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Effect of Gametic Disequilibrium on Selection in an Autotetraploid Population*

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Summary. The effects of a gametic disequilibrium (DSE) in an autotetraploid population on response to selection as measured by the covariance of selection were investigated. The theoretical responses were calculated for mass selection [Mass (1)] and half-sib progeny test selection (HSPT) in a two-allele (B and b), single locus, autotetraploid population. The complexity of calculations precluded analytical expressions for the covariances so numerical analysis was used assuming the following genetic models: monoplex dominance, partial monoplex dominance, duplex dominance, partial duplex dominance, and additive gene action.

The results indicated the DSE could greatly affect the covariance of selection. For a constant allele frequency the DSE might double the covariance expected with selection in a population at random mating equilibrium (RME) of gametes, but in other instances approach zero. For all genetic models and the two breeding methods investigated the covariance of selection was always increased when the frequency of BB gamete exceeded p^2 (where p is frequency of allele B) and decreased when the frequency of BB gamete was less than p^2. The possible incorporation of this information into a long term breeding program and some other ramifications were briefly discussed.

With the DSE the covariances of selection with HSPT and Mass (1) had a proportionality of 1:2, respectively, with the additive genetic model, but this relationship rarely occurred for other genetic models. The deviations from this ratio were not large in comparison to differences between selection in populations in DSE and RME.

Key words: Autopolyploid – Selection Response – Genetic Theory – *Medicago sativa* L.

Introduction

Theoretical studies of selection in autotetraploid genetics such as Hill and Haag (1974) and Rowe and Hill (1981) were concerned with development of expressions for genetic gains at a locus with two alleles in a single cycle of selection for various breeding methods. One underlying assumption of the genetic models in these studies was that selection was performed on a population in random mating equilibrium (RME). That is, the expected frequencies of gametes and genotypes are expressable in terms of frequency of the alleles in the population. In contrast most cycles of selection in a countinuing breeding project on a crop such as alfalfa (*Medicago sativa* L.) are performed on populations with gametic disequilibrium (DSE) due to prior selection for the same or a correlated trait with insufficient generations of random intercrossing between cycles of selection to attain RME.

If selections are made in populations in RME, many covariances of selection for intra-population selection methods simplify to a constant times $pq\alpha$ (Hill and Haag 1974) where α is the additive genetic effect of the population (Hill 1971) and p and q are the usual frequencies of the desired and undesired alleles, respectively. When selections are made in a population with DSE, the covariances are not simplifiable to terms which facilitate generalized comparisons of breeding methods. Such comparisons must be made on a numerical basis for specified genetic situations.

This research investigated the theoretical effects of the DSE in the selected population on the expected genetic gain in contrast to selection in a population with a gametic equilibrium. The specific statistic investigated for comparison of genetic gains was the covariance of selection which is a covariance between the frequency of desired allele in the clones or progenies to be considered for selection and the genotypic value of the corresponding observed units upon which

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selection is based. The observed units are usually the clones or progenies themselves or some related progenies.

Calculations

Genotype Frequencies

This study is focused on the genetics at a single locus in an autotetraploid population with two alleles, 'B', and 'b', whose frequencies in the population are, respectively, p and q. The frequency of allele B in the population is expected to change only in response to selection, and allele B is assumed to code for the desirable trait while b codes for the undesirable trait. Random chromosome inheritance is assumed.

If the given population of autotetraploid plants is in RME, the expected frequency of each genotype is given by expansion of the binomial $(p+q)$ to the fourth power (column f_{iRME} of Table 1) and the expected frequencies of the gametes is given by the square of the same binomial as p^2, $2pq$, and q^2 for gametes, BB, Bb, and bb, respectively. For the population in DSE the frequencies of gametes and genotypes are not expressable in terms of allele frequencies. Instead the frequencies of the genotypes are expressed in terms of the square of the trinomial $(x+2y+z)$ which represents the frequencies of the gametes in the population: frequency of gamete BB is x, the frequency of gamete Bb is 2y, and the frequency of gamete bb is z (column f_{iDSE} of Table 1).

