

Genetic components of combining ability in a complete diallel

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ABSTRACT - Obtained \hat{g}_i and \hat{s}_{ii} values were associated to theoretical concepts of the respective parameters in a complete diallel with 28 parents and the simulation of five hypothetical variables with five different d/a relations (0, 0.5, 1.0, 1.5, and 2.0). These were controlled by a single gene with two alleles whose parents were represented by different frequencies of the favorable allele (1/28, 2/28, ..., 28/28). The conclusion was drawn that the existence of dominance deviations in the loci regulating the trait influences the GCA estimates considerably and that there is a high correlation (0.96) between the absolute \hat{s}_{ii} and the respective \hat{g}_i values. The joint evaluation of \hat{g}_i and \hat{s}_{ii} estimates provides information on the genetic quality of the populations of the diallel.

Key words: combinatory ability, complete diallel, genetic components, genetic improvement.

INTRODUCTION

The expressions 'general combining ability' (GCA) and 'specific combining ability' (SCA) are being used since the past century (Sprague and Tatum 1942) to designate the properties of the evaluated populations in hybridization programs. One of the techniques that can verify the mean performance of a parent in a series of hybrid combinations (GCA) and make out certain hybrid combinations which are relatively superior or inferior to the expected based on the GCA of its parents (SCA), is the diallel analysis.

The complete diallel involves all crossing possibilities

within a parent group, and it is used to study polygenic systems that determine quantitative traits since it offers information regarding the predominant gene action. It can be used at initial, intermediate, or final stages of an improvement program. Depending on the nature of the parents, the conclusions based on the results are also useful for the formation of a basis population for intra or inter-population improvement (Viana et al. 1999).

The success of an improvement program is closely linked to the selection of the best parents (families, lines, etc). The estimates of the GCA, and effect SCA of the parent with itself, provide information on the quality and genetic

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diversity of the parents that compose the diallel. Although inferences on the genotypic values of individuals are of great interest, it is important to consider the genetic values of each allelic form. It is the case of the allogamous species, whose parents pass their alleles and not their genotypes on to the descendants (Falconer 1987).

On these premises, the aim of our study was to associate \hat{g}_i and \hat{s}_{ii} estimates obtained from simulated data to the theoretical concepts presented in literature and to identify the factors that can alter the estimates of the same.

MATERIAL AND METHODS

In our study we considered a complete diallel with $p = 28$ populations (parents). Five hypothetical variables controlled by a single gene with two alleles each were simulated, whose dominance degree was represented by d/a relations of 0, 0.5, 1.0, 1.5, and 2.0, expressing the respective situations of absence, partial, and complete dominance, and two degrees of overdominance.

The k^{th} parents for $k = 1, 2, \dots, 28$, was represented by the favorable allele frequency equal to $k/28$. The analysis of the data obtained from the 28 parents and the $p(p-1)/2 = 378$ F_1 hybrids, a total of 406 genotypes, was realized by method 1, model 1 (for fixed effects) of Griffing (1956). We assumed that the maternal effects, effective population size, and inbreeding depression effects were all negligible or absent in the seeds of these 406 genotypes.

The statistical model is expressed by:

$$Y_{ij} = m + g_i + g_j + s_{ij} + \varepsilon_{ij},$$

where Y_{ij} is the observed average of the ij^{th} hybrid for $i \neq j$ or for the i^{th} parent, when $i = j$; with i and $j = 1, 2, \dots, p$; m is the overall mean; \hat{g}_i and \hat{g}_j are general combining ability effects (GCA); s_{ij} is the specific combining ability effect (SCA), and ε_{ij} is the random non-observable experimental error term.

The averages values used for the complete diallel were defined by the following equations:

$$Y_{ii} = \mu + a(2p_i - 1) + 2p_i(1 - p_i)d$$

and

$$Y_{ij} = \mu + a(p_i + p_j - 1) + (p_i + p_j - 2p_i p_j)d$$

where μ is the average genotypic value of the homozygote; a is the deviation between the largest genotypic homozygote value and μ ; d is the deviation between the genotypic heterozygote value and μ , called deviation due to dominance; and p_i and p_j are frequencies of favorable alleles for the i^{th} and j^{th} parents, respectively.

