STABILITY OF COMBINING ABILITY EFFECTS IN MAIZE HYBRIDS

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ABSTRACT: General and specific combining ability effects are important indicators in a maize (*Zea mays* L.) breeding program aiming hybrid development. The objectives of the present study were to estimate the general (GCA) and specific combining abilities (SCA) effects of commercial maize hybrids using a complete diallel scheme and to assess the stabilities of these estimates. Fifty-five entries were assessed; ten commercial single-crosses and all possible double-crosses. The experiments were carried out in 12 environments in the 2005/06 growing season. A randomized complete block design was used with three replications per environment. Ear yield was evaluated, corrected to 13% of moisture content. The combined diallel analysis involving all environments was performed and the stability of general and specific combining ability effects was investigated. The underlying nonparametric statistics evaluated the contribution of each effect to the genotype by environment interaction. Non-additive effects were more important for this set of hybrids than the additive effects. It was possible to select parents with high stability for combining ability and with high GCA.
Key words: *Zea mays* L., diallel, nonparametric statistics

ESTABILIDADE DOS EFEITOS DA CAPACIDADE DE COMBINAÇÃO EM HÍBRIDOS DE MILHO

RESUMO**:** Os efeitos da capacidade geral (CGC) e específica de combinação (CEC) são indicadores importantes em um programa de melhoramento milho (*Zea mays* L.) visando a obtenção de híbridos. Os objetivos do presente trabalho foram estimar os efeitos da capacidade geral e específica de combinação de híbridos comerciais de milho e avaliar a estabilidade das estimativas desses parâmetros. Para isso foram avaliados 55 tratamentos, sendo dez híbridos simples comerciais e os 45 híbridos duplos possíveis. Os experimentos foram conduzidos em 12 ambientes no ano agrícola de 2005/06. O delineamento empregado foi o de blocos casualizados com três repetições por ambiente, e o caráter avaliado foi o peso de espigas corrigido para 13% de umidade. Procedeu-se à análise dialélica conjunta envolvendo todos os ambientes e realizou-se o estudo da estabilidade dos efeitos da capacidade geral e específica de combinação, adotando-se a estatística não-paramétrica por meio da soma de postos. Os efeitos não aditivos foram mais importantes que os efeitos aditivos para o desempenho desse conjunto de híbridos. É possível selecionar genitores com alta estabilidade para a capacidade de combinação e com CGC de elevada magnitude.
Palavras-chave: *Zea mays* L., dialelo, estatística não-paramétrica

INTRODUCTION

The use of diallel crosses to study the genetic control of traits, and to select parents to obtain synthetics or hybrids, is frequent in maize (*Zea mays* L.) breeding (Rodrigues et al., 2006; Welcker et al., 2005). One of the most used procedures in the diallel analysis is Griffing's (1956) method, that estimates the general (GCA) and specific (SCA) combining ability of the parents.

Given the diversity of environments in which maize is cropped in Brazil, the hybrid by environment interaction is normally expressive (Aguiar et al., 2003; Gonçalves et al., 1999; Machado et al., 2008). Therefore it is necessary to identify hybrids that present not only wide adaptation, assessed by the mean yield, but also have high stability, i.e., with homeostasis to adjust to environmental changes. Some studies have already compared stability in different types of hybrids (Carvalho et al., 2005; Ribeiro et al., 2000).

However, there is little information regarding stability of the GCA and SCA effects. Probably, when identifying single-crosses with higher stability in the

GCA and SCA, the hybrid combinations (double-cross) obtained from these parents also present higher homeostasis for environmental variations. Pacheco et al. (1999) estimated GCA and SCA stability parameters, using the method developed by Eberhart & Russel (1966) in maize populations in Hardy-Weinberg equilibrium, and reported differences in GCA and SCA stability for the different populations assessed. However, no reports were found of studies using single-crosses as parents.

The objectives of the present study were to estimate the effects of the general and specific combining abilities of commercial maize hybrids using a complete diallel scheme and to assess the stabilities of these estimates.

MATERIAL AND METHODS

The experiments were carried out in 12 environments in Minas Gerais State in the 2005/06 growing season, in farms and experimental stations. These environments constituted a sample of the southern region of Minas Gerais and Alto Paranaíba that vary greatly in level of technology used, altitude and sowing date (Table 1).

Ten commercial single-crosses were used (A, B, C, D, E, F, G, H, I and J), which differed regarding grain texture and cycle. These single-crosses (SC) were chosen because they are recommended for cropping in the southern region of Minas Gerais. Using the diallel scheme, all possible double-crosses (DC) were obtained in the 2004/05 agricultural season.

