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Theoretical value of estimates of general combining ability in the autotetraploid crop*

D. E. Rowe

Research Geneticist, USDA-ARS, Crop Science Research Lab., P.O. Box 5367, Mississippi State, MS 39762, USA

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Summary. The means of half-sib progenies have been indicated as selection criteria for intra-population improvement while the average of the means of full-sib progenies in diallel analyses have been proposed as predictors, in part, of the means of untested synthetic varieties. When these measures based on progeny means are expressed as deviations from a defined greater population of crosses, they are often termed the general combining ability (GCA). In this study the GCA estimates or a facsimile were theoretically investigated for the one locus, digene, autotetraploid model to verify the genetic basis and its value for selection and prediction in the presence of a naturally occurring phenomena of autopolyploids called gametic disequilibrium with three types of non-additive inheritance. Two breeding objectives were envisioned, the selection of best parents with recurrent selection based on GCA in the continued development of elite populations and the prediction of advanced generation synthetic variety performance. The first generation means of progenies with a potential bias due to gametic disequilibrium were compared to GCA estimation of same progenies in the absence of gametic disequilibrium. The results indicated that testcrossing plants to a population without gametic disequilibrium could be used for selection of best parents. The gametic disequilibrium in the cross may increase or depress selection response dependent on the array of genotypes which happen to be evaluated, on the type of genic action at the locus, and on the frequency of the desirable allele in the testor population. The GCA estimates for prediction of synthetic performance were potentially biased by gametic disequilibrium. An assumption of pollination by the same array of gametes was made for all plants, but obviously was unrealistic for GCA estimation with partial diallels, or with no selfing, and in other situations. The GCA estimate was shown to be an unreliable predictor of synthetic variety performance. When it was assumed that different plants were pollinated by different arrays of gametes, a more realistic situation, no genetic interpretation of GCA values was possible even with purely additive gene action at the locus.

Key words: Synthetic Variety – Alfalfa – *Medicago sativa* L. – Progeny test – Half-sib progeny – Selection

Introduction

Though the procedures that individual plant breeders use for development of alfalfa (*Medicago sativa* L.) cultivars as synthetic varieties can vary substantially, the underlying objectives can be sketched with some certainty. Commonly, one or more populations are improved with respect to one or more economic traits by some recurrent selection procedure. Then the synthetic variety is developed as a polycross of clones from one or more of the elite populations. The use of more than one population in synthetic variety development can facilitate a blending of several desirable traits into one cultivar, increase the potential of beneficial heterotic effects, and reduce the potential of inbreeding depression in advancing generations. At this point the breeder evaluates the synthetic varieties he has composed in comparative trials over years and locations.

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* Cooperative investigation of the Alfalfa Production Research Unit, United States Department of Agriculture, Agricultural Research Service, and the Nevada Agricultural Experiment Station, Reno, Nevada

The importance of heterozygosity in alfalfa is irrefutable (reviewed by Bingham 1980). Logically, then in an outcrossing crop such as alfalfa, the general combining ability (GCA) of a plant measured as the difference in the average performance of all crosses with that plant and the mean performance of all crosses in some population, either random or selected (Sprague and Tatum 1942) would be expected to be a useful trait for selection in synthetic variety development. Indeed, Allard (1960) suggests that the parents of the synthetic variety be selected on basis of GCA.

The attraction of GCA estimation is that it can provide an emperical estimate on the inheritance of a trait which may be very complex and it does suggest a basis for forecasting the value of a plant in untested crosses. To this end, Busbice (1970) considered the weighted GCA estimates for prediction of synthetic variety performance. The statistical analysis of GCA is straightforward, in an experimental design which may involve either comparing the polycrosses progenies in a half-sib family analysis or the average of individual crosses in a diallel analysis. The difficulty with GCA is not in its estimation, but in its interpretation and utilization.

The objective of alfalfa breeding is to develop a synthetic variety which is superior after its third or fourth generation of seed increase. Thus the intent is to produce a cultivar which is still superior when it is approximately in random mating equilibrium (RME). The frequencies of different genotypes for the population in RME are simply the products of the frequencies of the constituent genes and such a population is genetically stable in the absence of mutation, migration, and selection. The number of different combinations of synthetic parents may be very large which produce the same random mating equilibrium population. But for traits with nonadditive inheritance, the earlier generation means can be very different from the different parental combination due to differences in genetic structure of the populations. This deviation from RME is referred to as gametic disequilibrium (GDSE). Since in practice, the GCA estimates are based on the first generation means which can be biased by the GDSE (Rowe and Hill 1984), it is not obvious that the GCA estimates are informative with respect to identifying the best parents for intrapopulation improvement or for prediction of the means of untested synthetic varieties.

