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Diallel analysis and inbreeding depression of commercial maize hybrids aiming the formation of base populations

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Abstract

The development of base populations derived from high yield commercial hybrids is considered one of the main strategies to initiate a maize breeding program, mainly because these hybrids have already been tested in many environments, and so, associating high yield and a large proportion of favorable loci fixed. Therefore, the objective of the present study is to estimate the combining abilities and inbreeding depression of commercial maize hybrids for agronomic traits. Eighteen commercial hybrids divided in two groups accordingly to their respective companies, seventy-two F, combinations from a partial diallel scheme, eighteen S, populations and one check were evaluated in a randomized complete block design in two experiments, both in Sementes Balu Experimental Unit, Sabáudia (PR), Brazil, for growing seasons from 2011/2012 and 2012/2013. The Griffing method (1956), adapted to a partial diallel by Geraldi and Miranda Filho (1988) was applied for the evaluation of the general combining ability (GCA) and specific combining ability (SCA). The hybrids P1630, P4285, 30B39Y and DKB370 showed increased yield, and hybrids P1630, 32R22H, and DKB615 showed reduced plant and ear height. These hybrids can be recommended for the extraction of inbred lines and formation of composites followed by intrapopulation selection. The combinations P1630 x DKB330, P4285 x DKB245, 30F53 x DKB370, and 32R22H x DKB370 showed desirable SCA effects for grain yield and are recommended for use in interpopulation breeding programs. Among the hybrids with desirable GCA effects, 30B39Y showed the lowest inbreeding depression effect for the analyzed traits.

Keywords: Zea mays L, base populations, combining abilities, heterosis

Introduction

In any maize breeding program, the definition of the base population plays a major role in order to guarantee time and resources efficiency and can be designated as wide or narrow genetic base population (Hallauer et al, 2010). Narrow genetic base populations with the recycling of inbred lines is being widely adopted in maize breeding programs of private institutions (Carena, 2005; Zheng et al, 2008). According to Bernardo (2009) and Mikel (2011), maize breeding in the USA is largely focused on the development of improved versions of historical inbreds, such as A632, B73, H99, Mo17, Dk3llH6, Oh43, and Ph207, aiming to obtain high yield hybrids.

The use of high yield commercial hybrids to form base populations, currently denominated as second cycle breeding, is considered a viable strategy to initiate a breeding program aiming to obtain new inbreds, becoming a common practice between breeding programs (Lamkey et al, 1995).

To define which hybrids will be used to form base populations, it is important that these hybrids be selected based on the expression of the heterosis and combining abilities, both general and specific (Hallau-

er et al, 2010). Diallel analysis is an efficient method to estimate useful parameters in the choice of parents for understanding the genetic effects involved in the determination of a certain trait. Griffing's analysis of combining ability stands out as the most commonly used, based on a more simple genetic model, being easier to interpret and applicable to all species of plants (Viana et al, 2011).

The quantification of inbreeding depression constitutes another key point to define the potential of given genotypes in a breeding program, considering the extraction of inbred lines. As self-pollination promotes an increase in homozygosity, thus exposing the effects of recessive alleles, lower magnitudes of inbreeding depression are an indication of lower genetic loads, which results in a greater potential for extraction of superior inbred lines (Falconer and Mackay, 1996).

Our study aimed to estimate the general and specific combining abilities through diallel analysis, estimate the inbreeding depression effects, and identify more promising commercial maize hybrids for the constitution of base populations to be used in the maize breeding programs.

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Materials and Methods

Eighteen high yielding commercial maize hybrids adapted to the region were used as parents in the diallel crosses. These hybrids were divided in two groups, the first one consisting of 12 Pioneer Hi-Bred hybrids, and the second group consisting of 6 Dekalb/Monsanto hybrids. A total amount of 109 treatments were evaluated, obtained by the 18 hybrids to 72 hybrid combinations derived from diallel crosses in a partial diallel scheme, 18 S₁ progenies obtained from these parents and one check (Table 1).

