

Full Length Research Paper

Restricted maximum likelihood/best linear unbiased prediction (REML/BLUP) for analyzing the agronomic performance of corn

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Adoption of accurate and simplistic biometric models that estimate variance components, predicting genotypic effects are desired in plant breeding. The aim of this study was to estimate the variance components and predict genotypic values by REML/BLUP for combinations of maize inbred lines derived from two heterotic groups with F₁'s evaluation in four locations. The crosses originated 25 hybrids that were evaluated in four trials. Genotype x environment interaction provided oscillations regarding the best combinations in the environments and must be individually analyzed in each environment, the superior crosses for grain yield, except 15x3' combination, which achieved good performance in all the trials. The combination of 5x4' is promising for obtaining high grain yield in Itapiranga and Pato Branco. The 5x3' combination have a higher overall average, being higher than the other combinations in Clevelândia and Ampere environments for plot yield, providing hybrids with fewer branches in the tassel.

Key words: Best linear unbiased predictor, restricted maximum likelihood, *Zea mays* L.

INTRODUCTION

The success of a corn breeding program is achieved, among other factors, with the launch of a hybrid of equal

or superior performance than already commercially available. Biometric models used for genetic constitutions

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evaluation in preliminary trials aiming at increasing efficiency and accuracy in selection of lines' combinations are very important for breeding programs achieve their goal.

The need for robust and accurate models in evaluating complex experiments (multi-sites trials, multi-year trials), is making the mixed models-based on restricted maximum likelihood/best linear unbiased prediction (REML/BLUP) more and more popular in plant breeding programs (Resende, 2004) due in many cases, the effect of local/year considered random, where the inferences are general (Piepho et al., 2007). REML/BLUP-based procedures are scarcely penalized by the non-additive nature of traits and by the experimental unbalance as compared to ANOVA-based models (Hu, 2015). In maize, these methods were effective in assessing the performance of hybrids and in accurate prediction of the variance components and breeding values (Nardino et al., 2016; Baretta et al., 2016).

In annual or biennials plants, the use of mixed models is still limited, although growing, as reported in works by Borges et al. (2009). In Brazil, it has been used in several crops such as sugarcane (Bastos et al., 2007; Lopes et al., 2014), soybeans (De Melo Pinheiro et al., 2013), beans (Carbonell et al., 2007) oat (Coimbra et al., 2005) and in potato (Souza et al., 2005).

Adoption of accurate and simplistic biometric models that estimate variance components and predict the genotypic effects are desired in plant breeding, largely due to effects of genotype x environment interaction. In this context, the aim of this research was to estimate the variance components and predict genotypic values by REML/BLUP of maize inbred lines' combinations from two heterotic groups, crossed in partial diallel scheme with F_1 's evaluation in four locations.

MATERIALS AND METHODS

The tests were based on artificial crosses among inbred lines, from company's research station KSP Seeds Ltda., in the city of Clevelândia-PR, Brazil in 2010-2011 growing season. The crosses were carried out in partial diallel design resulting in 25 F_1 's hybrids, which were evaluated at different locations. The hybrid seeds were hand harvested, dried and prepared for the trials' sowing in four environments.

Sowing of trials was carried out in 2011-2012 growing season in four different locations of Santa Catarina and Paraná States, in southern part of Brazil (Table 1). In previous sowing, each experimental area was analyzed in order to identify potentially disruptive features. A randomized complete block design with three replications was used. Blocks were allocated in order to maintain homogeneity within the block and heterogeneity between the blocks. Experimental units were composed of two 5-m-long cultivar rows, spaced by 0.7 m, adjusting the stand to 42 plants per experimental unit, equivalent to 60,000 plants ha^{-1} .

The following traits were assessed: plot grain yield (GY, kg per plot), ear height (EH in centimeters) distance from the last node of the stem to the first branch of the tassel (DLN in centimeters), number of tassel branch (NTB, units) and thousand-kernel weight (TKW in grams), measured by counting eight replicates of 100

kernels.

Estimates of genetic parameters were carried out based on the restricted maximum likelihood and the best linear unbiased predictor (REML/BLUP). The data set was subjected to analyses in order to estimates genetic parameters based on the procedures of the restricted maximum likelihood and the best linear unbiased predictor (REML/BLUP). The softwares used in the analyses were Selegen (Resende, 2007b) and SigmaPlot v.11.

