

## Topics on the genetics of maize yield stability

Cleso Antônio Patto Pacheco\*<sup>1</sup>, Manoel Xavier dos Santos<sup>1</sup>, Cosme Damião Cruz<sup>1</sup>, Paulo Evaristo de Oliveira Guimarães<sup>1</sup>, Sidney Netto Parentoni<sup>1</sup> and Elto Eugênio Gomes e Gama<sup>1</sup>

<sup>1</sup>Embrapa Milho e Sorgo, Caixa Postal 151, Sete Lagoas, MG, Brazil, CEP 35701-970.; <sup>2</sup>UFV, DBG, Viçosa, MG, Brazil, CEP 36571-000. (\* Corresponding Author. E-mail: cleso@cnpms.embrapa.br)

### ABSTRACT

Diallel experiments were carried out in several environments to investigate the genetic control of maize yield stability. The analyses used the methodology developed by Pacheco (1997) which is useful when the genotype x environment interaction is significant and the genetic effects are not consistent across environments. The 28 population diallel assessed in ten environments allowed the following conclusions: a) dominance deviations were the main cause of yield instability; b) populations selected under environmental stress conditions, such as Saracura, produced more stable intervarietal hybrids through a reduction in the deviations from regression due to specific combining ability; c) selection for yield followed by selection for stability would increase the breeding program efficiency if the initial populations had high General and Specific Combining Abilities, broad adaptability and regression deviations close to zero.

**KEY WORDS:** Stability, diallel, maize, GCA, SCA.

### INTRODUCTION

Although breeders and statisticians have identified and recognized the importance of the genotype x environment interaction in selection, Rojas and Sprague (1952) were the first ones to investigate the consistency of the General Combining Ability (GCA) and Specific Combining Ability (SCA) estimates in experiments repeated in a series of locations or years. Indeed, better decisions can be made on the choice of parents to start a breeding program and on the selection methods to be used when the variances of the GCA and SCA effects are estimated from data obtained in several environments (Matzinger et al., 1959).

Eberhart and Russell (1966) partitioned the treatment sum of squares in GCA and SCA components and respective interactions in their assessment of two diallels, one with eleven and the other with eight maize lines, in eight and twelve environments, respectively. The authors presented the adaptability and stability estimates for the parents of the diallel but did not compare them with the estimates obtained from the derived hybrids. This procedure would allow an understanding of what happens when a stable line is crossed with an unstable one.

Gama and Hallauer (1980) assumed that maize yield stability is genetically controlled. They evaluated selected and unselected lines for grain yield and concluded that hybrids derived from selected line

hybrids had mean yield significantly higher than the unselected ones, but the two groups did not differ for adaptability and yield stability. They therefore suggested that the breeder should emphasize selection for yield and only then assess yield stability of the elite hybrid group.

This approach was shared by Torres (1988) who observed, using data from National Trials of Maize, that adaptability and yield must have independent genetic control given the lack of correlation between them and given the size of the coefficient of determination for grain yield, which was approximately twice that for adaptability. The author, however, did not refer to the stability estimated according to the deviations from linear regression nor did he discuss these traits inheritance.

Based on a simple one gene two allele model (BB, Bb and bb), similar to that presented by Falconer (1987), but considering several environments, Vencovsky and Barriga (1992) showed that the genotype x environment interaction ( $\sigma_{GA}^2$ ) component of variance is due to the instability of the *u*, *a* and *d* genotypic effects, which vary from one environment to another, that is, its origin is genetic. They drew attention to the fact that, contrary to the traditional variances, which are defined among genotypes within environments, is defined among environments within genotypes. It is a genetic variation among environments of intragenotypic origin.

This study aimed to investigate and interpret the genetic causes of yield stability using diallel crosses assessed in several environments.

## MATERIAL AND METHODS

The methodology used in this study was developed by Pacheco (1997) to investigate the genotype x environment interaction in diallel crosses assessed in a series of environments. The adaptability and stability parameters of Eberhart and Russell (1966) are partitioned into genetic effects of General (GCA) and Specific (SCA) Combining Abilities, and analyzed by Griffing's method II, model I (1956).

Details of the matrix calculations, in which the adaptability parameters are partitioned by the least squares method, are presented by Pacheco et al. (1999):

$$\beta = \begin{bmatrix} \beta_{0ij} \\ \beta_{1ij} \end{bmatrix} = \begin{bmatrix} \beta_{0t} \\ \beta_{1t} \end{bmatrix} = \begin{bmatrix} \beta_{0m} & \beta_{0g_i} & \beta_{0g_j} & \beta_{0s_{ij}} \\ \beta_{1m} & \beta_{1g_i} & \beta_{1g_j} & \beta_{1s_{ij}} \end{bmatrix}$$

where,

$\beta_{0ij} = \beta_{0t}$  : is the intercept or point at which the regression line cuts the Y axis, which corresponds to the mean of the *i*th genotype in the *k*th environment, according to the methodology of Eberhart and Russell (1966). It can be partitioned by the Griffing' (1956) effects so that:

$\beta_{0m}$  : is the general mean;

$\beta_{0g_i}$  : is the GCA effect of the *i*th genotype;

$\beta_{0g_j}$  : is the GCA effect of the *j*th genotype;

$\beta_{0s_{ij}}$  : is the SCA effect of the cross between the *i*th and *j*th genotype;

$\beta_{1ij} = \beta_{1t}$  : is the linear regression coefficient or the adaptability coefficient of Eberhart and Russell, which can be partitioned by the Griffing' effects (1956) so that,

$\beta_{1m}$  : is the linear regression coefficient associated to the general mean (  $\beta_{1m} = 1.0$  )

$\beta_{1g_i}$  : is the linear regression coefficient associated to the GCA effect of the *i*th genotype;

$\beta_{1g_j}$  : is the linear regression coefficient associated with the GCA effect of the *j*th genotype;]

