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Effect of gametic disequilibrium on means and on genetic variances of autotetraploid synthetic varieties *

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Summary. The occurrence and effects of a gametic disequilibrium (DSE) in the first generation of a theoretical two-population synthetic variety were investigated. Theoretical development was limited to the genetics at a single locus with two alleles in an autotetraploid species with random chromosome inheritance. Algebraic expressions were developed for the differences between the mean genotypic values of the two-population synthetic variety at generation one and in random mating equilibrium (RME). For the situation where both parents of the synthetic were in RME, a numerical analysis was performed for all possible allele frequencies assuming the following types of genic action: monoplex dominance, partial monoplex dominance, duplex dominance, partial duplex dominance, and additive. The result indicated that with non-additive genic action the DSE could, in some cases, greatly depress or inflate the mean genotypic value of the first generation (Syn-$1_{(\mathrm{RME})}$). Thus, any change of means over advancing generations with loss of DSE could be positive or negative. When additive genic action was assumed, there was no effect associated with DSE and when both parents had the same allele frequencies there was no DSE. The DSE, with only a minor exception, decreased the genetic variance and in numerous cases forced it near zero. Expressions were developed for mean genotypic values of a first generation synthetic with DSE in one parent (Syn-$1_{(\mathrm{DSE/RME})}$) or both parents (Syn-$1_{(\mathrm{DSE})}$). The deviation of these means from those of Syn-$1_{(\mathrm{RME})}$ was a function of digenic and quadragenic population effects. An inspection of the response equations for Syn-$1_{(\mathrm{RME})}$ indicated that in a series of crosses with one common parent the rankings of first generation means would be the same as the ranking of populations at equilibrium though the individual means would be biased. More importantly with DSE of one or both parents there are situations when a ranking of first generation mean genotypic values would not reflect relative frequency of desirable alleles in the populations. These results indicate that statistical analyses and selections based on means of the Syn-1 generation can have an error which is not avoidable by improvement in precision of evaluation.

Key words: Selection response – Genetic variance – Synthetic variety – *Medicago sativa* – Alfalfa

Introduction

Much of the effort expended in the long-term, continuing alfalfa (*Medicago sativa* L.) breeding project is in selection/screening of populations, in evaluation of progress as means of best families or crosses, and in estimation of combining abilities. Thus, the effectiveness of the breeding program is a function of estimation of population means and exploitation of genetic variance.

One of the known genetic realities potentially affecting genetic variance and population means is the gametic disequilibrium (DSE) first outlined by Haldane (1930). That is, the genotype frequencies in a random mating autotetraploid population may not be describable as the simple products of allele frequencies but

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also reflect a structure restriction due to meiotic processes. The comprehensive review by Demarly (1963) indicated that with four or five generations of random mating the genotype frequencies would be a function of allele frequencies, i.e. the population would be in random mating equilibrium (RME).

Although the DSE is a recognized phenomenon in synthetic varieties and expected to decrease by two thirds with each generation of random mating (Demarly 1963), its effects on individual synthetic varieties are not predictable and most theoretical investigations into means of advancing generations of the autotetraploid synthetic variety have investigated the effects of heterosis on means (Dudley 1964; Gallais 1974) and inbreeding (Gallais 1968; Busbice 1969).

This study is an investigation of some effects of the DSE and its interaction with types of genic action on a breeding program. The means and genetic variances are calculated and compared for the same synthetic with and without DSE, and the effects of using parents for synthetics which are not in RME are elucidated.