Forty five double-crosses and ten single-crosses (parents) were evaluated using a randomized complete block design with three replications per environment. The plots consisted of two 3 m long rows spaced 0.8 m between rows, using a population density of 55,000 plants per hectare. The other cultural practices were those normally used by farmers or experimental stations for maize (EMBRAPA, 2007). Experimental details of the environments where the experiments were carried out are shown in Table 1.

The trait evaluated was ear yield (kg ha^{-1}) corrected to 13% of moisture content and to ideal stand by covariance analyses (Vencovsky & Barriga, 1992).

Combined diallel analysis was performed and the quadratic components were estimated that expressed variability of the parents studied, regarding the GCA ($\hat{\phi}_g$) and SCA ($\hat{\phi}_s$). To verify whether the estimates of the general and specific combining abilities were different from zero, the t test was carried out (Zhang et al., 2005). Nonparametric statistics were used to obtain a measure of the stability of the parameters of the Griffing diallel analysis, base of the contribution of each estimate to the genotype by environment interaction (Machado et al., 2008; Truberg & Huehn, 2000).

The estimated effects of the GCA, obtained in the diallel analysis, were ranked in a double entry table among effects (placed on the lines) and environments (placed in the columns). The smallest estimate in each environment received the rank 1 and the greatest received the rank 10. The same procedure was adopted for the effects of the SCA but the greatest estimates in each environment received the rank 55.

From this classification, the ecovalence estimate (Wricke, 1965) was obtained using the following expression: $W_i^2 = \sum (R_{ij} - \overline{R}_{i.} - \overline{R}_{.j} + \overline{R}_{..})^2$ where: W_i^2: ecovalence; R_{ij}: rank for the observation of the estimate of the i parameter in the j environment; $\overline{R}_{i.}$: average rank of the i parameter estimate; $\overline{R}_{.j}$: average rank of the j environment; $\overline{R}_{..}$: grand mean. The stability analyses were carried out using R Program (R Development Core Team, 2006).

Table 1 - Data of locations in the State of Minas Gerais, Brazil, where the experiments were carried out.

Municipal district	Sown date	Harvest date	Latitude	Longitude	Altitude	Ear Yield	Technological level[1]
					m	kg ha^{-1}	
Lavras	11/08/2005	05/23/2006	21°13'S	44°58'W	910	10,803	E.S. (High technology)
Guarda-Mor	12/21/2005	06/02/2006	17°34'S	47°08'W	1,010	6,212	Small farmer
Lavras	11/12/2005	05/18/2006	21°12'S	44°58'W	951	6,246	Small farmer
São Gotardo	11/07/2005	05/27/2006	19°18'S	46°03'W	1,058	8,085	E.S. (High technology)
Ijaci	10/13/2005	03/23/2006	21°09'S	44°56'W	859	13,192	E.S. (High technology)
Ijaci	01/31/2006	07/27/2006	21°09'S	44°56'W	859	8,896	E.S. (Off season)
Lavras	11/28/2005	05/09/2006	21°13'S	45°03'W	918	8,685	Medium farmer
Ribeirão Vermelho	11/03/2005	04/27/2006	21°10'S	45°04'W	884	8,737	Medium farmer
Candeias	11/13/2005	05/02/2006	20°46'S	45°19'W	967	9,876	Commercial farmer
Paracatu	02/20/2006	07/04/2006	17°13'S	46°39'W	580	7,768	E.S. (Off season)
Carrancas	12/21/2005	06/01/2006	21°24'S	44°38'W	1,005	7,353	Medium farmer
Itutinga	12/06/2005	06/14/2006	21°23'S	44°46'W	958	8,041	Medium farmer

[1]Technological level similar of the classification made by EMBRAPA (2007). E.S.: Experimental station.

RESULTS AND DISCUSSION

Although most of the experiments were carried out on farms, the sources of variation in the analysis of variance, except error, explained 87.2% of the total variation, showing good experimental accuracy. Environmental means ranged from 6,212 kg ha^{-1} at a small farmer in a low technological level to 13,192 kg ha^{-1} at an experimental station in a high technological management system (Table 1).

Due to the diversity of environments, the significance of the Environment (E) source of variation was detected in the combined diallel analysis, ($p \leq 0.01$). Similarly, differences ($p \leq 0.01$) were detected for entries and for entries by environment interaction. In the partioning of the entries source of variation, according to the Griffing's (1956) method, significant differences were obtained for GCA and SCA.