RESULTS AND DISCUSSION

Components of variance estimated by REML shows that for the DLN trait, genetic variance (σ^2_G) represents 9.76% of total phenotypic variance (σ^2_F), and the variance of interaction ($\sigma^2_{G \times E}$) 16.71%, being the great part of total variation coming from environment (σ^2_E) 73.53%. Components of variance for the TKW trait show 11.40% for σ^2_G , 19.70% for $\sigma^2_{G \times E}$ and 68.90% for σ^2_E . Total variance for EH was explained by 12.61% σ^2_G , 20.43% σ^2_E and the great contribution was from $\sigma^2_{G \times E}$ (66.95%). Total variance for GY was decomposed into 65.52 % from $\sigma^2_{G \times E}$, 10.34% from σ^2_G and 24.14% from σ^2_E , indicating that much of the variation is due to effects of genotype x environment interaction. Variance components for NTB trait are great for σ^2_E (46.44%), for σ^2_G (39.31%) and for $\sigma^2_{G \times E}$ (14.25%). Variance component of GxE interaction is superior to the other variances, except phenotypic, for EH (66.95%) and GY (65.52%). For other traits, the environmental variance represents the largest fraction of the phenotypic variation; however, it can be considered that there is genetic variation among hybrids, especially for NTB trait (Figure 1).

The accuracy values show the precision of inferences of the average of genotype (Table 2). Accuracy values for the traits were classified as moderate too high (Resende and Duarte, 2007). According to Candido et al. (2009), obtaining a successful breeding program depends, among other on parameters for conducting trials with efficient analysis methodologies.

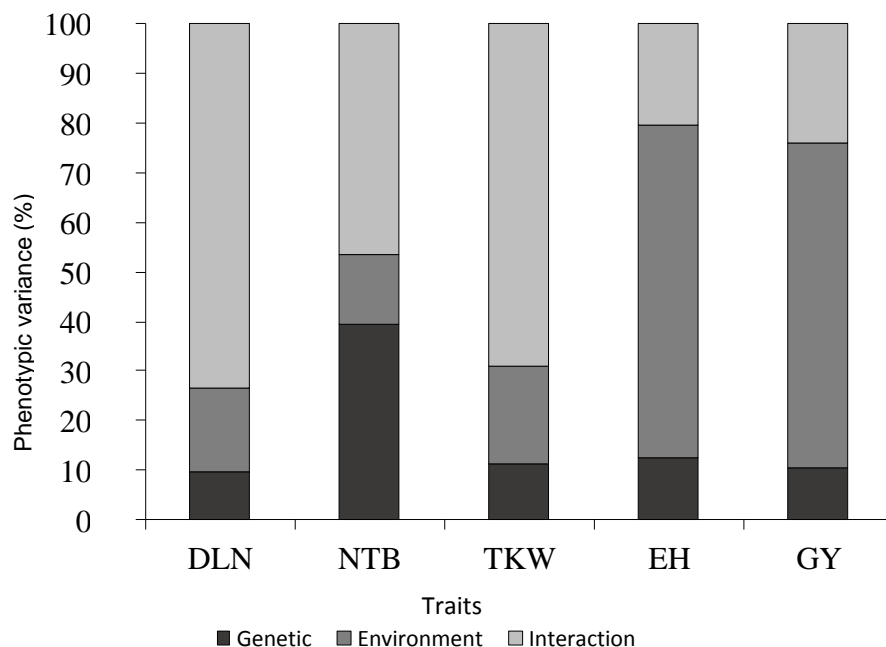
The magnitudes of $\sigma^2_{G \times E}$ were lower as compared to σ^2_G and H^2_G only for NTB trait, resulting in a genotypic correlation between the environments (r_{gloc}) of 73%. These results indicate the tendency of genotypes' stability in different locations, which is too upper and lower for the trait. For the other traits; however, the magnitude of $\sigma^2_{G \times E}$ was over σ^2_G and high as compared to h^2_G , resulting in lower values of r_{gloc} for DLN ($rg_{loc} = 0.37$), TKW ($rg_{loc} = 0.37$), EH ($rg_{loc} = 0.16$) and GY ($rg_{loc} = 0.15$).

Genetic correlations between environments for these last traits show that hybrids do not have the same behavior in different environments, occurring variations in the ordering of genotypes. GxE interaction contains a part related to the difference between the genetic variance of trait in different environments and over the lack of association between genetic treatments in one environment to another. The first is called simple

Table 1. Location and climate characteristics of experimental areas.

State	City	South LAT	West LONG	MASL	Climate ⁺	Average temperature ^{+,*} (°C)		Annual rainfall ⁺ (mm)
						T _{cold}	T _{hot}	
Santa Catarina	Itapiranga	27°10'10"	53°42'44"	206	Cfa			1760
	Ampére	25°54'65"	53°25'39"	580	Cfa	15.9	>22.0	1960
Paraná	Pato Branco	26°13'44"	52°40'15"	760	Cfa			1947
	Clevelândia	26°21'52"	52°28'22"	860	Cfb	13.4	20.0	2243

⁺ The climate classification is according to Alvarez et al. (2014). ^{*} Average air temperature for the two climate classifications presented in the trial areas. T_{hot} = Average air temperature in the hottest month of the year, T_{cold} = Average air temperature in the coldest month of the year.

