

Combining ability and analysis of genetic components of synthetic maize populations using a mixed model approach

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ABSTRACT: The aim of this study was to estimate the combined ability and analyze the genetic variance components of synthetic maize populations using diallel crossing with a mixed model approach. Twelve synthetic varieties were crossed following the complete diallel scheme without reciprocals, resulting in 66 intervarietal hybrids, which were evaluated along with the parental populations and four commercial cultivars in three different environments. An experiment was performed on 82 genotypes using a randomized complete block design with three repetitions. The evaluated traits were ear height (EH), plant height (PH) and grain yield (GY). Griffing's Model II, Method 2 and Gardner and Eberhart's Model II were combined for diallel analysis, along with the UPGMA method based on predicted breeding values (BLUP). The non-additive genetic effects were the most important for plant architecture and grain yield within each synthetic population, as based on the GCA and SCA. Clusters 1 and 2 separated by UPGMA can be included in breeding programs to obtain hybrids, and cluster 3 can be used to obtain genotypes with lower plant architectures and higher productivity in intrapopulation breeding programs.

Key words: general combining ability; heterosis; specific combining ability; *Zea mays* L.

Análise combinatória e componentes genéticos de populações sintéticas de milho utilizando abordagem de modelos mistos

RESUMO: Objetivou-se estimar a capacidade combinatória e analisar os componentes genéticos de populações sintéticas de milho em cruzamentos dialélicos utilizando abordagem de modelos mistos. Doze variedades sintéticas foram cruzadas em esquema dialélico completo sem recíproco, resultando em 66 híbridos intervarietais, que foram avaliados com as populações parentais e quatro cultivares comerciais em três ambientes distintos. Os experimentos, com 82 genótipos cada, foram conduzidos em delineamento de blocos ao acaso com três repetições. Foram avaliadas as características altura da espiga (AE), altura da planta (AP) e produtividade de grãos (PG). O modelo II, método II de Griffing e o modelo II de Gardner e Eberhart foram combinados para a análise dialélica juntamente com o método de agrupamento UPGMA com base nos valores genéticos preditos (BLUP). Os genes de efeito não aditivos foram os mais importantes para arquitetura de plantas e produtividades de grãos dentro de cada população de sintéticos, com base na CGC e CEC. Os grupos 1 e 2 separados pelo agrupamento UPGMA podem ser incluídos em programas de melhoramento para obtenção de híbridos e o grupo 3 pode ser utilizado para obtenção de genótipos com menores arquiteturas de planta e maior produtividade em programas de melhoramento intrapopulacional.

Palavras-chave: capacidade geral de combinação; heterose; capacidade específica de combinação; *Zea mays* L.

Introduction

The main objective of breeding programs is to develop commercial cultivars while deciding which genotypes and crossings should be used to obtain considerable gains in the traits of agronomic interest, and is critical to the success of such programs. Good performance of the genotypes or population only indicates its relative superiority, but does not necessarily reflect the ability to transfer the trait of interest when crossed with other genotypes.

The diallel breeding scheme is one of the methods which enables separating the performance of the parental and progeny populations into components to estimate the general (GCA) and specific (SCA) combining abilities. Many methods have been applied to perform analyses where the parents can be pure lines or open pollinated varieties (Gardner & Eberhart, 1966; Griffing, 1956a). In this context, the analyses allow for estimating the genetic parameters without bias, using (among other methods) the parents and their F_1 crossings. Furthermore, diallel analyses are employed to identify the best genotypes to be crossed to explore heterosis and select the best crossing for commercial use or as a source of variability in breeding programs.

Hallauer et al. (2010) showed that the expected cross value is the sum of the GCA of the two parents, while the deviations from these values are the SCA. Thus, GCA describes the general importance of the parent on a particular trait, while the SCA indicates the importance of joint action of the genes of that parent in the cross (Baker, 1978). According to Griffing (1956b), the expected gain of any trait from the GCA and SCA estimates will be proportional to their variances. The mean squares of GCA and SCA ratio are used to determine the prevalence of gene action (additive and non-additive) of the quantitative character. The closer this ratio is to the unit, the better the performance of the selected progeny based on GCA values (Murtadha et al., 2016).