Considering one locus, the GCA estimates are functions of the genetic differences of the parents and the mean effects of an allelic substitution and are directly associated to the additive effects of the genes when the tester frequency is 0.5 (Hallauer & Miranda Filho, 1988). In the present study, the testers used were single-crosses, and then their allelic frequencies are 0.5. In this case, GCA directly represents the additive effects.

The GCA estimates ($\hat{g}_i$) of the hybrids assessed ranged from -366.2 to 538.2 kg ha^{-1}. The highest estimates were obtained for the single-crosses F and B, indicating that these hybrids had a higher favorable allele frequency for ear yield. This fact can be verified by the mean yields obtained for these hybrids across environments. The smallest GCA estimates were obtained by the single-crosses E and C, with values of -366.2 and -357.2 kg ha^{-1}, respectively. They presented the lowest favorable allele frequency for the trait evaluated (Table 2).

The SCA effects are functions of dominance and the product of the differences in allele frequencies of the parents, consequently they are related to the effects of dominance and epistasis (Hallauer & Miranda Filho, 1988). The quadratic component for SCA ($\hat{\phi}_s$) was 4.3 times greater than the quadratic component for GCA ($\hat{\phi}_g$) indicating that the non-additive effects were more important than the additive effects for variation in this set of hybrids.

Concerning the specific combining ability estimates ($\hat{s}_{ij}$), it was verified that 15% were different from zero ($p \leq 0.05$). The percentage of positive and negative estimates was 38% and 62%, respectively, ranging from -1,604.9 to 1,726.3 kg ha^{-1} (Table 2). The $\hat{s}_{ij}$ effects, estimated as deviation in performance compared to the expected based on the general combining ability, are a measured from the non-additive effects, and are useful in identifying the best hybrid combinations among the parents assessed (Cruz et al., 2004).

Based on the significance of the GCA and SCA variation sources, parents differed in the combining ability, contributing differently to the crosses where they were involved and the hybrid performances were different from the expected due to the GCA effects. SCA is a function of the effects of dominance and the diversity of the parents. The existence of divergence was detected by the variation observed in the parents means (Table 2). When expressive SCA occurs, the

Table 2 - Estimates of general ($\hat{g}_i$) and specific ($\hat{s}_{ij}$) combining abilities (diagonal and upper diagonal) and ear yield means (kg ha^{-1}) (bellow the diagonal), from the diallel analysis.

Parent	A	B	C	D	E	F	G	H	I	J	Mean	$\hat{g}_i$
											kg ha^{-1}	
A	969.5**	270.9^{ns}	392.2^{ns}	-1,455.9**	150.7^{ns}	299.1^{ns}	-525.1^{ns}	520.6^{ns}	13.4^{ns}	-1,604.9**	9,376 b	-5.3^{ns}
B	9,062 b[1]	151.0^{ns}	124.8^{ns}	476.3^{ns}	-286.4^{ns}	-454.3^{ns}	121.6^{ns}	-192.5^{ns}	-398.9^{ns}	36.41^{ns}	9,327 b	379.4**
C	8,447 c	8,564 c	420.1^{ns}	-55.8^{ns}	-944.5*	-447.7^{ns}	-31.9^{ns}	335.8^{ns}	-160.0^{ns}	-53.2^{ns}	8,123 d	-357.2**
D	6,828 e	9,145 b	7,877 d	1,443.5**	44.9^{ns}	-230.3^{ns}	-1090.1**	-138.4^{ns}	687.9^{ns}	-1,125.5**	9,606 a	-127.5^{ns}
E	8,196 d	8,144 d	6,749 e	7,968 d	152.4^{ns}	-105.1^{ns}	464.9^{ns}	-37.6^{ns}	-32.4^{ns}	440.7^{ns}	7,837 d	-366.2**
F	9,249 b	8,880 c	8,150 d	8,598 c	8,484 c	491.0^{ns}	518.2^{ns}	-366.3^{ns}	-463.7^{ns}	267.9^{ns}	9,984 a	538.2**
G	8,043 a	9,074 b	8,184 d	7,356 e	8,672 c	9,630 a	637.6^{ns}	-692.9^{ns}	-164.8^{ns}	124.8^{ns}	9,367 b	156.3^{ns}
H	8,866 c	8,538 c	8,329 d	8,085 d	7,947 d	8,523 c	7,814 d	237.9^{ns}	-124.1^{ns}	219.7^{ns}	8,522 c	-66.4^{ns}
I	8,348 d	8,320 d	7,822 d	8,900 c	7,941 d	8,414 c	8,331 d	8,149 d	337.4^{ns}	-32.1^{ns}	8,600 c	-77.4^{ns}
J	6,733 e	8,759 c	7,933 d	7,090 e	8,418 c	9,149 b	8,624 c	8,496 c	8,234 d	1,726.3*	9,132 b	-74.0^{ns}

* and **Different from zero by the t test, at 5% and 1% , respectively. ^{ns}Not different. [1/]means followed by the same letter belong to the same group, by the Scott and Knott test (1974) at 5%.

