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Effects of Two-locus Linkage Disequilibrium on Progress from Reciprocal Recurrent Selection in Maize

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Summary. Because each population in a reciprocal recurrent selection program can be dually described as a tester for its reciprocal and as a population subject to selection, selection progress can be partitioned into algebraic terms that are (a) unaffected by initial linkage disequilibrium, (b) modified exclusively by initial linkage disequilibrium in the selection populations, (c) influenced solely by initial linkage disequilibrium in the tester populations, and (d) modulated jointly by initial linkage disequilibrium in both populations. If only additive genetic effects are present in the intercross population, linkage disequilibrium affects selection progress via only the selection populations. Initial linkage disequilibrium affects selection progress via the tester populations, and/or the selection and tester populations jointly, only in the presence of epistatic effects for which, out of all alleles involved in the interaction, two alleles emanate from the tester population. If only additive × additive epistasis is present, initial linkage disequilibrium affects progress via both the selection and tester populations, but the effect is permanent via only the selection populations. The effect of initial linkage disequilibrium via the tester populations, and/or the selection and tester populations jointly, is permanent only in the presence of additive × dominance and/or dominance × dominance epistasis in the intercross population.

Key words: Corn – *Zea mays* L. – Linkage – Reciprocal recurrent selection – Recombination

Introduction

The reciprocal recurrent selection procedure was proposed by Comstock et al. (1949). The purpose of the scheme was to improve the intercross population, M × N, of two separately maintained populations, M and N. In this selection method, plants in population M are simultaneously self-pollinated and crossed as male parents, each to an equal number of randomly chosen plants in population N used as female parents. Likewise, a number of plants in population N are simultaneously self-pollinated, and each is crossed to an equal number of randomly chosen plants in population M. Equal numbers of kernels from each female crossed by a common male are bulked to form the testcross of each male parent. The number of female parents in each testcross is assumed to be large enough to reduce sampling error to an acceptable level. Consequently, each testcross is assumed to have resulted from the union of a random sample of gametes from a single plant from one or the other of the populations with a sample of gametes drawn at random from the entire gametic array of the reciprocal population.

The testcrosses are evaluated in performance trials. Since all plants in each testcross are sired by a common male parent, the testcrosses are often called half-sib families. Consequently, in recent years, the selection method has received the adjuncted appellation of half-sib reciprocal recurrent selection (Hallauer and Miranda, Fo. 1981). Individual males from each population are selected on the basis of testcross performance, and the S1 progenies of selected individuals are separately intercrossed by a procedure that approximates random mating to form the bases of populations M and N for the next cycle of selection and recombination. The crucial features of the procedure are that (a) each population serves as a tester for individuals in the reciprocal population, (b) individuals are selected on the basis of testcross, or half-sib family, means, and (c) S1 progenies of selected individuals are recombined only within populations. Because half-sib family means are the units of selection, selection of individuals in both populations is made on the basis of general combining ability with the reciprocal population; and, because S1 progenies of selected individuals are recombined only

within each population, no genes are transferred between populations.

Griffing (1962) presented prediction formulae for gain from n cycles of reciprocal recurrent selection, followed by t generations of random mating without selection, for a two-locus model in which both populations are initially at linkage equilibrium. The prediction formulae indicated that permanent shifts in gene frequency are solely a function of the additive effects of the genes in the intercross population. The formulae also revealed that, although additive × additive epistatic effects are instrumental in immediate response to selection, only those due to epistatic effects of genes at locus-pairs from the same population contribute. Johnson (1982) developed prediction theory for progress from simple recurrent selection for a two-locus model that allowed for linkage disequilibrium in the initial gametic array of the population under selection and stipulated recombination of the self-derived progenies of selected parents. The theory suggested that initial disequilibrium permanently affects selection progress and that, if epistasis exists, additive × additive epistatic effects attributable to alleles from the population under selection are incident to the distortion.

The purpose of this paper is to present prediction formulae for gain from reciprocal recurrent selection based on a two-locus model that admits initial linkage disequilibrium in both populations and requires recombination of self-derived progenies of selected individuals. The following assumptions applicable to truncation selection will hold: (a) individuals constituting the top p percent of each population are selected each cycle on the basis of testcross performance; (b) the genetic effects at each locus-pair are small in comparison to the standard deviation of testcross means; and (c) the phenotypic variability, due to environmental and background genetic effects at numerous segregating loci, of testcross means is normally distributed with equal variance for each population. The assumption that genetic effects at each locus-pair are small in comparison to the standard deviation of testcross means implies that changes in the magnitudes of the genetic effects will be a relatively small and can reasonably be ignored for a few selection cycles. Over a large number of cycles, changes in the magnitudes of the genetic effects could be appreciable and would cause the prediction formulae to become increasingly inaccurate. Consequently, the formulae to be presented are valid only for a few cycles of selection.

