$${}_{ab}\mu_0 = \sum_{ik} ({}_a p_i) ({}_b p_k) ({}_{ab}d_{a_i b_k}) = 0.$$

In the remainder of the paper, the term "population mean" refers to the coded mean involving genotypic deviations as described above.

Associated with the genotypic deviation ${}_{ab}d_{a_i b_k}$ is the following gene model:

$${}_{ab}d_{a_i b_k} = {}_{ab}\alpha_{a_i} + {}_{ab}\alpha_{b_k} + {}_{ab}\delta_{a_i b_k},$$

where

$${}_{ab}\alpha_{a_i} = \sum_k ({}_b p_k) ({}_{ab}d_{a_i b_k}) = \text{additive effect of } ({}_a A_i) \text{ in } {}_{ab}\Pi_0,$$

and

$${}_{ab}\delta_{a_i b_k} = ({}_{ab}d_{a_i b_k} - {}_{ab}\alpha_{a_i} - {}_{ab}\alpha_{b_k}) = \text{interaction (dominance) effect associated with } ({}_a A_i) ({}_b A_k) \text{ in } {}_{ab}\Pi_0.$$

The quantities ${}_{ab}\delta_{a_i b_k}$ will be termed dominance effects since such effects, when defined within the framework of either of the base populations, are due to the dominance phenomenon. However, in some hybrid populations, where alleles in one population are not present in the other, these interaction effects need not reflect the basic dominance relationships existing in the multiple-allele system.

The partitioning of the total genotypic variance in the hybrid population may be represented symbolically as

$${}_{ab}\sigma_G^2 = {}_{ab}\sigma_{A_a}^2 + {}_{ab}\sigma_{A_b}^2 + {}_{ab}\sigma_{D_{ab}}^2,$$

where

$${}_{ab}\sigma_G^2 = \sum_{ik} ({}_a p_i) ({}_b p_k) ({}_{ab}d_{a_i b_k})^2 = \text{total genotypic variance,}$$

$${}_{ab}\sigma_{A_a}^2 = \sum_i ({}_a p_i) ({}_{ab}\alpha_{a_i})^2 = \text{additive genetic variance due to } {}_a A_i \text{ alleles,}$$

$${}_{ab}\sigma_{A_b}^2 = \sum_k ({}_b p_k) ({}_{ab}\alpha_{b_k})^2 = \text{additive genetic variance due to } {}_b A_k \text{ alleles,}$$

and

$${}_{ab}\sigma_{D_{ab}}^2 = \sum_{ik} ({}_a p_i) ({}_b p_k) ({}_{ab}\delta_{a_i b_k})^2 = \text{dominance variance.}$$

The parameters for ${}_a\Pi_0$ can be obtained from the above notation by substituting "a" for the subscript "b". Similarly the parameter for ${}_b\Pi_0$ can be obtained by making the inverse substitution.

It should be noted that in the above treatment the variances due to each effect are kept separate. Thus the total additive genetic variance in ${}_{ab}\Pi_0$ is

$${}_{ab}\sigma_A^2 = {}_{ab}\sigma_{A_a}^2 + {}_{ab}\sigma_{A_b}^2.$$

Besides the variances described above, there are certain covariances among additive effects in different populations which must be considered. These are

$$\text{Cov}({}_{aa}\alpha_a, {}_{ab}\alpha_a) = \sum_i ({}_a p_i) ({}_{aa}\alpha_{a_i}) ({}_{ab}\alpha_{a_i}),$$

and

$$\text{Cov}({}_{bb}\alpha_b, {}_{ab}\alpha_b) = \sum_k ({}_b p_k) ({}_{bb}\alpha_{b_k}) ({}_{ab}\alpha_{b_k}).$$

The g.c.a. effect of the genotype $(_aA_i)(_aA_j)$ in $_a\Pi_0$ when tested by $_b\Pi_0$ is the expected mean of the following half-sib array:

$$\frac{1}{2} \sum_k ({}_b p_k) [({}_a A_i)({}_b A_k) + ({}_a A_j)({}_b A_k)]$$

which is equal to

$${}_{ab} \gamma_{a_i a_j} = \frac{1}{2} ({}_{ab} \alpha_{a_i} + {}_{ab} \alpha_{a_j}).$$

General combining ability effects for the same genotype but with different test populations may be obtained by appropriate substitution of subscripts.

(ii) *Selection Values*.—The selection value associated with the genotype $(_aA_i)(_aA_j)$ of $_a\Pi_0$ tested with $_b\Pi_0$ is defined to be

$${}_{ab} w_{a_i a_j} = 1 + (i / {}_{ab} \sigma_{h.s.}^2) {}_{ab} \gamma_{a_i a_j},$$

where

i = selection differential measured in terms of g.c.a. effects,

and

${}_{ab} \sigma_{h.s.}^2$ = variance of the g.c.a. estimates.

The variance of the g.c.a. estimates will depend on the structure of the experimental design giving rise to the half-sib means. For a discussion of this problem and a more detailed argument concerning the definition of the selection values, see a previous paper by the author (Griffing 1962).

(iii) *Consequences of One Cycle of Selection*.—The consequences of one cycle of truncation selection can be determined most easily for all mating systems by first setting out the results for the generalized mating system ${}_{ab} M_{cd}$ and then making the appropriate subscript substitutions to obtain the results for each of the various mating systems.

Consider first the problem of obtaining the gametic array from the selected genotypes in $_a\Pi_0$ when tested by $_b\Pi_0$.