$\beta_{1s_{ij}}$  : is the linear regression coefficient associated with the SCA effect of the cross between the *i*th and *j*th genotype estimated by

$$\hat{\beta} = \begin{bmatrix} \sum_{k=1}^a m_k / a & \sum_{k=1}^a g_{ik} / a & \sum_{k=1}^a g_{jk} / a & \sum_{k=1}^a s_{ijk} / a \\ \sum_{k=1}^a I_k^2 / \sum_{k=1}^a I_k^2 & \sum_{k=1}^a g_{ik} I_k / \sum_{k=1}^a I_k^2 & \sum_{k=1}^a g_{jk} I_k / \sum_{k=1}^a I_k^2 & \sum_{k=1}^a s_{ijk} I_k / \sum_{k=1}^a I_k^2 \end{bmatrix}$$

The estimation of the adaptability parameters was emphasized by Pacheco et al. (1999) due to its simplicity and the small size of the matrixes involved. This was done, however, without hampering the understanding of the estimation of the stability parameters, whose demonstration is longer because the of the sum of the square matrixes. A simple presentation of the sum of the squares matrix of the regression deviations can simplify the understanding of the estimation, considering that

$$SSDes = SSE / G_{ij} - SE Re g$$

$$SSDes = r (Y'Y - C) - r (\hat{\beta}' X'Y - C)$$

$$SSDes = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & SSD_{g_i} & SSD_{g_i g_j} & SSD_{g_i s_{ijk}} \\ 0 & SSD_{g_i g_j} & SSD_{g_j} & SSD_{g_j s_{ijk}} \\ 0 & SSD_{g_i s_{ijk}} & SSD_{g_j s_{ijk}} & SSD_{s_{ijk}} \end{bmatrix}$$

As demonstrated above, the sum of the squares of the deviation matrix is composed of the sums of the squares of the deviations due to the Griffing (1956) GCA and SCA genetic effect variances on the diagonal, and to the covariance among these effects, outside the diagonal. Non-nil covariances indicate non-independence of the genetic effects. However, because of their difficult interpretation and, until now, small practical values, they were added and denominated double products (DP).

It is important to point out that the sum of the elements within the sum of the squares matrixes resulted in numbers that correspond to the respective sums of the squares obtained by the conventional Eberhart and Russell (1966) model. The relationship between the regression sum of squares and the environments within genotype sum of squares, defined as the total determination coefficient ( $R_t^2$ ), allowed the visualization of the raw data fitting the linear regression.

However, since these data are estimated from the sum squares of each genotype, the  $R_t^2$  is not the best measurement for comparing directly the magnitude of the deviations from regression mean squares among

the assessed genotypes. This comparison can be made by the Snedecor F statistics, where greater F values indicate greater deviations from regression mean squares.

Thus the most meaningful way to partition deviations from the regression in their components attributed to

$$F = \frac{MS(D_i)}{MSR} = \frac{MS(D_{gi}) + MS(D_{gj}) + MS(D_{sij}) + MS(D_{DP})}{MSR} = \frac{MS(D_{gi})}{MSR} + \frac{MS(D_{gj})}{MSR} + \frac{MS(D_{sij})}{MSR} + \frac{MS(D_{DP})}{MSR}$$

The components are not, however, associated to any probability function.

This methodology was applied by Pacheco (1997) to the yield data (kg/ha) of 28 maize open pollinated populations (P's), to their first selfed generation ( $S_{1s}$ ), to their 378 diallel crosses ( $F_{1s}$ ), and to seven controls in ten environments. Description of the populations are in Pacheco et al. (2002). The analyses were performed by the Genes Program (Cruz, 1997).

## RESULTS AND DISCUSSION

In the diallel cross (Table 1), the  $S_{1s} \times E$ 's interaction was not significant, the treatments were significant at the 5% level of probability and all the other variation sources were significant at the 1% level of probability.

Results were significant within the scope of this study, showing large differences across environments in the mean performance among and within treatment groups which form the diallel, justifying the application of the described methodology.

Observing the F statistics for the deviation from the regression mean squares for treatments involved in the diallel cross, as well as their partitions into genetic effects and double products, it can be noticed that the magnitudes of these F statistic data were strongly influenced by the magnitude of the deviations from the regression associated to SCA, both for the 28 populations (Table 2) and for the 378 intervarietal hybrids. Only the results from the 20 highest yielding intervarietal hybrids are presented in this study (Table 3).

The five populations that presented the largest deviations from the regression associated with the GCA effects were: BA III-Tusón (25), Cunha (24), BR-136 (19), CMS-23 (14) and CMS-50 (21). Deviations from the regression associated to the SCA effects indicated that the five most unstable populations were: CMS-01 (1), CMS-14C (11), CMS-

the Griffing genetic effects, preserving, at the same time, the relationships among genotypes, is to consider the relationship between their respective deviation mean squares and residual mean squares. This is also true for the double products, as partitions of the total F statistic.

50 (21), BR-105 (6) and Nitrodent (28). The regression deviations associated with the double products among the genetic effects also contributed to the magnitude of the F statistics, mainly in these five populations: CMS-39 (20), Cunha (24), BR-136 (19), CMS-04N (04) and CMS-23 (14) (Table 2).

The populations classified among the five least stable, by at least one of the genetic effects, also presented significant F test for total regression deviations, except BR-105 (6) and Nitrodent (28), where the F was non-significant because of its negative double products.

Since double products are due to the regression covariance among the genetic effects, they are difficult to interpret, and are further complicated by the sum of all the double products. They will not, therefore, be further discussed, but their importance for the value and for the significance of the F test is acknowledged.