The genetic GCA and SCA values were determined by a modified version of Vencovsky (1987)'s model, which considers only one locus controlling a quantitative trait with two alleles without epistatic effects in a diploid species with sexual reproduction, given by:

$$g_i = (p_i - \bar{p})[a + (1 - 2\bar{p})d] \quad (i)$$

and

$$s_{ii} = 2[(\bar{p} - p_i)(p_i - \bar{p})d] \quad (ii)$$

where \bar{p} is the average frequency of the favorable allele among the parents of the analyzed diallel, and the equation $a + (1 - 2\bar{p})d$ represents the mean effect of gene substitution (α).

The study was based on the estimation of GCA (\hat{g}_i) effects and also SCA effects of the i^{th} parent with itself (\hat{s}_{ii}) for the five hypothetical simulated variables, relating these estimates to the equations (i) and (ii), respectively. The simulations and diallel analyses were performed with software Genes (Cruz 1997).

RESULTS AND DISCUSSION

Table 1 shows the values of the 28 GCA estimates for the different hypothetical variables. Oscillations from one variable to the other were small for the same parent (population) in spite of the different dominance degree. This fact can be explained by the mean allelic frequency of 0.52. When the mean estimated allelic frequency in a diallele is 0.5, the dominance effects are cancelled. Consequently, the \hat{g}_i 's are predominantly function of the contribution of the additive effects and the gene frequency in parent i (Cruz and Vencovsky 1989). Thus, if the parents that compose the diallel have a broad genetic base (many segregant loci) and a gene frequency mean of 0.5, the greatest effects of the GCA for a quantitative trait will probably indicate the parents with the highest concentration of predominantly additive genes. However, we should bear in mind that despite the broad-based parents, some loci might have allelic frequencies that differ from 0.5, which does not necessarily cancel the expression $(1 - 2\bar{p})d$, whose GCA is influenced by the gene dominance.

The additional effect ascribed to the dominance deviation slightly reduced the \hat{g}_i estimates along with the increase of the d/a relation. Although the dominance effects hampered the selection of the parents, they allowed an exploration of the heterosis that, together with the right of the intellectual property warranted by the secret of the inbred line combinations, are the chief responsible for the success in maize improvement.

Table 1. Estimates of GCA effects for the hypothetical variables controlled by a single gene with two alleles and different dominance degrees (d/a ratios) for a complete diallel with 28 parents

Parents	d/a = 2.0	d/a = 1.5	d/a = 1.0	d/a = 0.5	d/a = 0
1	-4.676	-4.712	-4.749	-4.785	-4.822
2	-4.300	-4.342	-4.383	-4.424	-4.464
3	-3.928	-3.973	-4.018	-4.062	-4.107
4	-3.559	-3.605	-3.654	-3.702	-3.750
5	-3.193	-3.243	-3.292	-3.343	-3.393
6	-2.831	-2.882	-2.933	-2.985	-3.036
7	-2.472	-2.521	-2.575	-2.626	-2.679
8	-2.117	-2.168	-2.217	-2.270	-2.322
9	-1.764	-1.815	-1.864	-1.914	-1.964
10	-1.415	-1.465	-1.512	-1.559	-1.607
11	-1.069	-1.116	-1.160	-1.205	-1.250
12	-0.729	-0.770	-0.811	-0.852	-0.893
13	-0.391	-0.427	-0.463	-0.502	-0.536
14	-0.055	-0.086	-0.117	-0.148	-0.179
15	0.276	0.252	0.228	0.203	0.178
16	0.604	0.587	0.570	0.553	0.536
17	0.929	0.920	0.911	0.902	0.893
18	1.251	1.250	1.249	1.250	1.250
19	1.569	1.578	1.588	1.598	1.607
20	1.883	1.904	1.924	1.945	1.964
21	2.195	2.227	2.258	2.290	2.321
22	2.503	2.547	2.590	2.635	2.678
23	2.807	2.864	2.921	2.979	3.036
24	3.108	3.179	3.251	3.322	3.393
25	3.405	3.492	3.578	3.664	3.750
26	3.700	3.802	3.903	4.005	4.107
27	3.991	4.109	4.227	4.346	4.464
28	4.278	4.414	4.550	4.686	4.821