The frequency of $(_aA_i)(_aA_j)$ following selection is

$$({}_a p_i)({}_a p_j)({}_{ab} w_{a_i a_j}).$$

Hence the gametic array from all selected individuals is

$$\begin{aligned} & \frac{1}{2} \sum_{ij} ({}_a p_i)({}_a p_j)({}_{ab} w_{a_i a_j}) [({}_a A_i) + ({}_a A_j)] \\ & = \sum_i ({}_a p_i^1)({}_a A_i), \end{aligned}$$

where

$${}_a p_i^1 \cong ({}_a p_i) [1 + \{i/2({}_{ab} \sigma_{h.s.}^2)\} ({}_{ab} \alpha_{a_i})].$$

Similarly the gametic array from all selected individuals of $_c\Pi_0$ when tested with $_d\Pi_0$ is

$$\sum_k ({}_c p_k^1)({}_c A_k),$$

where

$${}_c p_k^1 \cong ({}_c p_k) [1 + \{i/2({}_{cd} \sigma_{h.s.}^2)\} ({}_{cd} \alpha_{c_k})].$$

The mean of the hybrid population which results from the mating of selected individuals from ${}_a\Pi_0$ with those from ${}_c\Pi_0$ is

$$\begin{aligned} {}_{ac}\mu_1 &= \sum_{ik} ({}_ap_i^1)({}_cp_k^1)({}_{ac}d_{a_ik}) \\ &= [i/2({}_{ab}\sigma_{h.s.}^2)]\text{Cov}({}_{ab}\alpha_a, {}_{ac}\alpha_a) + [i/2({}_{cd}\sigma_{h.s.}^2)]\text{Cov}({}_{ca}\alpha_c, {}_{cd}\alpha_c). \end{aligned}$$

The mean for ${}_a\Pi_1$ can be obtained by substituting the subscripts "a" for "c" and "b" for "d". Likewise, the mean for ${}_c\Pi_1$ can be obtained by the inverse substitutions.

The specific means for the various mating systems will be given after the next section which briefly reviews the approximate consequences of n cycles of selection.

(iv) *Consequences of n Cycles of Selection.*—The mean of the hybrid population, ${}_{ac}\Pi_n$, which results from n cycles of selection involving the generalized mating system ${}_{ab}M_{cd}$ can be shown to be approximately equal to

$$\sum_{ik} ({}_ap_i^n)({}_cp_k^n)({}_{ac}d_{a_ik}),$$

where

$${}_ap_i^n \cong ({}_ap_i)[1 + \frac{1}{2}n(i/{}_{ab}\sigma_{h.s.}^2)({}_{ab}\alpha_{a_i})],$$

and

$${}_cp_k^n \cong ({}_cp_k)[1 + \frac{1}{2}n(i/{}_{cd}\sigma_{h.s.}^2)({}_{cd}\alpha_{c_k})].$$

In terms of gene effects this generalized mean is equal to

$${}_{ac}\mu_n = \frac{1}{2}n[(i/{}_{ab}\sigma_{h.s.}^2)\text{Cov}({}_{ab}\alpha_a, {}_{ac}\alpha_a) + (i/{}_{cd}\sigma_{h.s.}^2)\text{Cov}({}_{ca}\alpha_c, {}_{cd}\alpha_c)].$$

The specific means for the various selection systems are given in Table 1.

If more than one locus is considered and epistasis and linkage ignored, the total genotypic effect is the sum of increments over all loci. However, if linkage and epistasis occur, the *immediate* response to selection may be affected. These complications are considered in the next section which deals with populations generated by alleles at two linked loci.

(b) *Selection among Genotypes Generated by Alleles at Two Loci which may be Linked*

(i) *Parameters of the Population.*—This section is concerned with selection involving random-mating populations generated by an arbitrary number of alleles at each of two loci which may be linked.

As with the single-locus case, the usual gene model and variance partitioning must be extended to accommodate the hybrid population ${}_{ab}\Pi_0$ which results from crossing ${}_a\Pi_0$ and ${}_b\Pi_0$.

Let

$$\sum_i ({}_rp_i^1)({}_rA_i^1) = \text{allelic array at locus (1) for the } r\text{th population.}$$

$$\sum_k ({}_rp_k^2)({}_rA_k^2) = \text{allelic array at locus (2) for the } r\text{th population,}$$

y = recombination frequency for the two loci,

and

$\sum_{ijkl} ({}_a f_{a_i a_k}) ({}_b f_{b_j b_l}) ({}_a A_i^1) ({}_a A_k^2) ({}_b A_j^1) ({}_b A_l^2) =$ zygotic array for the hybrid population,

where

$${}_a f_{a_i a_k} = ({}_a p_i^1) ({}_a p_k^2) = \text{frequency of the gamete } ({}_a A_i^1) ({}_a A_k^2) \text{ from } {}_a \Pi_0,$$

and

$${}_b f_{b_j b_l} = ({}_b p_j^1) ({}_b p_l^2) = \text{frequency of the gamete } ({}_b A_j^1) ({}_b A_l^2) \text{ from } {}_b \Pi_0.$$

