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Two-locus Theory in Recurrent Selection for General Combining Ability in Maize

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Summary. Two-locus theory for recurrent selection for general combining ability in maize was developed. The theory featured: (a) recombination of the selfed progeny of selected parents; and (b) linkage disequilibrium in the initial gametic array. The theory indicated: (a) that initial linkage disequilibrium exerts a permanent influence upon selection progress; (b) that interposition of one or more generations of random mating before each cycle reduces the permanent effect in ensuing cycles; and (c) that random mating done before initiation of selection is more efficient in removing the influence of linkage disequilibrium on selection progress than random mating done between subsequent cycles.

Key words: Maize – Corn – *Zea mays* L. – Recurrent selection – General combining ability

Introduction

In recurrent selection for general combining ability in maize, the foundation population is often formed by a random (or balanced) intermating of homozygous inbred lines. Usually, each of the lines is relatively superior for some economically important traits but is relatively inferior for others. For example, some lines may exhibit early maturity in hybrid combination but also transmit poor stalk quality. Other lines may generally confer high yield along with excessively high ear-placement, and so on. The aim of recurrent selection is usually the joint improvement of all traits which, when considered together, can be subsumed by a single trait called net merit. Net merit may be variously determined, but regardless of the method of determination, net merit will be assumed to be consistently measurable, numerically representable, and continuously distributed. The foundation set of inbred lines is representative of the initial gametic array of the population. With regard to net merit, then, the initial gametic array may often be in a state of linkage disequilibrium in which, with respect to the relatively favorable alleles in the allelic arrays of many pairs of loci, the frequency of repulsion phase gametes is in excess. Moreover, for even single traits, if the set of foundation inbred lines is nonrandomly chosen, the frequency of repulsion phase gametes may (though not necessarily) be in excess in the initial gametic array.

The gametic array is said to be in negative linkage disequilibrium when the frequency of repulsion gametes is in excess, and in positive linkage disequilibrium when the frequency of coupling gametes is in excess. If the initial array is in negative linkage disequilibrium, selection progress will be retarded. Consequently, the foundation population is often randomly mated for a number of generations prior to initiation of selection in order to dispel the influence of negative linkage disequilibrium on selection progress. If, however, the influence of initial linkage disequilibrium upon achieved gain is dissipated by random mating, a more efficient procedure might be to insert a number of random mating generations between selection cycles and reduce the number of random mating generations before starting selection.

In maize, individual plants from the population under selection (the selection population) are evaluated by means of testcrosses to a tester population. The testcrosses are evaluated in performance trials, and superior individuals are selected on the basis of their testcross performance. Because maize is an annual, the selected individuals themselves cannot be intermated to form the population base for the next cycle of selection. Rather, the selfed progeny (S1 families) of selected individuals are intercrossed by some procedure that approximates random mating to form the base of the next selection cycle.

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If (a) the top p percent of the individuals in the selection population are selected each cycle on the basis of their testcross performance, (b) the genetic effects for each pair of loci are small compared to the standard deviation of the testcross means, and (c) environmental effects are normally distributed with constant variance for all testcrosses, two-locus truncation selection theory can be employed to examine the influence of initial linkage disequilibrium on selection progress. Griffing (1962) presented one-locus, two-locus, and general theory of recurrent selection for general combining ability. The presentation of Griffing, however, did not address the problem of linkage disequilibrium in the initial gametic array nor did it make allowance for recombination of selfed progeny of selected individuals.

In this paper, two-locus selection theory that allows for initial linkage disequilibrium and recombination of selfed progeny of selcted individuals will be developed. The theory will be focused on the influence of random mating in dispelling the effect of initial linkage disequilibrium on selection progress.