Theory

Let the initial gametic arrays in populations M and N be $g_{M_0} = \sum p_{ik} A_i B_k$ $(i = 1, 2, \ldots, a;\ k = 1, 2, \ldots, b)$ and $g_{N_0} = \sum p_{rt} A_r B_t$ $(r = 1, 2, \ldots, e;\ t = 1, 2, \ldots, f)$, respectively, where p_{ik} is the frequency of gamete $A_i B_k$ (summation is over all subscripts unless otherwise indicated). Random union of gametes between arrays g_{M_0} and g_{N_0} produces the initial intercross population genotypic array $G_{M_0 \times N_0} = \sum p_{ik} p_{rt} A_i B_k / A_r B_t$. Let the genotypic value of $A_i B_k / A_r B_t$ be denoted as

$$Y_{ikrt} = \mu + \alpha_i + \beta_k + \alpha_r + \beta_t + \delta_{ir} + \gamma_{kt} + \varepsilon_{ik} + \varepsilon_{it} + \varepsilon_{rk} + \varepsilon_{rt} + \tau_{irt} + \eta_{krt} + \tau_{ikr} + \eta_{ikt} + \omega_{ikrt}. \quad (1)$$

The parameters of the model (1) are the dually defined genetic effects (Stuber and Cockerham 1966) of an intercross population for which the parental gametic arrays g_{M_0} and g_{N_0} are in linkage equilibrium; i.e., $p_{ik} = p_i p_k$, $p_{rt} = p_r p_t$ for $p_i = \sum_k p_{ik}$, $p_k = \sum_i p_{ik}$, $p_r = \sum_t p_{rt}$, and $p_t = \sum_r p_{rt}$. With regard to the linkage equilibrium intercross population, μ is the mean; α_i and β_k are the additive effects of alleles A_i and B_k, respectively; δ_{ir} and γ_{kt} are the dominance effects attributable to the intralocus interactions within the allele duplexes (A_i, A_r) and (B_k, B_t), respectively; ε_{ik} is the additive × additive interaction effect attributable to the interlocus interaction within the duplex (A_i, B_k); τ_{irt} and η_{krt} are the additive × dominance interaction effects attributable to interactions within the triplets (A_i, A_r, B_t) and (A_r, B_k, B_t), respectively; and ω_{ikrt} is the dominance × dominance interaction effect attributable to interaction within the quadruplet (A_i, A_r, B_k, B_t). Remaining parameters have the obvious similar definitions.

The mean of the initial intercross population in terms of the model (1) is

$$\mu_{M_0 \times N_0} = \sum p_{ik} p_{rt} Y_{ikrt} = \mu + E_M + E_N + \Xi_{MN}, \quad (2)$$

where $E_M = \sum \Delta_{ik} \varepsilon_{ik}$, $E_N = \sum \Delta_{rt} \varepsilon_{rt}$, and $\Xi_{MN} = \sum \Delta_{ik} \Delta_{rt} \omega_{ikrt}$ for $\Delta_{ik} = p_{ik} - p_i p_k$ and $\Delta_{rt} = p_{rt} - p_r p_t$.

Random union of gametes within the arrays g_{M_0} and g_{N_0} produces the intrapopulation genotypic arrays:

$$G_{M_0 \times M_0} = \sum p_{ik} p_{jl} A_i B_k / A_j B_l$$

and

$$G_{N_0 \times N_0} = \sum p_{rt} p_{sv} A_r B_t / A_s B_v,$$

respectively. The gametic arrays produced by $A_i B_k / A_j B_l$ and $A_r B_t / A_s B_v$ are

$$(1/4)\,[(1+\lambda)\,A_i B_k + (1-\lambda)\,A_i B_l + (1-\lambda)\,A_j B_k + (1+\lambda)\,A_j B_l]$$

and

$$(1/4)\,[(1+\lambda)\,A_r B_t + (1-\lambda)\,A_r B_v + (1-\lambda)\,A_s B_t + (1+\lambda)\,A_s B_v],$$

respectively, where λ is the linkage coefficient (Schnell 1961).

Random mating of individuals in population M with those in population N produces the genotypic array:

$$G_{(MN)_0} = (1/16) \sum p_{ik}\, p_{jl}\, p_{rt}\, p_{sv} [(1+\lambda)^2 (A_i B_k/A_r B_t + \ldots + A_j B_l/A_s B_v) + (1-\lambda^2)(A_i B_k/A_r B_v + \ldots + A_i B_l/A_s B_v + A_j B_k/A_r B_t + \ldots + A_j B_l/A_s B_t) + (1-\lambda)^2 (A_i B_l/A_r B_v + \ldots + A_j B_k/A_s B_t)]. \quad (3)$$

In terms of (1), the genotypic value of the progeny of the mating of $A_i B_k/A_j B_l$ with $A_r B_t/A_s B_v$ is

$$\begin{aligned} Y_{ikjlrtsv} &= \mu + (1/2)(\alpha_i + \beta_k + \alpha_j + \beta_l + \alpha_r + \beta_t + \alpha_s + \beta_v) \\ &+ (1/4)(\delta_{ir} + \delta_{is} + \delta_{jr} + \delta_{js} + \gamma_{kt} + \gamma_{kv} + \gamma_{lt} + \gamma_{lv}) \\ &+ (1/4)(1+\lambda)(\varepsilon_{ik} + \varepsilon_{jl} + \varepsilon_{rt} + \varepsilon_{sv}) \\ &+ (1/4)(1-\lambda)(\varepsilon_{il} + \varepsilon_{jk} + \varepsilon_{rv} + \varepsilon_{st}) \\ &+ (1/8)(1+\lambda)(\tau_{irt} + \eta_{krt} + \tau_{jrt} + \eta_{lrt} + \tau_{ikr} + \eta_{ikt} + \tau_{iks} + \eta_{ikv} + \tau_{isv} + \eta_{ksv} + \tau_{jsv} + \eta_{lsv} + \tau_{jlr} + \eta_{jlt} + \tau_{jls} + \eta_{jlv}) \\ &+ (1/8)(1-\lambda)(\tau_{irv} + \eta_{krv} + \tau_{jrv} + \eta_{lrv} + \tau_{ilr} + \eta_{ilt} + \tau_{ils} + \eta_{ilv} + \tau_{ist} + \eta_{kst} + \tau_{jst} + \eta_{lst} + \tau_{jkr} + \eta_{jkt} + \tau_{jks} + \eta_{jkv}) \\ &+ (1/16)(1+\lambda)^2 (\omega_{ikrt} + \omega_{iksv} + \omega_{jlrt} + \omega_{jlsv}) \\ &+ (1/16)(1-\lambda^2)(\omega_{ikrv} + \omega_{ikst} + \omega_{ilrt} + \omega_{ilsv} + \omega_{jkrt} + \omega_{jksv} + \omega_{jlrv} + \omega_{jlst}) \\ &+ (1/16)(1-\lambda)^2 (\omega_{jlrv} + \omega_{ilst} + \omega_{jkrv} + \omega_{jkst}). \end{aligned} \quad (4)$$