Regarding the selection of the best crosses in breeding programs, a cluster analysis enables identifying groups that show high intra-group and inter-group homogeneity. Hierarchical clustering methods are generally used to study the genetic diversity in plants. Among others, the UPGMA method has been commonly used to cluster agronomical and morphological traits using Euclidean distance (Setimela et al., 2016). Combined with the diallel crossing analysis and estimates of genetic components, these methods are used to identify parental groups with good capacity for intra- and intercross to obtain superior genotypes in breeding programs (Badu-Apraku et al., 2016).

Thus, the objective of this study was to estimate the combining ability and analyze the genetic components in synthetic populations of maize using diallel crossing.

Material and Methods

Twelve synthetic maize varieties from local commercial varieties were crossed following the complete diallel scheme

without reciprocals. Sixty-six (66) intervarietal hybrids were evaluated along with the 12 parental varieties and four commercial cultivars, totaling 82 genotypes.

The experiment was carried out in the 2009-2010 harvest year, in three environments. The first (first environment) and second (second environment) crops were grown on an experimental farm at Jaboticabal (21°15'17" S, 48°19'20" W; 605 m a.s.l.) São Paulo, Brazil, and a second crop (third environment) in Campo Alegre de Goiás (17°37'59" S, 47°46'42" W; 877 m a.s.l.), Goiás, Brazil. The climates in both places are classified as tropical Aw according to the Koppen classification, with 60 mm average rainfall in the driest month and average temperature of 18°C in the coldest month of the year. The average temperature in the rainy season is 29°C. The soils are classified as Eutrophic Red Latosol and Dystrophic Red Latosol, respectively (Embrapa, 2006).

All experiments followed a randomized complete block design (RCBD) with three replications. The plots consisted of four 5-meter long rows, spaced 0.9 m from one another. The population density was 55,555 plants.ha⁻¹ and only the two central rows were considered in the evaluation. All experiments had the following cultivars as controls: AG-7000 (simple hybrid), BR106 (open-pollinated variety), Bandeirantes (open-pollinated variety) and Campeão (open-pollinated variety). The evaluated traits were ear height (EH, cm), plant height (PH, cm), and grain yield (GY, kg.ha⁻¹). The plot production data was corrected to 13% moisture and adjusted based on the covariance method, and then converted to kg.ha⁻¹.

The normal distribution of the data was checked by Levene and Kolmogorov-Smirnov for all traits. The deviance analysis used the linear mixed model Eq. 1:

$$y = X\beta + Z_1g + Z_2w + e \quad (1)$$

where y - is the vector of phenotypic observations; β - is the vector of fixed effects due to blocks, environments and general average; g - is the vector of the genotype effects, assumed as random; w - is the vector of the effects of the genotypes x environments interaction (random); X , Z_1 and Z_2 are the matrices of incidence of these effects; and e is the random residual vector $N(0, \sigma^2)$. Where, 0 - is the empty vector; φ - is the empty matrix; G - is the inter- genotypic variance matrix; W - is the matrix of genotypic interaction; R - is the genotypic variance matrix, and considering the BLUE model for β of the fixed effects and BLUP for the random effects, g and w . The estimates of the variance components necessary to obtain the breeding values (BLUP) of the individuals were determined iteratively using the multivariate Restricted Maximum Likelihood (REML) method.

Estimates of genotypic values ($u + g + ge$) (Bernardo, 1996) were used in the UPGMA clustering analysis by Euclidean distance, resulting in a dendrogram with clustered cultivars. To determine whether the clusters represented the observed relationship between the parents, the cophenetic correlation coefficient between the cophenetic and dissimilarity matrices was estimated (Laude & Carena, 2015).

Control cultivars were removed from the dataset for the diallel analysis. The macro Diallel-05 of SAS software (Zhang et al., 2005) was used, which included the diallel analysis proposed by Gardner & Eberhart (1966) Model II. It analyzes the crosses and parental relations without reciprocals, unfolding the sum of squares to inter-varietal and parental hybrids in variety and heterotic effects using the following model Eq. 2:

$$Y_{jj'} = \mu_v + 0.5(v_j + v_{j'}) + v\bar{h} + v(h_j + h_{j'}) + vs_{jj'} \quad (2)$$

