# Genetic divergence among maize hybrids and correlations with heterosis and combining ability

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**ABSTRACT.** Twelve corn hybrids recommended for cropping in the south-central region of the Paraná State and 66 crossings obtained among these hybrids were evaluated for agronomic and morphological traits. These genotypes were evaluated in three experiments performed in Laranjeiras do Sul, Guarapuava and Cantagalo, Paraná State, Brazil. Heterosis and specific combining ability (SCA) were estimated for yield of husked ears. Data from measuring 22 morphological/agronomical traits of the parents were subjected to a multivariate joint analysis of variance and cluster analysis to group the parental hybrids via the neighbor method, using the generalized Mahalanobis distance. Pearson correlation coefficients between heterosis, SCA, $D^2$ and yield of husked ears were obtained. The cross P30F44 x Sprint displayed a high mean and a high heterosis for yield of husked ears, but a moderate estimate of genetic divergence. Estimates of genetic divergence were not effective at predicting the most heterotic crossings, as Pearson correlation coefficients between $D^2$ and heterosis and $D^2$ and CEC were not significant. Positive significant correlations were observed between yield means and CEC and heterosis.

**Keywords:** *Zea mays*, specific combining ability, Mahalanobis distance, plant breeding.

## Divergência genética entre híbridos de milho e correlações com heterose e capacidade de combinação

**RESUMO.** Doze híbridos de milho recomendadas para a região centro-sul do Paraná e os 66 cruzamentos obtidos entre eles foram avaliados quanto a caracteres agronômicos e morfológicos em Laranjeiras do Sul, Guarapuava e Cantagalo, Estado do Paraná. Foi calculada a heterose e estimada a capacidade específica de combinação (CEC) dos cruzamentos para o caráter produção de espigas despalhadas. Foram tomadas medidas de 22 caracteres morfoagronômicos dos 12 genitores e os dados foram submetidos à análise multivariada conjunta com agrupamento pelo método hierárquico do vizinho mais próximo, utilizando a distância generalizada de Mahalanobis ($D^2$). Foram obtidas correlações entre a heterose, CEC, $D^2$ e média da produtividade. O cruzamento P30F44 x Sprint revelou média alta e elevada heterose para peso de espigas despalhadas, embora tenha apresentado estimativa moderada da divergência genética. As estimativas de divergência genética não foram eficientes na predição dos cruzamentos mais heteróticos, pois as correlações entre $D^2$ e heterose e entre $D^2$ e CEC foram não significativas. Houve correlações positivas e significativas entre as médias de produção de espigas, a CEC e a heterose.

**Palavras-chave:** *Zea mays*, capacidade específica de combinação, distância de Mahalanobis, melhoramento vegetal.

## Introduction

The choice of germplasm is an essential and crucial step in any plant breeding program, whether for the development of varieties or to produce hybrids, and can determine the success or failure of the selection process (ARAÚJO; NASS, 2002).

The presence of genetic divergence among accessions of germplasm is essential; however, satisfactory results are obtained only if the germplasm employed in the cross also present high values for the traits of interest (CARVALHO et al., 2003).

In maize breeding programs, the choice of base populations with high potentials for grain yield is fundamental to the process of obtaining superior inbred lines. Accordingly, populations generated from commercial hybrids represent an interesting potential base population, as they have been previously tested in various environments. Thus, these hybrids generally present high yield and desirable agronomic characteristics, with large proportions of favorable loci previously selected (AMORIM; SOUZA, 2005). The use of populations with different heterotic patterns is a

strategy that allows exploration and capitalization on heterosis to produce new corn hybrids (PINTO et al., 2001; VIEIRA et al., 2009).

Heterosis, expressed in crosses between individuals from different populations, depends on the presence of genes with non-additive effects in controlling desirable characteristics and the genetic divergence between them. Thus, in the choice of parents for these populations, divergent and previously adapted individuals are preferentially chosen (FUZATTO et al., 2002; GORGULHO; MIRANDA FILHO, 2001). In the case of any degree of dominance greater than zero, heterosis is due to differences in allele frequency between the parents (FALCONER; MACKAY, 1996).

The study of genetic divergence can assist in the choice of genotypes to be used in breeding programs for the development of new populations (CRUZ; REGAZZI, 1997). Genetic divergence is related to the degree of distance between populations in the set of genetic characters that differ between the populations. However, in most cases genetic distance is positively correlated with heterosis (PATERNIANI et al., 2008). Thus, the magnitude of heterosis is generally proportional to the genetic distance between the parents.