Procedural Details and Genetic Consequences

To produce the selfed progeny and testcrosses, individual plants in the selection population are simultaneously self-pollinated and crossed as male parents, each to an equal number of randomly chosen plants in the tester population used as female parents. The tester population may be the selection population itself or a more or less unrelated population. The crossing procedure is often called a design I mating scheme because, presumably, of its resemblance to the Experiment I design outlined by Comstock and Robinson (1952). The number of plants used as female parents in each testcross is assumed to be large enough to reduce sampling variation to an acceptable level, and equal numbers of kernels from all females crossed by a common male are bulked to form the testcross of each male parent. Consequently, each testcross is assumed to have resulted from the union of a random sample of the gametes produced by an individual plant in the selection population with a random sample of the gametes produced by the entire tester population.

The set of testcrosses under performance-trial evaluation is called the testcross population. By virtue of the assumption of random sampling of gametes from the tester population, for each testcross in the testcross population, the expected value of the following genetic effects is zero: (a) all effects involving dominance; (b) all single-locus additive effects attributable to alleles from the tester population; and (c) all additive × additive epistatic effects attributable to the interaction of alleles from the selection population with alleles from the tester population. If the performance trials have been properly designed, the expected value of all environmental effects is also zero. If the gametic array from the tester population is not in linkage equilibrium, the expected value of the additive × additive epistatic effects attributable to alleles from the tester population is not zero. However, this expectation is constant over all testcrosses and is merely part of the testcross population mean. Consequently, the expected value of the deviation of each testcross mean from the testcross population mean is expressible as a function of the single-locus additive and additive × additive epistatic interaction effects attributable to alleles from the selection population. Because the genetic value of each individual in the selection population is measured by the magnitude of the deviation of its testcross mean from that of the testcross population, the genetic value of each individual is essentially determined by the value of its gametic array in combination with the gametic array of the tester and is expressable in terms of single-locus additive and additive × additive epistatic effects in the testcross population that are attributable to alleles from the selection population.

Theory

Let gamete $A_i B_k$ ($i = 1, 2, \ldots, g$; $k = 1, 2, \ldots, h$) occur in the initial gametic array with frequency p_{ik}. The gametic array is then $\Sigma\, p_{ik} A_i B_k$ (throughout, summation is over all subscripts, unless otherwise noted). Following random union of gametes, the genotypic array is $\Sigma\, p_{ik} p_{jl} A_i B_k / A_j B_l$ ($i, j = 1, 2, \ldots, g$; $k, l = 1, 2, \ldots, h$). The gametic array produced by $A_i B_k / A_j B_l$ is $(1/4)$ $[(1+\lambda) A_i B_k + (1-\lambda) A_i B_l + (1-\lambda) A_j B_k + (1+\lambda) A_j B_l]$, where $\lambda = 1 - 2\varrho$, ϱ being the recombination frequency (Schnell 1961). The expected value of the testcross mean of $A_i B_k / A_j B_l$ is $(1/4)$ $[(1+\lambda) Z_{ik} + (1-\lambda) Z_{il} + (1-\lambda) Z_{jk} + (1+\lambda) Z_{jl}]$, where Z_{ik} is the expected value of gamete $A_i B_k$ in the testcross population.

If truncation selection on the basis of testcross performance is imposed on the array $\Sigma\, p_{ik} p_{jl} A_i B_k / A_j B_l$, the genotypic array following selection is

$$\Sigma\, p_{ik} p_{jl} \left\{1 + (K/4\sigma^2)\left[(1+\lambda) z_{ik} + (1-\lambda) z_{il} + (1-\lambda) z_{jk} + (1+\lambda) z_{jl}\right]\right\} A_i B_k / A_j B_l, \text{ where } z_{ik} = Z_{ik} - \Sigma\, p_{ik} Z_{ik},$$

etc., K is the selection differential, and σ^2 is the variance of testcross means. The selfed progeny array is

$$(1/16)\,\Sigma\, p_{ik} p_{jl} \left\{1 + (K/4\sigma^2)\left[(1+\lambda) z_{ik} + (1-\lambda) z_{il} + (1-\lambda) z_{jk} + (1+\lambda) z_{jl}\right]\right\} \times \left\{(1+\lambda) A_i B_k + (1-\lambda) A_i B_l + (1-\lambda) A_j B_k + (1+\lambda) A_j B_l\right\}^2. \quad (1)$$