Thus the objectives of this study were to theoretically investigate the genetic basis of GCA estimation or a related measure for intrapopulation improvement and for synthetic variety development.

Materials and methods

This study assumes a theoretical, digene (B and b), one locus, random mating population with random chromosome inheritance. The frequencies of genes B and b are p and q, respectively. When the population is in RME, the genotype frequencies are expressed as the expansion of the binomial $(p+q)^4$, Table 1. For the population in GDSE, the genotype frequencies are expressed as the square of the progenitor gamete frequencies x, 2y, and z for gametes BB, Bb, and bb, respectively. Any population not in RME will approach the equilibrium with loss of two-thirds of the disequilibrium with each generation of random mating (Haldane 1930). This disequilibrium will approach zero in the fourth or fifth generation of random mating (Demarly 1963).

It was assumed that population phenotypes were the sum of environmental and genetic effects and that the expectation of the environmental effect was zero. Then the expected value for the phenotype was equivalent to the mean genotypic value of the population. The genotypic values were assigned to genotypes to reflect the following different types of genic action at the B locus: monoplex dominance (MD), duplex dominance (DD), and recessive (REC), see Table 1. Additive gene action was omitted since that population mean is not biased by the GDSE (Rowe and Hill 1984). The means of populations are found as the $\Sigma f_i G_i$ where f_i is the frequency of the i^{th} genotype frequencies in RME or not in RME and G_i is the genotypic value of the i^{th} genotype for a given type of gene action (Table 1).

In a hypothetical breeding program it is assumed that GCA estimates are being made on a set of clones which have a GDSE because they are selections or the product of only one or two generations of random mating of selected materials. These selections are evaluated using either polycrossed families or a diallel analysis.

One case to be considered is the testcross of the clones to a population which is assumed to be in RME with respect to the B gene. The assumed objective of this procedure was to select the best clones on basis of their progeny performances. With the testor population in RME and the evaluated clones in GDSE, the mean of all testcross progenies was not predictable because it was a function of the sample of genotypes which happen to occur in the tested population. Thus in lieu of calculating GCA values for each of the five genotypes, the differences between progenies of crosses of clones which differ by a single gene substitution of B for b was elucidated for

Table 1. The genotypes, their frequencies with or without RME, genotypic values for three types of inheritance, and cross reference code for genotypic values

Genotypes	Frequencies of genotypes		Genotypic values			
	In RME	Not in RME	Monoplex dominance	Duplex dominance	Recessive	Code
BBBB	p^4	x^2	1	1	1	G4
BBBb	$4p^3q$	$4xy$	1	1	0	G3
BBbb	$6p^2q^2$	$4y^2+2xz$	1	1	0	G2
Bbbb	$4pq^3$	$4zy$	1	0	0	G1
bbbb	q^4	z^2	0	0	0	G0

Table 2. Equations for means of progenies produced by crossing the five genotypes to a testor population either in RME or not in RME. Mean genotypic values calculated using genotypic value codes of Table 1

Genotype	Progeny means for testor in RME
BBBB	$p^2(G4) + 2pq(G3) + q^2(G2)$
BBBb	$(p^2/2)(G4) + (pq + (p^2/2))(G3) + (pq + (q^2/2))(G2) + (q^2/2)(G1)$
BBbb	$(p^2/6)(G4) + (2p^2 + pq)(1/3)(G3) + (p^2 + q^2 + 8pq)(1/6)(G2) + (pq + 2q^2)(1/3)(G1) + (q^2/6)(G0)$
Bbbb	$(p^2/2)(G3) + ((p^2/2) + pq)(G2) + (pq + (q^2/2))(G1) + (q^2/2)(G0)$
bbbb	$p^2(G2) + 2pq(G1) + q^2(G0)$
	Progeny mean for testor not in RME
BBBB	$x(G4) + 2y(G3) + z(G2)$
BBBb	$(x/2)(G4) + ((2y/2) + (x/2))(G3) + ((z/2) + (2y/2))(G2) + (z/2)(G1)$
BBbb	$(x/6)(G4) + ((2y/6) + (2x/3))(G3) + ((x/6) + (4y/3) + (z/6))(G2) + ((2/3)z + (2y/6))(G1) + (z/6)(G0)$
Bbbb	$(x/2)(G3) + ((2y/2) + (x/2))(G2) + ((z/2) + (2y/2))(G1) + (z/2)(G0)$
bbbb	$x(G2) + 2y(G1) + z(G0)$