The crosses were performed in the second harvest of 2011, in Iguatemi, PR, Brazil (Latitude 23°25'S and Longitude 51°57'W at an altitude of 550 m), which, according to the Brazilian System of Soil Identification (SiBCS), presents a Dystrophic Red Latosol (Oxisol). To perform the crosses, all possible combinations among the 18 parents in a partial diallel scheme were sown in paired rows, each plot consisting in two rows of 10 m each. Each combination was sown in two different days, to ensure the synchronization of parental flowering time. Self-pollinations plots were set up for each parent, consisting of a single row of 10 m each. All rows were 0,80 m spaced, and consisted of 5 plants m⁻¹.

The experiments were performed in Sabaúdia, PR, Brazil, at an altitude of 725 m, located at 23°19'S and 51°33'W latitude and longitude, respectively. The 109 treatments were evaluated in the growing seasons of 2011-2012 and 2012-2013, in a randomized complete block design with replications, in which each plot consisted of two rows of 5 m each, spaced

Table 1 - Origin and description of the commercial hybrids used as parents in the partial diallel.

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^{*:} SH: Simple Hybrid, TH: Triple Hybrid, and DH: Double Hybrid.

0.90 m apart, resulting in a useful area of 9 m². Each plot was thinned at 30 days to a density of 5 plants m⁻¹, resulting in a population of approximately 55,500 plants ha⁻¹ at harvest time. Fertilization consisted of the application of 350 kg ha⁻¹ of the formulation 4-20-20 at sowing, and 140 kg ha⁻¹ of N using urea in the covering at 35 days after seedling emergency.

All of the treatments in both experiments were evaluated for plant height (PH), average height for insertion of the ears (EH) from the data collected in 6 competitive plants per plot. Grain yield data was obtained from the productivity of husked ears per plot, standardized at 13% moisture content. A covariance analysis according to Vencovsky and Cruz (1991) was adopted for the stand adjustment, considering an ideal stand of 50 plants per plot.

The analysis of variance for each experiment were performed, followed by the evaluation of homogeneity of variances using the Hartley test (Hartley, 1950). The joint analysis for the environments was performed according to the statistical model $Y_{ijk} = \mu + R/E_{jk} + G_i + E_j + GE_{ij} + \epsilon_{ijk}$, in which Y_{ijk} is the meanphenotypic value of the plot; μ is the overall mean of the experiment; R/E_{jk} is the effect of the k^{th} repetition in j^{th} environment; G_i is the fixed effect of the i^{th} genotype; E_j is the effect of j^{th} environment; GE_{ij} is the effect of the interaction of i^{th} genotype with j^{th} environment, and ε_{ijk} is the experimental error. Then, the data was submitted to Scott-Knott (1974) cluster analysis of grouping means.

The joint partial diallel analysis was performed using data from all F, generation according to model 4 from Griffing (1956) methodology adapted to partial diallel scheme by Geraldi and Miranda Filho (1988), aiming to evaluate the combining abilities and their interaction with environment, according to the following model: $Y_{ij} = \mu + g_i + g_j + s_{ij} + E_k + GE_{ik} + GE_{jk} + SE_{ijk}$ $+\overline{e}_{ii}$, in which Y_{ii} is the mean value of the hybrid combination between ith parental from group 1 and the jth parental from group 2; µ is the overall mean; g is the GCA of the i, parental from group I; g, is the GCA of the jth parental of group II; s, is the SCA between ith parental from group 1 and jth parental from group 2; E, is the effect of environment k; GE, and GE, are the effects of the interaction between the GCA associated with the ith and jth parents from groups 1 and 2, respectively, with the environments; SE; the effect of the interaction between the SCA between the ith and jth parents and the environments; and e is the average experimental error.