Calculations

Equations

This theoretical study is restricted to the genetics at one locus in an autotetraploid population with two alleles designated 'B' and 'b' where B effects a more desirable trait. One of the two theoretical populations, 'P', has alleles B and b at frequencies p and q, respectively, and has gametes BB, Bb, and bb at frequencies x, 2y, and z, respectively. With random mating the frequencies of genotypes BBBB, BBBb, BBbb, Bbbb, and bbbb are, respectively, x^2, 4xy, $(4y^2+2xz)$, 4yz, and z^2. When population P is in random mating equilibrium, gamete and genotype frequencies are expressable as second and fourth power expansions, respectively, of the binomial $(p+q)$ with the following equivalences: $x=p^2$, $2y=2pq$, $z=q^2$, $x^2=p^4$, $4xy=4p^3q$, $(4y^2+2xz)=6p^2q^2$, $4yz=4pq^3$, and $z^2=q^4$.

The second theoretical population 'R' has alleles B and b at frequencies r and s and gammetes BB, Bb, and bb at frequencies u, 2v, and w, respectively. Expressions for genotype frequencies in population R are found as shown for population P. In all cases random chromosome segregation was assumed. The genotypic value parameters (Table 1) used to model the populations are A, D, T, and F where A is the effect due to each allele (B) singly, D is the effect due to interaction of two alleles (BB), T is the effect due to interaction of three alleles (BBB) and F is the effect due to interaction of four alleles (BBBB) (Hill, 1971). With five genotypes, a population is describable in four population parameters (α, β, γ, and δ) as defined for population P in RME (Table 1).

The mean of population P in RME is:

$$\bar{P}=4pA+6p^2D+4p^3T+p^4F. \qquad (1)$$

The mean genotypic value of the two populations (P by R) synthetic variety which is in RME ($\mathrm{Syn}_{\mathrm{RME}}$) is that of the single population with a mean allele frequency $(p+r)/2$ (Rowe and Hill 1981).

Table 1. The mathematical model of genotypic values of genotypes in population P and the equations for population parameters. (Hill 1971)

Genotypes	Genotypic value
BBBB	$4A+6D+4T+F$
BBBb	$3A+3D+T$
BBbb	$2A+D$
Bbbb	A
bbbb	0
Genetic effects	
Additive (α)	$=A+3pD+3p^2T+p^3F$
Digenic (β)	$=D+2pT+p^2F$
Trigenic (γ)	$=T+pF$
Quadragenic (δ)	$=F$

$$\begin{aligned}\mathrm{Syn}_{\mathrm{RME}}&=(2p+2r)A+[(3/2)p^2+3pr+(3/2)r^2]\,D\\&+[(1/2)p^3+(3/2)p^2r+(3/2)pr^2+(1/2)r^3]\,T \qquad (2)\\&+[(1/16)p^4+(4/16)p^3r+(6/16)p^2r^2+(4/16)pr^3+(1/16)r^4]\,F.\end{aligned}$$

An expression for the mean genotypic value of the first generation (i.e. Syn-1) of the two-population synthetic (P by R) is found as the cross products of gamete array frequencies (p^2, 2pg, q^2) and (r^2, 2rs, s^2) and associated genotypic values. Thus the mean genotypic value of Syn-1 where both parents were in RME is:

$$\begin{aligned}\text{Syn-1}_{(\mathrm{RME})}&=p^2r^2(\mathrm{BBBB})+(2pqr^2+2p^2rs)(\mathrm{BBBb})\\&+(q^2r^2+4rspq+p^2s^2)(\mathrm{BBbb})+(2pqs^2+2q^2rs)(\mathrm{Bbbb})\\&+s^2q^2(\mathrm{bbbb})\end{aligned}$$

where the genotypes are replaced by respective genotypic values from Table 1 and simplified to get the following expression:

$$\begin{aligned}\text{Syn-1}_{(\mathrm{RME})}&=(2p+2r)A+(p^2+4pr+r^2)D+(2p^2r+2pr^2)T\\&+p^2r^2F. \qquad (3)\end{aligned}$$

The difference between equations (2) and (3) is an expression for the effect of DSE on mean genotypic value of the Syn-1. The effect of DSE is found by subtraction.