TABLE 1
MEANS RESULTING FROM n CYCLES OF SELECTION FOR POPULATIONS
GENERATED BY MULTIPLE ALLELES AT ONE LOCUS

	T_{aa}	T_{ab}	T_{ba}	T_{bb}
T_{aa}	${}_{aa}M_{aa}$ $\mu_n = 2U$	${}_{aa}M_{ab}$ $\mu_n = U + Y$	${}_{aa}M_{ba}$ $\mu_n = Y + W$	${}_{aa}M_{bb}$ $\mu_n = Y + Z$
T_{ab}		${}_{ab}M_{ab}$ $\mu_n = 2Y$	${}_{ab}M_{ba}$ $\mu_n = V + W$	${}_{ab}M_{bb}$ $\mu_n = V + Z$
T_{ba}			${}_{ba}M_{ba}$ $\mu_n = 2Z$	${}_{ba}M_{bb}$ $\mu_n = Z + X$
T_{bb}				${}_{bb}M_{bb}$ $\mu_n = 2X$

where

$$\begin{aligned}
 U &= \frac{1}{2}n(i/{}_{ab}\sigma_{h.s.}^2) {}_{aa}\sigma_{A_a}^2 & X &= \frac{1}{2}n(i/{}_{ab}\sigma_{h.s.}^2) {}_{bb}\sigma_{A_b}^2 \\
 V &= \frac{1}{2}n(i/{}_{ab}\sigma_{h.s.}^2) {}_{ab}\sigma_{A_a}^2 & Y &= \frac{1}{2}n(i/{}_{ab}\sigma_{h.s.}^2) [\text{Cov}({}_{aa}\alpha_a, {}_{ab}\alpha_a)] \\
 W &= \frac{1}{2}n(i/{}_{ab}\sigma_{h.s.}^2) {}_{ab}\sigma_{A_b}^2 & Z &= \frac{1}{2}n(i/{}_{ab}\sigma_{h.s.}^2) [\text{Cov}({}_{ab}\alpha_b, {}_{bb}\alpha_b)]
 \end{aligned}$$

The genotypic value for $({}_a A_i^1) ({}_a A_k^2) ({}_b A_j^1) ({}_b A_l^2)$ is characterized by the gene model

$$\begin{aligned}
 {}_{ab}d_{a_i a_k, b_j b_l} &= {}_{ab}\alpha_{a_i} + {}_{ab}\alpha_{a_k} + {}_{ab}\alpha_{b_j} + {}_{ab}\alpha_{b_l} + {}_{ab}\delta_{a_i b_j} + {}_{ab}\delta_{a_k b_l} + {}_{ab}(\alpha\alpha)_{a_i a_k} \\
 &\quad + {}_{ab}(\alpha\alpha)_{a_i b_l} + {}_{ab}(\alpha\alpha)_{b_j a_k} + {}_{ab}(\alpha\alpha)_{b_j b_l} + {}_{ab}(\alpha\delta)_{a_i, a_k b_l} + {}_{ab}(\alpha\delta)_{b_j, a_k b_l} \\
 &\quad + {}_{ab}(\delta\alpha)_{a_i b_j, a_k} + {}_{ab}(\delta\alpha)_{a_i b_j, b_l} + {}_{ab}(\delta\delta)_{a_i b_j, a_k b_l}
 \end{aligned}$$

where

- ${}_{ab}\alpha_{a_i}$ = additive effect of the ${}_a A_i^1$ allele,
- ${}_{ab}\delta_{a_i b_j}$ = dominance effect associated with the genotype $({}_a A_i^1) ({}_b A_j^1)$,
- ${}_{ab}(\alpha\alpha)_{a_i a_k}$ = additive \times additive epistatic effect associated with genes $({}_a A_i^1)$ and $({}_a A_k^2)$,

$ab(\alpha\delta)_{a_i, a_k b_l}$ = additive \times dominance epistatic effect associated with the gene $(_a A_i^1)$ and the genotype $(_a A_k^2)(_b A_l^2)$, and

$ab(\delta\delta)_{a_i b_j, a_k b_l}$ = dominance \times dominance epistatic effect associated with the genotypes $(_a A_i^1)(_b A_j^1)$ and $(_a A_k^2)(_b A_l^2)$.

The genotypic values are chosen so that

$$\sum_{ijkl} (_a p_i^1)(_a p_k^2)(_b p_j^1)(_b p_l^2)(ab d_{a_i a_k, b_j b_l}) = 0.$$

The partitioning of the total genotypic variance may be represented symbolically as

$$ab\sigma_G^2 = ab\sigma_{A_a}^2 + ab\sigma_{A_b}^2 + ab\sigma_{D_{ab}}^2 + ab\sigma_{A_a A_a}^2 + ab\sigma_{A_a A_b}^2 + ab\sigma_{A_b A_a}^2 + ab\sigma_{A_b A_b}^2 + ab\sigma_{A_a D_{ab}}^2 + ab\sigma_{A_b D_{ab}}^2 + ab\sigma_{D_{ab} A_a}^2 + ab\sigma_{D_{ab} A_b}^2 + ab\sigma_{D_{ab} D_{ab}}^2,$$

where

$$ab\sigma_{A_a}^2 = \sum_i (_a p_i^1)(ab\alpha_{a_i})^2 + \sum_k (_a p_k^2)(ab\alpha_{a_k})^2$$

= additive genetic variance,

$$ab\sigma_{D_{ab}}^2 = \sum_{ij} (_a p_i^1)(_b p_j^1)(ab\delta_{a_i b_j})^2 + \sum_{kl} (_a p_k^2)(_b p_l^2)(ab\delta_{a_k b_l})^2$$

= dominance variance,

$$ab\sigma_{A_a A_b}^2 = \sum_{il} (_a p_i^1)(_b p_l^2)[ab(\alpha\alpha)_{a_i b_l}]^2$$

= additive \times additive variance,

$$ab\sigma_{A_a D_{ab}}^2 = \sum_{ikl} (_a p_i^1)(_a p_k^2)(_b p_l^2)[ab(\alpha\delta)_{a_i, a_k b_l}]^2$$

= additive \times dominance variance, and

$$ab\sigma_{D_{ab} D_{ab}}^2 = \sum_{ijkl} (_a p_i^1)(_a p_k^2)(_b p_j^1)(_b p_l^2)[ab(\delta\delta)_{a_i b_j, a_k b_l}]^2$$

= dominance \times dominance variance.