**Figure 1.** Partitioning of phenotypic variance into genetic, environment and interaction effects.**Table 2.** Variance components (VC) estimated by restricted maximum likelihood (REML) for the traits distance from the last node to the first branch of the tassel (DLN), number of tassel branch (NTB, units), thousand-kernel weight (TKW), ear height (EH) and grain yield (GY).

VC	DLN(cm)	NTB (units)	TKW (g)	EH (cm)	GY (kg)
σ^2_G	1.01	4.8	168.37	20.33	0.09
$\sigma^2_{G \times E}$	1.73	1.74	290.91	107.9	0.57
σ^2_E	7.61	5.67	1017.44	32.93	0.21
σ^2_F	10.35	12.21	1476.72	161.16	0.87
h^2_{gIndiv}	0.098(±0.05)	0.392(±0.10)	0.117(±0.05)	0.126 (±0.05)	0.112(±0.05)
C^2_{int}	0.17	0.14	0.19	0.67	0.66
h^2_{min}	0.48	0.84	0.52	0.41	0.43
\hat{r}_a	0.70	0.91	0.72	0.64	0.60
rg_{loc}	0.37	0.73	0.37	0.16	0.15
Overall average	21.82	15.90	334.42	121.85	8.47

σ^2_G : gen|Etic variance; $\sigma^2_{G \times E}$: variance of Gx E interaction; σ^2_E : environmental variance; σ^2_F : phenotypic variance; h^2_{gIndiv} : individual heritability without interaction effects; C^2_{int} : coefficient of determination of the interaction; h^2_{min} : Average heritability; \hat{r}_a : selective accuracy; rg_{loc} : correlation between locations.

Table 3. Estimates of average components by best linear unbiased predictor (BLUP) for the traits distance from the last node to the first branch of the tassel (DLN), number of tassel branch (NTB, units), thousand-kernel weight (TKW), ear height (EH) and grain yield (GY).

Ranking*	DLN (cm)		NTB (units)		TKW (g 1000 kernels ⁻¹)		EH (cm)		GY (kg plot ⁻¹)	
	Cross***	u+g**	Cross	u+g	Cross	u+g	Cross	u+g	Cross	u+g
1	2x3	23.82	5x3	18.92	15x5	351.92	15x3	122.50	5x3	8.88
2	11x3	22.90	14x4	18.80	13x3	347.88	10x5	122.05	5x4	8.77
3	5x3	22.73	4x7	17.47	1x4	345.29	6x3	122.01	1x4	8.75
4	4x6	22.58	15x3	17.12	15x2	342.54	13x3	121.91	15x3	8.73
5	4x7	22.77	2x3	17.10	5x3	342.48	1x1	121.60	13x3	8.63
6	4x3	22.73	4x3	17.03	4x7	339.34	12x3	121.53	12x3	8.57
7	3x1	22.44	6x3	16.75	10x5	338.33	5x3	119.34	15x2	8.51
8	14x4	22.40	11x3	16.42	3x1	338.23	4x3	119.16	11x3	8.51
9	6x4	22.33	7x4	16.22	15x3	337.41	15x8	119.10	4x7	8.49
10	8x4	22.32	6x4	16.12	6x3	335.95	7x4	119.10	10x5	8.48
11	3x4	22.29	3x4	16.12	12x3	334.68	1x4	118.89	6x3	8.46
12	6x3	22.27	4x6	15.92	4x3	333.79	13x4	118.88	9x4	8.46
13	13x3	22.14	12x3	15.86	5x4	333.55	15x5	118.80	3x4	8.44
14	7x4	22.13	3x1	15.63	4x6	331.81	2x3	118.56	1x1	8.43
15	13x4	22.03	1x1	15.42	13x4	331.32	15x2	118.08	7x4	8.42
16	1x1	21.94	8x4	15.14	9x4	330.38	11x3	117.94	4x3	8.41
17	15x3	21.90	13x4	14.91	2x3	328.49	8x4	117.52	6x4	8.37
18	5x4	21.81	9x4	14.75	3x4	327.89	4x7	117.05	2x3	8.37
19	1x4	21.76	10x5	14.70	7x4	326.16	3x4	116.50	15x5	8.37
20	15x2	21.74	1x4	14.43	1x1	325.29	3x1	116.43	4x6	8.33
21	15x5	21.74	13x3	14.42	15x8	323.96	9x4	115.92	3x1	8.33
22	10x5	21.66	15x5	14.37	6x4	322.69	14x4	114.30	15x8	8.32
23	9x4	21.65	15x8	13.69	11x3	321.95	6x4	113.53	13x4	8.29
24	15x8	21.45	5x4	12.52	14x4	318.66	5x4	112.70	14x4	8.28
25	12x3	21.22	15x2	11.82	8x4	318.59	4x6	112.13	8x4	8.14

*Classification in descending order by the predicted average of the cross's combinations of partial diallel; **Component of genotypic average without GxE interaction for 25 combinations of a partial diallel; ***Combination related to the crosses in partial diallel scheme of 25 hybrids obtained.

interaction and the second complex or cross interaction (Resende, 2007a). The presence of complex interaction always indicate the existence of specifically adapted cultivars to specific environments, which require the adoption by cautious measures for recommending cultivars (Ramalho et al., 2012).