$$\begin{aligned}\text{Syn-1}_{(\mathrm{RME})}-\mathrm{Syn}_{\mathrm{RME}}&=-(p-r)[(1/2)(p-r)D\\&+[(1/2)(p^2+r^2)]T-(1/16)[r^2(5p+r)-p^2(5r+p)]\,F]. \qquad (4)\end{aligned}$$

A two-population (P by R) synthetic variety where one population (R) is not in RME has the following mean genotypic value:

$$\begin{aligned}\text{Syn-1}_{(\mathrm{RME/DSE})}&=p^2u(\mathrm{BBBB})+(2pqu+2p^2v)(\mathrm{BBBb})\\&+(uq^2+4pqv+p^2w)(\mathrm{BBbb})+(2pqw+2vq^2)(\mathrm{Bbbb})\\&+wq^2(\mathrm{bbbb})\end{aligned}$$

where genotypic values are substituted for respective genotypes and simplified to give

$$\begin{aligned}\text{Syn-1}_{(\mathrm{RME/DSE})}&=(2p+2r)A+(p^2+4pr+u)D\\&+(2pu+2p^2r)T+p^2uF. \qquad (5)\end{aligned}$$

The effect on mean genotypic value of a DSE in one of the parents in comparison to both parents in RME is:

$$\begin{aligned}\text{Syn-1}_{(\mathrm{RME})}-\text{Syn-1}_{(\mathrm{RME/DSE})}&=(u-r^2)(D+2pT+p^2F)\\&=(u-r^2)\beta_{(\mathrm{P})}. \qquad (6)\end{aligned}$$

Which is digenic effect $\beta_{(\mathrm{P})}$ of population P multipled by the deviation of the frequency of BB gamete in population R from its expected value when in RME. When neither population is in RME the mean genotypic value of Syn-1 is:

$$\text{Syn-1}_{(\text{DSE})} = ux(\text{BBBB}) + (2vx + 2uy)(\text{BBBb}) + (wx + 4vy + uz)(\text{BBbb}) + (2vz + 2yw)(\text{Bbbb}) + wz(\text{bbbb}).$$

The genotypic values are substituted into the equation for the respective genotypes and simplified to:

$$\text{Syn-1}_{(\text{DSE})} = (2p + 2r)A + (x + 4pr + u)D + (2xr + 2up)T + uxF. \tag{7}$$

The effect of two populations in DSE versus both populations in RME in the Syn-1 is:

$$\text{Syn-1}_{(\text{DSE})} - \text{Syn-1}_{(\text{RME})} = (x - p^2)\beta_{(R)} + (u - r^2)\beta_{(P)} + (r^2 - u)(p^2 - x)\delta. \tag{8}$$

The difference in mean genotypic values due to having one and both populations in DSE is:

$$\text{Syn-1}_{(\text{DSE})} - \text{Syn-1}_{(\text{RME/DSE})} = (x - p^2)(\beta_{(R)} + (u - r^2)\delta). \tag{9}$$

The differences between genotypic values of $\text{Syn-1}_{(\text{DSE})}$ and those of $\text{Syn-1}_{(\text{RME})}$ and $\text{Syn-1}_{(\text{RME/DSE})}$ are functions of digenic and quadragenic population parameters and measures of DSE, $(x-p^2)$ and $(u-r^2)$.

The genetic variances of the Syn_{RME} and $\text{Syn-1}_{(\text{RME})}$ were evaluated as $\Sigma^5_{i=1} f_i (x_i - \bar{x})^2$ where x_i is the genotypic value of the i^{th} genotype, f_i is the frequency of the i^{th} genotype, and $\bar{x}$ is the mean genotypic value of $\text{Syn-1}_{(\text{RME})}$ (equation 3) or Syn_{RME} (equation 2) accordingly.