Considering that to be significant at least at the 5% level of probability, the total F had to be at least 1.94, the deviations due to the double products alone would be responsible for the significance of the F test in two treatments: CMS-22 x PH 4 (13x23) and CMS-50 x PH 4 (21x23) (Table 3). The deviations from regression due to SCA would be responsible for the significance in the CMS-50 x PH 4 (21x23) and in 57 other treatments.

Although the deviations from regression due to SCA and double products were the strongest determinants of yield instability in 50 treatments (54.63% of those with significant F), the combination of small deviations of all effects was responsible for the significance of the F test in 49 other treatments, or 45.37% of those with significant F (Table 4).

Table 4 gives an overview of the performance of the parents and their crosses, based on the significance of the total deviations from regression and on the relationship deviation from the SCA mean squares / effective mean error greater than 1.94. The penultimate

**Table 1.** Combined analysis of variance for the 10 environments, with adjusted means of the 28 parents, their 378 inter varietal hybrids, 28 S<sub>1</sub>'s and 7 checks. Ear weight (kg/ha) in 10 environments. 1991/92 and 1992/93.

Sources of variation	Degrees of freedom	Sum of squares	Mean square	F
Environments (E)	9	27131576320	3014619648	142.41 <sup>1/</sup>
Treatments (T)	440	11952547840	27164882	16.78 <sup>1/</sup>
Diallel (D)	405	3833901824	9466424	5.85 <sup>1/</sup>
F <sub>1</sub> 's	377	3068670720	8139710	5.03 <sup>1/</sup>
S <sub>0</sub> 's	27	520497984	19277704	11.91 <sup>1/</sup>
S <sub>1</sub> 's	27	228345760	8457250	5.22 <sup>1/</sup>
(S <sub>0</sub> - S <sub>1</sub> )	(27)	206111136	7633746	4.14 <sup>1/</sup>
Cov[(S <sub>1</sub> , (S <sub>0</sub> -S <sub>1</sub> )]	(27)	43021728	1593397	
Checks (C)	6	117279128	19546522	12.07 <sup>1/</sup>
T x E	3960	6410868736	1618906	1.63 <sup>1/</sup>
D x E	3645	5594575872	1534863	1.55 <sup>1/</sup>
F <sub>1</sub> 's x E	3393	5138250752	1514368	1.53 <sup>1/</sup>
S <sub>0</sub> 's x E	243	421869632	1736089	1.75 <sup>1/</sup>
S <sub>1</sub> 's x E	243	172484256	709811	0.72 ns
(S <sub>0</sub> - S <sub>1</sub> ) x E	(243)	447878304	1843120	1.86 <sup>1/</sup>
Cov[(S <sub>1</sub> , (S <sub>0</sub> -S <sub>1</sub> )] x E	(243)	-99241280	-408400	
C x E	54	166298912	3079609	3.11 <sup>1/</sup>
Effective error	4000	3963328800	990832	

  

Groups of treatments	Means	% relative	Range	
			Less Productive	More Productive
28 Progenitors	6458	100.0	3865	8157
378 F <sub>1</sub> 's	7144	110.6	5170	9034
28 S <sub>1</sub> 's	3285	50.9	2119	4971
7 Checks	7943	123.0	6333	9570
441 Treatments	6868	106.3	2119	9570

column shows that the parents differed in yield stability, both *per se* and in crosses. The BA III – Tusón (25) population was unstable and contributed to the instability of 48.1% in the crosses in which it participated as parent. On the other hand, the Saracura population (26) was stable and contributed to the stability of the crosses in which it participated. Only 7.4% of the derived crosses were unstable, showing its genetic influence on yield stability.

The last column in Table 4 shows that the contribution of the SCA deviations to the significance of the deviations from regression also varied according to treatment. Thus, while 22.2% of the crosses derived from the CMS-01 population (1) presented significant F for total deviations from regression based exclusively on the contribution of the SCA deviations, none of the crosses in which BR-136 (19) participated had significant deviations based only on the SCA deviations, indicating that the populations also differed on the type of genetic action for stability.

It should be pointed out, however, that in the populations already selected under some environmental stress, the importance of the deviations

related to SCA was smaller. The CMS-04 population is a good example once it was split in two sub-populations during breeding, CMS-04N (4) and CMS-04C (5), which were then submitted to selection in fertile soils and in soils under Cerrado vegetation, respectively. Divergent selection caused changes in the genetic frequencies of the two versions which can be ascertained in the results obtained for the two sub-populations *per se* (Table 2) and in crosses with other populations of this diallel (Table 3).

Table 3 also shows that the two versions differed in their  $\hat{g}_i$  and  $\hat{s}_{ii}$  effects (Table 2). Further, there was greater genetic complementation between them ( $\hat{s}_{ij}$  of 138.50) than in the cross between the BR-105 (6) and BR-106 (7) populations (of 33.80), which were submitted to several reciprocal recurrent selection cycles (Table 3). Although both versions presented wide adaptability, CMS 04C (5) showed lower yielding and tended to be less responsive to improvement in the environmental conditions than the fertile soil version. The main difference between them, however, was yield stability. According to the F total criteria, only the version selected for the

Cerrado can be considered stable.

Table 4 shows the large difference in stability performance in the intervarietal hybrids from the two sub-populations. The Cerrado version was much more efficient (11.1%) than the fertile soil (22.2%) in producing stable F1's when assessment was based on SCA related deviations from regression. The "intervarietal hybrid (IVH)" derived from the CMS 04N x CMS 04C (4x5) cross is also very representative since it joined the characteristics of greater yield and stability that were separated in the two parents (Table 3), indicating that selection in the two environments may have acted on different adaptation mechanisms.

The smaller contribution of the SCA related deviations from regression in crosses involving populations that had been selected under environmental stress conditions was also observed in the BR-136 (19), CMS-30 (18) and CMS-14C (11) populations, which were selected in soils under Cerrado vegetation, in CMS-22 (13), Nitrodent (28)

and Nitroflint (27), which were selected in soils with nitrogen stress, and especially in Saracura (26), which was developed to tolerate marshy soils.