The predicted estimates of crossings BLUP, resulting in a hybrid with smaller distance from the last node to the first branch of the tassel, are sought, because the greater length of the tassel have negative effects on grain yield (Table 3). This is due to increased demand for assimilates and low performance of hybrids in biotic and abiotic stress conditions (Sangoi et al., 2002b); thus, crosses with average genotypic of lesser magnitude would be desired for selection. The combinations between lines 13x3', 7x4', 13x4', 1x1', 15x3', 5x4', 1x4', 15x2', 15x5', 10x5', 9x4', 15x8' and 12x3' have revealed predictions below genotypic overall average (Table 3), standing out among the other combinations. The main

contributing factor for selecting smaller size tassel in breeding programs, is because the tassel mass is directly related to the size, negatively influencing the production of grain due to competition with the ear by nutrients. Because of this, larger tassels would be greater-power sink, reducing the availability of assimilates to the ear (Hallauer et al., 2010).

Regarding the predicted components for NTB trait, averages of crossings with lower magnitude are prioritized, because smaller tassels require less assimilate and nutrients. This minimizes protandric nature of the plant, reducing the ontogenic interval between male and female flowering (Sangoi et al., 2002a). The power demand and lower apical dominance of the tassel over the spikes are important characteristics for nutrients to be used for balanced allometric development of inflorescences of the plant. This is reflected in a greater number of ears per plant and best floral synchrony of modern hybrids, especially in high densities. In this

context, the predicted genotypic averages of crosses between the hybrids 3x1', 1x1', 8x4', 13x4', 9x4', 10x5', 1x4', 13x3', 15x5', 15x8', 5x4' and 15x2' are lesser than other crosses (Table 3).

For the TKW trait, the crosses between inbred lines 15x5', 13x3', 1x4', 15x2', 5x3', 4x7', 10x5', 3x1', 15x3', 6x3', 12x3', 4x3' and 5x4' has shown magnitudes largest than overall average (Table 3), being considered as promising crosses to increase TKW and contribute to produce hybrids with high grain yield.

Regarding the predicted components for EH trait, the crosses combination of 15x2', 11x3', 8x4', 4x7', 3x4', 3x1', 9x4', 14x4', 6x4', 5x4' and 4x6' can be highlighted due its average, which is lesser than overall average (Table 3). Such criteria are established due to the maize genetic breeders seeking lines with lower height of ear insertion, being among the major changes sought with the lowest height on the cob, the higher nitrogen use efficiency, allow the center of gravity of plant to stay more balanced, reducing lodging and stem's breakage and favoring the absorption and translocation of nutrients to the grain filling (Sangoi et al., 2002b).

Combination with genotypic averages for GY that can be highlighted among predicted estimates are respectively: 1x3', 1x4', 5x4', 15x3', 12x3', 13x3', 15x2', 10x5' and 11x3' (Table 3). These crosses have greater GY than the overall genotypic average of the trials, proving to be promising to produce hybrids with increased GY in the four environments. In this context, the identification of promising crosses for a greater number of environments becomes important, since there are components of genetic, environmental and GxE origin involved in phenotypic expression, which can make difficult and complicate the breeders' work. Ramalho et al. (2012) points out that not always do hybrids with broader adaptation have higher grain yield. This fact can prevent a generalized way recommendation, being the most widely used alternative to solve this problem, to identify hybrids with greater phenotypic stability for different environments and to make a stratification of environments aiming to discover locations' groups within which the variance component associated with the effect of interaction is minimized.

Individual BLUPs in each location allow analysis of each combination in a more thorough form, informing the oscillations of the hybrid and selecting the best combination for a specific micro-region (environment). In this sense, using REML/BLUP-based procedures has numerous advantages and provides more security to the breeder. Resende and Duarte (2007) points that for selection, genotypic averages will represent better the future average of genotypes than phenotypic averages. According to the same authors, even which the assessments are in the same place or region, the effects of blocks and plots are unlikely to be repeated, thus, if the tests are conducted in different regions, the effect on the average will be higher.