where $Y_{jj'}$ - is the average of parental genotypes when $j=j'$ and average cross when $j \neq j'$, μ_v - is the average of all parental genotypes, v_j and $v_{j'}$ - are the effects of varieties j and j' , respectively, when parental genotypes are included in the analysis with the restriction $\sum v_j = 0$, h - is the average heterosis, h_j and $h_{j'}$ - is the varietal effect for the j and j' varieties, respectively, and $s_{jj'}$ - is the specific heterosis with the restriction $\sum_j s_{jj} = \sum_{j'} s_{j'j'} = 0$. In addition, the diallel analysis by the Griffing's Model II, Method 2 was performed to analyze the parental crosses, estimating the general (GCA) and specific (SCA) combining ability. Griffing (1956b) proposed to analyze the diallel table decomposing the mean v_{ij} in the following effects in Eq. 3:

$$v_{ij} = \mu_x + g_i + g_j + s_{ij} + \frac{1}{b} \sum_k b_k + \frac{1}{b} \sum_k (bv)_{ijk} + \frac{1}{bc} \sum_k \sum_l e_{ijkl} \quad (3)$$

where, v_{ij} - is the average phenotypic value observed in the plot for the i^{th} and j^{th} genotype; μ_x - is the effect of general average; g_i and g_j - are the GCA effects, associated to the i^{th} and j^{th} parent, respectively; s_{ij} - is the SCA effect of the cross ij , given that $s_{ij} = s_{ji}$; k - is the number of blocks varying from 1,2,3, ..., b ; bv - effect of the block x genotype interaction; $c = p^2 - p + 1$ where p - is the number of parents; e_{ijkl} - is the average random error associated with the $ijkl$ observations.

The following restrictions apply in this model: $\sum_j g_j = 0$ and $\sum_{i \neq j} s_{ij} = 0$ (for each j). The additive and non-additive effects of traits were calculated by the sum of square GCA and SCA ratio for each trait, estimated by the Griffing (1956b) method according to the following Eq. 4 proposed by Baker (1978):

$$CGC : CEC = \frac{SQ_{CGC}}{(SQ_{CGC} + SQ_{CEC})} \quad (4)$$

Results and Discussion

Considering the traits GY, PH and EH, there was a highly significant effect to all random and fixed effects of the model, except for synthetics vs. controls to PG (Table 1). A significant variance was observed for genotypes, synthetic varieties, crosses and commercial controls, as well as the following contrasts: crosses vs. controls and synthetic vs. crosses, showing significant inter- and intra-group differences for all studied traits. The synthetic vs. controls were not significantly different for grain yield (GY), showing that the synthetic varieties did not differ from controls on average GY, but PH and EH were significantly different.

The traits (except for EH) were significantly affected by the environment (Murtadha et al., 2016). In addition, there was a significant genotypes x environments interaction for all traits, indicating a different genotypic performance in response to environmental changes. According to Abdel-Moneam et al. (2009), these results suggest that testing varieties in different environments enable accurate selection of a stable parent with productive potential. Thus, parental testing in various environments is important to ensure the stability of genotypes.

The average performances of the 12 synthetic varieties and 10 best crosses are presented in Table 2. Overall, all crosses performed better compared to the parental populations and commercial varieties, and the C-8x12 crossing was superior to

Table 1. Deviance analysis by the likelihood ratio test (LRT) for random effects and analysis of variance of fixed effects via mixed models for the 12 synthetic varieties, 66 hybrids and four commercial cultivars evaluated in three environments.

Components of variance of random effects							
FV	GL (χ^2)	GY		PH		EH	
		σ^2	LRT ²	σ^2	LRT ²	σ^2	LRT ²
Synthetics	1	491578	48***	77.69	6.4*	58.19	10***
Gen x Env	1	428093	25.1***	117.79	215.7***	81.31	193.6*
Residue		1757266		90.77		61.22	
Mean square of fixed effects							
FV	GL	GY		PH		EH	
Environments	2	181673684.50***		19607.00***		6590.85 ^{ns}	
Genotypes	81	5659888.80***		705.20***		503.25***	
Controls	3	9070547.00**		6264.39***		1951.57***	
Crosses	65	2880175.70*		273.63***		269.05***	
Syn vs Controls	1	2616140.70 ^{ns}		19523.4***		11856.01***	
Crosses vs Controls	1	193117605.00***		1110.32*		1513.05**	
Syn vs Crosses	1	37279170.10***		11343.77***		5771.39***	
Average amplitude (Synthetics)		2209.48		43.78		37.00	

***, **, *, ns, significant at 0.001, significant at 0.01, significant at 0.05 and non-significant respectively, Syn: Synthetics; Env: Environments, GEN: Genotypes, FV: source of variation, GL (χ^2): degrees of freedom of the chi-square analysis; GL: degrees of freedom; PH: plant height (cm), EH: ear height (cm), GY: grain yield (kg.ha⁻¹).