The gametic array produced by (1) is

$$(1/4)\,\Sigma\, p_{ik}\, p_{jl}\left\{1+(K/4\,\sigma^2)\,[(1+\lambda)\,z_{ik}+(1-\lambda)\,z_{il} +(1-\lambda)\,z_{jk}+(1+\lambda)\,z_{jl}]\right\} \times\left\{(1+\theta)\,A_i\,B_k+(1-\theta)\,A_i\,B_l+(1-\theta)\,A_j\,B_k +(1+\theta)\,A_j\,B_l\right\}, \quad (2)$$

where $\theta=(1/2)\,\lambda\,(1+\lambda)$.

In terms of the model $Z_{ik}=\mu+\alpha_i+\beta_k+\varepsilon_{ik}$, where μ, α_i, β_k, and ε_{ik} are the mean and the additive, and additive × additive interaction effects of A_i and B_k, respectively, in the testcross population when the selection population is at random mating and linkage equilibrium, (2) can be written as

$$\begin{aligned}\Sigma\,\{&[p_i\,p_k+(1/2)\,(1+\theta)\,\Delta_{ik}]\,[1+(K/2\,\sigma^2)\,(\alpha_i+\beta_k)]\\ &+[(1+\lambda\,\theta)\,p_i\,p_k+(1/2)\,(1+\lambda)\,(1+\theta)\,\Delta_{ik}]\\ &\quad\times(K/4\,\sigma^2)\,\varepsilon_{ik}\\ &+(1/2)\,(1-\theta)\,(K/2\,\sigma^2)\,(p_i\,\textstyle\sum_i\Delta_{ik}\,[\alpha_i+(1/2)\\ &\quad\times(1+\lambda)\,\varepsilon_{ik}]\\ &+p_k\,\textstyle\sum_k\Delta_{ik}\,[\beta_k+(1/2)\,(1+\lambda)\,\varepsilon_{ik}])\\ &+(1-\lambda)\,(1-\theta)\,(K/8\,\sigma^2)\,\textstyle\sum_{jl}\Delta_{il}\,\Delta_{jk}\,\varepsilon_{jl}\\ &-[(1+\lambda)\,(1+\theta)\,(p_i\,p_k+\Delta_{ik})+2\,(1+\lambda)\,(1-\theta)\,p_i\,p_k]\\ &\quad\times(K/8\,\sigma^2)\,\Sigma\,\Delta_{ik}\,\varepsilon_{ik}\}\,A_i\,B_k. \end{aligned}\quad (3)$$

By ignoring second order terms and assuming that the genetic effects change very little during selection, the gametic array produced by the selfed progeny of selected parents of the n^{th} cycle is approximately

$$\begin{aligned}\Sigma\,\{&[p_i\,p_k+\Phi^n\,\Delta_{ik}]\,[1+(n\,K/2\,\sigma^2)\,(\alpha_i+\beta_k)]\\ &+[\textstyle\sum_{r=0}^{n-1}\Phi^r(1+\lambda\,\theta)\,p_i\,p_k+n\,(1+\lambda)\,\Phi^n\,\Delta_{ik}]\\ &\quad\times(K/4\,\sigma^2)\,\varepsilon_{ik}\\ &+(1/2)\,(1-\theta)\textstyle\sum_{r=0}^{n-1}(r+1)\,\Phi^r(K/2\,\sigma^2)\,(p_i\sum_i\Delta_{ik}\,[\alpha_i\\ &+(1/2)\,(1+\lambda)\,\varepsilon_{ik}]+p_k\textstyle\sum_k\Delta_{ik}\,[\beta_k+(1/2)\,(1+\lambda)\,\varepsilon_{ik}])\\ &+(1-\lambda)\,(1-\theta)\textstyle\sum_{r=n-1}^{2(n-1)}\Phi^r(K/8\,\sigma^2)\sum_{jl}\Delta_{il}\,\Delta_{jk}\,\varepsilon_{jl}\\ &-(1+\lambda)\,[(n/2)\,\Phi^n\,(p_i\,p_k+\Delta_{ik})+(1-\Phi)\textstyle\sum_{r=0}^{n-1}(r+1)\\ &\times\Phi^r\,p_i\,p_k]\,(K/2\,\sigma^2)\,\Sigma\Delta_{ik}\,\varepsilon_{ik}\}\,A_i\,B_k, \end{aligned}\quad (4)$$