Models of genic action

Due to complexities of equations for mean genotypic values, comparisons were possible only with numerical analyses which assumed specific types of genic action. For this study five types of genic action were assumed for locus B. They were monoplex dominance (MD), partial monoplex dominance (PMD), duplex dominance (DD), partial duplex dominance (PDD), and additive (ADD). For each genic model the respective genotypic value codes in terms of the same maximum genotypic value (h) (Table 2) indicate the meaning of the five types of genetic action.

Response surfaces

The means for $\text{Syn-1}_{(\text{RME})}$ and Syn_{RME} were calculated for all frequencies from 0.0 to 1.0 in increments of 0.05 or 0.10 for each of the four types of non-additive genic action. The effect of DSE was shown by expressing $\text{Syn-1}_{(\text{RME})}$ mean genotypic value as a percent of the Syn_{RME} mean. The percents were plotted as a response surface over all possible values of p and r for each genic model (Fig. 1). Similarly, the total genetic variance was calculated for $\text{Syn-1}_{(\text{RME})}$ and Syn_{RME} populations for each of the five types of genic action and the variance of $\text{Syn-1}_{(\text{RME})}$ was expressed as a percent of Syn_{RME} genetic variance and plotted as a response surface over allele frequencies p and r (Fig. 2).

Table 2. The genotypic values for five models of genic action and solutions for parameters of genotypic values

Genotypes	Genotypic values (h)[a]				
	MD	PMD	DD	PDD	ADD
BBBB	1	1	1	1	1
BBBb	1	1	1	1	0.75
BBbb	1	1	1	0.5	0.50
Bbbb	1	0.5	0	0	0.25
bbbb	0	0	0	0	0
Parameters					
A	1	0.5	0	0	0.25
D	−1	0	1	0.5	0
T	1	−0.5	−2	−0.5	0
F	−1	0	3	0	0

[a] h is an arbitrary constant of the trait

Results

There are some situations when the DSE does not have an effect on the means. When ADD genic action is assumed, $D = T = F = 0.0$ and equations expressing the effect of DSE on genotypic value ((4), (6), (8), and (9)) go to zero and implicitly the DSE has no effect on the means. For the cross of two populations which are in RME, the mean genotypic value of $\text{Syn-1}_{(\text{RME})}$ is equivalent to that of Syn_{RME} when $p = r$ (see equation (4)) regardless of type of genic action because the DSE is zero, but when either parent of the cross deviates from RME there is a DSE effect as shown by equations (6) and (8).

Figure 1 demonstrates the possible disparity in mean genotypic values of the first and equilibrium generations of the synthetic variety when some type of dominance exists at locus B. With MD and PMD genic action any change in the mean genotypic value in advancing generations with loss of DSE will necessarily be a decrease. But with DD and PDD the changes are greater and more unpredictable (the vertical scale for DD and PDD is double that of MD and PMD). Assuming DD genic action, a change in the genotypic mean over advancing generations will be positive if allele frequencies p and r were less than 0.5, but for greater allele frequencies any change in the synthetic mean would be a decrease. With PDD genic action nearly all possible changes in synthetic mean in advancing generations would be positive.

The means of populations are used as criteria for selection/elimination and for estimation of combining abilities. For this theoretical study with a given type of dominance genetic action the means of a set of populations in RME (Syn_{RME}) will have relative rankings reflecting relative frequency of allele B. The distance between population means are a function of allele frequency and type of genic action of allele B for Syn_{RME}, but for the means of the first generation the rankings do not always have a one-to-one correspondence to allele frequencies.