Inbreeding depression was quantified in the first generation of self-pollination of the parents present in the diallel, according to the equation:

$$D = \frac{(F_1 - S_1)}{F_1} x 100$$

in which D = inbreeding depression, F_1 = mean for the commercial hybrid and S_1 = mean for the S_1 population of the commercial hybrid. The potential of the commercial hybrids as sources of inbred lines was

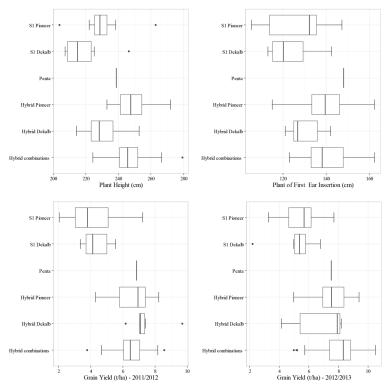


Figure 1 - Boxplot of the minimum, maximum and medium values – 25, 50, and 75 quartiles – of the plant height, plant of first ear insertion and grain yield.

studied according to the method proposed by Gardner (1965) and explained by Vencovsky and Barriga (1992), from the expression $\overline{L}_i = \overline{u} + \hat{a} = 2 \, \overline{S}_{1i} - \overline{S}_{0i}$ in which $\overline{L}_i =$ expected means of the pure inbred lines; $\overline{S}_{1i} =$ phenotypic mean value after one generation of self-fertilization; and $\overline{S}_{0i} =$ original phenotypic mean value of the genotypes. The analysis and calculations were performed using the programs Genes (Cruz, 2016) and software R (http://www.r-project.org).

Results and Discussion

The effects of treatments for all of the evaluated traits in the joint analysis of variance indicated differences (p < 0.05) between the genotypes included in this study. This response constitutes a key element for breeding programs, justifying the partitioning of treatments variance. Differences for all traits were observed from the partitioning of the treatment sum of squares for both F_1 and S_1 generations, regarding the group of most interest. Parental effects were similar (p > 0.05) for grain yield (GY), as well as for plant height (PH) and GY in relation to the Treatments vs. Checks interaction. Meanwhile, the effect of Environment indicates a major environmental influence on the averages of ear height (EH) and GY.

Considering the source of variation Treatments vs Environments (T x E) interaction, GY was the only trait with different performances from these genotypes in function of environmental variations from one year to the next. In the partitioning the T x E interaction mean

square for GY, the Diallel vs Season (D x E) and the Parents vs Seasons (P x E) were the only groups of interests to show differences. The similar effect for F_1vs Environment (F_1 x E) is an indication that the plasticity of these hybrid combinations facing environmental diversity was sufficient to guarantee stability in their performance in these two years of experimentation. This result is in disagreement with that obtained by Senhorinho et al (2015), in which they evaluated 22 commercial maize hybrids, $96 \ F_1$ combinations from a partial diallel scheme, $22 \ S_1$ populations and four controls. They found differences for the majority of sources of variation in the partitioning the variance of the T x E interaction for GY.

The experimental coefficients of variation (CVs.) obtained in the experiments were 5%, 7%, and 14% for PH, EH, and GY, respectively. According to the CVs. classification proposed by Fritsche-Neto et al (2012), the obtained values in this present study can be considered intermediate, indicating satisfactory experimental precision.

Considering the traits PH and EH, Dekalb hybrids showed the lowest values (230.70 \pm 13.30 cm and 129.95 \pm 8.35 cm, respectively) when compared with Pioneer HiBred hybrids (248.89 \pm 10.33 cm and 138.87 \pm 12.72 cm, respectively), having 4 hybrids (DKB330, DKB240, DKB 615 and DKB390) grouped, according to Scott Knott (1974), in groups with the lowest values for both traits (Figures 1 and 2). The hybrid combinations obtained average values of 246.85

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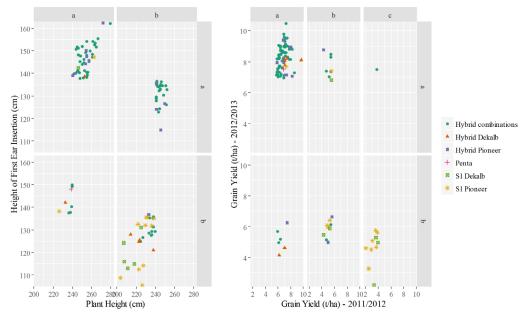


Figure 2 - Scott-Knott grouping means for plant height, height of first ear insertion and grain yield of 18 commercial hybrids, 72 hybrid combinations from a partial diallel scheme, 18 S₁ populations and one check (cv. Penta) evaluated in seasons 2011-2012 and 2012-2013.