The mean of the genotypic array (3) is then

$$\mu_{(MN)_0} = \sum p_{ik}\, p_{jl}\, p_{rt}\, p_{sv}\, Y_{ikjlrtsv} = \mu + \psi E_M + \psi E_N + \psi^2 \Xi_{MN}, \quad (5)$$

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

The genotypic arrays in populations M and N following truncation selection of individuals based on testcross performance are

$$\begin{aligned} \tilde{G}_{M_0} &= \sum p_{ik}\, p_{jl} \{1 + (K/2\sigma^2)[(\alpha_i + \psi Z_i) + (\beta_k + \psi H_k) + (\alpha_j + \psi Z_j) + (\beta_l + \psi H_l) \\ &+ \psi(\varepsilon_{ik} + \psi \Omega_{ik}) + (1-\psi)(\varepsilon_{il} + \psi \Omega_{il}) + (1-\psi)(\varepsilon_{jk} + \psi \Omega_{jk}) + \psi(\varepsilon_{jl} + \psi \Omega_{jl}) \\ &- 2\psi (E_M + \psi \Xi_{MN})]\} A_i B_k/A_j B_l, \end{aligned} \quad (6)$$

and

$$\begin{aligned} \tilde{G}_{N_0} &= \sum p_{rt}\, p_{sv} \{1 + (K/2\sigma^2)[(\alpha_r + \psi Z_r) + (\beta_t + \psi H_t) \\ &+ (\alpha_s + \psi Z_s) + (\beta_v + \psi H_v) + \psi(\varepsilon_{rt} + \psi \Omega_{rt}) \\ &+ (1-\psi)(\varepsilon_{rv} + \psi \Omega_{rv}) + (1-\psi)(\varepsilon_{st} + \psi \Omega_{st}) \\ &+ \psi(\varepsilon_{sv} + \psi \Omega_{sv}) - 2\psi (E_N + \psi \Xi_{MN})]\} A_r B_t/A_s B_v, \end{aligned} \quad (7)$$

respectively, where K is the selection differential, σ^2 is the phenotypic variance of testcross means for both populations, $Z_i = \sum_{rt} \Delta_{rt}\, \tau_{irt}$, $H_k = \sum_{rt} \Delta_{rt}\, \eta_{krt}$, and $\Omega_{ik} = \sum_{rt} \Delta_{rt}\, \omega_{ikrt}$, etc.

The gametic arrays produced by the selfed progeny of selected individuals in populations M and N are

$$\begin{aligned} g_{M_1} &= \sum \{[p_i p_k + \varphi \Delta_{ik}][1 + (K/2\sigma^2) \times (\alpha_i + \psi Z_i + \beta_k + \psi H_k)] \\ &+ (1-\varphi)(K/2\sigma^2)\, p_i \sum_i \Delta_{ik} [\alpha_i + \psi Z_i + \psi(\varepsilon_{ik} + \psi \Omega_{ik})] + (1-\varphi)(K/2\sigma^2)\, p_k \\ &\times \sum_k \Delta_{ik} [\beta_k + \psi H_k + \psi(\varepsilon_{ik} + \psi \Omega_{ik})] \\ &+ [(1-\psi)(1-\varphi) p_i p_k + \psi\varphi (p_i p_k + \Delta_{ik})](K/2\sigma^2) \\ &\times [\varepsilon_{ik} + \psi \Omega_{ik}] + (1-\psi)(1-\varphi)(K/2\sigma^2) \sum_{jl} \Delta_{il} \Delta_{jk} \\ &\times [\varepsilon_{jl} + \psi \Omega_{jl}] - [2\psi(1-\varphi) p_i p_k + \psi\varphi (p_i p_k + \Delta_{ik})] \\ &\times (K/2\sigma^2)[E_M + \psi \Xi_{MN}]\} A_i B_k, \end{aligned} \quad (8)$$