Regarding the predicted estimate and their confidence intervals for the 25 combinations for the DLN trait (Figure 2), considering location's average as discriminatory parameter to identify the best combinations, the intersections whose average are lower than the overall average were highlighted, due to the increased demand for energy directed to the growth and development of the tassel, providing competition with the ear (Sangoi et al., 2002a). In Ampère, it was highlighted, the combinations of 1x4', 10x5', 12x3', 13x4' and 15x2' with the smallest magnitudes in relation to overall average (21.73 cm). In Clevelândia, the combinations that can be highlighted are 1x1', 9x4' and 15x8', considering the predicted overall average (22.98 cm). For Itapiranga, the lowest magnitudes for the overall average (21.5) are the crosses, 1x4', 8,4', 9x4', 12x3' and 15x8'. In Pato Branco, the combinations 12x3', 15x2' and 15x8' were lower than overall average (21.44 cm). Based on obtained estimates, it can be considered that none combinations were the same for the four environments.

Individual BLUPs for NTB trait (Figure 3), it is considered as optimal combinations, those that reveal lower magnitudes to predict average in each location. In Ampère, the crosses 5x4', 9x4', 13x3', 15x5', 15x8' and 15x2' has shown lower magnitudes than average of this environment (15). In Clevelândia, the combinations 1x4', 4x6', 5x4', 15x8' and 15x2' are lower than average of this location (15.79). In Itapiranga, the crosses 5x4', 15x5', 15x8' and 15x2' showed lower magnitude than predicted average (16.05). In Pato Branco, there were lower magnitudes of the crosses 15x8' and 15x2', considering the average of 14.7 branches.

Regarding MMG trait (Figure 4), the crosses that were higher than the local average in Ampere (302 g) are, respectively, 1x4', 5x3' 13x3' 15x3', 15x5' and 15x2' in Ampere environment. The higher predicted estimates in Cleveland are 1x4', 4x7' and 13x3' whose predicted average was 378.79 g, showing that there was a high homogeneity of the crossings for this site. In Itapiranga, the average predicted was 312.63 g, and the superior combinations for this estimate were the combinations 1x4', 4x7', 6x3', 10x5', 12x3' and 15x5'. The promising combinations in Pato Branco are 1x4', 3x1', 5x3', 10x5', 13x3', 15x5' and 15x2' above average of 344.97 g. Combinations with superior magnitudes for this trait are desirable in maize breeding, because this trait presents positive association with grain yield.

The ear height allows the plant, together with the stem diameter allows greater resistance to lodging. The predicted average for EH in Ampere was 113.24 cm (Figure 5). The crosses with the lower estimates than local average were 3x4', 4x7', 4x6', 5x4', 6x4', 13x4' and 15x8'. In Clevelândia, crosses with the predicted average that stood out are 2x3', 3x1', 4x6' , 5x4', 6x3', 6x4', 9x4', 10x5' and 11x3' below average of this location (136.49 cm). Under the conditions of Itapiranga, smaller ear heights were achieved by the combinations 3x4', 4x7',

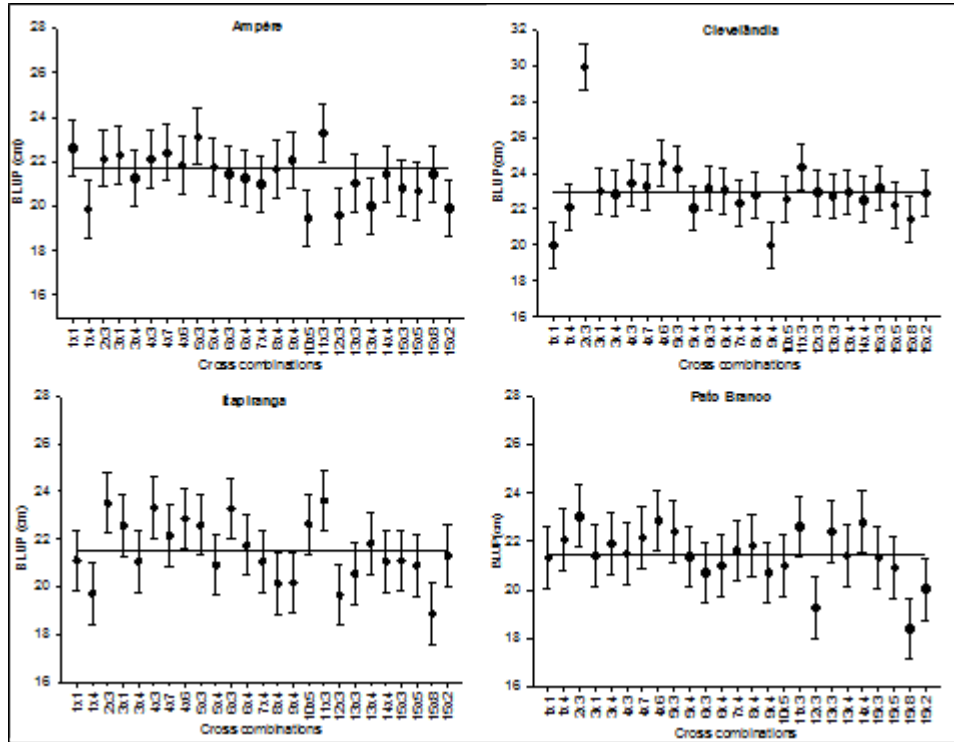


Figure 2. Estimates of genotypic averages for the trait distance from the last node to the first branch of the tassel in Ampère, Clevelândia, Itapiranga and Pato Branco regarding 25 combinations of a partial diallel.