According Cargnelutti Filho et al. (2008), genetic divergence (evaluated based on the genetic distance between individuals) is a predictive feature that allows for the identification of crosses with a higher probability of success. Specifically, the evaluation of divergence can identify those crosses that will optimize heterosis while avoiding undesirable features.

In the prediction of genetic divergence between genotypes, multivariate methods, such as principal component analysis, canonical variables and agglomerative methods, can be applied. Agglomerative methods differ from the commonly utilized approaches, primarily because they rely on previously estimated dissimilarity measures, such as the Mahalanobis distance (CRUZ; REGAZZI, 1997).

The goal of this study was to evaluate the genetic divergence among 12 commercial corn hybrids, as well as the heterosis and specific combining ability of the 66 crosses between these hybrids. Further, we aimed to evaluate the efficiency of the estimates of genetic divergence in predicting the most heterotic crosses between the parental hybrids.

## Material and methods

Twelve commercial corn hybrids (P30F53, P30F44, AG8021, GNZ2005, GNZ2004, Penta, Premium Flex, Sprint, AS1575, 2B587, 2B688 and DKB234) were intercrossed with each other. The 66 crosses obtained, together with the 12 parental hybrids and three checks (P30R50, AS1560 and

DKB214) were evaluated by a randomized block design with three replicates in three experiments conducted at different locations in the central-south region of Paraná State during the 2007/2008 harvest.

The first experiment was carried out in Laranjeiras do Sul, located at latitude 25º24'15"S and longitude 52º28'22"O, with an altitude of 790 meters and soil classified as Typic Eutrophic (EMBRAPA, 2006). The second experiment was conducted in Guarapuava, located at latitude 25°23'02"S and longitude 51º29'43"O, an altitude of 1026 meters, with soil classified as Distroferric Oxisoil (EMBRAPA, 2006). The third experiment was conducted in Cantagalo, located at latitude 25°22'28"S and longitude 52º07'35"O, at an altitude of 790 meters with soil classified as Typic Eutrophic (EMBRAPA, 2006).

Each plot consisted of two rows of 5 meters in length, spaced at 0.80 meters, with a total area of 8 $m^2$ with 5 plants per linear meter and a population equivalent to 62,500 plants $ha^{-1}$.

To obtain the estimates of heterosis of the 66 crossings, five agronomic traits were assessed at each location: male flowering (MF) - number of days, counted from sowing to the issuance of 50% mature tassels in the plot; prolificacy (PR) - the ratio between the number of ears per plot and the final stand; plant height (PH) and ear insertion height (EH) in meters, sampled from five competitive plants from each plot; yield of husked ears (YHE) t $ha^{-1}$, with 13% moisture and stand corrected by covariance (RAMALHO et al., 2000), considering the ideal stand as 50 plants per plot. Heterosis values were calculated based on average data from three locations: H = $F_1$-($MP_i$ + $MP_j$) / 2, where H is heterosis, $F_1$ is the mean of the $F_1$ generation, and MP is the mean of parental $P_i$ or $P_j$. The heterosis estimates were also calculated as a percentage and the significance was determined with a *t* test (FUZATTO et al., 2002).

For the assessment of genetic diversity among the 12 parental hybrids (in addition to the five characteristics mentioned) 20 other morphological characteristics were evaluated from five competitive plants per plot in experiments at Laranjeiras do Sul and Guarapuava: total number of internodes (NI); length of the internode below the ear (IL); diameter of the stalk at the internode below the ear (SD); leaf length at ear height (LL); leaf width at ear height (LW); number of leaves below the ear (NLB); number of leaves above the ear (NLA); angle between the leaf (at ear height) and the stalk (AL) - scores (1 = 20º, 2 = 30º, 3 = 40º, 4 = 50º and 5 ≥ 60º); length of the main stem of the tassel (LMS); length of the secondary stem of the first lateral branch of the tassel (LSS); number of secondary

stems of the tassel (NSS); angle between the main and secondary stem of the tassel (ASS) - scores (1 = 20°, 2 = 30°, 3 = 40°, 4 = 50° e 5 ≥ 60°); ear placement (EP) - score of the angle between the ear and the stalk (1 = ear parallel to stalk , 2 = 30°, 3 = 45°, 4 = 60° and 5 = ear fully decumbent in relation to stalk); husk coverage of the ear (HC) - scores from 1 to 5 (1 = ear with excellent husk coverage; 5 = ear with very bad husk coverage); number of rows of kernels on the ear (NRK); number of kernels per row (NKR); length of the ear (EL); diameter of the ear (ED); diameter of the cob (CD); color of the cob (CC) - scores (1 = purple, 2 = dark red, 3 = clear red, 4 = beige and 5 = white).