where $\Phi=(1/2)\,(1+\theta)$.

By assuming the value of $A_i\,B_k$ in the testcross population to be $Z_{ik}=\mu+\alpha_i+\beta_k+\varepsilon_{ik}$, and by applying the algebraic device for obtaining the n^{th} partial sum of a geometric series to appropriate terms in (4), the testcross mean of selfed progeny of plants selected in the n^{th} cycle is approximately

$$\begin{aligned}\mu_n=\mu&+\Phi^n\,\Sigma\Delta_{ik}\,\varepsilon_{ik}\\ &+(K/\sigma^2)\,\{(n/4)\,\sigma_A^2+(1/16)\,(1+\lambda\,\theta)\,(1-\Phi^n)\\ &\quad\times(1-\Phi)^{-1}\,\sigma_{AA}^2\\ &+(1-\Phi^n)\,(1-\Phi)^{-1}\,\Sigma\Delta_{ik}\,\alpha_i\,\beta_k\\ &+[(n/2)\,\Phi^n+(1/4)\,(1+\lambda)\,(1-\Phi^n)\,(1-\Phi)^{-1}]\,\Sigma\Delta_{ik}\\ &\quad\times(\alpha_i+\beta_k)\,\varepsilon_{ik}\\ &+(1/4)\,(1+\lambda)\,\Phi^n\,[\Sigma\Delta_{ik}\,\varepsilon_{ik}^2-(\Sigma\Delta_{ik}\,\varepsilon_{ik})^2]\\ &+(1/4)\,(1-\lambda)\,\Phi^{(n-1)}\,(1-\Phi^n)\,\Sigma\Delta_{il}\,\Delta_{jk}\,\varepsilon_{ik}\,\varepsilon_{jl}\}, \end{aligned}\quad (5)$$

where $\sigma_A^2=2\,\Sigma\,p_i\,p_k\,(\alpha_i^2+\beta_k^2)$, and $\sigma_{AA}^2=4\,\Sigma\,p_i\,p_k\,\varepsilon_{ik}^2$. Because of the assumption of constancy of genetic effects, which holds only if gene frequencies remain constant, the approximations (4) and (5) are good for only a few selection cycles.

If the population from the n^{th} cycle is randomly mated without selection for m generations, the mean decomposes to approximately

$$\begin{aligned}\mu_{n.m}=\mu&+\Psi^m\,\Phi^n\,\Sigma\Delta_{ik}\,\varepsilon_{ik}\\ &+(K/\sigma^2)\,\{(n/4)\,\sigma_A^2+(1/16)\,(1+\lambda\,\theta)\,\Psi^m\,(1-\Phi^n)\\ &\quad\times(1-\Phi)^{-1}\,\sigma_{AA}^2\\ &+(1-\Phi^n)\,(1-\Phi)^{-1}\,\Sigma\Delta_{ik}\,\alpha_i\,\beta_k+[(n/2)\,\Phi^n\\ &+(1/4)\,(1+\lambda)\,(1-\Phi^n)\,(1-\Phi)^{-1}]\,\Sigma\Delta_{ik}\,(\alpha_i+\beta_k)\,\varepsilon_{ik}\\ &+(1/4)\,(1+\lambda)\,\Psi^m\,\Phi^n\,[\Sigma\Delta_{ik}\,\varepsilon_{ik}^2-(\Sigma\Delta_{ik}\,\varepsilon_{ik})^2]\\ &+(1/4)\,(1-\lambda)\,\Psi^m\,\Phi^{(n-1)}\,(1-\Phi^n)\,\Sigma\Delta_{il}\,\Delta_{jk}\,\varepsilon_{ik}\,\varepsilon_{jl}\}, \end{aligned}\quad (6)$$