 \pm 9.51 cm for PH and 139.61 \pm 9.05 cm for EH, in which, 12 hybrid combinations were grouped in the groups with the lowest values of PH and EH. The S $_1$'s genotypes from Dekalb obtained average values of 219.29 \pm 14.85 cm and 123.62 \pm 11.45 cm for PH and EH, respectively, while Pioneer HiBred hybrids obtained average values of 229.77 \pm 11.45 cm and 127.39 \pm 13.44 cm for PH and EH, respectively. The check genotype «Penta», performed 238.75 cm and 148.00 cm for PH and EH, respectively.

Considering GY, the average values of both groups of hybrids were similar, having Pioneer Hi-Bred hybrids performing 6.62 ± 1.18 t ha⁻¹ and 7.52 ± 1.25 t ha⁻¹ in 2011-2012 and 2012-2013 main harvests, respectively, while Dekalb hybrids performed 7.41 ± 1.19 t ha⁻¹ and 6.81 ± 1.90 t ha⁻¹ in 2011-2012 and 2012-2013 main harvests, respectively (Figure 1). Pioneer HiBred hybrids (P3646, P1630, 30B39Y, 32R22H, P4285, P30F36, 30R50, and 30B30), and Dekalb hybrids (DKB330, DKB245, DKB240, and DKB370) were alocated in groups with the highest average values in both harvests (Figure 2).

Mean values for GY of hybrid combinations were 6.51 ± 0.86 t ha⁻¹ in the first and 8.10 ± 1.06 t ha⁻¹ in the second year, with 84% of all hybrid combinations clustered in groups with the highest grain yield for both years of study (Figure 2). This result demonstrates the potential of high yielding commercial maize hybrids in the development of base populations for breeding programs (Senhorinho et al, 2015; Souza Neto et al, 2015). The check genotype «Penta» was alocated in the group with the highest average for both harvests (6.86 t ha⁻¹ and 7.51 t ha⁻¹ for 2011-2012 and 2012-2013 havests, respectively; Figure 2).

Considering the average values of S_1 's genotypes, Pioneer HiBred and Dekalb performed, respectively, $4.13 \pm 1.48 \, t \, ha^{-1}$ and $4.33 \pm 0.87 \, t \, ha^{-1}$ for 2011-2012 harvest and $5.57 \pm 1.25 \, t \, ha^{-1}$ and $5.09 \pm 1.55 \, t \, ha^{-1}$ for 2012-2013 harvest.

The diallel analysis indicated different effects of GCA for group 1 and 2 for all evaluated traits, while SCA showed only for GY. In both groups, the magnitude of the mean squares of GCA were greater then the mean squares of SCA for all evaluated traits, suggesting a predominance of additive effects. This result is in agreement to that reported by many authors, in which there is a predominance of additive effects and partial dominance for PH, EH, and GY (Comstock and Robinson, 1948; Gardner et al, 1953; Oliboni et al, 2013; Senhorinho et al, 2015).

In general, the variability of \hat{g} 's indicates that the commercial hybrids used as parents had different contributions in the supply of favorable alleles with additive effects to their progeny. Furthermore, the variability of the \hat{s}_{ij} 's indicates hybrid combinations with different performances in relation to what would be expected based only on the GCA effects. This result reflects the possibility to perform intrapopulation breeding, aiming to obtain superior inbred lines with a propensity to present higher levels of heterosis for GY (Hallauer et al, 2010). There were similar effects of the interaction between hybrid combinations and cropping seasons (F_1 x E), indicating a similar performance of genotypes in both years.

Among Pioneer genotypes, 3021, P1630, 32R22H, and 30F80 were highlighted for plant height, while the highlighted Dekalb genotypes were DKB330, DKB245, and DKB615 (Table 2). Such results permit

Table 2 - Estimates of the effects for \hat{g}_i and \hat{g}_j for plant height, ear height, and grain yield.