Data were subjected to analysis of variance for each individual location, and after confirmation of homoscedasticity by the Hartley test (RAMALHO et al., 2000), joint analysis of variance was performed.

Data on morphological and agronomic characteristics obtained from the 12 parental hybrids were subjected to a multivariate joint analysis of variance to obtain the matrices of the sum of squares and sum of products of the error. The dissimilarity methodology was used to form the groups, by the method of single linkage cluster of the nearest neighbor (JOHNSON; WICKERN, 1988) from the dissimilarity matrix, based on the Mahalanobis distance ($D^2$).

To establish the cut-off point in the dendrogram for the identification of groups, the procedure used by Marchioro et al. (2003) was employed. However, as the number of genotypes (12) was smaller than the number of traits (22), the SAS routine (SAS, 1988) was modified, replacing the matrix of variance and covariance for the parametric matrix. The $D^2$ (cutoff line) was obtained with 95% of probability using 5,000 simulations.

Estimates of specific combining ability SCA ($\hat{s}_{ij}$) were obtained according to Method 2 of Griffing's Model I. Pearson correlation coefficients (STEEL; TORRIE, 1980) were obtained between $D^2$, the estimates of heterosis, SCA ($\hat{s}_{ij}$) and the yield of husked ears (YHE) to check whether the genetic diversity, estimated by multivariate distances, could be used as a predictive factor to identify the most promising hybrid combinations. Analyses were performed using the statistical software GENES (CRUZ, 2006).

## Results and discussion

The values of heterosis for male flowering (MF) were positive for all crosses, indicating the absence of bidirectional dominance deviations. Among the 58 crosses that showed significant heterosis by t test, estimates ranged from 1.5 days (1.9%) to 7.5 days (10.1%) for the cross Premium Flex x Sprint (data not shown).

In the case of prolifacy (PR), only 14 crossings showed statistically significant heterosis values, ranging from -0.08 (-6.9%) to 0.15 (15.5%) (data not shown). These data indicate that expression of bidirectional dominance deviations. The positive estimates of the greatest values were presented by the crosses GNZ2005 x Sprint and GNZ2005 x Penta, which demonstrated a desirable increase in the average number of ears per plant.

Reduction in plant height and ear insertion height are desirable traits, and nine estimates of heterosis presented significant negative values for both for plant height (PH) and ear insertion height (EH) (data not shown). The cross P30F44 x 2B688 displayed the most negative heterosis values for PH (-0.15 m or -6.3%) and EH (-0.17 m or -12.3%).

Estimates of heterosis for yield of husked ears (YHE) are presented in Table 1. Only one significant negative estimate of heterosis of YHE was identified, the cross Premium Flex x Sprint (-2.22 t ha$^{-1}$ or -21.2%).

All estimates of heterosis from crosses involving both parents from the same breeding program (P30F53 x P30F44, GNZ2005 x GNZ2004, Penta x Premium Flex, Premium Flex x Sprint, Penta x Sprint and 2B587 x 2B688) were negative or equivalent to zero (Table 1). This is likely the result of low genetic complementarity of loci with non-additive effects, possibly because these crosses displayed some degree of parental relationship. Pfann et al. (2009) identified negative estimates of specific combining ability (SCA) for grain yield for the cross Penta x Premium Flex in diallelic evaluation of two locations in the central-south region of Paraná State (Guarapuava and Goioxim). These data agree with the findings of this study, as SCA and heterosis are related parameters.

Significant positive estimates of heterosis for YHE were identified for 38 crosses, ranging from 1.18 (9.3%) for the cross AS1575 x 2B688 to 3.76 t ha$^{-1}$ (35.5%) for the combination P30F44 x Sprint (Table 1). Hallauer and Miranda Filho (1981) and Falconer and Mackay (1996) argue that in addition to the existence of genes with some degree of dominance controlling the character, the expression of heterosis also depends on the divergence between genotypes, as differences in allele frequencies are required at loci involved in the expression of desirable characteristics.

The mean values for the traits obtained from the joint analysis of variance involving the two locations (Laranjeiras do Sul and Guarapuava) were used to evaluate genetic divergence between the 12 parental hybrids, since no significant 'genotypes x locations' interaction were identified for most traits (Table 2).