The parameters for $_a \Pi_0$ and $_b \Pi_0$ can be obtained from those given above by appropriate substitutions of subscripts.

Besides the variances listed above and the covariances of additive effects in different populations as given in the argument for a single locus, there are two further covariances that need to be considered. These concern the cross-products of additive \times additive effects in different populations, i.e.

$$\text{Cov}[_{aa}(\alpha\alpha)_{aa}, ab(\alpha\alpha)_{aa}] = \sum_{ik} (_a f_{a_i a_k})[_{aa}(\alpha\alpha)_{a_i a_k}][ab(\alpha\alpha)_{a_i a_k}],$$

and

$$\text{Cov}[_{bb}(\alpha\alpha)_{bb}, ab(\alpha\alpha)_{bb}] = \sum_{jl} (_b f_{b_j b_l})[_{bb}(\alpha\alpha)_{b_j b_l}][ab(\alpha\alpha)_{b_j b_l}].$$

Finally, the g.c.a. effect of the genotype $(_a A_i^1)(_a A_k^2)(_b A_j^1)(_b A_l^2)$ from $_a \Pi_0$ when tested by $_b \Pi_0$ is given by

$$ab\gamma_{a_i a_k, a_j a_l} = \frac{1}{2}[ab\alpha_{a_i} + ab\alpha_{a_k} + ab\alpha_{a_j} + ab\alpha_{a_l}] + \frac{1}{2}(1-y)[ab(\alpha\alpha)_{a_i a_k} + ab(\alpha\alpha)_{a_j a_l}] + \frac{1}{2}y[ab(\alpha\alpha)_{a_i a_l} + ab(\alpha\alpha)_{a_j a_k}].$$

(ii) *Selection Values.*—In a manner analogous to that given for the case of a single locus, the selection value for the genotype $(aA_i^1)(aA_k^2)(aA_j^1)(aA_l^2)$ from ${}_a\Pi_0$ tested by ${}_b\Pi_0$ is

$$abw_{a_ia_k, a_ja_l} = 1 + (i/ab\sigma_{h.s.}^2)(ab\gamma_{a_ia_k, a_ja_l}).$$

(iii) *Consequences of One Cycle of Selection.*—Prediction formulae will be obtained for the generalized mating system ${}_abM_{cd}$. Specific cases can then be obtained by appropriate substitution of subscripts.

TABLE 2
MEANS RESULTING FROM A SINGLE CYCLE OF SELECTION FOR POPULATIONS GENERATED BY ALLELES AT TWO LINKED LOCI

	T_{aa}	T_{ab}	T_{ba}	T_{bb}
T_{aa}	${}_{aa}M_{aa}$ $\mu_1 = 2U'_1$	${}_{aa}M_{ab}$ $\mu_1 = U'_1 + Y'_1$	${}_{aa}M_{ba}$ $\mu_1 = Y'_1 + W'_1$	${}_{aa}M_{bb}$ $\mu_1 = Y'_1 + Z'_1$
T_{ab}		${}_{ab}M_{ab}$ $\mu_1 = 2Y'_1$	${}_{ab}M_{ba}$ $\mu_1 = V'_1 + W'_1$	${}_{ab}M_{bb}$ $\mu_1 = V'_1 + Z'_1$
T_{ba}			${}_{ba}M_{ba}$ $\mu_1 = 2Z'_1$	${}_{ba}M_{bb}$ $\mu_1 = Z'_1 + X'_1$
T_{bb}				${}_{bb}M_{bb}$ $\mu_1 = 2X'_1$

where

$$U'_1 = (i/ab\sigma_{h.s.}^2)\{\frac{1}{2}({}_{aa}\sigma_{A_a}^2) + \frac{1}{4}(1 + \delta_y)({}_{aa}\sigma_{A_a A_a}^2)\},$$

$$V'_1 = (i/ab\sigma_{h.s.}^2)\{\frac{1}{2}({}_{ab}\sigma_{A_a}^2) + \frac{1}{4}(1 + \delta_y)({}_{ab}\sigma_{A_a A_a}^2)\},$$

$$W'_1 = (i/ab\sigma_{h.s.}^2)\{\frac{1}{2}({}_{ab}\sigma_{A_b}^2) + \frac{1}{4}(1 + \delta_y)({}_{ab}\sigma_{A_b A_b}^2)\},$$

$$X'_1 = (i/ab\sigma_{h.s.}^2)\{\frac{1}{2}({}_{bb}\sigma_{A_b}^2) + \frac{1}{4}(1 + \delta_y)({}_{bb}\sigma_{A_b A_b}^2)\},$$

$$Y'_1 = (i/ab\sigma_{h.s.}^2)\{\frac{1}{2}[\text{Cov}({}_{aa}a_a, {}_{ab}a_a)] + \frac{1}{4}(1 + \delta_y)[\text{Cov}({}_{aa}(aa)_{aa}, {}_{ab}(aa)_{aa})]\},$$

and

$$Z'_1 = (i/ab\sigma_{h.s.}^2)\{\frac{1}{2}[\text{Cov}({}_{ab}a_b, {}_{bb}a_b)] + \frac{1}{4}(1 + \delta_y)[\text{Cov}({}_{ab}(aa)_{bb}, {}_{bb}(aa)_{bb})]\}.$$