In a series of crosses where population P is crossed to n other populations ($R_1, R_2, \ldots, R_n$) and where all parent populations are in RME the means are given by

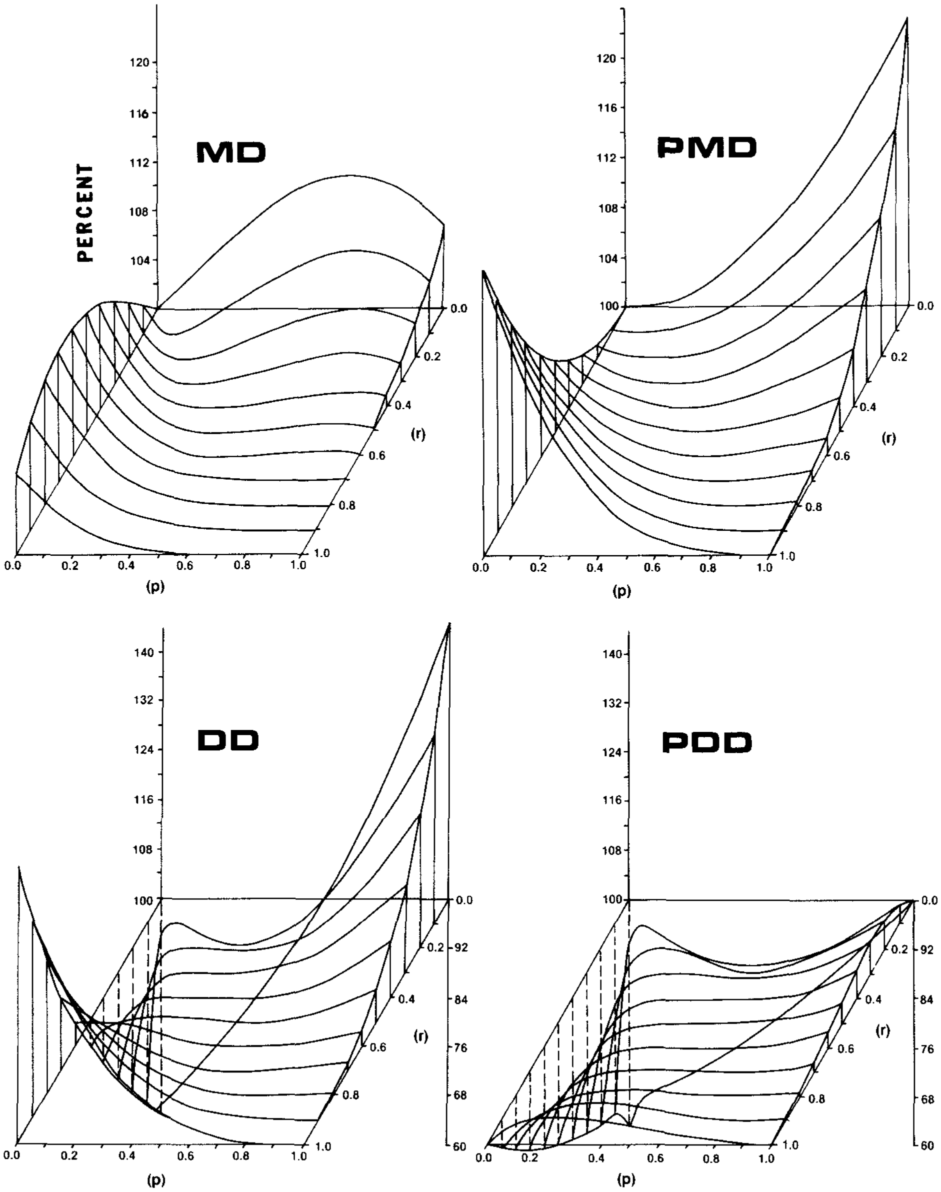

Fig. 1. Response surfaces for the mean genotypic values of Syn-1(RME) expressed as a percent of the mean genotypic values of $\mathrm{Syn}_{\mathrm{RME}}$ with allele B frequencies p and r in the populations P and R, respectively, for four types of genic action

equation (3). For each type of dominance considered in this study, the solutions for A, D, T, and F (found in Table 1) are substituted into equation (3) and simplified. With frequency p fixed, the equation for each type of genic action can be shown to be monotone increasing for increasing values of r on the interval (0, 1). Thus the ranking of the crosses with $R_1, R_2, \ldots, R_n$ have an expected ranking of means the same as that of $\mathrm{Syn}_{\mathrm{RME}}$, though the means are biased from those of $\mathrm{Syn}_{\mathrm{RME}}$ as indicated by equation (4).