**Table 1**. Mean estimates of heterosis of yield of husked ears (YHE) of the 66 crosses obtained from 12 corn hybrids evaluated in three locations in the South-Central region of the Paraná State, Brazil.

| Cross | Heterosis YHE | | Cross | Heterosis YHE | |
|---|---|---|---|---|---|
| | t ha$^{-1}$ | % | | t ha$^{-1}$ | % |
| P30F53 x P30F44 | -0.39$^{ns}$ | -3.2 | GNZ2005 x Sprint | 2.60$\star$ | 23.3 |
| P30F53 x AG8021 | 0.26$^{ns}$ | 2.2 | GNZ2005 x AS1575 | 1.40$\star$ | 12.5 |
| P30F53 x GNZ2005 | 1.28$\star$ | 11.4 | GNZ2005 x 2B587 | 1.28$\star$ | 11.6 |
| P30F53 x GNZ2004 | 1.49$\star$ | 12.8 | GNZ 2005 x 2B688 | 0.21$^{ns}$ | 2.1 |
| P30F53 x Penta | 1.95$\star$ | 16.6 | GNZ2005 x DKB234 | 1.79$\star$ | 16.7 |
| P30F53 x Premium Flex | 0.44$^{ns}$ | 3.7 | GNZ2004 x Penta | 2.44$\star$ | 22.5 |
| P30F53 x Sprint | 2.37$\star$ | 21.1 | GNZ2004 x Premium Flex | 2.39$\star$ | 23.4 |
| P30F53 x AS1575 | 0.73$^{ns}$ | 5.8 | GNZ2004 x Sprint | 1.68$\star$ | 14.5 |
| P30F53 x 2B587 | -0.24$^{ns}$ | -1.9 | GNZ2004 x AS1575 | 1.28$\star$ | 11.0 |
| P30F53 x 2B688 | -0.01$^{ns}$ | -0.1 | GNZ2004 x 2B587 | 1.56$\star$ | 13.3 |
| P30F53 x DKB234 | 0.41$^{ns}$ | 3.6 | GNZ2004 x 2B688 | 1.43$\star$ | 13.8 |
| P30F44 x AG8021 | 1.28$\star$ | 11.7 | GNZ2004 x DKB234 | 1.32$\star$ | 12.0 |
| P30F44 x GNZ2005 | 1.79$\star$ | 16.9 | Penta x Premium Flex | 0.29$^{ns}$ | 2.6 |
| P30F44 x GNZ2004 | 1.70$\star$ | 15.5 | Penta x Sprint | -0.59$^{ns}$ | -5.7 |
| P30F44 x Penta | 0.89$^{ns}$ | 8.0 | Penta x A 1575 | 0.40$^{ns}$ | 3.4 |
| P30F44 x Premium Flex | 1.96$\star$ | 17.4 | Penta x 2B587 | 0.89$^{ns}$ | 7.6 |
| P30F44 x Sprint | 3.76$\star$ | 35.5 | Penta x 2B688 | 1.58$\star$ | 13.4 |
| P30F44 x AS1575 | 1.30$\star$ | 10.9 | Penta x DKB234 | 1.36$\star$ | 13.0 |
| P30F44 x 2B587 | 0.67$^{ns}$ | 5.6 | Premium Flex x Sprint | -2.22$\star$ | -21.2 |
| P30F44 x 2B688 | 1.59$\star$ | 13.1 | Premium Flex x AS1575 | 0.33$^{ns}$ | 2.8 |
| P30F44 x DKB234 | 1.93$\star$ | 18.0 | Premium Flex x 2B587 | 1.58$\star$ | 13.3 |
| AG8021 x GNZ2005 | 2.60$\star$ | 25.6 | Premium Flex x 2B688 | 0.99$^{ns}$ | 8.3 |
| AG8021 x GNZ2004 | 1.57$\star$ | 14.9 | Premium Flex x DKB234 | 0.68$^{ns}$ | 6.4 |
| AG8021 x Penta | 1.51$\star$ | 14.2 | Sprint x 1575 | 1.09$^{ns}$ | 9.8 |
| AG8021 x Premium Flex | 1.98$\star$ | 18.3 | Sprint x 2B587 | 1.85$\star$ | 16.5 |
| AG8021 x Sprint | 2.15$\star$ | 21.1 | Sprint x 2B688 | 1.04$^{ns}$ | 9.2 |
| AG8021 x AS1575 | 0.88$^{ns}$ | 7.6 | Sprint x DKB234 | 1.85$\star$ | 18.6 |
| AG8021 x 2B587 | 0.69$^{ns}$ | 5.9 | AS1575 x 2B587 | 0.80$^{ns}$ | 6.4 |
| AG8021 x 2B688 | 0.10$^{ns}$ | 0.8 | AS1575 x 2B688 | 1.18$\star$ | 9.3 |
| AG 8021 x DKB234 | 1.54$\star$ | 14.9 | AS1575 x DKB234 | 0.79$^{ns}$ | 7.0 |
| GNZ2005 x GNZ2004 | 0.06$^{ns}$ | 0.6 | 2B587 x 2B688 | -0.87$^{ns}$ | -6.9 |
| GNZ2005 x Penta | 2.24$\star$ | 21.5 | 2B587 x DKB234 | 0.90$^{ns}$ | 7.9 |
| GNZ2005 x Premium Flex | 1.95$\star$ | 19.9 | 2B688 x DKB234 | 1.90$\star$ | 16.6 |