The analysis of the 20 highest yielding intervarietal hybrids showed that BR-106 (7) was the parent in 50% of them (Table 3). Three out of these 10, including the top yielding, presented significant deviations from regression and, for one of them, the F statistic would be significant based only on the SCA related deviations from regression. On the other hand, BR-106 (7) was also the parent of the four most stable of the 20 highest yielding hybrids, in crosses with CMS-04N (4), CMS-14C (11), CMS-04C (5), and Saracura (26). This confirms the importance of increasing the frequency of genes for adaptation to some environmental stress for yield stability.

Since stability is conditioned mainly by the SCA effect, certain hybrid combinations can perform better or worse than expected, based on the mean performance of the parental lines involved. This occurred with the CMS 04N x BR 106 (4x7) cross, which, contrary to

**Table 2.** Eberhart and Russell (1966) adaptability and stability parameter estimates and their partition in Griffing's (1956) general and specific combining abilities. Diallel cross between 28 maize populations assessed in ten environments.

Tratamentos	$\hat{\beta}_{0t}$	$\hat{\beta}_{0gi}$	$\hat{\beta}_{0sij}$	$\hat{\beta}_{0sii}$	$\hat{\beta}_{1t}$	$\hat{\beta}_{1gi}$	$\hat{\beta}_{1sij}$	$\hat{\beta}_{1sij}$	$\hat{R}_t^2$	F	$\frac{MS(D_{gi})}{MSR}$	$\frac{MS(D_{sij})}{MSR}$	$\frac{MS(D_{sij})}{MSR}$	$\frac{MS(D_{DP})}{MSR}$
1 CMS 1	4744.81	-515.80	-515.80	-1320.04	0.4559**	-0.0856	-0.0856	-0.3730**	36.45	2.97**	0.16	0.16	3.20	-0.55
2 CMS 2	5486.81	-392.02	-392.02	-825.61	0.6885*	-0.0221	-0.0221	-0.2673*	88.60	0.50	0.24	0.24	1.01	-0.99
3 CMS 3	6050.86	-198.61	-198.61	-648.37	0.9050	0.0207	0.0207	-0.1364	82.96	1.38	0.11	0.11	0.75	0.41
4 CMS 4N	7550.54	250.28	250.28	-46.47	1.1392	0.0410	0.0410	0.0572	79.78	2.69**	0.15	0.15	1.15	1.25
5 CMS 4C	7012.02	104.41	104.41	-293.26	1.0563	0.0008	0.0008	0.0547	87.40	1.32	0.07	0.07	1.39	-0.21
6 BR 105	8156.64	533.73	533.73	-7.26	1.2263	0.0724	0.0724	0.0816	91.21	1.19	0.09	0.09	1.70	-0.70
7 BR 106	7784.99	868.60	868.60	-1048.66	0.8909	0.1373	0.1373	-0.3837**	78.03	1.83	0.19	0.19	1.36	0.10
8 BR 107	6586.75	-227.50	-227.50	-54.71	0.9427	-0.0415	-0.0415	0.0256	86.64	1.12	0.05	0.05	0.69	0.34
9 BR 111	6619.58	43.26	43.26	-563.40	0.9960	0.0362	0.0362	-0.0763	94.43	0.48	0.08	0.08	1.18	-0.86
10 BR 112	6400.37	-189.23	-189.23	-317.63	0.7401*	-0.0454	-0.0454	-0.1692	73.70	1.60	0.07	0.07	1.35	0.10
11 CMS 14C	6771.04	179.41	179.41	-684.23	1.0746	0.0154	0.0154	0.0438	74.23	3.28**	0.04	0.04	2.26	0.94
12 CMS 15	6950.98	-222.24	-222.24	299.00	0.8787	-0.0371	-0.0371	-0.0471	96.91	0.20	0.03	0.03	0.24	-0.10
13 CMS 22	6063.45	-162.79	-162.79	-707.43	0.8389	-0.0240	-0.0240	-0.1132	79.44	1.49	0.13	0.13	0.74	0.50
14 CMS 23	5344.55	-692.39	-692.39	-367.12	0.7404*	-0.1076	-0.1076	-0.0444	69.05	2.01*	0.30	0.30	0.34	1.08
15 BR 126	5352.12	-78.70	-78.70	-1586.94	0.8370	-0.0381	-0.0381	-0.0868	90.26	0.62	0.21	0.21	0.47	-0.28
16 CMS 28	6648.19	226.21	226.21	-900.68	1.1140	0.0817	0.0817	-0.0493	90.41	1.08	0.13	0.13	1.03	-0.22
17 CMS 29	6279.25	-352.81	-352.81	-111.59	0.8874	-0.0495	-0.0495	-0.0136	87.69	0.91	0.13	0.13	0.88	-0.24
18 CMS 30	5995.99	-250.63	-250.63	-599.20	0.6016**	-0.0748	-0.0748	-0.2489*	66.13	1.52	0.09	0.09	0.75	0.59
19 BR 136	6362.09	-18.37	-18.37	-697.63	0.9898	-0.0047	-0.0047	-0.0008	75.41	2.62**	0.33	0.33	0.48	1.48
20 CMS 39	7062.31	246.37	246.37	-526.88	0.9871	0.0180	0.0180	-0.0488	69.30	3.53**	0.23	0.23	1.25	1.83
21 CMS 50	6670.08	345.02	345.02	-1116.42	0.9231	0.0807	0.0807	-0.2384*	67.58	3.35**	0.29	0.29	1.78	0.98
22 Sintético Elite	7382.33	373.44	373.44	-461.01	1.1061	0.0781	0.0781	-0.0500	94.15	0.62	0.02	0.02	0.57	0.02
23 África do Sul ph4	5501.36	-297.48	-297.48	-1000.13	0.8439	-0.0369	-0.0369	-0.0823	89.55	0.68	0.26	0.26	1.03	-0.87
24 Cunha	5776.74	-50.78	-50.78	-1218.15	0.6493**	-0.0672	-0.0672	-0.2162	46.25	4.01**	0.51	0.51	1.30	1.69
25 BA III - Tusón	3865.33	-632.96	-632.96	-1965.20	0.7678	-0.0972	-0.0972	-0.0378	66.76	2.40*	0.59	0.59	0.93	0.30
26 Saracura	7613.47	330.40	330.40	-143.79	0.8996	0.0273	0.0273	-0.1551	78.92	1.77	0.10	0.10	1.31	0.27
27 Nitroflint	7234.76	303.19	303.19	-468.08	0.9262	0.0598	0.0598	-0.1934	82.38	1.50	0.10	0.10	0.80	0.50
28 Nitrodent	7568.54	478.00	478.00	-483.91	0.9727	0.0624	0.0624	-0.1520	84.33	1.44	0.08	0.08	1.57	-0.29