Table 2. Genotypic value, means and standard deviations for grain yield, plant height and ear height for 12 synthetic varieties, top 10 intervarietal crossings, and four commercial cultivars.

Genotypes	GY	PH	EH
	(kg ha ⁻¹)	(cm)	
S-01	5554.78	198.44	107.77
S-02	5367.56	196.66	111.22
S-03	5391.22	199.88	115.11
S-04	5502.56	204.11	114.66
S-05	4680.89	202.44	117.77
S-06	4634.11	214.44	123.44
S-07	3888.89	209.44	123.44
S-08	4522.22	215.11	123.44
S-09	3705.89	218.00	131.55
S-10	4519.67	215.66	125.55
S-11	3893.11	174.22	94.55
S-12	3661.44	205.44	124.33
C-8x12	9065.00**	195.44 a	110.33 ab
C-2x9	7152.10 ab	209.66 a	114.55 ab
C-4x12	6793.33 abc	209.00 a	122.22 a
C-5x10	6708.67 abc	206.77 a	120.44 ab
C-3x4	6699.67 abc	199.00 a	111.11 ab
C-4x8	6625.33 abc	203.88 a	113.11 ab
C-3x8	6595.89 abc	205.55 a	119.77 ab
C-6x10	6542.22 abc	207.33 a	118.44 ab
C-5x8	6536.22 abc	202.44 a	110.55 ab
C-1x12	6535.80 abc	199.11 a	113.00 ab
AG-7000	7159.33	202.78	119.49
BR 106	4610.19	204.49	117.74
Bandeirantes	5394.67	233.15	138.52
Campeão	5799.67	233.70	135.60
CV (%)	11.06	6.61	9.06
Mean (Sint)	4610.19	204.49	117.74
SD (Sint)	537.76	14.23	10.41
Mean (Cruz)	6071.38	201.01	113.60
Mean (Test)	5740.96	218.53	127.83
SD (Test)	1003.91	14.88	8.68

CV (%): coefficient of environmental variance; PH: plant height (cm), EH: ear height (cm), GY: grain yield (kg,ha⁻¹); CRUZ : Cross; SINT: Synthetic variety; TEST: commercial controls; SD: standard deviation; **: significant difference by 1% the Dunnett test with respect to the average of the simple hybrid AG-7000; Means followed by the same lowercase letter in the column do not differ by the Tukey test at 5% significance.

the average of the AG-7000 hybrid (Table 2). The coefficient of variation for all variables are within the acceptable range according to Fritsche-Neto et al. (2012), confirming the accuracy of the experiment and estimated averages.

The GCA effects were significant for PH and EH (Table 3), indicating variability among genotypes regarding the frequency of favorable alleles due to the additive genetic effects of these traits. According to Hallauer et al. (2010), the variety effect and GCA do not have the same meaning in the Gardner & Eberhart (1966) method, because the varietal effect is the contribution of the varieties in crosses and contribution *per se*, so the GCA estimated by the Griffing (1956b) method might be more accurate to interpret the additive genetic effects. Likewise, the SCA effect was significant for all traits (Table 3), indicating whether the hybrid combinations performed better or worse than expected based on the GCA of the synthetic varieties. This result showed the high degree

Table 3. Summary of variance analysis of diallel crossings by the Gardner and Eberhart method II (1966) and Griffing's method II (1956), Model 2 for grain yield, plant height, and ear height.

FV	GL	Mean square		
		GY	PH	EH
GCA ⁺⁺	11	3603561.80 ^{ns}	579.05 ^{**}	685.70 ^{**}
SCA ⁺⁺	66	5744970.30 ^{**}	345.62 ^{**}	269.59 ^{**}
GCA: SCA	-	0.09	0.21	0.29
Additive Variance	-	14414247.20	2316.20	2742.80
Variance of dominance	-	22979881.20	1382.48	1078.48
Degree of dominance	-	1.78	1.08	0.88
Crossings	65	5748116.94 ^{**}	345.63 ^{ns}	269.60 [*]
Mean heterosis	1	195040603.76 [*]	1172.30 ^{ns}	1559.73 ^{ns}
Varietal heterosis	11	3646103.99 ^{**}	940.94 ^{**}	590.42 ^{**}
Specific heterosis	54	2672954.59 ^{ns}	209.06 ^{ns}	180.00 [*]
Synthetics x Environments	22	3663489.70 ^{**}	265.42 ^{**}	158.00 ^{**}
M. Heterosis x Env	2	4049960.14 ^{ns}	9081.10 ^{**}	3407.40 ^{**}
V. Heterosis x Env	22	1105814.92 ^{ns}	261.20 ^{**}	141.01 ^{**}
S. Heterosis x Env	108	3413581.04 ^{**}	158.12 ^{**}	120.44 ^{**}
Residue (Ajs)	621	-	-	-
Heritability ⁺⁺⁺ (%)	-	39.27	64.13	73.43