$\star$, $^{ns}$: significant and not significant at 5% de probability by $t$ test.

**Table 2**. Summary of joint analysis of variance concerning the morphological/agronomical traits evaluated in Laranjeiras do Sul and Guarapuava to study the genetic divergence among the 12 parental corn hybrids.

| Trait | QM | | Error | Mean | CV (%) |
|---|---|---|---|---|---|
| | Genotype | Genotypes x locations | | | |
| MF | 21.6515$\star$ | 16.1212$^{ns}$ | 8.0492 | 75.41 | 3.76 |
| PR | 0.0343$\star$ | 0.0061$^{ns}$ | 0.0054 | 1.05 | 6.97 |
| YHE | 9.9931$\star$ | 2.8629$\star$ | 2.8629 | 11.70 | 14.45 |
| PH | 0.0558$^{ns}$ | 0.0162$^{ns}$ | 0.0140 | 2.48 | 4.77 |
| EH | 0.0728$\star$ | 0.0104$^{ns}$ | 0.0081 | 1.49 | 6.00 |
| NI | 3.3000$\star$ | 0.3731$^{ns}$ | 0.2270 | 15.31 | 3.11 |
| IL | 9.9797$\star$ | 0.7057$^{ns}$ | 0.6717 | 16.51 | 4.96 |
| SD | 0.0843$\star$ | 0.0232$^{ns}$ | 0.0343 | 1.29 | 14.27 |
| LL | 0.0527$^{ns}$ | 0.0328$^{ns}$ | 0.0683 | 0.95 | 27.45 |
| LW | 1.9227$^{ns}$ | 0.8167$^{ns}$ | 1.2828 | 10.20 | 11.10 |
| NLB | 1.4634$\star$ | 0.0840$^{ns}$ | 0.0817 | 6.08 | 4.69 |
| NLA | 2.1513$\star$ | 0.3436$^{ns}$ | 0.1824 | 9.22 | 4.62 |
| LA | 0.5751$\star$ | 0.2320$^{ns}$ | 0.3420 | 2.93 | 19.91 |
| LMS | 62.4149$\star$ | 7.6839$^{ns}$ | 5.4761 | 42.60 | 5.49 |
| LSS | 25.0825$\star$ | 8.4534$^{ns}$ | 5.7666 | 21.32 | 11.26 |
| NSS | 1.2357$\star$ | 0.2284$^{ns}$ | 0.1191 | 1.41 | 24.32 |
| ASS | 28.5503$\star$ | 3.0303$^{ns}$ | 1.6389 | 9.50 | 13.47 |
| EP | 0.8001$\star$ | 0.4138$^{ns}$ | 0.1305 | 2.50 | 14.40 |
| HC | 1.7301$\star$ | 0.6866$^{ns}$ | 0.2886 | 1.95 | 27.47 |
| NRK | 19.9589$\star$ | 0.4304$\star$ | 0.6504 | 15.85 | 5.08 |
| NKR | 23.4744$\star$ | 7.0256$\star$ | 4.2183 | 35.94 | 5.71 |
| EL | 4.7888$\star$ | 2.2873$^{ns}$ | 1.1500 | 17.47 | 6.13 |
| ED | 0.8935$\star$ | 0.0398$^{ns}$ | 0.0230 | 4.50 | 3.36 |
| CD | 0.4627$\star$ | 0.0168$\star$ | 0.0070 | 2.33 | 3.58 |
| CC | 0.7254$\star$ | 0.0454$^{ns}$ | 0.0985 | 4.51 | 6.94 |

MF = male flowering, PR = prolificacy, YHE = yield of husked ears, PH = plant height, EH = ear insertion height, NI = number of internodes, IL= internode length, SD = diameter of the stalk, LL = Leaf length, LW = leaf width, NLB = number of leaves below the ear, NLA = number of leaves above the ear, LA = angle of the leaf, LMS = length of main stem of the tassel, LSS = length of secondary stem of the tassel, NSS = number of secondary stems of the tassel, ASS = angle of the secondary stem of the tassel, EP = ear placement, HC = husk coverage of the ear = NRK = number of rows of kernels on the ear, NKR = number of kernels per row, EL = length of the ear, ED = diameter of the ear, CD = diameter of the cob, CC = color of the cob. $\star$, $^{ns}$: significant and not significant at 5% probability by F test.