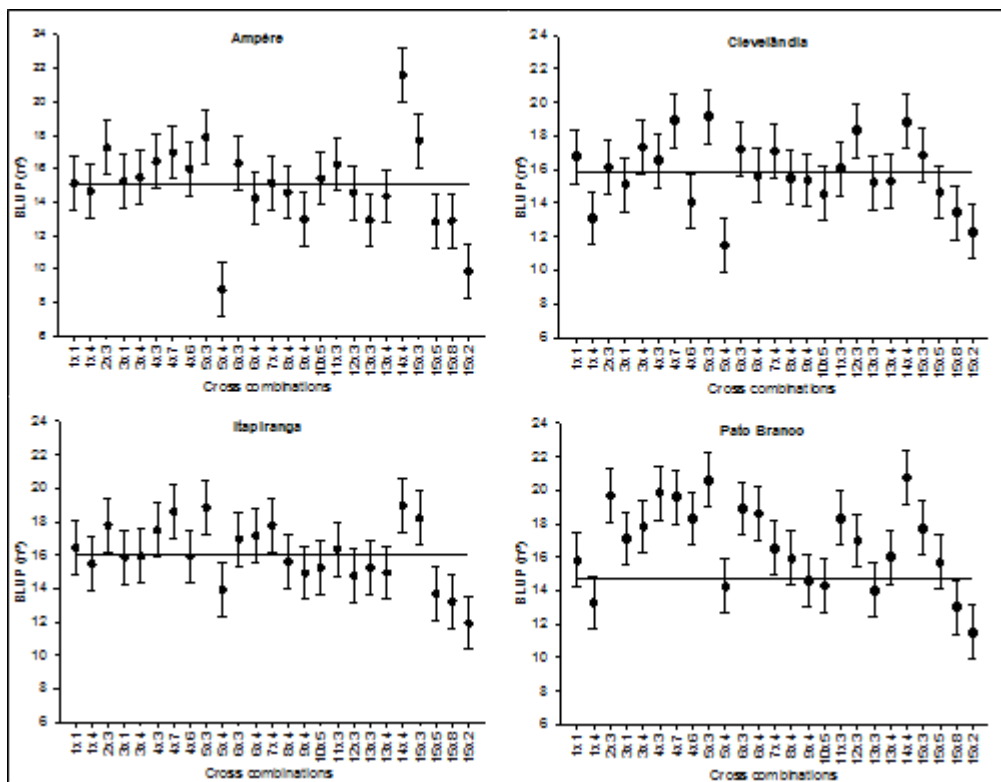


Figure 3. Estimates of genotypic averages for the trait number of tassel branch in Ampère, Clevelândia, Itapiranga and Pato Branco regarding 25 combinations of a partial diallel.