It can be shown that the frequency of the gamete $(aA_i^1)(aA_k^2)$ from selected members of ${}_a\Pi_0$ on testing with ${}_b\Pi_0$ is

$$af_{a_ia_k}^1 = af_{a_ia_k} \left(1 + (i/ab\sigma_{h.s.}^2)\left\{ \frac{1}{2}({}_{ab}\alpha_{a_i} + {}_{ab}\alpha_{a_k}) + \frac{1}{4}(1 + \delta_y)[{}_{ab}(\alpha\alpha)_{a_ia_k}] \right\} \right),$$

where

$$\delta_y = (1 - 2y)^2.$$

Similarly the frequency of the gamete $(cA_j^1)(cA_l^2)$, from selected members of $c\Pi_0$ on testing with $a\Pi_0$ is

$$cf_{c_jc_l}^1 = cf_{c_jc_l} \left(1 + (i/ca\sigma_{h.s.}^2) \left\{ \frac{1}{2}(ca\alpha_{c_j} + ca\alpha_{c_l}) + \frac{1}{4}(1 + \delta_y)[ca(\alpha\alpha)_{c_jc_l}] \right\} \right).$$

Hence, the mean of the hybrid population obtained by crossing the selected members of $a\Pi_0$ with those from $c\Pi_0$ is

$$ac\mu_1 = (i/ab\sigma_{h.s.}^2) \left\{ \frac{1}{2}\text{Cov}(ab\alpha_a, ac\alpha_a) + \frac{1}{4}(1 + \delta_y)\text{Cov}[ab(\alpha\alpha)_{aa}, ac(\alpha\alpha)_{aa}] \right\} \\ + (i/ca\sigma_{h.s.}^2) \left\{ \frac{1}{2}\text{Cov}(ca\alpha_c, ac\alpha_c) + \frac{1}{4}(1 + \delta_y)\text{Cov}[ca(\alpha\alpha)_{cc}, ac(\alpha\alpha)_{cc}] \right\}.$$

It is interesting to note that of the four classes of additive \times additive epistatic effects which occur in the hybrid population, only those that involve two alleles coming from the same population contribute to the genetic advance.

The specific results for the various mating systems are given in Table 2.

(iv) *Consequences of n Cycles of Selection.*—It can be shown that after n cycles of selection the frequency of the gamete $(aA_i^1)(aA_k^2)$ from selected individuals of $a\Pi_{n-1}$ is approximately

$$af_{a_i a_k}^n = af_{a_i a_k} \left(1 + (i/ab\sigma_{h.s.}^2) \left\{ \frac{1}{2}n(ab\alpha_{a_i} + ab\alpha_{a_k}) + \frac{1}{4}(1 + \delta_y) \left(\sum_r^n b^{r-1} [ab(\alpha\alpha)_{a_i a_k}] \right) \right\} \right),$$

where

$$b = 1 - y.$$

Similarly, the frequency of the gamete $(cA_j^1)(cA_l^2)$ from selected individuals of $c\Pi_{n-1}$ is approximately

$$cf_{c_jc_l}^n = cf_{c_jc_l} \left(1 + (i/ca\sigma_{h.s.}^2) \left\{ \frac{1}{2}n(ca\alpha_{c_j} + ca\alpha_{c_l}) + \frac{1}{4}(1 + \delta_y) \left(\sum_r^n b^{r-1} [ca(\alpha\alpha)_{c_jc_l}] \right) \right\} \right).$$

Hence, the mean of the hybrid population $ac\Pi_n$ is approximately

$$ac\mu_n = (i/ab\sigma_{h.s.}^2) \left\{ \frac{1}{2}n\text{Cov}(ab\alpha_a, ac\alpha_a) + \frac{1}{4}(1 + \delta_y) \left(\sum_r^n b^{r-1} \text{Cov}[ab(\alpha\alpha)_{aa}, ac(\alpha\alpha)_{aa}] \right) \right\} \\ + (i/ca\sigma_{h.s.}^2) \left\{ \frac{1}{2}n\text{Cov}(ca\alpha_c, ac\alpha_c) + \frac{1}{4}(1 + \delta_y) \left(\sum_r^n b^{r-1} \text{Cov}[ca(\alpha\alpha)_{cc}, ac(\alpha\alpha)_{cc}] \right) \right\}.$$

The means of the various mating systems are derivable from the general formulation above and are given in Table 3. It is clear that linkage and epistasis can cause disturbance to the prediction formulae for *immediate* genetic gains.

(v) *Consequences of Relaxation after n Cycles of Selection.*—It is assumed that n cycles of selection have occurred with the mating system abM_{cd} . This is then followed by t generations of random mating without selection, such that elements of $a\Pi_n$ mate at random to produce the population $a\Pi_{n,t}$, and elements of $c\Pi_n$ mate at random to produce $c\Pi_{n,t}$. The problem, then, is to predict the mean of the hybrid population $ac\Pi_{n,t}$.