The analysis of variance revealed no significant differences for plant height (PH), leaf length (LL) or width of leaves (WL), indicating that there are no genetic differences between the genotypes for these traits (Table 2). Thus, these traits were disregarded in the assessment of genetic diversity.

The amplitude of the generalized Mahalanobis distances ($D^2$) ranged from 406.7 for the most divergent pair of hybrids (DKB234 and 2B688) to 26.8 between the least divergent hybrids (Penta and Premium Flex) (Table 3). These data are supported by the findings of by Pfann et al. (2009). Larger magnitudes of divergence, in descending order, were found between the pairs AG8021 and Sprint, GNZ2005 and DKB234, Sprint and DKB234 and the pair GNZ2004 and 2B688. The lowest estimates of divergence were observed for the pairs P30F44 and Penta, Premium Flex and 2B587, followed by P30F44 and Premium Flex.

Miranda et al. (2003) reported that estimates of the generalized Mahalanobis distances ($D^2$) clearly indicate that the pairs of popcorn cultivars are more divergent and more similar genetically. Fonseca and Silva (1999) reported the effectiveness of the cluster technique, with measures of genetic diversity represented by the Mahalanobis distance, for the identification of duplicate accessions of beans. This method has also been applied to several studies with corn (FERREIRA et al., 1995; FUZATTO et al., 2002; MELO et al., 2001).

The cross between the most divergent hybrids (2B688 x DKB234) (Table 3) showed an increase of 1.90 t ha$^{-1}$ over the average of these two parental hybrids, representing a heterosis of 16.6% (Table 1). Moreover, the cross between hybrids P30F44 and Sprint, which presented a low estimate of genetic divergence (Table 3), displayed a YHE of 14.34 t ha$^{-1}$, which represents an increase of 3.76 t ha$^{-1}$ over the parental average, representing for heterosis of 35.5% (Table 1). These data indicate that estimates of genetic divergence may not be enough to reveal which combinations of genotypes can be successfully used for breeding. Our data suggest that the means of yield and heterosis should be considered jointly. According to Hallauer and Miranda Filho (1981), it is preferable to cross genotypes with high yield that display intermediate genetic divergence than to cross genotypes with intermediate yield and wide divergence.

We performed a cluster analysis based on multivariate distances from the dissimilarity using the nearest neighbor method. The dendrogram from this analysis revealed the formation of five groups (Figure 1) when adopting a cutoff of 67.73 in the distance scale with 95% probability, according to Marchioro et al. (2003).
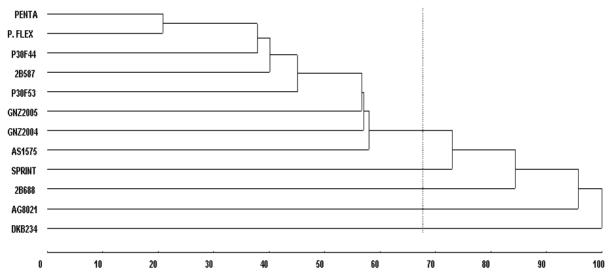
According to the magnitude of divergence, the five groups discriminated: group I, formed by the hybrid DKB234, group II formed by the hybrid AG8021, group III by 2B688, group IV by Spirnt and group V by Penta, Premium Flex, P30F44, 2B587, P30F53, GNZ005, GNZ2004 and AS1575, a group with an internal divergence lower than the cutoff level.

The interaction between SCA and location was not significant for YHE (data not shown). Thus, estimates of the SCA ($\hat{s}_{ij}$) are presented as the average of three locations and the respective means of the YHE of the crosses (Table 4). The Pearson correlation coefficient demonstrated a significant ($p < 0.05$) relationship between $\hat{s}_{ij}$ and heterosis (0.885), YHE and $\hat{s}_{ij}$ (0.818) and between heterosis and YHE (0.646) (Table 5).