where $\Psi=(1/2)(1+\lambda)$.

If t generations of random mating are interposed before each generation of selection, including the first, the gametic array after $n\,(t+1)$ generations is approximately

$$\begin{aligned}\Sigma\,\{&[p_i\,p_k+\Phi^n\,\Psi^{nt}\Delta_{ik}]\,[1+(n\,K/2\,\sigma^2)\,(\alpha_i+\beta_k)]\\ &+[\textstyle\sum_{r=0}^{n-1}\Phi^r\,\Psi^{rt}\,(1+\lambda\,\theta)\,p_i\,p_k+n\,(1+\lambda)\,\Phi^n\,\Psi^{nt}\Delta_{ik}]\\ &\quad\times(K/4\,\sigma^2)\,\varepsilon_{ik}\\ &+[(1-\Phi)\,(\Psi^t)\textstyle\sum_{r=0}^{n-1}\Phi^r\,\Psi^{rt}+(1-\Phi\Psi^t)\sum_{r=1}^{n-1}r\,\Phi^r\,\Psi^{rt}]\\ &\quad\times(K/2\,\sigma^2)\,(p_i\textstyle\sum_i\Delta_{ik}\,[\alpha_i+(1/2)\,(1+\lambda)\,\varepsilon_{ik}]\\ &+p_k\textstyle\sum_k\Delta_{ik}\,[\beta_k+(1/2)\,(1+\lambda)\,\varepsilon_{ik}])\\ &+(1-\lambda)\,(1-\theta)\textstyle\sum_{r=n-1}^{2(n-1)}\Phi^r\,\Psi^{2rt}\,(K/8\,\sigma^2)\sum_{jl}\Delta_{il}\,\Delta_{jk}\,\varepsilon_{jl}\\ &-(1+\lambda)\,[(n/2)\,\Phi^n\,\Psi^{nt}\,(p_i\,p_k+\Delta_{ik})+(1-\Phi)\,(\Psi^t)\\ &\quad\times\textstyle\sum_{r=0}^{n-1}\Phi^r\,\Psi^{rt}\,p_i\,p_k\\ &+(1-\Phi\,\Psi^t)\textstyle\sum_{r=1}^{n-1}r\,\Phi^r\,\Psi^{rt}\,p_i\,p_k]\,(K/2\,\sigma^2)\,\Sigma\Delta_{ik}\,\varepsilon_{ik}\}\,A_i\,B_k, \end{aligned}\quad (7)$$