Effect of g, and g,	PH (cm)	EH (cm)	GY (t ha ⁻¹)						
Average Environment (GROUP I)									
30F53	1.396	0.972	-0.384						
3021	-5.896	-2.778	-0.19						
P3646	4.438	3.222	0.379						
P1630	-4.021	-11.069	0.463						
30B39Y	7.979	5.806	0.432						
32R48	-1.646	-0.754							
32R22H	d -3.396 -6.7		-0.854						
P4285	2.229 3.800		0.489						
P30F36	1.271 1		0.066						
30R50	-1.396 2.764		0.264						
30B30	3.021	2.764	0.109						
30F80	-3.979 1.514		-0.02						
Ave	Average Environment (GROUP II)								
DKB330	-3.854	-2.299	-0.412						
DKB245	-3.188 5.285		0.058						
DKB240	-0.188 -7.861		-0.392						
DKB370	13.542	8.326	0.568						
DKB615	-7.417	-5.757	-0.129						
DKB390	1.104	2.306	0.307						

to infer that these parents are able to provide favorable genes to their progenies so as to promote a reduction in plant height. On the other hand, considering EH, the highlighted genotypes were P1630 and 32R22H for \hat{g}_i and DKB240 and DKB615 for \hat{g}_i .

The parents P1630, P4285, 30B39Y, and DKB370 showed the highest estimates of \hat{g}_i and \hat{g}_j for GY, favoring an increasing of averages in their respective hybrid combinations, when compared to the general performance of all F_1 's generations. All of the above mentioned parents showed higher yields, therefore, are considered promissing for a breeding program, for associating high GY and GCA.

The formation of composites for intrapopulation selection is a viable alternative to obtain genotypes with an accumulation of desirable characteristics. Since the choice of genotypes to be used in the synthesis of a composite depends on the general combining ability of the parents, our results allow us to indicate the hybrids P1630, P4285, 30B39Y, and DKB370 for their high GCA for grain yield, and hybrids 3021 and DKB615 by their additive genetic contribution associated with reduced plant and ear height. They should be promising genotypes for the formation of a base populations in a breeding program.

The selection of the most promising hybrid combinations should be made not only from the SCA estimates but also from the parental g_i values. However, it is important that hybrids with a high SCA are formed from at least one parent with high GCA, that is, a parent with a particularly high frequency of favorable genes (Cruz et al, 2007). Based on these assumptions, the hybrid combinations with the largest values were P1630 x DKB330, P4285 x DKB245, 30F53 x DKB370, and 32R22H x DKB370 (Figure 3), since ge-

netic complementation in these crosses should have increased the means of the evaluated traits as a consequence of the non-additive genetic effects.

High estimates of \hat{s}_{ij} involving at least one parent with a high GCA estimate may be an indication that populations generated by these parents can be useful in reciprocal recurrent selection (RRS), as this method was designed to exploit both general and specific combining abilities (Comstock et al, 1949), and successful results have been reported regarding the improvement of agronomic traits of diverse populations under cycles of RRS (Hallauer, 1970; Keeratinijakal and Lamkey, 1993; Pena-Asin et al, 2013; Raposo et al, 2004; Santos et al, 2005; Santos et al, 2007; Souza Júnior et al, 2010).

Considering the estimates of $\hat{\mu}$ + \hat{a} and inbreeding depression (% ID), the parents 3021, P3646, 30B39Y, and DKB390 were considered the most promising for extraction of inbred lines for the evaluated traits, because they associate the lowest % ID with the highest $\hat{\mu}$ + \hat{a} (Table 3). The estimates of $\hat{\mu}$ + \hat{a} and % ID are an indicative of the potential that a certain population will have in relation to the demand of superior inbred lines. Therefore, the lower the % ID of a certain population, the lower the contribution of dominant effects over the means, and consequently, higher the estimates of $\hat{\mu}$ + \hat{a} (Vencovsky and Barriga, 1992).