General mean ( $\hat{m}$ ): 7096.45 kg/ha;  $\hat{\beta}_{1m}$ : 1.0; \* and \*\* indicates significance at the 5% and 1% level of probability by the F or t tests; MSD: mean square of the deviations from regression; MSR: residual mean square of the joint ANOVA;  $R_t^2$ : total determination coefficient.

what was expected, showed more stability than the IVH CMS 04C x BR-106 (5x7) cross.

A preliminary analysis of the deviations from regression and the combining ability of a variety with itself ( $\hat{S}_{ii}$ ), which, according to Cruz and Vencovsky (1989), are important indicators of unidirectional dominance and varietal heterosis, suggested that the most heterozygous materials were more stable than the most homozygous materials, since those materials in which the varietal heterosis was negative, such as the Saracura (26) population, were more stable than those in which the varietal heterosis was positive, such as the BA-III-Tusón (25) population (Table 2). However, it must be emphasized that, when the dominance deviations are predominantly positive, the positive varietal heterosis is due to the contribution of the loci to heterozygosis, resulting from all the possible crosses with a given population. Consequently, the varietal heterosis needs to be interpreted as an specular image of the population genome. The most homozygous populations, with the highest frequency of homozygous loci, either favorable or unfavorable, will present large and positive varietal heterosis. Therefore, the negative varietal heterosis can be used as an indicator of the

degree of heterozygosity in the population, that is, the smallest (most negative) the varietal heterosis the greatest the frequency of heterozygous loci.

In the context of this study, and, according to Cruz and Vencovsky (1989), the varietal heterosis can be better understood when the parents are included, according to Cruz and Vencovsky (1989), although the Gardner and Eberhart diallel (1966) is more parameterized than that of Griffing (1956), the two methodologies do not differ in the quality of information generated and the following relationships among the parameter is presented:

$$\hat{g}_i = \frac{1}{2} \hat{v}_i + \frac{p-2}{p+2} \hat{h}_i$$

$$\hat{S}_{ii} = -\frac{p-1}{p+1} \hat{h} - \frac{2(p-2)}{p+2} \hat{h}_i$$

$$\left( \frac{\sum_{i=1}^p \hat{S}_{ii}}{p} \right) = -\left( \frac{p-1}{p+1} \right) \hat{h}$$

The mean for  $\hat{S}_{ii}$  (-638.03) is indirectly important

**Table 3.** Eberhart and Russell (1966) adaptability and stability parameter estimates and their partition in function of the Griffing (1956) general and specific combining abilities for the 20 highest yielding intervarietal hybrids. Diallel between 28 maize populations assessed in ten environments.