and the mean is approximately

$$\begin{aligned}\mu_{n(t+1)}=\mu&+\Phi^n\,\Psi^{nt}\,\Sigma\Delta_{ik}\,\varepsilon_{ik}\\ &+(K/\sigma^2)\,\{(n/4)\,\sigma_A^2+(1/16)\,(1+\lambda\,\theta)\\ &\quad\times(1-\Phi^n\,\Psi^{nt})\,(1-\Phi\,\Psi^t)^{-1}\,\sigma_{AA}^2\\ &+\Psi^t\,(1-\Phi^n\,\Psi^{nt})\,(1-\Phi\,\Psi^t)^{-1}\,\Sigma\Delta_{ik}\,\alpha_i\,\beta_k\\ &+[(n/2)\,\Phi^n\,\Psi^{nt}+(1/4)\,(1+\lambda)\,\Psi^t(1-\Phi^n\,\Psi^{nt})\\ &\quad\times(1-\Phi\,\Psi^t)^{-1}]\,\Sigma\Delta_{ik}\,(\alpha_i+\beta_k)\,\varepsilon_{ik}\\ &+(1/4)\,(1+\lambda)\,\Phi^n\,\Psi^{nt}\,[\Sigma\Delta_{ik}\,\varepsilon_{ik}^2-(\Sigma\Delta_{ik}\,\varepsilon_{ik})^2]\\ &+(1/8)\,(1-\lambda)\,(1-\theta)\,\Phi^{(n-1)}\,\Psi^{2(n-1)t}\,(1-\Phi^n\,\Psi^{2nt})\\ &\quad\times(1-\Phi\,\Psi^{2t})^{-1}\,\Sigma\Delta_{il}\,\Delta_{jk}\,\varepsilon_{ik}\,\varepsilon_{jl}\}. \end{aligned}\quad (8)$$

For $t=0$, Eqs. (5) and (8) are identical.

Experimental evidence suggests that epistasis is unimportant in the inheritance of most quantitative traits of maize (Sprague and Eberhart 1977). If epistasis

is ignored, Eq. (8) reduces to

$$\mu_{n(t+1)} = \mu + (K/\sigma^2)\,[(n/4)\,\sigma_A^2 + \Psi^t(1-\Phi^n\,\Psi^{nt}) \times (1-\Phi\,\Psi^t)^{-1}\,\Sigma\,\Delta_{ik}\,\alpha_i\,\beta_k]. \quad (9)$$

The relative reduction in selection progress over n cycles of selection due to initial disequilibrium is

$$R_n = 1 - \Psi^t(1-\Phi^n\,\Psi^{nt})\,[(1-\Phi\,\Psi^t)\,(n/4)\,\sigma_A^2]^{-1}\,\Sigma\,\Delta_{ik}\,\alpha_i\,\beta_k. \quad (10)$$

For $s \leqq n$, the relative influence of initial disequilibrium on gain from the $(s-1)^{th}$ to the s^{th} cycle, compared to the cumulative influence of initial disequilibrium over n cycles with no random mating generations interposed, is

$$D_{s(s-1)/n} = \Phi^{(s-1)}\,\Psi^{st}\,(1-\Phi)\,(1-\Phi^n)^{-1}. \quad (11)$$

For fixed s and variable t, Eq. (11) indicates the relative effect of random mating between any two given consecutive cycles. For fixed t and variable s, Eq. (11) gives the relative influence of random mating across succeeding cycles.

Table 1. Percent reduction in selection gain over three cycles of selection for several levels of initial negative linkage disequilibrium, degrees of linkage (λ), and numbers of random mating generations interposed prior to each selection cycle (t). The trait under selection is governed by two loci with equal and additive effects, and each locus is segregating initially for two equally frequent alleles

λ	t	Negative linkage disequilibrium of initial gametic array			
		1/32	1/16	1/8	1/4
0	0	7	15	29	58
	1	3	5	11	22
	2	1	2	5	10
	3	1	1	2	4
0.25	0	8	16	32	64
	1	4	8	16	31
	2	2	4	8	17
	3	1	2	5	9
0.50	0	9	18	36	72
	1	6	11	22	45
	2	4	7	14	29
	3	2	5	10	19
0.75	0	10	21	42	84
	1	8	16	33	66
	2	6	13	26	52
	3	5	10	21	42
0.99	0	12	25	50	99
	1	12	25	49	98
	2	12	24	49	97
	3	12	24	48	96

Table 2. Percent influence of initial linkage disequilibrium on selection gain from cycle to cycle compared to the cumulative influence of initial disequilibrium over three cycles with no random mating generations interposed