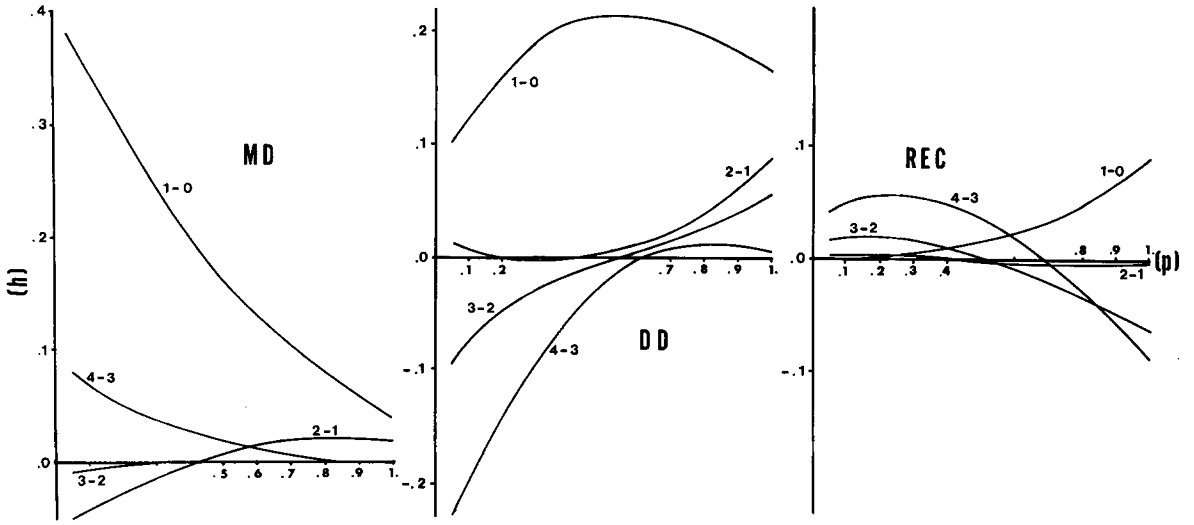

Fig. 1. The bias for three types of gene action of the following differences in the means of respective progenies, codes in parenthesis: BBBB and BBBb (4-3), BBBb and BBbb (3-2), BBbb and Bbbb (2-1), and Bbbb and bbbb (1-0)

three types of genic action at the B locus. This was informative because the greater the expected differences between progeny means, the lower the likelihood of making errors in ranking of the clones and thus errors in selection of best clones. The effect of the GDSE on the selection process was assessed by comparing the differences between progeny means with and without GDSE. The expressions for expected progeny means for each testcross are in Table 2, the mean of the RME population was determined using the given gene frequency of that population and the RME distribution in Table 1 and the different types of genic action. Figure 1 is the progeny mean for each genotype cross at RME minus the mean of the GDSE population with all possible gene frequencies in the testor population.

In the second part of this study, the assumption of testor population in RME is relaxed to reflect the genetics of GCA estimation from diallel analyses with selected clones or from the half-sib progenies produced from polycrossing among only the selected clones. Under these conditions the genotype frequencies of population or progeny are described in terms of gamete frequencies x, 2y, and z of the testor population such that $x + 2y + z = 1.0$. All possible gamete frequencies can be defined in terms of x and 2y since z is then $(1 - x - 2y)$. The equations for the expected means of the progenies of each clone crossed to the testor population in GDSE appear in Table 2.

For GCA estimation the mean of all crosses must be known, but this is not easily described since the genotypes of evaluated materials has not been specified. For simplification it was assumed that the overall mean is determined by random pairing of the gametes with frequencies x, 2y, and z. This implies the population of evaluated clones in the diallel or polycross was sufficiently large that the presence or absence of a single clone will, on average, have a negligible effect on the population mean. This assumption is also reasonable if selfing where to occur naturally in the polycrossed progeny at a frequency of (1/N) where N is the number of evaluated clones. The GCA was then calculated as the difference of