The approach to RME by the random mating population in DSE is asymptotic with two-thirds of the DSE lost each generation (Demarly 1963). Thus the frequencies of each type of gamete in the next generation, indicated by a prime, are $x' = (1/3)(x) + (2/3)(p^2)$, $2y' = (1/3)(2y) + (2/3)(2pq)$, and $z' = (1/3)(z) + (2/3)(q_2)$.

Modeling

Five types of genetic action were assumed for investigation in this study: monoplex dominance (MD), partial monoplex dominance (PMD), duplex dominance (DD), partial duplex dominance (PDD), and additive genetic action (ADD). The genotypic values for each genetic model is in terms of maximum genotypic value 'h' in Table 2. The array of genotypes exhibiting some dominance, MD, PMD, DD, and PDD, differ sequentially by subtraction of 0.5 h from one genotype.

Covariance of Selection

The genetic gain with selection was assumed to be proportional and constant to the covariance of selection (Falconer 1960). The covariance of selection was calculated for two selection methods: mass selection [Mass (1)] and half-sib progeny test selection (HSPT). With Mass (1) the selections are made on basis of

Table 1. The genotype frequencies, allele frequencies, and genotypic values for calculation of covariance of selection with Mass (1) and HSPT. Gamete frequencies after one generation of random mating are indicated by a prime

Genotype	Indicator	Frequency of Genotype		Frequency of 'B'	Genotype Value	Genotypes	Genotypic Value[a]
	i	f_{iRME}	f_{iDSE}	B_i	V_i		V'_i
BBBB	1	p^4	x^2	1	G1	BBBB BBBb BBbb	$(x')G1 + (2y')G2 + (z')G3$
BBBb	2	$4p^3q$	$2(x)(2y)$	3/4	G2	BBBB BBBb BBbb Bbbb	$(x'/2)G1 + ((2y'/2) + (x'/2))G2 + ((z'/2) + (2y'/2))G3 + (z'/2)G4$
BBbb	3	$6p^2q^2$	$((2y)^2 + 2xz)$	1/2	G3	BBBB BBBb BBbb Bbbb bbbb	$(x'/6)G1 + ((2y'/6) + (2/3)x')G2 + ((x'/6) + (2/3(2y') + (z'/6))G3 + ((2/3)z' + (2y'/6))G4 + (z'/6)G5$
Bbbb	4	$4pq^3$	$2(2y)(z)$	1/4	G4	BBBb BBbb Bbbb bbbb	$(x'/2)G2 + ((2y'/2) + (x'/2))G3 + ((z'/2) + (2y'/2))G4 + (z'/2)G5$
bbbb	5	q^4	z^2	0	G5	BBbb Bbbb bbbb	$(x')G3 + (2y')G4 + (z')G5$

[a] The G's of Genotypic Value must be cross-referenced to values of a particular genetic model in Table 2

individual phenotypes and the selections are randomly intercrossed to produce the improved population. It is assumed that the pollen parents of the intercrosses are limited to the selections. Second is HSPT where half-sib progenies are produced for each plant by randomly intercrossing the original populations and making selections of parents on basis of half-sib progeny performance. The selections are then randomly intercrossed to produce the improved population. These covariances of selection in a population in DSE or in RME were calculated as follows from information outlined in Table 1:

$$\mathrm{Mass(1)_{DSE}} = \sum_{i=1}^{5} f_{iDSE} B_i V_i - \left(\sum_{i=1}^{5} f_{iDSE} B_i\right)\left(\sum_{i=1}^{5} f_{iDSE} V_i\right)$$

$$\mathrm{Mass(1)_{RME}} = \sum_{i=1}^{5} f_{iRME} B_i V_i - \left(\sum_{i=1}^{5} f_{iRME} B_i\right)\left(\sum_{i=1}^{5} f_{iRME} V_i\right)$$

$$= \sum_{i=1}^{5} f_{iRME} B_i V_i - p\left(\sum_{i=1}^{5} f_{iRME} V_i\right)$$

$$\mathrm{HSPT_{DSE}} = \sum_{i=1}^{5} f_{iDSE} B_i V_i' - \left(\sum_{i=1}^{5} f_{iDSE} B_i\right)\left(\sum_{i=1}^{5} f_{iDSE} V_i'\right)$$

Where f_{iRME} and f_{iDSE} are the frequencies of the ith genotype in a population in RME or in DSE, respectively. The B_i is the frequency of B allele in ith genotype and V_i and V_i' are genotypic values of the individuals and their half-sib progenies, respectively, (Table 1). The x′, 2y′ and z′ are gamete frequencies after one generation of random mating as discussed in an earlier paragraph.