and

$$\begin{aligned} g_{N_1} &= \sum \{[p_r p_t + \varphi \Delta_{rt}][1 + (K/2\sigma^2)(\alpha_r + \psi Z_r + \beta_t + \psi H_t)] \\ &+ (1-\varphi)(K/2\sigma^2)\, p_r \\ &\times \sum_r \Delta_{rt} [\alpha_r + \psi Z_r + \psi(\varepsilon_{rt} + \psi \Omega_{rt})] \\ &+ (1-\varphi)(K/2\sigma^2)\, p_t \\ &\times \sum_t \Delta_{rt} [\beta_t + \psi H_t + \psi(\varepsilon_{rt} + \psi \Omega_{rt})] \\ &+ [(1-\psi)(1-\varphi) p_r p_t + \psi\varphi (p_r p_t + \Delta_{rt})] \\ &\times (K/2\sigma^2)[\varepsilon_{rt} + \psi \Omega_{rt})] \\ &+ (1-\psi)(1-\varphi)(K/2\sigma^2) \sum_{sv} \Delta_{rv} \Delta_{st} [\varepsilon_{sv} + \psi \Omega_{sv}] \\ &- [2\psi(1-\varphi) p_r p_t + \Psi\varphi (p_r p_t + \Delta_{rt})](K/2\sigma^2) \\ &\times [E_N + \Xi_{MN}]\} A_r B_t, \end{aligned} \quad (9)$$

respectively, where $\varphi = (1/2)[1 + (1/2)\lambda(1+\lambda)]$.

If second order terms are ignored, the gametic arrays produced after n cycles of selection followed by m generations of random mating in each population without selection is

$$\begin{aligned} g_{M_{n,m}} &= \sum ([p_i p_k + \psi^m \varphi^n \Delta_{ik}][1 + (K/2\sigma^2) \times \{n(\alpha_i + \beta_k) + \psi\, \pi(n)(Z_i + H_k)\}] \\ &+ p_i (K/2\sigma^2) \sum_i \Delta_{ik} [\{\pi(n) - n\psi^m \varphi^n\}\{\alpha_i + \psi \varepsilon_{ik}\} \\ &+ \psi\, \pi(n)\{\Upsilon(n) - \psi^m \varphi^n\}\{Z_i + \psi \Omega_{ik}\}] \\ &+ p_k (K/2\sigma^2) \sum_k \Delta_{ik} [\{\pi(n) - n\psi^m \varphi^n\}\{\beta_k + \psi \varepsilon_{ik}\} \\ &+ \psi\, \pi(n)\{\Upsilon(n) - \psi^m \varphi^n\}\{H_k + \psi \Omega_{ik}\}] \\ &+ \psi^m [(1-\psi)(1-\varphi) + \psi\varphi]\, p_i p_k (K/2\sigma^2) \\ &\times [\pi(n)\, \varepsilon_{ik} + \psi\, n\, \varphi^{(n-1)} \Omega_{ik}] \end{aligned}$$

$$+\psi^{(m+1)}\varphi^{n}\Delta_{ik}\,(K/2\sigma^2)\,[n\,\varepsilon_{ik}+\psi\,\pi\,(n)\,\Omega_{ik}]$$
$$+\psi^{m}(1-\psi)\,(1-\varphi)\,\varphi^{(n-1)}\,(K/2\sigma^2)$$
$$\times\sum_{jl}\Delta_{il}\,\Delta_{jk}\,\pi\,(n)\,[\varepsilon_{jl}+\psi\,\Upsilon(n)\,\Omega_{jl}]$$
$$-\psi\,p_i\,p_k\,(K/2\sigma^2)\,[\{2\,\pi\,(n)-n\,\psi^{m}\varphi^{n}\}\,E_M$$
$$-\psi\,\pi\,(n)\,\{2\,\Upsilon(n)-\psi^{m}\varphi^{n}\}\,\Xi_{MN}]$$
$$-\psi^{(m+1)}\varphi^{n}\,\pi\,(n)\,\Delta_{ik}\,(K/2\sigma^2)$$
$$\times[E_M+\psi\,\Upsilon(n)\,\Xi_{MN}])\,A_i\,B_k, \qquad (10)$$

and

$$g_{N_{n\cdot m}}=\sum([p_r\,p_t+\psi^{m}\varphi^{n}\Delta_{rt}]\,[1+(K/2\sigma^2)$$
$$\times\{n\,(\alpha_r+\beta_t)+\psi\,\pi\,(n)\,(Z_r+H_t)\}]$$
$$+p_r\,(K/2\sigma^2)\sum_{r}\Delta_{rt}\,[\{\pi\,(n)-n\,\psi^{m}\varphi^{n}\}\,\{\alpha_r+\psi\,\varepsilon_{rt}\}$$
$$+\psi\,\pi\,(n)\,\{\Upsilon(n)-\psi^{m}\varphi^{n}\}\,\{Z_r+\psi\,\Omega_{rt}\}]$$
$$+p_t\,(K/2\sigma^2)\sum_{t}\Delta_{rt}\,[\{\pi\,(n)-n\,\psi^{m}\varphi^{n}\}\,\{\beta_t+\psi\,\varepsilon_{rt}\}$$
$$+\psi\,\pi\,(n)\,\{\Upsilon(n)-\psi^{m}\varphi^{n}\}\,\{H_t+\psi\,\Omega_{rt}\}]$$
$$+\psi^{m}\,[(1-\psi)\,(1-\varphi)+\psi\,\varphi]\,p_r\,p_t\,(K/2\sigma^2)$$
$$\times[\pi\,(n)\,\varepsilon_{rt}+\psi\,n\,\varphi^{(n-1)}\,\Omega_{rt}]$$
$$+\psi^{(m+1)}\varphi^{n}\Delta_{rt}\,(K/2\sigma^2)\,[n\,\varepsilon_{rt}+\psi\,\pi\,(n)\,\Omega_{rt}]$$
$$+\psi^{m}\,(1-\psi)\,(1-\varphi)\,\varphi^{(n-1)}\,(K/2\sigma^2)$$
$$\times\sum_{sv}\Delta_{rv}\,\Delta_{st}\,\pi\,(n)\,[\varepsilon_{sv}+\psi\,\Upsilon(n)\,\Omega_{sv}]$$
$$-\psi\,p_r\,p_t\,(K/2\sigma^2)\,[\{2\,\pi\,(n)-n\,\psi^{m}\varphi^{n}\}\,E_N$$
$$-\psi\,\pi\,(n)\,\{2\,\Upsilon(n)-\psi^{m}\varphi^{n}\}\,\Xi_{MN}]$$
$$-\psi^{(m+1)}\varphi^{n}\,\pi\,(n)\,\Delta_{rt}\,(K/2\sigma^2)$$
$$\times[E_N+\psi\,\Upsilon(n)\,\Xi_{MN}])\,A_r\,B_t, \qquad (11)$$