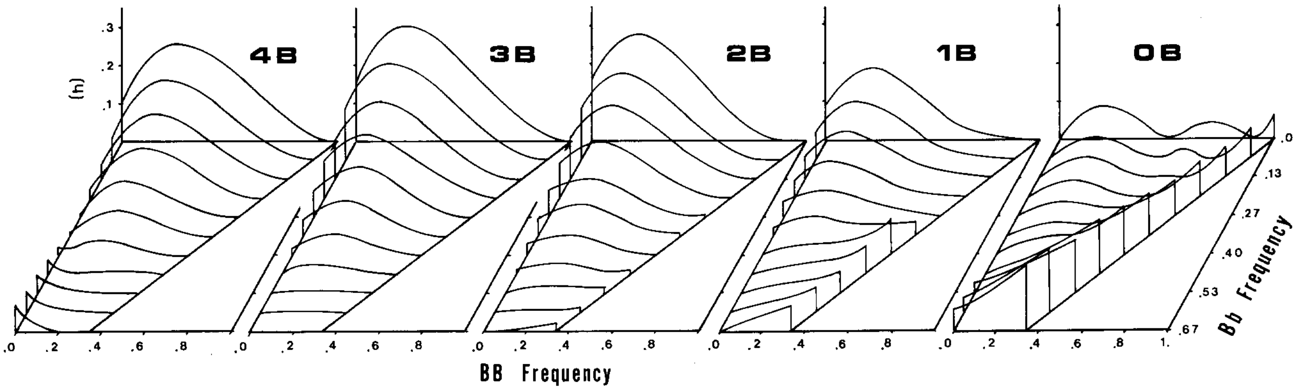

Fig. 2. Response surface for the absolute difference in genotypic value h of GCA estimates in the presence and absence of random mating equilibrium for genotypes BBBB (4B), BBBb (3B), BBbb (2B), Bbbb (1B), and bbbb (0B) with monoplex dominance

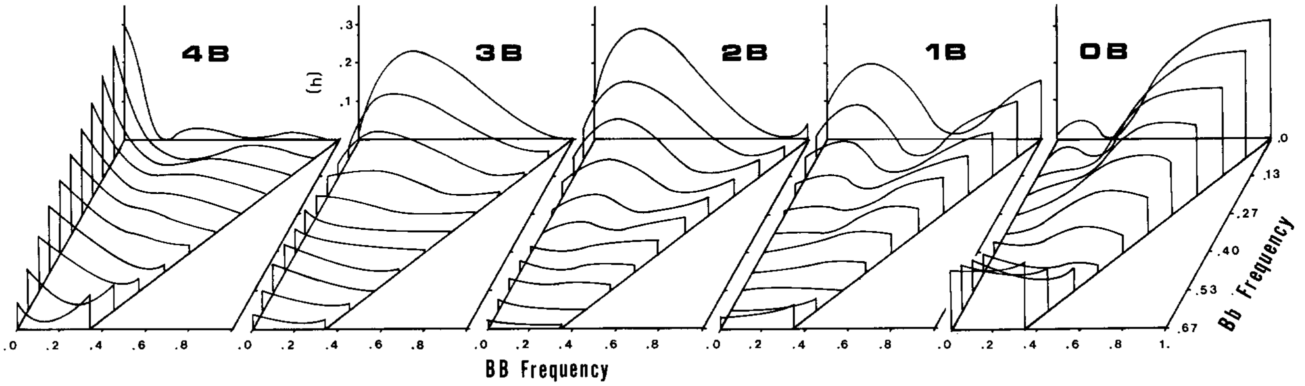

Fig. 3. Response surface for the absolute difference in genotypic value h of GCA estimates in the presence and absence of random mating equilibrium for genotypes BBBB (4B), BBBb (3B), BBbb (2B), Bbbb (1B), and bbbb (0B) with duplex dominance

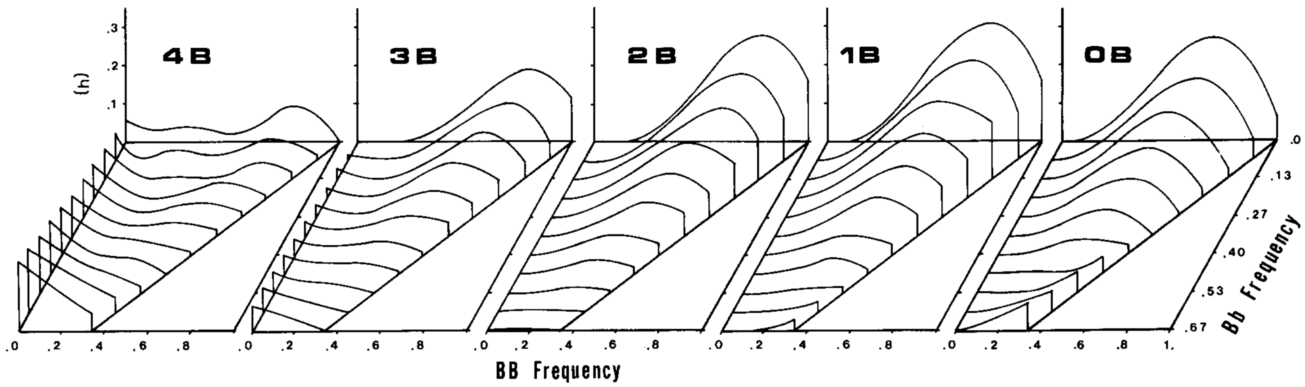

Fig. 4. Response surface for the absolute difference in genotypic value h of GCA estimates in the presence and absence of random mating equilibrium for genotypes BBBB (4B), BBBb (3B), BBbb (2B), Bbbb (1B), and bbbb (0B) with recessive gene action