Response Surfaces

The calculated covariances are depicted as response surfaces in a 3-dimensional figure whose base axes are the frequencies of gametes BB (x) and Bb (2y) and the vertical axes is the covariance of selection expressed as multiples of h, the genotypic value. The covariance is calculable above the triangle whose intercepts (2y, x) are (0, 0), (0, 1) and (1, 0) because $x+2y \leqq 1$. The relationship of frequency p to combinations of x and 2y is shown by diagonal lines in Fig. 1. The combinations of x and 2y which are identical to p^2 and 2pq, respectively, appear as the curved dotted line from (0, 0) to (0, 1) in Fig. 1.

Though a response surface is depicted for all possible combinations of x and 2y in Figs. 2, 3 and 4, not all combinations of x and 2y are expected with normal meiosis. No genotype produces the Bb gamete at a frequency of 1.0. The monoplex, duplex, and triplex genotypes produce the Bb gamete at frequencies of 0.50, 0.67, and 0.50, respectively.

Thus in Fig. 1 the combinations of x and 2y on and to the left of the dashed line indicates all possible gamete frequencies with normal meiosis.

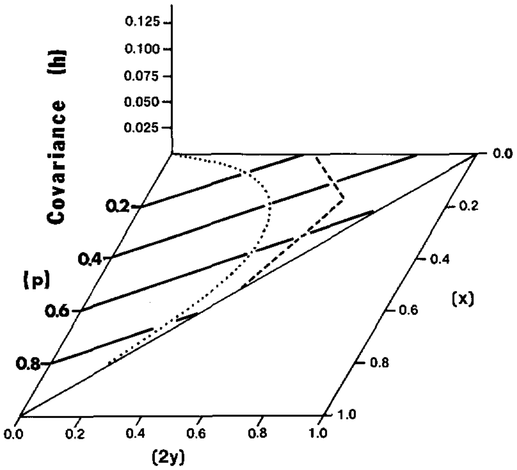

Fig. 1. The (x) and (2y) axes representing frequencies of gametes BB and Bb, respectively, and their relationship to frequency (p) of allele B, gamete frequencies possible with normal meiosis (on and to the left of the dashed line), and gamete frequencies equal to those at random mating equilibrium (the dotted line)

Results

The covariance of selection for Mass (1) selection in a population in DSE, Fig. 2, suggests a continuity in progression of the contours of the response surfaces coinciding to decreases in level of dominance for genetic models MD, PMD, and DD followed by a general decrease in surface height for the PDD genetic model. The surface for ADD genetic model appears similar to that of PDD, but the continuity and smoothness of change between these two surfaces is suspect because the difference in genotype values for the models is much more than a single addition or subtraction of 0.5 h for a single genotype (Table 2) as it is for MD to PMD to DD to PDD.

These covariances are maximized for 2y approaching zero with intermediate frequencies of x and are zero when x, 2y, or z are unity. In vicinity of the line given by $x+2y=1$, i.e. $z=0$, the response surface approaches zero and is nearly horizontal for MD genetic model. This same region of the response surface becomes increasingly steep for PMD and for DD. With

Table 2. The genotypic values and cross-reference codes for five genetic models

Genotypes	Genotypic values (h)[a]					Code for cross-reference
	MD	PMD	DD	PDD	ADD	
BBBB	1	1	1	1	1	G1
BBBb	1	1	1	1	0.75	G2
BBbb	1	1	1	0.5	0.5	G3
Bbbb	1	0.5	0	0	0.25	G4
bbbb	0	0	0	0	0	G5

[a] h is an arbitrary constant of the trait

PDD the covariance is no longer zero for all values at $z=0$. Concurrent with increases in the covariance near $z=0$ there is a decrease in the covariance in the vicinity of the origin (0, 0).