The frequency of the gamete $(aA_i^1)(aA_k^2)$ from $a\Pi_{n,t-1}$ is approximately

$$af_{a_i a_k}^{n,t} = (af_{a_i a_k}) \left(1 + (i/ab\sigma_{h.s.}^2) \left\{ \frac{1}{2}n(ab\alpha_{a_i} + ab\alpha_{a_k}) + \frac{1}{4}(b^t)(1 + \delta_y) \left(\sum_r^n b^{r-1} [ab(\alpha\alpha)_{a_i a_k}] \right) \right\} \right).$$

Likewise, the frequency of the gamete $(cA_j^1)(cA_l^2)$ from ${}_c\Pi_{n, t-1}$ is approximately

$$cf_{c_j c_l}^{n, t} = (cf_{c_j c_l}) \left(1 + (i/cd\sigma_{h.s.}^2) \left\{ \frac{1}{2}n(cd\alpha_{c_j} + cd\alpha_{c_l}) + \frac{1}{4}(b^t)(1 + \delta_y) \left(\sum_{r=1}^n b^{r-1} [cd(\alpha\alpha)_{c_j c_l}] \right) \right\} \right).$$

TABLE 3

MEANS RESULTING FROM n CYCLES OF SELECTION FOR POPULATIONS GENERATED BY ALLELES AT TWO LINKED LOCI

	T_{aa}	T_{ab}	T_{ba}	T_{bb}
T_{aa}	$\begin{matrix} {}_{aa}M_{aa} \\ \mu_n = 2U'_n \end{matrix}$	$\begin{matrix} {}_{aa}M_{ab} \\ \mu_n = U'_n + Y'_n \end{matrix}$	$\begin{matrix} {}_{aa}M_{ba} \\ \mu_n = Y'_n + W'_n \end{matrix}$	$\begin{matrix} {}_{aa}M_{bb} \\ \mu_n = Y'_n + Z'_n \end{matrix}$
T_{ab}		$\begin{matrix} {}_{ab}M_{ab} \\ \mu_n = 2Y'_n \end{matrix}$	$\begin{matrix} {}_{ab}M_{ba} \\ \mu_n = V'_n + W'_n \end{matrix}$	$\begin{matrix} {}_{ab}M_{bb} \\ \mu_n = V'_n + Z'_n \end{matrix}$
T_{ba}			$\begin{matrix} {}_{ba}M_{ba} \\ \mu_n = 2Z'_n \end{matrix}$	$\begin{matrix} {}_{ba}M_{bb} \\ \mu_n = Z'_n + X'_n \end{matrix}$
T_{bb}				$\begin{matrix} {}_{bb}M_{bb} \\ \mu_n = 2X'_n \end{matrix}$

where

$$U'_n = (i/ab\sigma_{h.s.}^2) \left\{ \frac{1}{2}n({}_{aa}\sigma_{A_a}^2) + \frac{1}{4}(1 + \delta_y) (\sum b^{r-1}) ({}_{aa}\sigma_{A_a A_a}^2) \right\},$$

$$V'_n = (i/ab\sigma_{h.s.}^2) \left\{ \frac{1}{2}n({}_{ab}\sigma_{A_a}^2) + \frac{1}{4}(1 + \delta_y) (\sum b^{r-1}) ({}_{ab}\sigma_{A_a A_a}^2) \right\},$$

$$W'_n = (i/ab\sigma_{h.s.}^2) \left\{ \frac{1}{2}n({}_{ab}\sigma_{A_b}^2) + \frac{1}{4}(1 + \delta_y) (\sum b^{r-1}) ({}_{ab}\sigma_{A_b A_b}^2) \right\},$$

$$X'_n = (i/ab\sigma_{h.s.}^2) \left\{ \frac{1}{2}n({}_{bb}\sigma_{A_b}^2) + \frac{1}{4}(1 + \delta_y) (\sum b^{r-1}) ({}_{bb}\sigma_{A_b A_b}^2) \right\},$$

$$Y'_n = (i/ab\sigma_{h.s.}^2) \left\{ \frac{1}{2}n[\text{Cov}({}_{aa}\alpha_a, {}_{ab}\alpha_a)] + \frac{1}{4}(1 + \delta_y) (\sum b^{r-1}) [\text{Cov}({}_{aa}(\alpha\alpha)_{aa}, {}_{ab}(\alpha\alpha)_{aa})] \right\},$$

and

$$Z'_n = (i/ab\sigma_{h.s.}^2) \left\{ \frac{1}{2}n[\text{Cov}({}_{ab}\alpha_b, {}_{bb}\alpha_b)] + \frac{1}{4}(1 + \delta_y) (\sum b^{r-1}) [\text{Cov}({}_{ab}(\alpha\alpha)_{bb}, {}_{bb}(\alpha\alpha)_{bb})] \right\}.$$

Hence, the mean of ${}_c\Pi_{n, t}$ is

$$ac\mu_{n, t} = (i/ab\sigma_{h.s.}^2) \left\{ \frac{1}{2}n\text{Cov}({}_{ab}\alpha_a, {}_{ac}\alpha_a) + \frac{1}{4}(b^t)(1 + \delta_y) \left(\sum_{r=1}^n b^{r-1} \text{Cov}[_{ab}(\alpha\alpha)_{aa}, {}_{ac}(\alpha\alpha)_{aa}] \right) \right. \\ \left. + (i/cd\sigma_{h.s.}^2) \left\{ \frac{1}{2}n\text{Cov}[_{cd}\alpha_c, {}_{ac}\alpha_c] + \frac{1}{4}(b^t)(1 + \delta_y) \left(\sum_{r=1}^n b^{r-1} \text{Cov}[_{cd}(\alpha\alpha)_{cc}, {}_{ac}(\alpha\alpha)_{cc}] \right) \right\} \right\}.$$

The above result demonstrates that as t becomes large the contributions due to linkage and epistasis tend to disappear, leaving as permanent gains only those contributions due to the additive genetic variances and covariances. These limiting results are identical to those developed earlier for independent, non-interacting loci.

(c) *Generalizations*

To consider genetic situations which are more complicated than that due to two loci, it is convenient to consider a different approach which depends on generating the random-mating population by "squaring" the zygotic array (for a single population) or "multiplying" the zygotic array of one population with that of the other (for a hybrid population). This permits the framework of families to become apparent in the population structure. The responses to selection may, then, be framed in terms of covariances among relatives.