respectively, where $\pi\,(n)=(1-\varphi^{n})\,(1-\varphi)^{-1}$, and $\Upsilon(n)=(1+\varphi^{n})\,(1+\varphi)^{-1}$.

Because each population serves dually as a tester for its reciprocal and as a population subject to selection, the mean of the intercross of arrays $g_{M_{n\cdot m}}$ and $g_{N_{n\cdot m}}$ is expressable as a sum partitioned according to terms that are (a) unmodified by initial linkage disequilibrium, (b) influenced by initial disequilibrium in the selection populations exclusively, (c) affected by initial disequilibrium in the tester populations exclusively, and (d) modified by initial disequilibrium in the tester and selection populations jointly, *viz.*:

$$\mu^{(R)}_{M_{n\cdot m}\times N_{n\cdot m}}=\mu+(K/2\sigma^2)\,\{n\,[\sum p_i\,\alpha_i^2+\sum p_k\,\beta_k^2+\sum p_r\,\alpha_r^2+\sum p_t\,\beta_t^2]$$
$$+\psi^{m}\,\pi\,(n)\,[(1-\psi)\,(1-\varphi)+\psi\,\varphi]\times[\sum p_i\,p_k\,\varepsilon_{ik}^2+\sum p_r\,p_t\,\varepsilon_{rt}^2]\}, \qquad (12.1)$$

plus

$$\mu^{(\Delta S)}_{M_{n\cdot m}\times N_{n\cdot m}}=(1/2)\,\psi^{m}\,\varphi^{n}\,(E_M+E_N)+(K/2\sigma^2)$$
$$\times\{2\,\pi\,(n)\,[\sum\Delta_{ik}\,\alpha_i\,\beta_k+\sum\Delta_{rt}\,\alpha_r\,\beta_t]+[n\,\psi^{m}\varphi^{n}+\psi\,\pi\,(n)]$$
$$\times[\sum\Delta_{ik}\,(\alpha_i+\beta_k)\,\varepsilon_{ik}+\sum\Delta_{rt}\,(\alpha_r+\beta_t)\,\varepsilon_{rt}]$$
$$+\psi^{(m+1)}\,\varphi^{n}\,[n\,(\sum\Delta_{ik}\,\varepsilon_{ik}^2+\sum\Delta_{rt}\,\varepsilon_{rt}^2)$$
$$-\pi\,(n)\,(E_M^2+E_N^2)]+\psi^{m}\,(1-\psi)\,(1-\varphi)\,\varphi^{(n-1)}\,\pi\,(n)$$
$$\times[\sum_{jl}\Delta_{il}\,\Delta_{jk}\,\varepsilon_{ik}\,\varepsilon_{jl}+\sum_{sv}\Delta_{rv}\,\Delta_{st}\,\varepsilon_{rt}\,\varepsilon_{sv}]\}, \qquad (12.2)$$

plus

$$\mu^{(\Delta T)}_{M_{n\cdot m}\times N_{n\cdot m}}=(1/2)\,\psi^{m}\,\varphi^{n}\,(E_M+E_N)+(K/2\sigma^2)$$
$$\times\{[n\,\psi^{m}\varphi^{n}+\psi\,\pi\,(n)]\,[\sum p_i\,\alpha_i\,Z_i+\sum p_k\,\beta_k\,H_k+\sum p_r\,\alpha_r\,Z_r+\sum p_t\,\beta_t\,H_t]+\psi^{(m+1)}\varphi^{n}\,\pi\,(n)$$
$$\times[\sum p_i\,Z_i^2+\sum p_k\,H_k^2+\sum p_r\,Z_r^2+\sum p_t\,H_t^2]$$
$$+\psi^{m}\,[\psi^{m}\varphi^{n}\,\pi\,(n)+n\,\psi\,\varphi^{(n-1)}]\,[(1-\psi)\,(1-\varphi)+\psi\,\varphi]$$
$$\times[\sum p_i\,p_k\,\varepsilon_{ik}\,\Omega_{ik}+\sum p_r\,p_t\,\varepsilon_{rt}\,\Omega_{rt}]$$
$$+n\,\psi^{(2m+1)}\,\varphi^{(2n-1)}\,[(1-\psi)\,(1-\varphi)+\psi\,\varphi]$$
$$\times\sum p_i\,p_k\,\Omega_{ik}^2+\sum p_r\,p_t\,\Omega_{rt}^2]\}, \qquad (12.3)$$

