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Heterosis and combining ability in crosses between two groups of open-pollinated maize populations

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Abstract – *The rapid expansion of corn in Brazil indicates the need to explore new sources of germplasm. Thus, the wider use of local germplasm, and the introduction of exotic ones seem to be an advisable strategy to achieve higher levels of yield and adaptability. The objective of this work was to generate information about the potential of two groups of populations (NAP – exotic; HG – local) and their heterotic pattern in hybrid combinations for the synthesis of new populations. Populations and hybrids were evaluated in complete randomized block designs with four replications, in two locations, and three yield traits were studied (GY – grain yield, EY – ear yield, SW – specific weight). The basic strategy was the selection of one HG population as base for the incorporation of each exotic population. The expected yield gain of the best combinations varied from 1 to 22%. Average heterosis for grain yield was 34.5%.*

Key words: Exotic germplasm, synthesis of population, incorporation, prediction.

INTRODUCTION

Leaf diseases in maize crop are an old and well known concern in tropical areas, so that the resistance to several kinds of pathogens has been systematically considered in most maize breeding programs (Miranda Filho 1985, Renfro 1985, Miranda Filho and Viégas 1987). The rapid increase in the acreage for maize crop in the last two decades, including new frontiers in the Central West region of Brazil, and the possibility of a second crop (usually maize after soybean) in the same year, contributed to decrease the discontinuity of crops in space and time. Thus, it favored the increase of the inoculum potential, which affects directly the level of damage, and may culminate in an epidemic disease under favorable environmental conditions. For this reason, a joint effort involving several public and private institutions was done aiming at the evaluation of 1273 accesses of a maize germplasm bank for resistance to five foliar diseases caused by *Physopella zeae*, *Phaeosphaeria maydis*, *Puccinia polysora*, *Exserohilum turcicum* and *corn stunt* complex (Miranda Filho et al. 2000).

Since the populations resulted from accesses of germplasm from Brazil and other origins, they were considered exotic in the traditional area for maize crop in the country, according to the concept given by Hallauer (1978). In fact, several authors have emphasized the importance of incorporation of exotic germplasm in maize breeding programs (Goodman 2005), and this subject acquires additional importance when dealing with disease resistance. An important aspect related to the introduction of exotic germplasm is that in most instances adaptation, in general, does not reach an acceptable level to be used directly in breeding programs. For this reason, the incorporation of exotic germplasms into local and adapted material has been recommended by several authors (Goodman 2005).

In Brazil, besides the wide genetic base, including local races and populations of several origins (Brieger et al. 1958), the introduction of exotic germplasm has largely contributed for the enhancement of yield and agronomic patterns of cultivars. After the first phase using local germplasm represented by old varieties, such as Cateto and Dente Paulista, an extraordinary advance occurred with the introduction of exotic germplasm. For instance, tuxpeño and related races of Mexico and Central America largely contributed for the development of high yielding semident

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hybrids (Miranda Filho and Viégas 1987). The importance of the introduction of the race Tuxpeño in maize breeding in Brazil was emphasized by Paterniani (1990).

The phenomenon of heterosis (hybrid vigor) has been exploited extensively in maize breeding and it has been attractive for more than 100 years, starting with the inbred-hybrid scheme suggested by Shull (1909) for the production of hybrid seeds. Actually, the heterosis effect depends on the type of gene action controlling the trait, and on the genetic divergence level between the parents in the biparental crosses (Hallauer and Miranda Filho 1988). However, heterosis is also important in the development of new populations obtained by intercrosses of two or more parents of narrow or broad genetic base; in fact, higher average heterosis of the parent crosses is directly related to the genetic variability expected in the newly formed population (Miranda Filho 1999). On the other hand, the heterosis effect does not dissipate after recombination, but is simply rearranged in the newly formed population, according to the types of crosses used (Hallauer and Miranda Filho 1988, Miranda Filho 2010).

The main focus in the present work was the study of nine exotic open-pollinated populations, previously obtained by intercrossing accesses of the Brazilian Germplasm Bank, selected for resistance to specific leaf diseases. Particular attention was given to the potential of these populations for the expression of heterosis and combining ability in crosses with a group of local and adapted populations derived from commercial hybrids. The final objective was to establish criteria to guide the synthesis of new populations; which increases the opportunities for using the semiexotic germplasm.