***, **, *, ns, significant at <1%, 1%, 5% and non-significant, respectively; Env: Environments; FV: source of variation; GL: degrees of freedom; PH: plant height (cm); EH: ear height (cm); GY: grain yield (kg,ha⁻¹); GCA⁺⁺ and SCA⁺⁺: general and specific combining ability estimated by the Griffing method (1956); ⁺⁺⁺: narrow sense heritability.

of genetic complementation in relation to the frequencies of the alleles in the loci that have dominance or overdominance in hybrids (Vencovsky & Barriga, 1992).

The GCA:SCA ratio was lower than the unit for all examined traits (Table 3). The closer this ratio is to the unit, the greater the chance of predicting the performance of progeny and obtaining information on highly heritable traits simply by using GCA values (Murtadha et al., 2016). These results suggest the existence of a dominant gene effect controlling these variables, as also reported by Bello & Olawuyi (2015). Moreover, the estimated degree of dominance ($(2V_d/V_a)^{0.5}$) was greater than the unit to GY and PH for interpopulation crosses, thereby indicating a dominance effect and the narrow sense heritability estimate additionally indicates that the non-additive gene effect is the most important for these traits. On the other hand, the $(2V_d/V_a)^{0.5}$ for ear height was less than the unit, showing partial dominance for this trait. These results are directly related to the selection of parental populations with desired traits for producing superior hybrids and are corroborated by Abdel-Moneam et al. (2009), Laude & Carena (2014), Gowda et al. (2013) and Solalinde et al. (2014). These authors stated that non-additive effects such as overdominance are the most important for grain yield.

There was a significant effect of synthetics x environments interaction for all traits, indicating that the selection of parents based on the GCA must be made for each environment. The significant specific heterosis vs. environment interaction shows different responses regarding the dominance effects of the crosses for the different evaluated environments (Table 3).

The GY heterosis was estimated as 1461.55 kg,ha⁻¹ and average heterosis was approximately 25% (Table 4). Ribeiro et al. (2014) also estimated high heterosis values as being 102%

Table 4. Estimation of the variety effects (v_i), general combining ability (g_i), varietal heterosis (h_i), overall mean, mean heterosis and mean heterotic effect according to Gardner and Eberhart's model II (1966) and Griffing's model II, method 2 (1956).

Synthetic	GY			PH			EH		
	v_i	g_i	h_i	v_i	g_i	h_i	v_i	g_i	h_i
S-01	944.58	3.08	-512.96	4.72	-5.23**	-3.38	-6.55	-5.30**	-2.85
S-02	757.36	75.80	-386.95	1.61	0.57	-0.01	7.44	-2.29**	-5.71
S-03	781.02	22.42	-438.42	-6.72	-1.76	-2.45	-4.88	-0.55	0.08
S-04	892.36	41.14	-292.88	-3.72	0.72	-1.58	-10.22	0.16	2.45
S-05	70.69	197.97	44.38	-5.38	-0.91	0.67	-3.22	-1.86*	-0.18
S-06	23.91	174.39	-80.42	-0.05	-0.27	-0.25	-0.88	-0.14	2.48
S-07	-721.30	-529.38*	-80.42	8.94	0.38	-3.85	12.44	1.48	-3.28
S-08	-87.97	-240.02*	386.40	9.94	2.05*	-1.22	1.77	0.96	0.05
S-09	-904.30	-19.66	372.03	5.94	3.27*	-0.62	11.44	4.25**	-3.58
S-10	-90.52	182.03	-27.18	7.94	1.99*	-0.58	13.11	2.08*	-5.45
S-11	-717.08	162.11	205.69	-19.72	-1.50	14.64	-22.55	0.13	16.21
S-12	-948.75	133.21	728.12	0.95	0.68*	0.24	6.59	1.07	-2.66
Overall mean ⁺		5845.92			201.41			114.24	
Mean Heterosis		1461.55			-3.58			-4.13	
Heterosis (%)		24.99			-1.77			-3.61	