If, in another instance, population P in RME is crossed to the n populations $R_1, R_2, \ldots, R_n$ which are not in RME, the expected means of the crosses are given by equation (5). With the assumptions of a fixed p and non-additive genic action at locus B, the ranking of the means of the crosses is then a function of u and r. Since the genotypic mean is not strictly a function of frequency r, the rankings of the means of the crosses will not necessarily reflect relative frequency of B allele.

If the RME and DSE situation were reversed, i.e. $R_1, R_2, \ldots, R_n$ are in the RME, then the equation (5) would still apply with a substitution of variables representing populations P and R. Thus p and x representing frequencies of B and BB in population P would be constants. Substitution of the values for A, D, T, and F for each type of non-additive genic action

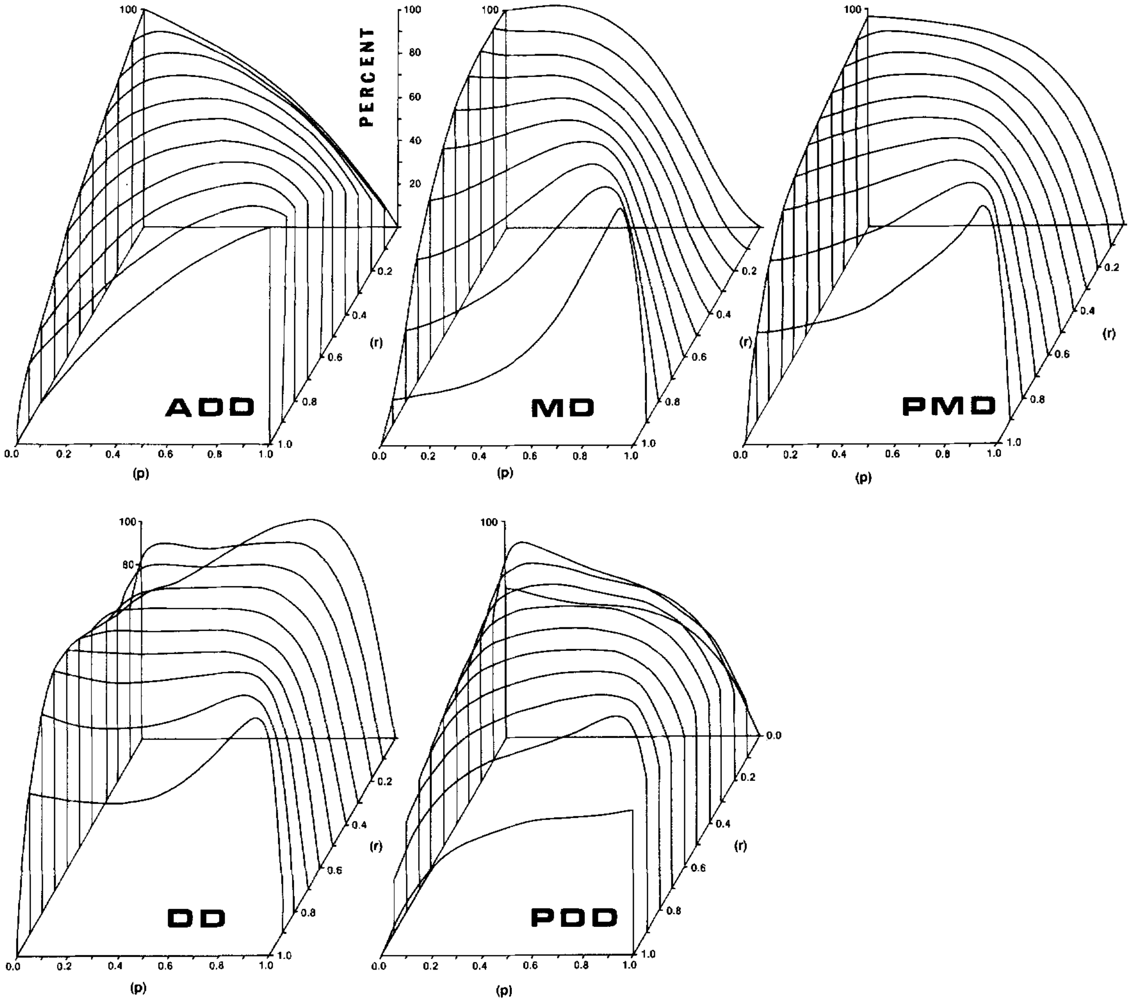

Fig. 2. Response surfaces for the genetic variance of Syn-1(RME) expressed as a percent of the genetic variance of SynRME for allele B frequencies p and r in populations P and R, respectively, for five types of genic action

results in four monotone increasing functions for increasing values of r on the interval (0, 1). Thus the expected rankings of genotypic means would be consistent with frequency of allele B though means would be biased, as shown by equation (6).

If population P were crossed to the n populations $R_1, R_2, \ldots, R_n$ and all populations involved had DSE, then the ranking of means of Syn-1 generation is not expected to accurately reflect the relative frequency of the desirable allele.

The relative amounts of genetic variance of the Syn-$1_{(RME)}$ and Syn_{RME} for values of p and r and each type of genic action appear in Fig. 2. Though only a fraction of the total variance (except for ADD) contributes to the expected gain with selection, the generally negative effect of DSE on selection in synthetic variety is indicated. With MD, PMD, or DD genic action and fixation of allele B in either of the parents results in zero genetic variance of the Syn-$1_{(RME)}$. Except for the situation of DD genic action, the genetic variance of Syn-$1_{(RME)}$ did not exceed that of Syn_{RME} and was equal when $p = r$. With DD genic action the Syn-$1_{(RME)}$ was a maximum of 103% of the Syn_{RME} variance when (p, r) frequencies were (0, 0.75) or the reverse.