population mean and the progeny means both of which were not in RME. The GCA was also calculated for the same population and progenies assuming they were in RME. Though the usual GCA is not a difference in populations in RME, it was assumed that this modified GCA had more relevance to the mean of the synthetic variety at RME. The effects of GDSE on the GCA estimate was indicated as the absolute difference between the GCA estimates as a response surface above all possible gamete frequencies of x and 2y. The 2y axis has a maximum value with normal meiosis of two-thirds and the sum of these two frequencies can not exceed 1.0 which accounts for the partially diagonal line seen in the bases of Figs. 2, 3, and 4. The response variable is the absolute difference between the two measures of GCA in terms of the arbitrary genotypic value h.

Results and discussion

The efficacy of selection in a finite population is dependent not only on the contiguity of phenotypic value and genotypic value, but also on the magnitude of the difference between mean genotypic values of the progenies of different genotypes. Given that the progeny phenotype can be biased by random measurement error and random environmental effects, the probability of correctly ranking two different genotypes for their relative genotypic values is dependent on the magnitude of the difference of their mean genotypic values. As this difference increases, the probability of making errors in the relative ranking of the two clones decreases with a proportional improvement in the success of selection.

Figure 1 indicates the effects of GDSE on the difference between progeny means of topcrosses. All diagrams are on the same scale with the $h=0.0$ position moved to accommodate the different response curves. When the response curve is positive, the GDSE has suppressed the difference between progenies in contrast to the same comparison made for the progenies in RME. When the curve is negative, the GDSE has inflated the difference between the means.

Obviously the GDSE has suppressed the difference between the progenies of genotypes Bbbb and bbbb with either DD or MD genic action at the locus. A less dramatic suppression occured for the contrast of BBBB and BBBb with MD, of BBbb and Bbbb with DD, and Bbbb and bbbb with REC. The effect of GDSE was negligible for the contrast of genotypes BBbb and Bbbb with REC gene action, and genotypes BBBb and BBbb with MD. For all other cases the GDSE effect was both positive and negative depending on the frequency of B in the testor population.

An earlier study (Rowe 1982) briefly considered the effect of GDSE on selection with half-sib progeny testing, but this current study elucidated in much more detail the complexity of the effect of GDSE on selection. Rowe and Hill (1981) found the use of testor population with frequency of gene B of zero was optimum for intra-population improvement using a testcross. This result assumed the original population was in RME and infinite. In the finite population the gain with selection is problematical and dependent on the sample of genotypes exposed to selection (Hill 1969). In the selection process the GDSE effect modifies all generalities such that without knowing the type of genic action aprior, the best testor for selection is not known.

The objective of synthetic variety development is the improvement of the cultivar mean in an advanced generation when that population is near RME, not the early generation mean. The use of GCA estimates for selection and for prediction of synthetic variety performance (Busbice 1970) implies a useful relationship between performance of single cross progenies and the contribution to the performance of the advanced generation mean. The distance between the equilibrium and biased GCA estimates in Figs. 2, 3, and 4 for three types of non-additive gene action at the B locus shows the possible disparity of the GCA measurement.

It is a paradox that the plant breeder often constructs synthetic varieties from very diverse sources in order to maximize heterotic effects, but when the synthetic variety attains an equilibrium most of the plants will be produced from crosses of closely related genotypes. The original parents are often genetically very different and hence the crosses which are measured in the first generation occur only rarely in the equilibrium population. Thus prediction of synthetic performance at equilibrium from the performance of first generation crosses or the first generation of the synthetic appears to be very unreliable if nonadditive gene action is important and if the synthetic variety is composed of heterogeneous parents. Thus it appears that GCA estimates from the diallel or from the polycross of selections are not reliable predictors of synthetic variety performance.

An earlier assumption in the model development was that the testor population genotype was constant, but if this is not true and each clone is pollinated with a different genotype, the situation becomes even more confusing. In the absence of the genetically constant testor population, differences in progenies will not be interpretable for either selection or prediction, even with purely additive gene action at the B locus.

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