GY: grain yield (kg ha⁻¹); PH: plant height (cm); EH: ear height (cm); +: mean diallel.

in corn, and Werle et al. (2014) reported values ranging from 40.5 to 386.4% in crosses involving 12 elite parental lines of corn. The difference between heterosis estimates and the differences between heterotic synthesis populations and lines are justified, and were found in the literature and reported in this work. These results suggest that inter-population methods can be successfully applied to obtain and select superior genotypes.

According to Soladinde et al. (2014), the variety (v_i) and GCA (g_i) effects may be used as selection criteria for promising varieties or forming a superior hybrid, or both. According to Hallauer (2010), the effects of general combining ability (g_i) are used for this purpose due to the relationship $g_i = 0.5v_i + h_i$.

In general, the S-01, S-02, S-03, and S-04 synthetics stood out for GY due to the high effects of v_i considering the overall average environments and were the most promising for inclusion in breeding programs to obtain superior genotypes. On the other hand, the S-08, S-09, S-11, and S-12 synthetics had negative estimates for v_i and g_i , indicating the potential of these parents to reduce plant height and ear height, respectively.

The hierarchical classification method (UPGMA) used the dissimilarity matrix between the 12 synthetic varieties and commercial controls, and separated the genotypes into three distinct clusters regarding the analyzed traits. The cophenetic correlation coefficient (r_c) based on Mantel statistics was 0.89. Sokal (1986) suggested that the correlation coefficient value should be greater than 0.85 so that the similarity matrix used represents the actual relationship between the clustered parents. The cutoff point was based on knowledge derived from results from the estimates of SCA, GCA, v_i and g_i for each population (Figure 1).

Cluster 1 had four synthetic similar varieties with high h_i estimates for grain yield. Cluster 2 grouped the varieties that resembled the commercial variety Champion, with positive g_i estimates, except for S-08. Clusters 1 and 2 have low CGA and high SCA estimates for intra- and inter-groups, respectively, indicating good complementarity between these groups, as

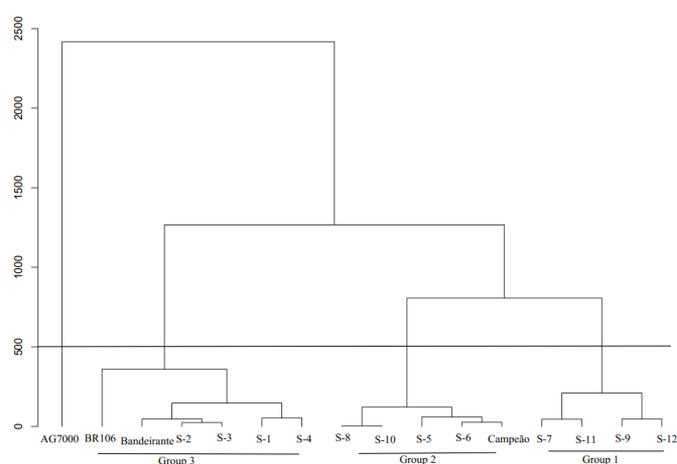


Figure 1. Dendrogram of the genetic relationships among 12 synthetic varieties and controls clustered by the UPGMA method based on the BLUP of grain yield, plant height and ear height.

confirmed by the best cross between the synthetics for GY (C-8x12), and PH and EH (C- 6x9). Cluster 3 grouped the varieties with superior performance and higher v_i and g_i estimates, but with negative h_i estimates, indicating that this group has high performance for intra-population breeding aiming at high grain yield populations. Laude & Carena (2014) and Vancetovic et al. (2015) determined maize heterotic groups using diallel analysis and multivariate clustering methods (UPGMA) and concluded that the UPGMA method was efficient to cluster maize for use in breeding programs.

Conclusions

Non-additive genetic effects are the most important in plant architecture and grain yield within each population of synthetics, as based on the GCA and SCA. Genotypes classified in the clusters 1 and 2 by the UPGMA method can be included in breeding programs to obtain hybrids, while genotypes of

cluster 3 can be used to obtain plants with lower architecture and increased yield in intra-population breeding programs.

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