Moreover, the estimates of correlations between $D^2$ and all other parameters were not significant ($p > 0.05$), indicating poor predictability between multivariate parameters and YHE behavior of the crosses. Ferreira et al. (1995) also obtained low estimates for correlations between $D^2$ and other parameters in maize. Fuzatto et al. (2002) found low correlations between the estimates of $D^2$ and $\hat{s}_{ij}$ (0.051), $D^2$ and heterosis (0.398) and $D^2$ and grain yield (0.082).

**Table 3**. Estimates of genetic dissimilarity between pairs of the 12 parental hybrids based on 22 morphological characteristics based on Mahalanobis distance ($D^2$).

| Hybrid | P30F44 | AG8021 | G2005 | G2004 | Penta | Premiun Flex | Sprint | AS1575 | 2B587 | 2B688 | DKB234 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| P30F53 | 65.5 | 141.2 | 136.4 | 96.8 | 84.2 | 92.9 | 107.4 | 141.9 | 100.1 | 130.7 | 162.9 |
| P30F44 | | 148.6 | 106.5 | 141.6 | 53.0 | 58.3 | 90.3 | 168.5 | 71.9 | 165.8 | 201.1 |
| AG8021 | | | 222.8 | 132.8 | 180.0 | 157.4 | 321.8 | 191.9 | 117.9 | 245.3 | 129.4 |
| G2005 | | | | 160.2 | 64.7 | 80.7 | 98.7 | 128.2 | 99.1 | 151.7 | 321.6 |
| G2004 | | | | | 174.5 | 169.1 | 218.8 | 177.3 | 141.7 | 256.3 | 158.7 |
| Penta | | | | | | 26.8 | 92.3 | 75.7 | 87.9 | 127.8 | 237.0 |
| P. Flex | | | | | | | 127.2 | 105.0 | 54.2 | 112.2 | 253.4 |
| Sprint | | | | | | | | 193.7 | 139.7 | 183.0 | 299.2 |
| AS1575 | | | | | | | | | 134.9 | 217.5 | 254.4 |
| 2B587 | | | | | | | | | | 150.0 | 192.8 |
| 2B688 | | | | | | | | | | | 406.7 |

**Figure 1**. Dendrogram illustrating the pattern of dissimilarity, established through a single linkage obtained from the cluster analysis via the nearest neighbor method, based on the Mahalanobis distance ($D^2$) of 22 morphological traits among the 12 parental hybrids.

**Table 4**. Mean estimates of specific combining ability ($\hat{s}_{ij}$) (up diagonal) and yield of husked ears (t ha$^{-1}$) (down diagonal) of the 66 crosses obtained from the 12 parental corn hybrids evaluated in three locations in the South-Central region of the Paraná State, Brazil.

| | P30F53 | P30F44 | AG8021 | GNZ 2005 | GNZ 2004 | Penta | Premium Flex | Sprint | AS175 | 2B587 | 2B688 | DKB 234 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P30F53 | **-0,352**[1] | -1.389 | -0.540 | 0.368 | 0.632 | 1.200 | 0.069 | 1.498 | 0.248 | -0.575 | -0.426 | -0.382 |
| P30F44 | 11.59 a | **-1,650** | -0.165 | 0.231 | 0.198 | 0.379 | 0.934 | 2.235 | 0.167 | -0.317 | 0.530 | 0.496 |
| AG 8021 | 11.81 a | 12.20 a | **-1,248** | 1.240 | 0.264 | 0.309 | 1.155 | 0.829 | -0.051 | -0.087 | -0.762 | 0.302 |
| GNZ2005 | 12.47 a | 12.35 a | 12.73 a | **-1,479** | -1.362 | 0.920 | 0.998 | 1.166 | 0.347 | -0.622 | -0.760 | 0.434 |
| GNZ2004 | 13.07 a | 12.65 a | 12.06 a | 10.22b | **-1,356** | 1.291 | -0.469 | 0.304 | 0.297 | 0.716 | 0.517 | 0.023 |
| Penta | 13.64 a | 12.84 a | 12.14 a | 12.51a | 13.21a | **-1,162** | -0.491 | -1.870 | -0.487 | -0.146 | 0.761 | 0.165 |
| P. Flex | 12.29 a | 13.18 a | 12.77 a | 12.37a | 11.53b | 11.22b | **-0,407** | -3.112 | -0.192 | 1.208 | 0.553 | -0.138 |
| Sprint | 13.58 a | 14.34 a | 12.30 a | 12.39a | 11.86a | 9.70b | 8.23b | **-1,395** | 0.090 | 0.992 | 0.113 | 0.543 |
| AS1575 | 13.28 a | 13.22 a | 12.37 a | 12.52a | 12.80a | 12.03a | 12.11a | 12.24a | **-0,625** | 0.328 | 0.640 | -0.137 |
| 2B587 | 12.35 a | 12.63 a | 12.22 a | 11.44b | 13.12a | 12.56a | 13.40a | 13.04a | 13.32 a | **-0,324** | -1.265 | 0.124 |
| 2B688 | 12.68 a | 13.65 a | 11.73 a | 11.48b | 13.09a | 13.35a | 12.92a | 12.33a | 13.81 a | 11.80a | **-0,471** | 1.039 |
| DKB234 | 11.75 a | 12.64 a | 11.82 a | 11.70a | 11.63a | 11.79a | 11.25b | 11.79a | 12.06 a | 12.21a | 31.31a | **-1,235** |