Tratamentos	$\hat{\beta}_{0t}$	$\hat{\beta}_{0gi}$	$\hat{\beta}_{0gj}$	$\hat{\beta}_{0sij}$	$\hat{\beta}_{1t}$	$\hat{\beta}_{1gi}$	$\hat{\beta}_{1gj}$	$\hat{\beta}_{1sij}$	$\hat{R}_t^2$	F	MS (D <sub>gi</sub> ) MSR	MS (D <sub>gj</sub> ) MSR	MS (D <sub>sij</sub> ) MSR	MS (D <sub>DP</sub> ) MSR
7 x 21	9034.10	868.60	345.02	724.03	1.2410*	0.1373	0.0807	0.0229	82.41	2.69**	0.19	0.29	2.79	-0.58
7 x 28	8893.64	868.60	478.00	450.59	1.2377	0.1373	0.0624	0.0380	86.95	1.88	0.19	0.08	1.84	-0.23
4 x 7	8652.61	250.28	868.60	437.28	1.0268	0.0410	0.1373	-0.1515	93.73	0.58	0.15	0.19	1.56	-1.32
6 x 26	8639.35	533.73	330.40	678.77	1.2496*	0.0724	0.0273	0.1499	91.45	1.20	0.09	0.10	0.98	0.02
11 x 28	8554.50	179.41	478.00	800.64	1.2592*	0.0154	0.0624	0.1815	93.56	0.89	0.04	0.08	0.62	0.15
6 x 7	8532.58	533.73	868.60	33.80	1.3765**	0.0724	0.1373	0.1669	94.00	0.99	0.09	0.19	0.78	-0.07
24 x 28	8531.82	-50.78	478.00	1008.15	1.3173**	-0.0672	0.0624	0.3221**	86.86	2.15*	0.51	0.08	2.46	-0.90
6 x 22	8529.85	533.73	373.44	526.23	1.1629	0.0724	0.0781	0.0125	90.94	1.10	0.09	0.02	1.17	-0.17
4 x 28	8516.30	250.28	478.00	691.57	1.1347	0.0410	0.0624	0.0314	88.42	1.38	0.15	0.08	0.70	0.45
7 x 11	8515.15	868.60	179.41	370.70	1.2998*	0.1373	0.0154	0.1471	96.71	0.47	0.19	0.04	0.32	-0.08
7 x 9	8484.01	868.60	43.26	475.70	1.1573	0.1373	0.0362	-0.0162	86.61	1.70	0.19	0.08	1.23	0.20
5 x 7	8465.78	104.41	868.60	396.32	1.3493**	0.0008	0.1373	0.2112	95.98	0.62	0.07	0.19	0.47	-0.11
7 x 27	8391.29	868.60	303.19	123.05	1.3584**	0.1373	0.0598	0.1613	80.88	3.57**	0.19	0.10	2.10	1.18
6 x 24	8360.63	533.73	-50.78	781.23	1.0061	0.0724	-0.0672	0.0010	81.04	1.94*	0.09	0.51	0.91	0.43
6 x 13	8328.31	533.73	-162.79	860.92	1.1060	0.0724	-0.0240	0.0577	89.71	1.15	0.09	0.13	0.64	0.29
3 x 6	8249.28	-198.61	533.73	817.71	0.9200	0.0207	0.0724	-0.1730	89.87	0.78	0.11	0.09	0.73	-0.15
7 x 26	8248.59	868.60	330.40	-46.86	1.1134	0.1373	0.0273	-0.0513	95.87	0.44	0.19	0.10	1.06	-0.91
10 x 21	8234.39	-189.23	345.02	982.15	1.1252	-0.0454	0.0807	0.0899	86.43	1.63	0.07	0.29	0.64	0.63
2 x 7	8215.67	-392.02	868.60	642.64	1.1420	-0.0221	0.1373	0.0268	81.73	2.39*	0.24	0.19	1.31	0.65
24 x 27	8202.08	-50.78	303.19	853.22	1.1416	-0.0672	0.0598	0.1490	93.84	0.70	0.51	0.10	0.51	-0.42
4 x 5	7589.65	250.28	104.41	138.50	1.1060	0.0410	0.0008	0.0641	90.62	1.04	0.15	0.07	0.87	-0.05
13 x 23	6735.28	-162.79	-297.48	99.10	1.0648	-0.0240	-0.0369	0.1257	70.29	3.92**	0.13	0.26	1.56	1.98
21 x 23	5169.90	345.02	-297.48	-1974.10	0.9710	0.0807	-0.0369	-0.0728	57.47	5.71**	0.29	0.26	2.86	2.30

General mean ( $\hat{m}$ ): 7096.45 kg/ha;  $\hat{\beta}_{1m}$ : 1.0; \* and \*\* indicates significance at the 5% and 1% level of probability by the F or t tests; MSD: mean square of the deviations from regression; MSR: residual mean square of the joint ANOVA;  $R_t^2$ : total determination coefficient.

since it has a symmetrical interpretation of the mean heterosis ( $\bar{h}$ ), revealing the importance of the dominance deviations and variance of the genetic frequency in the diallel for the trait under study (Cruz and Vencovsky, 1989). On the other hand, it has direct importance to the  $\hat{S}_{ii}$  estimated for each population, whose variation is due only to varietal heterosis ( $\hat{h}_i$ ), once the fraction of the mean heterosis in  $\hat{S}_{ii}$  is constant for all the populations. Therefore, larger  $\hat{S}_{ii}$  absolute values imply larger  $\hat{h}_i$  and, consequently, lower contribution of the favorable homozygous loci in the general combining ability ( $\hat{g}_i$ ).

This means that, for the data under discussion, the value  $\hat{S}_{ii} = -638.03$  is exclusively due to the mean heterosis, and that only values lower than this (larger and negative) will indicate positive effects due to varietal heterosis. Thus, varieties that presented values greater than  $-638.03$  were those that reduced the number of heterozygous loci as an average of all

crosses in which they participated. These varieties were less interesting for breeding purposes than those that increased the number of these loci.

In a diallel cross, the population with the largest  $\hat{S}_{ii}$ , although more divergent genetically, will be that with largest contribution to the varietal heterosis, by the predominance of loci in heterozygosis in the mean of the crosses in which it participated. This population, however, is less appropriate for intrapopulation breeding due to its low frequency of favorable alleles. This is highlighted when the  $\hat{S}_{ii}$  are associated to large negative  $\hat{g}_{i's}$ , as is the case of the BA-III – Tusón (25) population, which had the largest  $\hat{S}_{ii}$ , and the second smallest  $\hat{g}_i$ . These values suggested that this population has the highest frequency of homozygous recessive loci among the 28 assessed.

Under the genetic conditions of this study, the contributions of the homozygous and heterozygous loci to the general combining ability will average out when

**Table 4.** Identification of the parents and their crosses by the significance of the total deviations from regression and the relationship among the deviations from regression due to SCA and effective mean error.