plus

$$\mu^{(\Delta S\,\Delta T)}_{M_{n\cdot m}\times N_{n\cdot m}}=\psi^{2m}\,\varphi^{2n}\,\Xi_{MN}+(K/2\sigma^2)$$
$$\times\{2\,\psi^{(m+1)}\varphi^{n}\,\pi\,(n)\,\Upsilon(n)\,[\sum\Delta_{ik}\,Z_i\,H_k+\sum\Delta_{rt}\,Z_r\,H_t]$$
$$+\pi\,(n)\,[\psi^{m}\varphi^{n}+\psi\,\Upsilon(n)]\,[\sum\Delta_{ik}\,\alpha_i\,H_k+\sum\Delta_{ik}\,Z_i\,\beta_k+\sum\Delta_{rt}\,\alpha_r\,H_t+\sum\Delta_{rt}\,Z_r\,\beta_t]$$
$$+[n\,\psi^{2m}\varphi^{2n}+\psi^{2}\,\pi\,(n)\,\Upsilon(n)]\,[\sum\Delta_{ik}\,(\alpha_i+\beta_k)\,\Omega_{ik}+\sum\Delta_{rt}\,(\alpha_r+\beta_t)\,\Omega_{rt}]$$
$$+2\,\psi^{(m+1)}\,\varphi^{n}\,\pi\,(n)\,[\sum\Delta_{ik}\,(Z_i+H_k)\,\varepsilon_{ik}+\sum\Delta_{rt}\,(Z_r+H_t)\,\varepsilon_{rt}]$$
$$+\psi^{(m+1)}\,\varphi^{n}\,\pi\,(n)\,[\psi^{m}\varphi^{n}+\psi\,\Upsilon(n)]$$
$$\times[\sum\Delta_{ik}\,(Z_i+H_k)\,\Omega_{ik}+\sum\Delta_{rt}\,(Z_r+H_t)\,\Omega_{rt}]$$
$$+\psi^{(m+1)}\,\varphi^{n}\,[n\,\psi^{m}\varphi^{n}+\psi\,\pi\,(n)]$$
$$\times[\sum\Delta_{ik}\,\varepsilon_{ik}\,\Omega_{ik}+\sum\Delta_{rt}\,\varepsilon_{rt}\,\Omega_{rt}]$$
$$-\psi^{(m+1)}\,\varphi^{n}\,\pi\,(n)\,[\psi^{m}\varphi^{n}+\psi\,\Upsilon(n)]\,[E_M+E_N]\,\Xi_{MN}$$
$$+\psi^{(2m+2)}\,\varphi^{2n}\,\pi\,(n)$$
$$\times[\sum\Delta_{ik}\,\Omega_{ik}^2+\sum\Delta_{rt}\,\Omega_{rt}^2-2\,\Upsilon(n)\,\Xi_{MN}^2]$$
$$+\psi^{m}\,(1-\psi)\,(1-\varphi)\,\varphi^{(n-1)}\,\pi\,(n)\,[\psi^{m}\varphi^{n}+\psi\,\Upsilon(n)]$$
$$\times[\sum_{jl}\Delta_{il}\,\Delta_{jk}\,\varepsilon_{ik}\,\Omega_{jl}+\sum_{sv}\Delta_{rv}\,\Delta_{st}\,\varepsilon_{rt}\,\Omega_{sv}]$$
$$+\psi^{(2m+1)}\,(1-\psi)\,(1-\varphi)\,\varphi^{(2n-1)}\,\pi\,(n)\,\Upsilon(n)$$
$$\times[\sum_{jl}\Delta_{il}\,\Delta_{jk}\,\Omega_{ik}\,\Omega_{jl}+\sum_{sv}\Delta_{rv}\,\Delta_{st}\,\Omega_{rt}\,\Omega_{sv}]\}. \qquad (12.4)$$

The sum of equations (12.1), (12.2), (12.3), and (12.4) minus equation (2) equals selection advance from n generations of selection followed by m generations of random mating within each population without selection:

$$\mu^{(A)}_{M_{n\cdot m}\times N_{n\cdot m}}=\mu^{(R)}_{M_{n\cdot m}\times N_{n\cdot m}}+\mu^{(\Delta S)}_{M_{n\cdot m}\times N_{n\cdot m}}+\mu^{(\Delta T)}_{M_{n\cdot m}\times N_{n\cdot m}}+\mu^{(\Delta S\,\Delta T)}_{M_{n\cdot m}\times N_{n\cdot m}}-\mu_{M_0\times N_0}. \qquad (13)$$

Numerical Example

Consider the gain from three cycles of reciprocal recurrent selection, with no subsequent generations of random mating without selection, based on a model in which (a) the initial gametic arrays of the two populations are identical to one another and possess two equally frequent alleles at each locus, (b) the genetic effects ascribable to the genotypes $A_i B_k/A_r B_t$ (i, k, r, t = 1, 2) in the intercross population are as listed in Table 1, (c) the phenotypic variance of testcross means in the intercross population has a constant value of

Table 1. Values of the genetic effects ascribable to the genotypes A_iB_k/A_rB_t(i, k, r, t = 1,2) of the intercross population