The GCA estimates of the parents 1 and 28 of smallest and greatest frequency of the favorable allele were the highest in absolute values for all presented dominance degrees. On the contrary, the GCA estimates for the intermediate parents tended to be zero, principally in parent 14, whose difference ($p_i - \bar{p}$) was the smallest.

If the parents are considered open pollination populations, the greatest GCA effect is related to the population with greatest frequency of genes that increase the trait expression and/or that presents the greatest difference between its gene frequency and the mean frequency of the populations involved in the diallel. If the parents are inbred or pure lines, the greatest GCA effect is related to the line of the largest number of genes that increase the expression of the trait and, consequently, the greatest number of positive

differences between its gene frequency and the mean frequency of the lines involved in the diallel (Viana 2000).

The GCA effect is therefore an indicator for the superiority of a parent and/or of its greatest divergence regarding the parents of the diallel, besides making information on the parameters of the population effect (v_j) and of the varietal heterosis (H_j) of the Gardner and Eberhart (1966) model available, as Pacheco et al. (2002) have pointed out.

Cruz and Vencovsky (1989), who studied the SCA parameter of a parent with itself (\hat{s}_{ii}), considered it an indicator of varietal heterosis and the existence of unidirectional dominance, which is negative for predominantly positive dominance deviations and vice-versa. They further showed that the sum of the is a linear function of the mean

heterosis, and that method 2 proposed by Griffing (1956), which includes the parents, spawns basically the same information as the methodology of Gardner and Eberhart (1966).

The s_{ii} effects, like any SCA effect, are strongly linked to the dominance effects and the allelic frequencies (Table 2). This is made evident by the variations in the d/a relations that tend to increase the s_{ii} effect with the increase of d for the same parent.

Since a single gene was considered in this study, the s_{ii} estimates were negative because of the unidirectional dominance. It was also verified that the parents with extreme

allelic frequencies, 1 and 28, had the highest absolute s_{ii} values, which made them genetically the most divergent in relation to the others.

The correlation established in this study between the absolute g_i and s_{ii} values were 0.96 for any dominance degree ($d/a \neq 0$). Viana (2000) found similar results.

This correlation between populations is the correlation between the inter-population and intra-population combination ability. If the additive and dominant effects are significant in the studied diallel, the populations with high (positive) \hat{s}_{ii} and \hat{g}_i have the highest heterozygous

Table 2. Estimates of s_{ii} effects for the hypothetical variables controlled by a single gene with two alleles and different dominance degrees (d/a ratios) for a complete diallel with 28 parents

Parents	d/a=2.0	d/a=1.5	d/a=1.0	d/a=0.5	d/a=0
1	-8.787	-6.587	-4.395	-2.195	-0.004
2	-7.550	-5.658	-3.768	-1.888	0.001
3	-6.404	-4.806	-3.198	-1.601	-0.003
4	-5.352	-4.021	-2.676	-1.341	0.003
5	-4.404	-3.306	-2.199	-1.100	-0.001
6	-3.548	-2.658	-1.778	-0.886	0.004
7	-2.786	-2.089	-1.393	-0.693	0.000
8	-2.116	-1.585	-1.059	-0.525	-0.004
9	-1.551	-1.162	-0.775	-0.387	0.001
10	-1.069	-0.801	-0.540	-0.267	-0.003
11	-0.691	-0.520	-0.343	-0.175	0.003
12	-0.402	-0.302	-0.202	-0.101	-0.001
13	-0.218	-0.158	-0.107	-0.051	0.004
14	-0.119	-0.089	-0.060	-0.030	0.000
15	-0.122	-0.085	-0.060	-0.031	-0.004
16	-0.218	-0.156	-0.104	-0.051	0.001
17	-0.408	-0.302	-0.206	-0.099	-0.003
18	-0.691	-0.522	-0.342	-0.176	0.003
19	-1.068	-0.808	-0.539	-0.272	-0.001
20	-1.546	-1.159	-0.772	-0.385	0.004
21	-2.119	-1.585	-1.060	-0.526	0.000
22	-2.785	-2.085	-1.394	-0.695	-0.004
23	-3.544	-2.660	-1.775	-0.883	0.001
24	-4.406	-3.300	-2.205	-1.100	-0.003
25	-5.360	-4.015	-2.679	-1.343	0.003
26	-6.410	-4.805	-3.200	-1.605	-0.001
27	-7.551	-5.659	-3.778	-1.887	0.004
28	-8.786	-6.589	-4.393	-2.196	0.000
Heterosis mean -	3.215	- 2.410	- 1.607	- 0.803	0.000