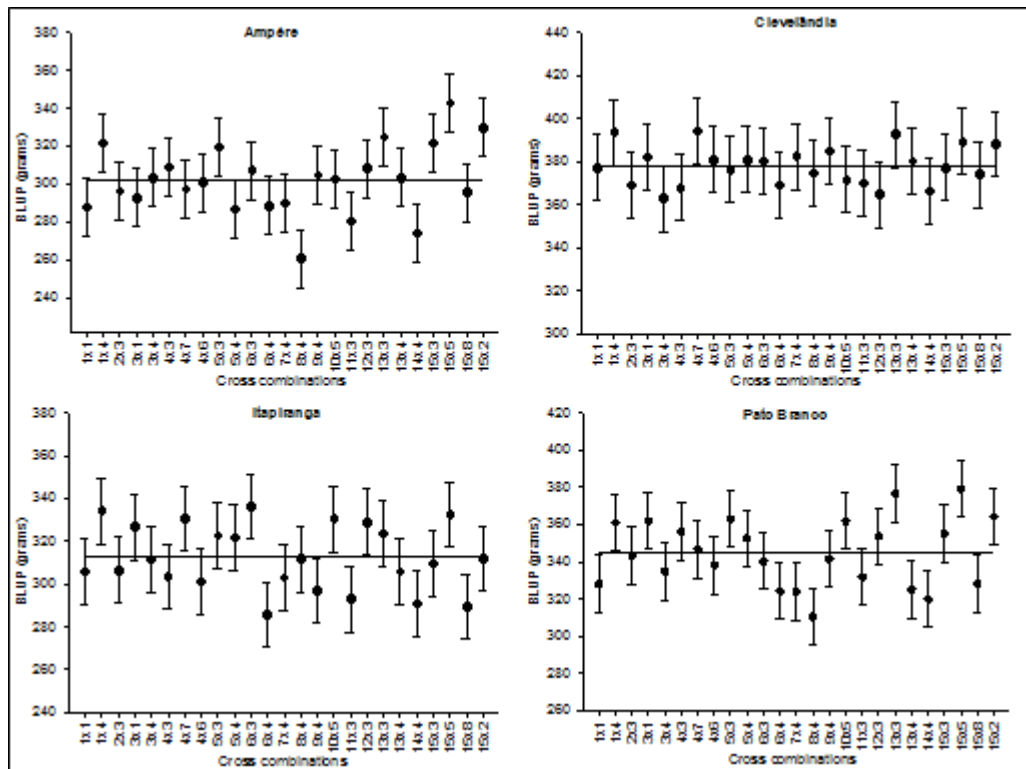


Figure 4. Estimates of genotypic averages for the trait thousand-kernel weight in Ampère, Clevelândia, Itapiranga and Pato Branco regarding 25 combinations of a partial diallel.

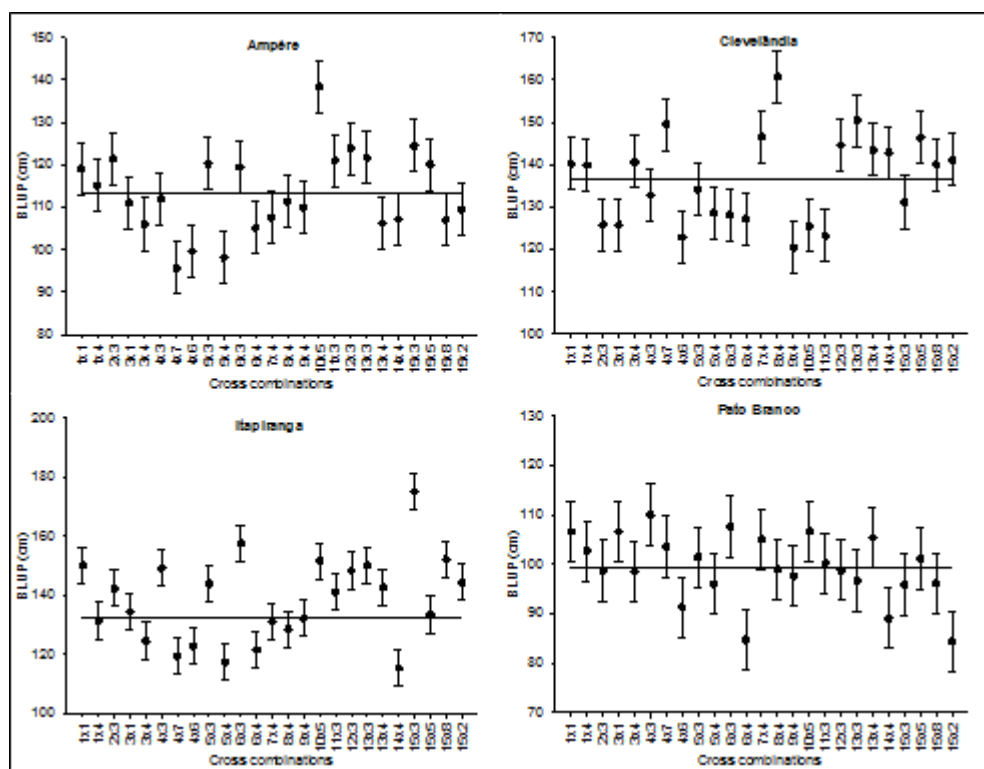


Figure 5. Estimates of genotypic averages for the trait ear weight in Ampère, Clevelândia, Itapiranga and Pato Branco regarding 25 combinations of a partial diallel.