(i) *Parameters of the Various Populations.*—Let

$\sum_i ({}_r f_i)({}_r G_i)$ = gametic array for the r th population,

$\sum_{ij} ({}_r f_i)({}_r f_j)({}_r H_{ij})$ = zygotic array of the r th population, where ${}_r H_{ij}$ represents the diploid genotype resulting from the mating of ${}_r G_i$ and ${}_r G_j$.

The hybrid population ${}_{ab}\Pi_0$ may be obtained by multiplying the zygotic arrays of ${}_a\Pi_0$ and ${}_b\Pi_0$ as follows:

$$\begin{aligned} {}_{ab}\Pi_0 &= [\sum_{ij} ({}_a f_i)({}_a f_j)({}_a H_{ij})][\sum_{kl} ({}_b f_k)({}_b f_l)({}_b H_{kl})] \\ &= \sum_{ijkl} ({}_a f_i)({}_a f_j)({}_b f_k)({}_b f_l)({}_{ab}H_{ij, kl}), \end{aligned}$$

where

$${}_{ab}H_{ij, kl} = \text{expected full-sib array from the cross } {}_a H_{ij} \times {}_b H_{kl}.$$

The mean genotypic value of the full-sib array ${}_{ab}H_{ij, kl}$ is ${}_{ab}h_{ij, kl}$, such that

$$\sum_{ijkl} ({}_a f_i)({}_a f_j)({}_b f_k)({}_b f_l)({}_{ab}h_{ij, kl}) = 0.$$

The half-sib family mean (or g.c.a. value) associated with ${}_a H_{ij}$ when tested by ${}_b \Pi_0$ is

$${}_{ab}h_{ij, ..} = \sum_{kl} ({}_b f_k)({}_b f_l)({}_{ab}h_{ij, kl}).$$

Similarly, when testing elements of ${}_c \Pi_0$ with the tester population ${}_d \Pi_0$, the hybrid population,

$${}_{cd}\Pi_0 = \sum_{rstu} ({}_c f_r)({}_c f_s)({}_d f_t)({}_d f_u)({}_{cd}H_{rs, tu}),$$

must be considered.

The genotypic mean of the full-sib array ${}_{cd}H_{rs, tu}$ is ${}_{cd}h_{rs, tu}$, such that

$$\sum_{rstu} ({}_c f_r)({}_c f_s)({}_d f_t)({}_d f_u)({}_{cd}h_{rs, tu}) = 0.$$

The half-sib mean associated with the genotype ${}_cH_{rs}$ is

$${}_c h_{rs}, \dots = \sum_{tu} ({}_a f_t)({}_a f_u)({}_c h_{rs}, tu).$$

To describe genetic advances due to selection in the various populations, it is necessary to extend the notion of covariance of half-sibs to accommodate not only the hybrid populations themselves, but to also include a corresponding quantity which involves different hybrid populations. The most useful general form of the

TABLE 4
MEANS RESULTING FROM ONE CYCLE OF SELECTION FOR THE GENERAL GENETIC SITUATION

	T_{aa}	T_{ab}	T_{ba}	T_{bb}
T_{aa}	${}_{aa}M_{aa}$ $\mu_1 = 2U^*$	${}_{aa}M_{ab}$ $\mu_1 = U^* + Y^*$	${}_{aa}M_{ba}$ $\mu_1 = Y^* + W^*$	${}_{aa}M_{bb}$ $\mu_1 = Y^* + Z^*$
T_{ab}		${}_{ab}M_{ab}$ $\mu_1 = 2Y^*$	${}_{ab}M_{ba}$ $\mu_1 = V^* + W^*$	${}_{ab}M_{bb}$ $\mu_1 = V^* + Z^*$
T_{ba}			${}_{ba}M_{ba}$ $\mu_1 = 2Z^*$	${}_{ba}M_{bb}$ $\mu_1 = Z^* + X^*$
T_{bb}				${}_{bb}M_{bb}$ $\mu_1 = 2X^*$

where

$$U^* = (i/ab\sigma_{h.s.}^2)[\text{Cov}_{aa, aa}(\text{HS})] \quad X^* = (i/ab\sigma_{h.s.}^2)[\text{Cov}_{bb, bb}(\text{HS})]$$

$$V^* = (i/ab\sigma_{h.s.}^2)[\text{Cov}_{ab, ab}(\text{HS})] \quad Y^* = (i/ab\sigma_{h.s.}^2)[\text{Cov}_{aa, ab}(\text{HS})]$$

$$W^* = (i/ab\sigma_{h.s.}^2)[\text{Cov}_{ba, ba}(\text{HS})] \quad Z^* = (i/ab\sigma_{h.s.}^2)[\text{Cov}_{ba, bb}(\text{HS})]$$

covariance of half-sibs is defined as the expected cross-product of elements in ${}_a\Pi_0$ when tested with ${}_b\Pi_0$, and the same elements in ${}_a\Pi_0$ when tested with ${}_c\Pi_0$, i.e.

$$\text{Cov}_{ab, ac}(\text{HS}) = \sum_{ij} ({}_a f_i)({}_a f_j)({}_a b h_{ij}, \dots)({}_a c h_{ij}, \dots).$$

(ii) *Consequences of One Cycle of Selection.*—The frequency of ${}_a H_{ij}$ in ${}_a\Pi_0$ when tested by ${}_b\Pi_0$ is

$$({}_a f_i)({}_a f_j)({}_a b w_{ij}) = ({}_a f_i)({}_a f_j)[1 + (i/ab\sigma_{h.s.}^2)({}_a b h_{ij}, \dots)].$$