Genotype	Genetic effects										
	α_i	β_k	α_r	β_t	ε_{ik}	ε_{rt}	τ_{irt}	η_{krt}	τ_{ikr}	η_{ikt}	ω_{ikrt}
A_1B_1/A_1B_1	1	1	1	1	1	1	1	1	1	1	1
A_1B_1/A_1B_2	1	1	1	−1	1	−1	−1	−1	1	−1	−1
A_1B_1/A_2B_1	1	1	−1	1	1	−1	−1	−1	−1	1	−1
A_1B_1/A_2B_2	1	1	−1	−1	1	1	1	1	−1	−1	1
A_1B_2/A_1B_1	1	−1	1	1	−1	1	1	−1	−1	−1	−1
A_1B_2/A_1B_2	1	−1	1	−1	−1	−1	−1	1	−1	1	1
A_1B_2/A_2B_1	1	−1	−1	1	−1	−1	−1	1	1	−1	1
A_1B_2/A_2B_2	1	−1	−1	−1	−1	1	1	−1	1	1	−1
A_2B_1/A_1B_1	−1	1	1	1	−1	1	−1	1	−1	−1	−1
A_2B_1/A_1B_2	−1	1	1	−1	−1	−1	1	−1	−1	1	1
A_2B_1/A_2B_1	−1	1	−1	1	−1	−1	1	−1	1	−1	1
A_2B_1/A_2B_2	−1	1	−1	−1	−1	1	−1	1	1	1	−1
A_2B_2/A_1B_1	−1	−1	1	1	1	1	−1	−1	1	1	1
A_2B_2/A_1B_2	−1	−1	1	−1	1	−1	1	1	1	−1	−1
A_2B_2/A_2B_1	−1	−1	−1	1	1	−1	1	1	−1	1	−1
A_2B_2/A_2B_2	−1	−1	−1	−1	1	1	−1	−1	−1	−1	1

Table 2. Total gain and its partition into components that are (a) disequilibrium-free, (b) affected exclusively by disequilibrium in the selection populations, (c) affected solely by disequilibrium in the tester populations, and (d) affected jointly by disequilibrium in both populations

Linkage coefficient (λ)	Initial negative disequilibrium	Total gain	Disequilibrium-free component	Disequilibrium-affected components		
				Selection populations	Tester populations	Joint populations
0	1/32	5.46	6.05	−0.40	−0.21	0.02
	1/16	4.93		−0.80	−0.41	0.09
	1/8	4.02		−1.60	−0.80	0.37
	1/4	2.76		−3.20	−1.49	1.41
0.25	1/32	5.43	6.15	−0.45	−0.31	0.04
	1/16	4.80		−0.90	−0.60	0.14
	1/8	3.75		−1.81	−1.13	0.54
	1/4	2.48		−3.67	−2.04	2.04
0.50	1/32	5.46	6.41	−0.52	−0.48	0.06
	1/16	4.64		−1.06	−0.93	0.22
	1/8	3.37		−2.16	−1.72	0.84
	1/4	2.13		−4.52	−2.89	3.13
0.75	1/32	5.55	6.93	−0.64	−0.83	0.10
	1/16	4.42		−1.31	−1.57	0.38
	1/8	2.83		−2.76	−2.78	1.45
	1/4	1.95		−6.06	−4.13	5.22
0.99	1/32	5.72	7.86	−0.81	−1.50	0.18
	1/16	4.08		−1.71	−2.76	0.69
	1/8	2.19		−3.74	−4.58	2.65
	1/4	2.47		−8.76	−5.36	8.74

16.0, and (d) the selection intensity is 0.10. Only genetic effects intrinsic to the shift in the intercross population mean are listed in Table 1.

The initial gametic arrays of the two populations are identically $(1/4 + \Delta_{11})\,A_1B_1 + (1/4 + \Delta_{12})\,A_1B_2 + (1/4 + \Delta_{21})\,A_2B_1 + (1/4 + \Delta_{22})\,A_2B_2$. In this array, $\Delta_{11} = \Delta_{22} = -\Delta_{12} = -\Delta_{21}$, and, for this example, $\Delta_{11} = \Delta_{22} < 0$ will be arbitrarily regarded as a state of negative disequilibrium.

For the hypothetical selection model, disequilibrium-free gain increased with tightened linkage, was markedly offset by the effects of initial negative disequilibrium attributable solely to either the selection or tester populations, and was enhanced by joint disequilibrium effects from both populations (Table 2). For all levels of linkage, total gain was curtailed in proportion to the magnitude of initial disequilibrium; and, for the most part, the effect of initial disequilibrium was magnified in conformance to the level of linkage.

Discussion

Equation (12.2) indicates that only additive and additive × additive epistatic effects are involved with linkage disequilibrium in altering selection gain via the selection populations. Equations (12.3) and (12.4) reveal that the genetic terms constituent to the testers that modify selection gain are

$$E_N = \sum \Delta_{rt}\,\varepsilon_{rt},\ Z_i = \sum_{rt} \Delta_{rt}\,\tau_{irt},\ H_k = \sum_{rt} \Delta_{rt}\,\eta_{krt},$$

$$\Omega_{ik} = \sum_{rt} \Delta_{rt}\,\omega_{ikrt},\ E_M = \sum \Delta_{ik}\,\varepsilon_{ik},\ Z_r = \sum_{ik} \Delta_{ik}\,\tau_{ikr},$$

$$H_t = \sum_{ik} \Delta_{ik}\,\eta_{ikt},\ \Omega_{rt} = \sum_{ik} \Delta_{ik}\,\omega_{ikrt},\ \text{and}$$

$$\Xi_{MN} = \sum \Delta_{rt}\,\Omega_{rt} = \sum \Delta_{ik}\,\Omega_{ik} = \sum \Delta_{ik}\,\Delta_{rt}\,\omega_{ikrt}.$$

Each of these terms comprises a sum of cross products with each cross product being composed of (a) initial disequilibrium in the tester times (b) a corresponding epistatic effect for which, out of the total number of alleles involved in the interaction, two alleles emanate from the tester population. If epistasis is absent, initial linkage disequilibrium affects selection gain only via the selection populations and has no effect via the tester populations. If epistasis is present, equations (12.3) and (12.4) show that selection gain is influenced by the effect of initial linkage disequilibrium via the testers. The effect of initial linkage disequilibrium via the testers is permanent, however, only in the presence of additive × dominance and/or dominance × dominance epistasis.