For every combination of 2y and x, the corresponding covariance assuming RME instead of DSE is given by Fig. 3. A progression of response surfaces very different from those to Fig. 2, is seen from genetic models MD to PMD to DD, followed by a general decrease in height for PDD genetic model. The ADD genetic model does appear similar to that for PDD genetic model.

With RME the covariance of selection is a function of frequency p. From Fig. 3 the MD genetic model appears maximized near $p=0.2$ which is a line from (0.4, 0.0) to (0.0, 0.2) for (2y, x). With PMD, DD, PDD, and ADD genetic models the approximate allele frequencies for which each covariance is maximized are, respectively, 0.3, 0.4, 0.45, and 0.5.

The curve in Fig. 1 which indicates where x and 2y are equal to p^2 and 2pq, respectively, is also the demarcation line separating where the DSE improves the covariance above that expected with selection in a population in RME and where the DSE results in a decrease in the covariance. To the right of this curve the DSE has reduced the covariance and to the left the DSE had enhanced the covariance of selection.

A comparison of response surfaces for the same genetic models of Figs. 2 and 3 indicates the covariance of selection can be greatly affected by DSE. On average for nontrivial values of p, i.e. $p \neq 0$ or 1, and with $x \gg p^2$ the covariance associated with DSE may be double that for RME and when $x \ll p^2$ the covariance of selection is much reduced for a given p value and can approach 0.

The response surfaces representing the covariance of selection with HSPT selection in a population in RME are not presented in this paper because these covariances are exactly half of those with Mass (1) selection, Fig. 3.

The covariances for HSPT selection in a population in DSE are represented as the response surfaces of Fig. 4. These surfaces have the general shape of those in Fig. 2 except their height is much reduced. With the ADD genetic model the covariance with HSPT selection is exactly half of that with Mass (1) selection as it is with selection in a population in RME, but for the other four genetic models this relationship rarely applies. The dotted curves across the x by 2y bases of MD, PMD, DD, and PDD genetic models of Fig. 4 are the regions where the covariance with HSPT is half of the covariance with Mass (1) selection. Those base regions designated with 'h' are where the HSPT covariance is greater than half of Mass (1) covariance and the unmarked regions are where the HSPT covariance is less than half of that with Mass (1) selection. The

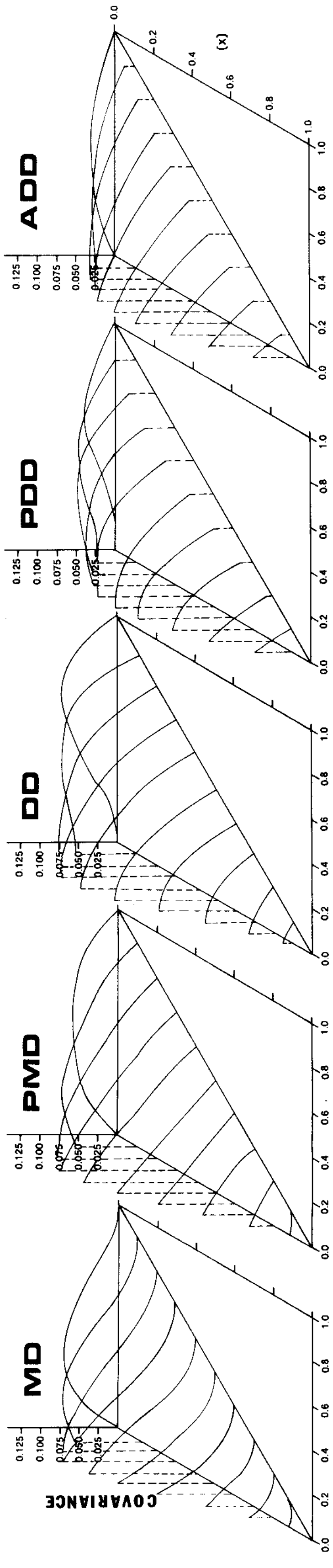

Fig. 2. Response surface for covariance of selection associated with Mass selection and gamete frequencies x(BB) and 2y(Bb) for five types of genetic action at locus B