Likewise, the frequency of ${}_c H_{ki}$ in ${}_c\Pi_0$ after testing with ${}_a\Pi_0$ is

$$({}_c f_k)({}_c f_i)({}_c a w_{ki}) = ({}_c f_k)({}_c f_i)[1 + (i/ca\sigma_{h.s.}^2)({}_c a h_{ki}, \dots)].$$

Consequently, the progeny mean resulting from mating the selected individuals may be evaluated as

$$\begin{aligned} {}_{ac}\mu_1 &= \sum_{ijkl} [({}_a f_i)({}_a f_j)({}_a b w_{ij})][({}_c f_k)({}_c f_i)({}_c a w_{ki})]({}_a c h_{ij, ki}) \\ &= (i/ab\sigma_{h.s.}^2)[\text{Cov}_{ab, ac}(\text{HS})] + (i/ca\sigma_{h.s.}^2)[\text{Cov}_{ca, ca}(\text{HS})]. \end{aligned}$$

The means for the various mating systems may be obtained by substituting appropriate subscripts. These means are given in Table 4. It is clear that the selection advances given in Table 2 are merely an elaboration of half-sib covariances in terms of gene effects.

(iii) *Consequences of n Cycles of Selection.*—Mean of the hybrid population after n cycles of selection may be expressed as follows:

$$\sum_{ijkl} \{(af_i^{n-1})(af_j^{n-1})[1 + (i/ab\sigma_{h.s.}^2)(abh_{ij}, \dots)]\} \{(cf_k^{n-1})(cf_l^{n-1})[1 + (i/ca\sigma_{h.s.}^2)(cdh_{kl}, \dots)]\} (ach_{ij, kl})$$

Evaluation of this expression is approximately given as follows:

$$acl^{\mu_n} = acl^{\mu_{(n-1), 1}} + acl^{\mu_1}$$

This states that the mean of the hybrid population is approximately equal to two parts: the first is the mean of the hybrid population which results from mating the unselected $a\Pi_{n-1}$ with the unselected $c\Pi_{n-1}$, and the second part is the same as the increment advance in the hybrid population due to the first cycle of selection.

As pointed out in the argument for the two-locus case, relaxation causes the selected mean to regress to that given by only the additive genetic variance. It is, of course, assumed throughout all of the above analyses that natural selection is not operating.

IV. DISCUSSION

It is clear that in all the g.c.a. selection schemes considered above, genetic advances due to a single cycle of selection are functions of half-sib covariances. This is true for reciprocal and other closely related forms of selection. Therefore, in the final analysis, the changes in gene frequencies are a function of only the additive effects of the genes. Even when additive \times additive epistatic effects contribute to the *immediate* response to selection, it is only those additive \times additive effects due to genes at different loci from the *same* population ($a\Pi_0$ or $b\Pi_0$) that make a contribution. Thus, additive \times additive effects associated with genes, one of which derives from $a\Pi_0$ and the other from $b\Pi_0$, do not contribute to the genetic advance of the hybrid population.

As pointed out by Schnell (1961), this may seem surprising since reciprocal selection was designed to make maximum use of both general and specific combining ability (Comstock, Robinson, and Harvey 1949). However, it is true that reciprocal selection, eventually, does isolate and capitalize on exceptional gene combinations at overdominant loci in the hybrid population.

In the section on generalizations, the approach used is based on the principle that random-mating populations or hybrid populations may be represented in terms of family structure. The elements that generate this structure are the diploid genotypes themselves. The immediate responses to selection, then, are given in terms of covariances among relatives: the parent-offspring covariance is associated with selection based on individual phenotypes, and a half-sib covariance is associated with selection based on g.c.a. values.

This approach can be extended further to accommodate the selection of units comprising groups of individuals, i.e. full-sib families, half-sib families, etc. To illustrate, briefly consider the selection of any such unit. Denote the genotypic mean value of such a unit as u_i and its frequency as f_i . Let $u_{i,j}$ denote the mean genotypic value of the progeny resulting from the mass random mating of the i th and j th units. Suppose further, that the selection value of the i th unit is

$$w_i = 1 + (i/\sigma_u^2)\lambda_i,$$

where

$$\lambda_i = u_i \quad (\text{selection based on the unit}),$$

and

$$\lambda_i = u_{i.} \quad (\text{selection based on the g.c.a. of the unit}).$$

Then for selection based on the unit itself, the mean of the progeny can be shown to be approximately equal to

$$2(i/\sigma_u^2)\sum_i(f_i)(u_i)(u_{i.}).$$

This is a function of the parent-offspring covariance in terms of the units concerned.

The mean of the progeny, when selection is based on the g.c.a. value of the unit, can be shown to be approximately equal to

$$2(i/\sigma_{u(h.s.)}^2)\sum_i(f_i)(u_{i.})^2,$$

which is a function of the half-sib covariance.

This approach, which the author has used previously (Griffing 1960, 1962), is essentially the same as that based on the concept of heritability [as set out by Lush (1948) and Falconer (1960)], if the heritability is defined as the regression of the g.c.a. of the unit on the phenotypic values of the test criterion by which the unit is selected.

The assumptions required for both methods are the same. If linear regression is to provide the basis of accurate prediction, the g.c.a. values and the phenotypic values of the test criterion should jointly exhibit a bivariate normal distribution. Hence, in either case if the analyses deal with small non-interacting sub-sets of loci, the approximations required for the analyses should hold. In practical terms, a transformation should be used which makes the joint response of the two variables linear. Even so the predictions are valid for relatively few cycles of selection because of the approximations required in the theory.

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