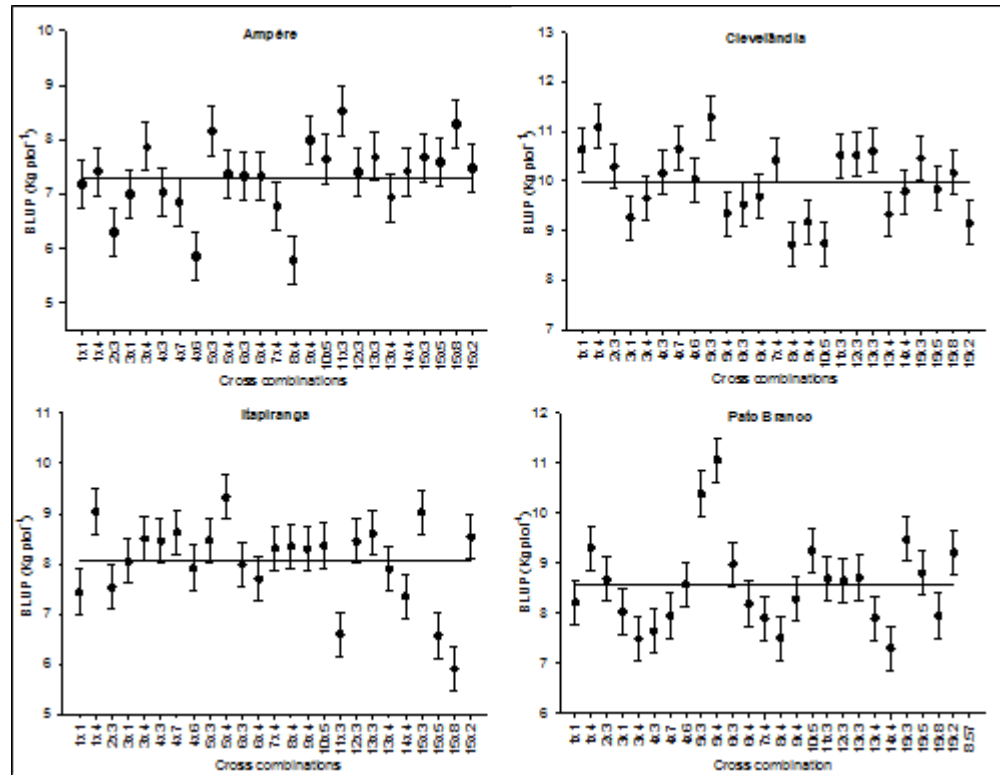


Figure 6. Estimates of genotypic averages for the grain yield per plot in Ampère, Clevelândia, Itapiranga and Pato Branco regarding 25 combinations of a partial diallel.

4x6', 5x4', 6x4' and 14x4', whose environmental average was 132.32 g. In Pato Branco environment, the combinations that revealed the magnitude smaller than the predicted average (99.37 cm) were 4x6', 6x4', 14x4' and 15x2'. According to Sangoi et al. (2002b), the reduced ear insertion height is among the traits which have improved absorption and transport of nutrients to the grain filling.

The GY (Figure 6), target trait of the breeders who seek incessantly cultivars or increasingly productive hybrids, is among the traits more influenced by environmental conditions, due to its complex action in response to different stimuli, resulting in a number of complications to identify more specific hybrids. Under the conditions of Ampere, combinations of superior crosses to average of 7.31 kg plot⁻¹ were from combinations 3x4', 5x3', 9x4', 11x3' and 15x8'. Cleveland revealed between the environments, the highest average (9.96 kg plot⁻¹), with the combinations 1x1', 1x4', 4x7', 5x3', 7x4', 11x3', 12x3', 13x3' and 15x3' located above this. The crosses that stood out for Itapiranga were 1x4', 3x4', 4x3', 4x7', 5x3', 5x4', 13x3', 15x3' and 15x2', with their average greater than 8.05 kg plot⁻¹. For Pato Branco combinations 1x4', 5x3', 5x4', 6x3', 10x5', 15x3' and 15x2' were, respectively, they were higher than the average of 8.57 kg plot⁻¹. The combination of lines 15x3' is higher than the average of the tests in all the environments. The

combinations that also showed themselves promising are between 5x4' lines in Itapiranga and Pato Branco environments and 5x3' that reveals superiority in the overall average of all combinations (Table 3), which is promising mainly for Clevelândia and Ampere. The fluctuations revealed by other diallel combinations are in agreement, because of the high effects shown in the variance component GxE. Grain yield is a complex and polygenic trait (Hallauer et al., 2010) controlled by a large number of genes. High effects of GxE interaction component is expected to occur, making it important biometric analysis with accurate models for estimating the components and predicting genotypic values, being REML/BLUP, favorable procedures in estimating these parameters (Resende, 2007a).

Conclusions

Estimates of variance component has revealed that the ear height and grain yield per plot suffer sharp action of GxE interaction.

The GXE interaction has provided oscillations regarding the best combinations in the environments and must be individually analyzed in each environment, the superior crosses for grain yield, except for 15x3' combination which achieved good performance in all

locations.

The combination 5x4' is promising to get high grain yields in Itapiranga and Pato Branco. The combination 5x3' has a higher overall average, which is higher than the other combinations in the environments of Clevelândia and Ampere and provides hybrid with fewer branches in the tassel.

Conflict of Interests

The authors have not declared any conflict of interests.

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Abbreviations

BLUP, Best linear unbiased prediction; **DLN**, distance from the last node of the stem to the first branch of the tassel; **EH**, ear height; **GY**, plot grain yield; **NTB**, number of tassel branch; **REML**, restricted maximum likelihood; **TKW**, thousand-kernel weight.

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