and homozygous loci frequencies. This condition ensures the required variability for a successful selection process and good performance, and indicates the most suitable populations for intra-population improvement. On the other hand, Pacheco et al. (2002) claim that the population with the greatest \hat{s}_{ii} together with a large negative \hat{g}_i in a diallel is not appropriate for intra-population improvement due to a high frequency of homozygous recessive loci. Likewise, a population with a very high \hat{g}_i and a small \hat{s}_{ii} , in spite of having a high frequency of favorable homozygous alleles and, consequently, high yield means, may not be the most indicated for intra-population improvement once the expected gains with selection tend to be small owing to its probably smaller genetic variability.

The negative heterosis may be attributed to the deviations of the negative dominance, indicating that the dominance effect tended to diminish the value of the trait. Since the dominance deviations in this simulation were unidirectional and positive, the varietal heterosis was negative for the parents 7 to 22, mainly for 14 and 15, since these contributed to reduce the heterosis of the crosses in which they participated and their heterozygous genotype manifestation.

The more homozygous a parent is, the greater the varietal heterosis, e.g., parents 1 and 28. Although the greatest absolute \hat{s}_{ii} value is related to parents with the highest favorable or unfavorable allele concentration (1 and 28,

respectively), they have no variability. The best parent should unite a high frequency of favorable alleles and high frequency of loci in heterozygosis. If several regulating loci of any trait were considered, instead of a single locus, the parents 24, 25, and 26 would probably be the most indicated for intra-population selection; besides the high concentration of favorable alleles, these have most individuals in the respective populations with heterozygote genotypes.

CONCLUSIONS

1. The GCA estimates are influenced by the dominance deviations in the regulating trait loci;
2. The high correlation between the absolute \hat{s}_{ii} values to the respective \hat{g}_i values in the evaluation of populations for a particular polygenic trait makes it possible to identify and select populations of good performance and a high genetic variability. The joint interpretation of these two genetic parameters provides complementary information on the genetic quality of the populations included in the improvement program.

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Componentes genéticos das capacidades de combinação do dialelo completo

RESUMO - Com o objetivo de associar os valores de \hat{g}_i e \hat{s}_{ii} obtidos, com os conceitos teóricos dos respectivos parâmetros, foi considerado um dialelo completo com 28 progenitores e a simulação de cinco variáveis hipotéticas com cinco diferentes relações d/a (0, 0,5, 1,0, 1,5 e 2,0). Estas foram governadas por apenas um gene com dois alelos, cujos progenitores foram representados por diferentes frequências do alelo favorável (1/28, 2/28, ..., 28/28). Concluiu-se que a existência de desvios da dominância nos locos reguladores da característica influencia consideravelmente nas estimativas de CGC e que existe uma alta correlação (0,96) entre os valores absolutos \hat{g}_i de \hat{s}_{ii} com os respectivos valores de \hat{g}_i . A avaliação das estimativas \hat{g}_i de \hat{s}_{ii} e conjuntamente, traz informações sobre a qualidade genética das populações do dialelo.

Palavras-chave: capacidade combinatória, dialelo completo, componentes genéticos, melhoramento genético.

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