Genitores	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	%Tot Dev.	%SCA Dev		
01 - CMS 01	<b>P</b>	<b>X</b>			<b>X</b>		<b>X</b>			S						<b>X</b>	<b>X</b>				<b>X</b>							X	25.9	22.2		
02 - CMS 02			X				X	X					<b>X</b>				<b>X</b>					S				<b>X</b>				25.9	14.8	
03 - CMS 03											<b>X</b>						X								X					14.8	3.7	
04 - CMS 04 N				P				<b>X</b>	X	<b>X</b>							<b>X</b>	X		<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>						33.3	22.2
05 - CMS 04 C																							X	X	<b>X</b>	<b>X</b>					18.5	11.1
06 - BR 105							X	<b>X</b>	<b>X</b>				<b>X</b>			S	X	X		X			X	X	<b>X</b>	<b>X</b>	X				37.0	14.8
07 - BR 106																<b>X</b>	X		<b>X</b>	<b>X</b>	X	S	X	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>				37.0	22.2
08 - BR 107										X									<b>X</b>						<b>X</b>						22.2	11.1
09 - BR 111										X							X							<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>				22.2	14.8
10 - BR 112												<b>X</b>					<b>X</b>	X	X					<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>				29.6	14.8
11 - CMS 14 C											<b>P</b>	<b>X</b>																			18.5	11.1
12 - CMS 15													X				<b>X</b>			X		<b>X</b>	X								25.9	14.8
13 - CMS 22													X	X					X	X	X		X								25.9	3.7
14 - CMS 23														P	X		<b>X</b>	X			S	X	S								25.9	7.4
15 - BR 126																	X		<b>X</b>	X			<b>X</b>	<b>X</b>	X		<b>X</b>				29.6	14.8
16 - CMS 28																X	X							X				X			25.9	7.4
17 - CMS 29																									X						18.5	11.1
18 - CMS 30																							X								37.0	11.1
19 - BR 136																			P	X	X										25.9	0.0
20 - CMS 39																					P	<b>X</b>	<b>X</b>								29.6	18.5
21 - CMS 50																						P		<b>X</b>							33.3	18.5
22 - Sint. Elite																									<b>X</b>						14.8	11.1
23 - PH 4																															18.5	11.1
24 - Cunha																								P				<b>X</b>			37.0	14.8
25 - BA III- Tus																									P		X				48.1	25.9
26 - Saracura																											<b>X</b>				7.4	7.4
27 - Nitroflint																												<b>X</b>			25.9	22.2
28 - Nitrodent																															18.5	7.4

X = cross and P = parent, with F significant for the total deviations from regression; **X** = cross and **P** = parent with the ratio: SCA MS deviations from regression/mean effective error, larger than 1.94; S = cross with non-significant F for the total deviations from regression and with the ratio: SCA MS deviations from regression/effective mean error larger than 1.94; %Tot. Dev = percentage of genotypes in which the ith parent contributed showing significant total deviations from regression; %SCA Dev = percentage of genotypes in which the ith parent contributed showing a ratio: SCA MS deviations from regression/effective mean error larger than 1.94.

the limit attained by  $\hat{S}_{ii}$  is at most 75% larger than -638.03 and is associated with a  $\hat{g}_i$  of at least 300.00, which is close to 50% of the mean heterosis.

In case of large contributions from the dominance deviations, very high  $\hat{g}_i$  associated with a low  $\hat{S}_{ii}$  indicates that the referred population may not be the most suitable for intrapopulation breeding. This happens despite the high frequency of homozygous favorable alleles and, consequently, high yield means; however, the expected gains from selection will tend to be small due to a probable low genetic variability. The population that best fitted this description was the BR-105 (6).

Therefore, due to the significance of the additive and dominant effects in this diallel, the ideal populations for *per se* or intrapopulation breeding will be those that present high  $\hat{S}_{ii}$  associated to high  $\hat{g}_i$ . These populations will have the highest frequency of homozygous and heterozygous loci, the first ensuring good performance due to the high frequency of favorable alleles, and the second, due to the variability necessary for successful selection. According to this line of thought, BR-106 (7) was the most indicated population present in this diallel for intrapopulation breeding, considering only the genetic effects involved.

In the CMS-50 (21) population, the  $\hat{g}_i$  and  $\hat{S}_{ii}$  genetic effects were, respectively, within the minimum and maximum limits of 50% and 175% of the mean and, consequently, it can be considered the second best population for intrapopulation breeding, although other populations presented higher general means.

The Saracura (26), Nitrodent (28), Sintético Elite (22), Nitroflint (27) and CMS-39 (20) populations with similar genetic performance were also considered promising. These five populations had larger than -638.03, indicating that the good magnitudes of their were due mainly to the contribution of the heterozygous loci of their genetic constitutions.

Negative varietal heterosis can also be attributed to negative dominance deviations, such as can be observed in Falconer (1987), indicating that the effect of dominance was towards decreasing the trait value. It is likely, however, that since the predominant dominance deviations in this diallel were positive, the negative varietal heterosis in the Saracura (26), Nitrodent (28), Sintético Elite (22), Nitroflint (27) and CMS-39 (20) populations were due to the strong heterozygous nature of their genomes. In average, these populations contributed to the reduction of heterosis in the crosses they participated.

It is worth noting that these five populations are

synthetic varieties or pools of broad genetic base (Parentoni et al., 1992; Machado et al., 1992; Santos et al., 1998; Pacheco et al., 1998) that were submitted to few mass selections and, or, half-sib progeny cycles. As they had not been selfed, their genetic variability were higher than those of other populations that had gone through selection methods which use selfed progenies (Lima et al., 1984), such as BR-105 (6) and BR-106 (7) (Pacheco et al., 2002).

By analyzing the effect of the specific combining ability between two different parents ( $\hat{S}_{ij}$ ) in terms of the parameters estimated by the complete model IV of Gardner and Eberhart (1966), and using the expressions presented by Cruz and Vencovsky (1989), the following expression is obtained:

$$\hat{S}_{ij} = \frac{2}{p+1} \hat{h} + \frac{4}{p+2} \hat{h}_i + \frac{4}{p+2} \hat{h}_j + \hat{S}'_{ij}$$

where  $\hat{S}'_{ij}$  refers to the specific heterosis of Gardner and Eberhart (1966) in the average of k environments. Thus the complete model for Griffing (1956) method 2 can be described by the expression:

$$\hat{Y}_{ij} = \hat{m} + \left( \frac{1}{2} \hat{v}_i + \frac{p-2}{p+2} \hat{h}_i \right) + \left( \frac{1}{2} \hat{v}_j + \frac{p-2}{p+2} \hat{h}_j \right) + \frac{2}{p+1} \hat{h} + \frac{4}{p+2} \hat{h}_i + \frac{4}{p+2} \hat{h}_j + \hat{S}'_{ij}$$

where  $\hat{m}$  is the general genotype mean in the k environments by the Griffing model (1956), where

$\hat{m} = \hat{m}_v + \left( \frac{p-1}{p+1} \right) \hat{h}$ . In this latter formula,  $\hat{m}_v$  is the general mean of the varieties in the k environments according to Gardner and Eberhart (1966) model (4), quoted by Cruz and Regazzi (1994).