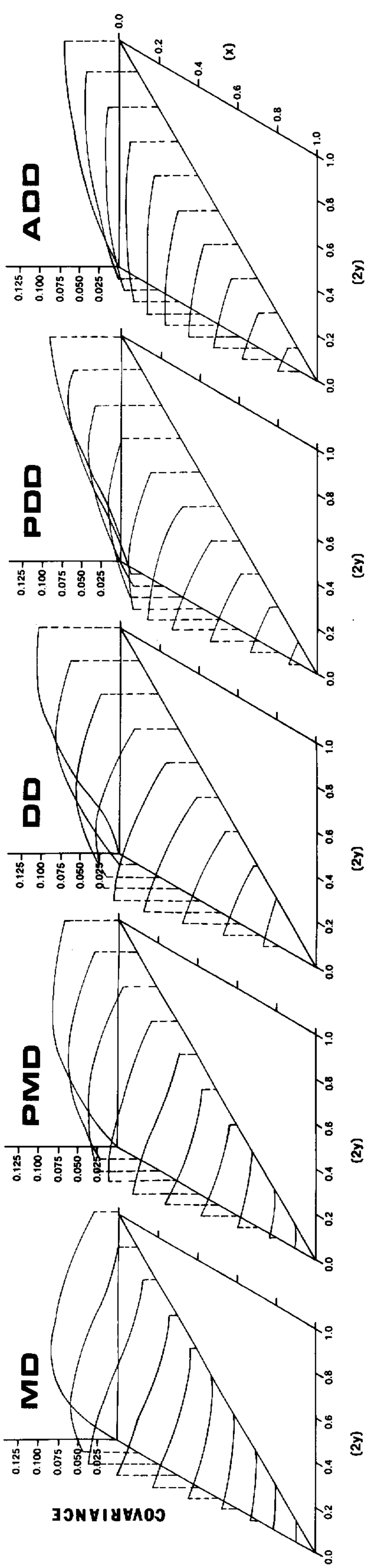

Fig. 3. Response surface for covariance of selection associated with Mass selection and gamete frequencies x(BB) and 2y(Bb) for five types of genetic action at locus B after random mating equilibrium has been attained in the population