As discussed earlier, the DSE did not have an effect on mean genotypic values when ADD genic action was assumed at B locus, but in some instances the DSE greatly reduced the genetic variance.

Discussion

The usefulness of a genic level theoretical study in making predictions of the dynamics of a real quantitative character is highly problematical, but can be used to expose the complexities of some of the underlying genetic processes. The results of this study suggest some interpretations for changes in the means of advancing generations of synthetic varieties and a bias in means of first generation synthetics which could have an effect on any genetic analysis of selection based on these means. The mean genotypic value of a progeny is a function of frequency of the beneficial allele, type of genic action at the locus, and a random variable called DSE.

Results of this study indicated that changes in the mean of advancing generations of the synthetic variety could be positive or negative which was briefly considered in a previous theoretical study by Gallais (1974). The absence of change in advancing generations of the synthetic variety could be the results of ADD genic action or other situations. In the cross of two populations each in RME and with equal allele frequencies there is no DSE and no change in mean genotypic value over generations.

Selections and evaluations performed on the Syn-1 generation may not be as accurate or effective as they would be at the $\mathrm{Syn}_{\mathrm{RME}}$ generation. From Fig. 2 it is obvious that the genetic variance is often zero when the B allele has been fixed in one parent. From this study it is apparent that the means of Syn-1 are not expected to be the same as those of $\mathrm{Syn}_{\mathrm{RME}}$ and that with a DSE in one or both parents of the two population synthetic the rankings of Syn-1 means will not contain much information about relative frequencies of allele B. For the special condition where populations P and R are single plants, there will be as DSE in each parent unless the allele has been fixed. This unpredictable bias in the means of Syn-1 is expected to bias variance component analyses, diallel analyses, estimates of heritabilities or realized gains, and predictions of means in advancing generations.

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