Table 3 - Ecovalence estimates for the general ($\hat{g}_i$) and specific ($\hat{s}_{ij}$) combining abilities estimates.

Parent	A	B	C	D	E	F	G	H	I	J	$\hat{g}_i$
A	0.6	1.9	1.3	0.8	2.3	1.6	1.2	0.7	1.9	0.2	11.3
B		3.4	2.7	2.7	2.4	1.5	2.4	1.1	1.2	3.2	9.7
C			2.4	1.3	0.4	2.9	2.5	1.3	2.8	2.4	6.7
D				0.8	4.0	3.0	0.2	0.9	1.7	1.1	13.5
E					2.5	1.3	1.3	0.6	1.4	1.5	8.8
F						1.9	1.4	1.9	0.8	2.1	3.4
G							2.6	1.3	1.7	1.1	9.5
H								2.0	3.1	2.0	14.4
I									3.6	2.9	6.9
J										1.9	15.7

effects of dominance were important for maize yield (Fuzatto et al., 2002; Hallauer & Miranda Filho, 1988; Souza Sobrinho et al., 2001).

The specific combining ability estimates of a parent with himself ($\hat{s}_{ii}$) was positive for all cases (Table 2). According to Cruz & Vencovsky (1989) this is an indication of unidirectional dominance in the sense of decreasing the expression of the trait. This result was expected, because the parents under assessment were single-crosses, with high yield potential, thus the double-crosses derived from their crosses would present lower yields, as reported in the present study.

Outstanding combinations were F×G, A×B, A×F and B×F, that presented high yield, high favorable allele frequency of their parents and the possibility of heterosis exploitation (Table 2).

The condition necessary for the study of stability in GCA and SCA is where these estimates interact with the environments (E). In the present study, the significance of the sources of variation GCA × E and SCA × E indicated that both the GCA and the SCA effects varied in the environments assessed.

Assuming that stability is under genetic control, breeders should include, as criteria to choose parents to form a base population for breeding programs, those that have stability of diallel analysis parameters. The diallel analysis parameters stability study confirmed that both the general combining ability ($\hat{g}_i$) and the specific combining ability ($\hat{s}_{ij}$) varied in function of environments, contributing differently to the interaction.

The ecovalence values (Wi^2%) obtained for the $\hat{g}_i$ effects represented the contribution of each estimate to the genotype by environment interaction and ranged from 3.4% to 15.7% (Table 3). Parents H and J presented the highest contributions for interaction, 14.4% and 15.7%, respectively, indicating that these genotypes have less stability for these parameters in the face of environmental variations. Parents C and F were at the opposite extreme, 6.7% and 3.4%, respectively. F parent showed the best stability and GCA effect (538.2 kg ha^{-1}) and high yield (9,984 kg ha^{-1}), indicating that it is an excellent source of inbreds. Studies of the stability parameter of the diallel analysis could facilitate the choice of base populations, generating more stable and productive hybrids (Pacheco et al., 1999). In this sense populations derived from the F hybrid would be outstanding.

There was a wide diversity of Wi^2% values for the SCA effects. The estimates ranged from 0.2% to 4.0%. At first it might seem that variation of the Wi^2% estimates among the different hybrids was small, but 55 treatments were assessed. Thus it was expected that the mean contribution of the hybrids would be small.

The hybrids that presented smallest stability for SCA estimates were the D×E and H×I hybrids with values of 4.0% and 3.1%, respectively, but the SCA values were not significant and these hybrids presented low yield. The $\hat{s}_{ij}$ effects with the smallest contribution to the interaction were normally associated to low magnitude estimates. A×J, C×E and D×G hybrids contributed with less than 0.50% to the interaction but presented negative $\hat{s}_{ij}$ equal to -1,604.9 kg ha^{-1}, -944.5 and -1,090.1 kg ha^{-1} respectively (Table 3). Our results did not allow us to identify parents that presented stability in the specific combining ability effects associated to a good performance in hybrid combinations.

CONCLUSIONS

The non-additive effects were more important than the additive effects for maize yield. It was possible to identify parents with high general combining ability estimates and stability of these parameters.

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