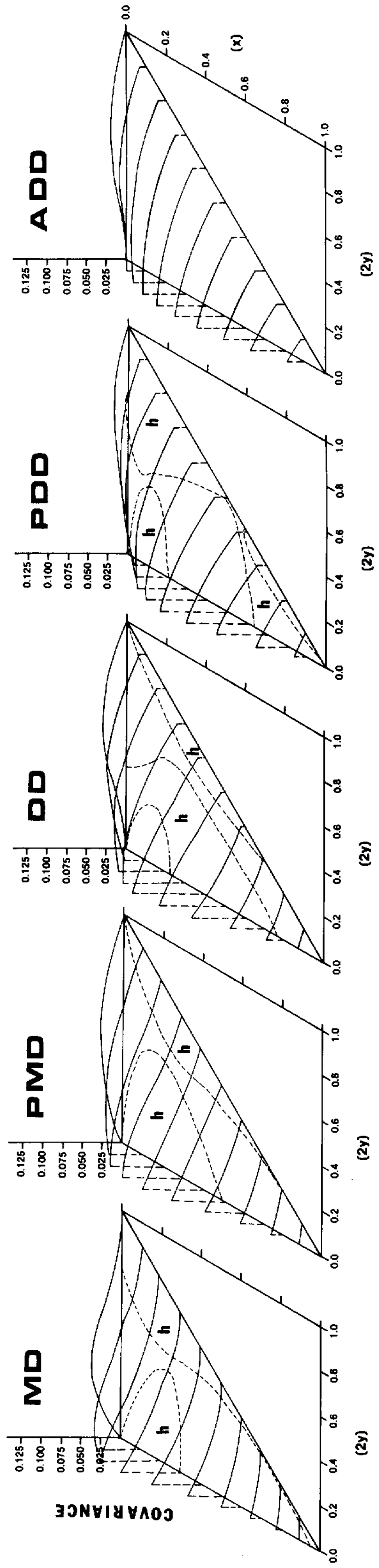

Fig. 4. Response surface for covariance of selection associated with half-sib progeny test selection and gamete frequencies x(BB) and 2y(Bb) for five types of genetic action at locus B. Regions (h) inside dashed lines have a covariance which is greater than 1/2 of the respective covariance with Mass selection in Fig. 2

regions where the HSPT covariance is greater or less than half the Mass (1) covariance are not constant among the genetic models. For each of the non-additive genetic models twice the HSPT covariance ranges, approximately, from a minimum of 80% to a maximum of 120% of the convariance with Mass (1). For HSPT the regions of x and 2y where the covariance of selection is increased by DSE with respect to the covariance with selection in a population in RME are the same as with Mass (1) selection (Fig. 1).

Discussion

In this modeling study the common assumption that gametes are at RME in the selected population was relaxed at the expense of losing generality for genetic models found in prior studies (Hill and Haag 1974; Rowe and Hill 1981). Hopefully the five genetic models used in this investigation encompass the genetic situations which are most frequently of interest to plant breeders.

The results of this study indicate the covariance of selection is affected in two ways when selections are made in populations in DSE instead of RME. First for a given p of allele B, the DSE may increase or decrease the covariance of selection in comparison to selection in RME except for trivial cases of p equal to 1.0 or 0.0. The covariance is increased when $x > p^2$ and decreased when $x < p^2$ for either HSPT or Mass (1). Secondly with HSPT the covariance is rarely half of that of Mass (1) except for additive genetic mode. Hill and Haag (1974) showed the covariance of selection with Mass (1) to be twice that of HSPT if the selected population was in RME. Those combinations of x and 2y where HSPT covariance is greater than half of the Mass (1) covariance differs for each genetic model. The above first point might be incorporated into breeding procedures, the the practical value to the plant breeder of the above second point is not obvious.

The difficulty for the plant breeder is knowing when an additional generation of random mating of selections is beneficial or detrimental to the rate of genetic improvement. An additional generation of random mating is expected to eliminate two-thirds of the DSE and approximately two-thirds of the difference in the covariances from Fig. 2 to Fig. 3. A second additional generation of random mating probably is not advisable because of the relatively small change in the covariance for the expense of the additional generation.

If a cycle of selection is performed on a population thought to be near RME, as might be the case with the initial cycle of selection, and which has a low frequency of desired allele, most selections would be monoplexes and their gametes would be bb and Bb. In such a situation the results of this study indicate an additional generation of random mating could improve the covariance of selection. This additional generation of random mating could be attained with continued improvement of the population if at this time selection were made for an uncorrelated trait. If the first cycle of selection were moderately successful in improving the frequency of allele B, the subsequent cycles of selection should be made in tandem with single generations of random mating in order to exploit the greater covariance of selection associated with selection in a population in DSE $x > p^2$.

The genetic gain with a given breeding procedure may be affected differently by forces acting at the single locus and at the multilocus levels. It was shown previously that the DSE associated with single generation of intercrossing in tandem cycles of selection would, in some instances, improve the covariance of selection far above that expected with selection in a population in RME. But in contrast, at the multilocus level this same procedure may hinder genetic gain because not all possible genotypes are produced in a single generation of random mating and moderately tight linkage groups are not expected to be broken. If two or more generations of random mating are used between the cycles of selection the improvement in covariance of selection associated with the increase in BB gametes would be reduced.

This author suggests that a reasonable compromise in the breeding procedures is the use of multiple generations of random intercrossing of selections for a given trait in the early phases of population improvement followed by single generations of random intercrosses with selection to attain high levels of a particular character towards the completion of population improvement.

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