By the expression previously presented for  $\hat{Y}_{ij}$ , it can be seen that varietal heterosis has greater effect on the GCA rather than on the SCA, mainly in the large diallels. In this study, where 28 parents were assessed, only 2/29 of the mean heterosis and 4/30 of the varietal heterosis due to each parent are computed in the SCA of an intervarietal hybrid.

According to Cruz and Regazzi (1994), the specific heterosis can also be estimated by the following expression:

$$\hat{S}'_{ij} = \left[ \hat{Y}_{ijk} - \frac{1}{2} (\hat{Y}_{iik} + \hat{Y}_{jjk}) \right] - \left( \frac{\hat{h}}{2} + \hat{h}_i + \hat{h}_j \right),$$



It can be noticed that  $\hat{S}_{ij}^t$  will be maximum when the mean and varietal heterosis are negative. However, considering that the dominance deviations in this diallel were predominantly positive and unidirectional and, consequently, the mean and the desirable varietal heterosis were positive, the ideal  $\hat{S}_{ij}^t$  would not be the  $\hat{S}_{ij}^t$  maximum, but that resulting from the cross between two parents bearers of  $\hat{g}_i$  and  $\hat{g}_j$  obtained by balanced homozygous and heterozygous potentials. These parents should also present good genetic complementation. Cruz and Vencovsky (1989) recommends that breeders should seek for the largest SCA effect within crosses with parents showing the largest GCA effect.

In most cases, larger  $\hat{S}_{ij}$  effects (Table 3) were related to lower  $\hat{g}_i$  of one of the parents, especially for the cross with the highest  $\hat{S}_{ij}$ , which was among the Cunha x Nitrodent (24x28) populations. Out of the 20 highest yielding intervarietal hybrids only four, CMS 14C x Nitrodent (11x28), CMS 04N x Nitrodent (4x28) and BR 105 x Saracura (6x26), besides the already quoted BR 106 x CMS 50 (7x21), presented both additive genetic effects positive. Only BR 106 x CMS 50 presented positive dominance deviations in both parents, showing, once again, the superiority of its SCA.

It is worth pointing out that the rule developed by Cruz and Vencovsky (1989) for the identification of the highest yielding HV by the largest  $\hat{S}_{ij}$  coupled with the parent with largest  $\hat{g}_i$  will apply only if the  $\hat{g}_i$  of this parent is due to positive effects from mean varietal  $\hat{v}_i$  and  $\hat{h}_i$  effects, as in the case of the BR-106 variety. In cases where this condition was not met, the highest yielding IHV could not be found by the suggested rule, as in some of the environments assessed in this study, in Napolini Filho et al. (1981) and in Eleutério et al. (1988).

This finding can be explained by the last expression presented, where the SCA will not mean good genetic complementation whenever the parent with the largest  $\hat{g}_i$  shows a negative  $\hat{h}_i$ , once the best parent will not be that with the highest frequency of favorable alleles. This parent will have not only high frequency of favorable homozygous loci but also high frequency of heterozygous loci. Thus the best complementation expected for this parent will come from a parent with a high frequency of unfavorable homozygous loci, therefore with negative  $\hat{g}_i$ . The resulting high  $\hat{S}_{ij}$ , therefore, may not be associated to the best intervarietal hybrid of all the diallel, which contradicts the rule suggested by Cruz and Vencovsky (1989).

Therefore, the SCA effect is more important within a

context of genetic complementation when associated with positive  $\hat{g}_{i's}$  in the two parents involved in the cross. This can be confirmed by the presence of those four, among the ten, previously quoted IHV with the highest yield. Only the Cunha x Nitrodent (24x28) hybrid resulted from the combination of a positive  $\hat{g}_i$  with another with negative. On the other hand, among the ten most productive IHV, only in BR 105 x BR 106 (6x7) the SCA was not significant.

## CONCLUSIONS

The main conclusions were: 1. the dominance deviations were the main effects responsible for the lack of yield stability; 2. the populations that were selected under some environmental stress conditions such as Saracura, contributed to the stability of the intervarietal hybrids in which they participated, mainly due to a reduction in the regression deviations caused by the specific combining ability; 3. selecting first for yield and then for stability would be more efficient if breeding programs started with populations with high general and specific combining ability, broad adaptability and regression deviations close to zero.

## RESUMO

### Considerações Sobre as Causas Genéticas da Estabilidade de Produção em Milho

O objetivo desse trabalho foi estudar os efeitos genéticos envolvidos na estabilidade de produção de milho em ensaios dialélicos conduzidos numa série de ambientes. Foi utilizada a metodologia desenvolvida por Pacheco (1997), útil quando a interação genótipos x ambientes é significativa e os efeitos genéticos não são consistentes de um ambiente para outro. A aplicação em um dialélico de 28 populações avaliado em dez ambientes, permitiu concluir que: a) os efeitos dos desvios devidos à dominância foram os principais responsáveis pela falta de estabilidade de produção; b) as populações selecionadas sob condição de estresse ambiental, como a Saracura, produziram híbridos intervarietais mais estáveis pela redução dos desvios da regressão devidos à capacidade específica de combinação; c) a prática de selecionar para produção e, entre os mais produtivos, identificar os mais estáveis, teria eficiência aumentada, se o programa de melhoramento fosse iniciado com populações cujos efeitos das capacidades geral e específica de

combinação, além de altos, tivessem adaptabilidade ampla e desvios da regressão próximos de zero.

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