For PH, the estimates of % ID ranged from -5.02 (DKB390) to 20.80 (P30F36), while for EH, ranged from -2.89 (DKB370) to 20.80 (P30F36). With respect to GY, the estimates ranged from -28.74 (3021) to 70.42 (32R22H) for 2011/2012 growing season

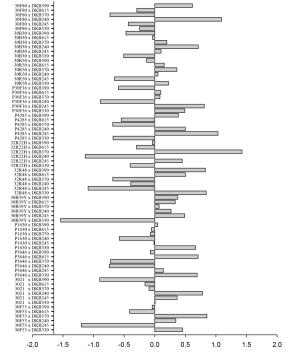


Figure 3 - Estimates of the effects of \hat{s}_{ij} on grain yield.

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Table 3 - Estimates of $\hat{\mu}$ + \hat{a} and relative percentage of inbreeding depression (% ID) for plant height (PH, cm), plant ear height (EH, cm) and grain yield (GY, t ha⁻¹).

Parents	F	PH		EH		GY - 2011/2012		12/2013
	μ̂ + â	% ID	μ̂ + â	% ID	μ̂ + â	% ID	μ̂ + â	% ID
30F53	204.75	9.73	114.00	12.00	-0.06	50.40	3.06	25.48
3021	227.50	1.18	134.25	0.91	6.74	-28.74	6.03	15.54
P3646	231.25	2.07	128.00	2.77	3.18	28.46	5.67	10.24
P1630	207.00	7.84	96.00	8.26	-0.74	55.35	2.20	36.15
30B39Y	253.50	3.40	132.25	9.24	6.23	12.15	8.31	-8.94
32R48	213.75	5.70	104.50	7.86	0.01	49.90	1.55	34.41
32R22H	196.00	10.72	98.50	11.07	-2.83	70.42	0.94	44.30
P4285	208.50	9.12	123.50	8.14	2.84	29.30	2.74	35.43
P30F36	150.25	20.80	71.75	25.39	-1.96	62.63	0.07	49.61
30R50	200.50	8.83	125.00	5.36	1.91	33.68	3.27	29.38
30B30	222.75	6.11	125.75	6.41	2.81	30.51	4.73	16.83
30F80	212.00	5.93	137.50	0.54	1.60	35.66	4.86	13.29
DKB330	192.00	7.05	106.50	7.57	-0.70	54.72	-3.81	73.26
DKB245	181.75	10.96	106.50	12.50	1.54	39.09	2.85	32.30
DKB240	198.50	8.30	109.00	4.96	0.77	44.59	2.14	36.25
DKB370	239.75	2.57	146.50	-2.89	1.38	42.87	5.47	16.28
DKB615	199.50	5.27	101.25	9.42	0.24	48.30	5.96	-14.78
DKB390	235.75	-5.02	134.00	-2.34	4.27	15.40	7.63	-42.37

and from -42.37 (DKB390) to 73.26 (DKB330) for 2012/2013 growing season. Senhorinho et al (2015), evaluating the % ID of 22 commercial hybrids, verified an average variation from -6.27 to 16.27 for PH, -11.17 to 25.09 for EH and -25.36 to 53.08 for GY. Bernini et al (2013) verified estimates of % ID ranging from 4.7 to 13.0 for PH, 0.8 to 9.7 for EH and 18.0 to 48.41 for GY.

Since most parents used in this experiment are single hybrids, high grain yield reduction levels indicate a large amount of genetic complementation between the parental inbred lines involved in their formation. This complementation results in high levels of heterosis from crossings between inbred lines of contrasting heterotic groups. In contrast, the hybrids that showed lower magnitudes of inbreeding depression were likely formed from crossings between inbred lines with higher frequencies of favorable alleles with additive effects that add up in each hybrid to constitute the important phenotypes in the evaluated environments.

Conclusions

The parents selected for grain yield (P1630, P4285, 30B39Y and DKB370), plant height (P1630, 3021, DKB330, DKB245 and DKB615) and ear height (P1630, 32R22H, DKB240 and DKB615) can be used in the formation of synthetics for the extraction of inbred inbred lines that reunite traits of interest.

The combinations P1630 x DKB330, P4285 x DKB245, 30B39Y x DKB245, 30F53 x DKB370 and 32R22h x DKB370 were the most promising with respect to grain yield.

The populations derived from the hybrids 3021, P3646, 30B39Y and DKB390 offer greater opportunities for success in the synthesis of inbred lines with superior grain yields.

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