The sum of equations (12.1) and (12.2) is consistent with equation (6) of Johnson (1982). {In equation (6) of Johnson (1982), the terms appearing as $[(n/2)\,\varphi^n + (1/4)\,(1+\lambda)\,(1-\varphi^n)\,(1-\varphi)^{-1} \sum \Delta_{ik}\,(\alpha_i + \beta_k)\,\varepsilon_{ik}$ and $(1/4)\,(1+\lambda)\,\psi^m\,\varphi^n[\sum \Delta_{ik}\,\varepsilon_{ik}^2 - (\sum \Delta_{ik}\,\varepsilon_{ik})^2]$ should be corrected to read $[(n/2)\,\psi^m\,\varphi^n + (1/4)\,(1+\lambda)\,(1-\varphi^n)\,(1-\varphi)^{-1} \sum \Delta_{ik}\,(\alpha_i + \beta_k)\,\varepsilon_{ik}]$ and $(1/4)\,(1+\lambda)\,\psi^m\,\varphi^n \times [n \sum \Delta_{ik}\,\varepsilon_{ik}^2 - (1-\varphi^n)\,(1-\varphi)^{-1}\,(\sum \Delta_{ik}\,\varepsilon_{ik})^2]$, respectively}. In simple recurrent selection, the tester is assumed to remain constant; i.e., to undergo no recombination. As a consequence, assuming for example that M and N are the selection and tester populations, respectively, in a simple recurrent selection program, E_N, Z_i, H_k, and Ω_{ik} remain completely confounded with μ, α_i, β_k, and ε_{ik}, respectively. Thus, even if epistasis exists, linkage disequilibrium in the tester affects progress in simple recurrent selection only by modifying the magnitude of additive, and additive × additive epistatic, effects attributable to alleles from the selection population.

The numerical example, featuring relatively large epistatic effects and gene frequencies equal to 0.5 in both populations, was constructed so as to illustrate vividly the effect of initial disequilibrium in the testers on selection progress. If, in actuality, epistasis is negligible, initial linkage disequilibrium in the testers is irrelevant, and only disequilibrium in the selection populations distorts selection progress. Even with considerable additive × dominance and dominance × dominance gene-action, choosing the initial populations on the basis of heterosis will ensure that many locus-pairs will be near or at fixation for particular allele-pair combinations in one population or the other. For a given locus-pair, the population near or at fixation for a particular allele-pair will in essence function solely as a tester for the reciprocal population while in the testcross population the additive × dominance and dominance × dominance gene action responsible for heterosis will be subsumed by additive and additive epistatic effects, respectively, attributable to alleles from the selection population. In addition, if a locus-pair is near or at fixation, linkage disequilibrium will be inconsequential or absent.

Evidence for important epistatic effects in the inheritance of quantitative traits in maize is inconclusive (Hallauer and Miranda, Fo. 1981); and, even if additive × dominance and dominance × dominance epistasis is important in heterosis, a model based on additive and additive × additive epistatic effects attributable to alleles from the selection population adequately describes progress from reciprocal recurrent selection if many loci-pairs are near or at fixation in one or the other population. If the initial populations have been chosen on the basis of heterosis, linkage disequilibrium in the testers is probably of no consequence. If, however, epistatic gene action is important at loci that are fixed in one or the other of the populations, intermat-

ing of the two populations to form a pooled base in which to reinitiate reciprocal recurrent selection will, in effect, create epistatic variation available to selection. Linkage disequilibrium could be substantial in the pooled population, and tester linkage disequilibrium could, consequently, play an important role in progress from reciprocal recurrent selection in the reconstituted populations.

In general, progress from reciprocal recurrent selection is a function of the covariance of half-sib progeny means of individuals in the parental populations with half-sib progeny means of the self-derived offspring. A comprehensive two-locus theory for the covariance of relatives is unavailable (Weir and Cockerham 1977), but such a theory would certainly be based on the concept of genic equivalence by descent. The parameters ψ and φ are explicit, linkage-dependent values of F^1 (the probability of equivalence by descent of two cis-arranged genes) for an individual belonging to the intercross population of (a) the parental populations and (b) the self-derived offspring, respectively. If (a) the two base populations are assumed to be unrelated and non-inbred, (b) recombination within each population is achieved by random mating, (c) inbreeding due to finite population size is ignored, and (d) selection in both populations is made on the basis of general combining ability with the reciprocal population, all other descent measures are zero or irrelevant. Elimination of all descent measures except F^1 obviates the necessity of casting the results in a general framework of equivalence by descent. In fact, a general context of equivalence by descent might divert attention from the underlying biological phenomenon of linkage. However, if a general theory of covariance of relatives is ever achieved, the derivations presented in this paper will be encompassed by the general theory.

Compared to the genetic-effects notation used in this paper, the notation of Weir and Cockerham (1977) could have greater mnemonic value but might also be more cumbersome. Either notational convention is likely to become increasingly ponderous as the theory is extended beyond two loci. A theory for arbitrary numbers of loci will probably require a novel, more elegant system of notation.

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