λ	t	Consecutive selection cycles		
		0–1	1–2	2–3
0	0	57	29	14
	1	29	14	7
	2	14	7	4
	3	7	4	2
0.25	0	52	30	17
	1	33	19	11
	2	20	12	7
	3	13	7	4
0.50	0	46	32	22
	1	35	24	16
	2	26	18	12
	3	20	13	9
0.75	0	40	33	27
	1	35	29	24
	2	30	25	21
	3	27	22	18
0.99	0	34	33	33
	1	33	33	33
	2	33	33	33
	3	33	33	33

Numerical Example

Consider a symmetrical genetic model in which both loci have equal and additive effects, and each locus segregates initially for two equally frequent alleles. The initial gametic array is

$$(1/4+\Delta_{11})\,A_1\,B_1 + (1/4+\Delta_{12})\,A_1\,B_2 + (1/4+\Delta_{21})\,A_2\,B_1 + (1/4+\Delta_{22})\,A_2\,B_2.$$

In this array, $\Delta_{11} = \Delta_{22} = -\Delta_{12} = -\Delta_{21}$. Let A_1 and B_1 denote the favorable alleles at their respective loci. Then, if $\Delta_{11} = \Delta_{22} > 0$, the array is in positive linkage disequilibrium; but if $\Delta_{11} = \Delta_{22} < 0$, the array is in negative linkage disequilibrium. In this model, the maximum possible disequilibrium is one-fourth.

By use of Eq. (10), the percent reduction in selection gain over three cycles for several levels of linkage disequilibrium, degrees of linkage, and numbers of random mating generations interposed prior to each selection cycle was calculated (Table 1). For all degrees of linkage, initial disequilibrium reduced progress, and interposition of one or more random mating generations before each cycle tempered the effect of initial disequilibrium.

By use of Eq. (11), the relative influence of initial disequilibrium on selection gain from cycle to cycle was

calculated. For all degrees of linkage, the influence of initial disequilibrium diminished with each succeeding cycle; and, as a consequence, the effect of random mating on reducing the influence of initial disequilibrium declined as well.

Discussion

Since the population mean can change only through alteration of the gametic array, expression (2) indicates that, in general, selection gain will be a function of the covariance of parent and selfed progeny, each being evaluated in the testcross population. With no initial linkage disequilibrium, Eqs. (5) and (6) are consistent with the results of Griffing (1962) with due allowances, of course, for: (a) differences in notation; (b) the linkage parameter θ, appropriate to the gametic array of the selfed progeny; and (c) presentation herein of summation series in partial summation form.

Equations (5) and (6) indicate that initial disequilibrium has a permanent effect upon selection progress, even after selection is relaxed. The permanent influence of disequilibrium is limited to cross product terms involving single-locus additive effects. Disequilibrium effects involving pure epistasis are dissipated upon relaxation of selection. Equation (8) indicates that interposition of one or more generations of random mating between cycles will not dissipate the permanent effect of disequilibrium upon achieved gain but will reduce the permanent effect in future cycles by forcing the gametic array closer to linkage equilibrium. Thus, since epistasis is relatively unimportant in maize, random mating done prior to initiation of selection should be more efficient in reducing the influence of initial disequilibrium than random mating done between succeeding cycles.

If the trait under selection is governed by many loci that are fairly evenly distributed over the genome, the average degree of linkage will probably be near zero. Nonetheless, Eq. (10) and the numerical results in Table 1 suggest that selection progress can be impeded by even small initial negative disequilibrium between independent loci. Equation (11) and the numerical results in Table 2 also indicate that reduction of the influence of initial disequilibrium on progress is accomplished most efficiently by random mating done prior to initiation of selection. Averaged over all pairs of loci, initial disequilibrium should usually be moderate or small. In most practical situations, three generations of random mating prior to initiation of selection should nullify the influence of initial disequilibrium on gain. Fewer random mating generations would likely be necessary if negative correlations between important traits in the initial array of inbred lines were small or absent.

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