[1]Diagonal = ($\hat{s}_{ii}$). Means followed by same letters do not differ by Scott Knott test at 5% of probability.

**Table 5**. Coefficients of linear Pearson correlations obtained from estimates of means of yield of husked ears (YHE), specific combining ability (SCA, $\hat{s}_{ij}$), heterosis and generalized Mahalanobis distance ($D^2$).

| | CEC ($\hat{s}_{ij}$) | Heterosis | ($D^2$) |
|---|---|---|---|
| YHE | 0.818★ | 0.646★ | -0.279 |
| CEC ($\hat{s}_{ij}$) | | 0.885★ | 0.105 |
| Heterosis | | | 0.161 |

★Significant at 5% of probability by $t$ test.

The literature asserts that heterosis and combining ability depend directly on genetic divergence between the parents and that there are more chances of generating promising combinations when more divergent genotypes are crossed (FERREIRA et al., 1995; PATERNIANI et al., 2008). However, in this study, the correlation between genetic divergence ($D^2$) and heterosis and between $D^2$ and $\hat{s}_{ij}$ were not significant (Table 5), contradicting the idea that to express high heterosis, it is necessary for the parental hybrids involved in the cross to be divergent. In fact, divergence of the parental is necessary for high levels of heterosis;

however, divergence does not ensure high levels of heterosis, because heterosis depends not only on differences in allele frequencies but also on dominance and epistatic interactions that were not considered in this work.

The lack of correlation between $\hat{s}_{ij}$ and $D^2$ was confirmed by the crosses GNZ 2005 x Penta, Premium Flex x 2B587 and P30F53 x Penta, which displayed high positive estimates of $\hat{s}_{ij}$ for YHE (1.291, 1.208 and 1.200 t ha$^{-1}$, respectively) (Table 4) while belonging to the same group (Figure 1). On the other hand, crosses between divergent parents, classified into distinct groups (Figure 1), did not always present satisfactory $\hat{s}_{ij}$. For example, the crosses P30F53 x AG 8021, P30F53 x DKB 234, P30F53 x 2B688, AG 8021 x 2B688, GNZ 2005 x GNZ 2004, GNZ 2005 x 2B688, GNZ 2004 x Premium Flex and 2B587 x 2B688 displayed negative estimates of $\hat{s}_{ij}$ for YHE (Table 4). These results are in agreement with those obtained by Melo et al. (2001) and Paterniani et al. (2008), which

indicated that crosses between some genotypes, even those with high estimates of divergence, do not guarantee high heterosis, resulting in high values of CEC.

Guimarães et al. (2007) reported non-significant correlation between mean yield and genetic distance of hybrids obtained by diallele crosses. Paterniani et al. (2008) reported that there was no correlation between heterosis, specific combining ability or yield of hybrids with genetic distance calculated by AFLP and SSR markers, indicating that it was not possible to infer the behavior of corn hybrids from the genetic divergence between the parental lines.

The results of our study show that genetic divergence is not sufficient to secure favorable heterosis and $\hat{s}_{ij}$. One hypothesis to explain this finding is the fact that when dealing with a quantitative characteristic, such as grain yield, one can encounter cases of bidirectional dominance, i.e. some loci are dominant in one direction and other loci are dominant in the opposite direction (FALCONER; MACKAY, 1996). Another hypothesis is that some characteristics used to estimate divergence did not significantly influence grain yield.

## Conclusion

Estimates of genetic divergence are not always sufficient to reveal which combinations should be used in breeding crosses. Instead, data related to the mean yield and heterosis should be assessed together in evaluating potential crosses. Genetic divergence is necessary for heterosis, however it is not sufficient to ensure heterosis at a high level.

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