MATERIAL AND METHODS

Basic germplasm

The present study was based on crosses between two groups of open-pollinated populations. Group I comprised nine populations synthesized in the NAP-Milho Project (*Núcleo de Apoio à Pesquisa do Milho – USP*) aiming at the development of germplasm with resistance to foliar diseases. Then, five populations were developed for resistance to *Exerohilum turcicum*, *Puccinia polysora*, *Physopella zeae*, *Phaeosphaeria maydis*, and *Corn stunt complex*, which were denominated NAP-HT, NAP-PP, NAP-PZ,, NAP-PM and NAP-CS, respectively. A sample of each NAP population was planted in isolated block for the second recombination; about 16,000 seeds were planted in each block. Visual phenotypic evaluation was used to select a sample of 200 open-pollinated ears (half-sib families), which represented the basic germplasm to initiate an intrapopulation recurrent selection program; in sequence, two cycles of recurrent selection were carried out. After selection of 200 ears to be used in the first cycle of recurrent selection, the remaning ears of the five blocks were harvested in bulk of individual ears, which were phenotypically selected according to ear type, sanity, grain color and texture, and other characters; these samples of selected ears originated four other populations, which were denominated NAP-FA, NAP-FL, NAP-FB and NAP-DB, which were related to endosperm types *yellow flint*, *orange flint*, *white flint* and *white dent*, respectively.

Group II was represented by six populations (F_2 generations) obtained from commercial hybrids in farm crops in the Southwestern region of Goiás; they were chosen for their yield potential and acceptable patterns for the expression of agronomic traits (plant architecture, sanity, resistance to plant lodging, etc.), besides their favorable pattern of adaptation to the Central Region, particularly the Southwest region of the state of Goiás. Group-II was identified by HG–34, HG–39, HG–41, HG–49, HG–71 and HG–78.

The crossing system followed the intergroup (Group I x Group II) partial diallel, which includes the 15 parental populations and the 54 hybrids with their reciprocal crosses, summing 123 experimental entries. The crossing system is an extension of the methodology suggested by Miranda Filho and Geraldi (1984). One commercial hybrid (BALU 480 PRO) was used as check, intercalated at every other 10 plots in each block. Trials were carried out in two locations (L1: Jataí; L2: Rio Verde) in the State of Goiás, in complete randomized block designs with four replications; plots were defined as two 5 m long rows, spaced 0.90m apart, with expected stand of 54 plants (two plants at the plot ends), resulting in a population density of 60 M plants per hectare. In the whole experiment, 14 quantitative traits were analyzed; however, for the purpose of the present study, only the yield traits were considered, which were: EY – ear yield (total ear weight in kg/plot), GY – grain yield (total grain weight in kg/plot), and SW – specific weight (grain weight per volume, in kg/m^3). All the information about yield traits were considered, but more details were directed to GY, since it was the most important to indicate the appropriate criterion to chose the local populations (HG) to be used as base for incorporation of the exotic germplasm.

Also, GY was adjusted for 13% grain moisture. Both EY and GY were corrected for stand variation using the methodology of covariance, as suggested by Miranda Filho (Vencovsky and Barriga 1992); correction was for expected stand (S_e=54) for individual plots using the formula $Y_c = Y_0 + b\,(S_e - S_0)$, where Y_c is the corrected yield, Y_o is the observed yield, b is the linear regression coefficient of Y_o over the variation of the observed stand (S_o).

Quantitative analysis

The preliminary analysis of variance for each location was carried out according to the randomized block design. In the whole set of data submitted for analysis, the parental populations were represented by two-row plots, and the hybrid combinations were represented by the two reciprocal crosses (each set in two-row plots, randomized in the experiment). The appropriate model is $Y_{ijx} = m + t_i + b_j + r_{x:i} + e_{ijx}$, where Y_{ijx} is the observed plot total or plot mean, m is the overall mean, t_i is a fixed treatment effect, b_j is the random effect of replications, $r_{x:i}$ is the difference between reciprocal crosses, and e_{ijx} is the experimental error with mean square M_E and $E(e_{ijx})^2 = \sigma^2$; the subscript **x** does not apply for the parental populations. In sequence, the analyses with partition of sums of squares according to the sources of variation were carried out with plot means over replications ($\overline{Y}_i$). Therefore, the model reduces to $Y_{ix} = m + t_i + r_{xi} + \bar{e}_{ix}$, so that $E(\bar{e}^{\,2}_{ix}) = \frac{1}{r}\sigma^2 = \underline{\sigma}^2$, and in the analysis with treatment means, the mean square error must be adjusted to $M_{\underline{E}} = \frac{1}{r}\ M_E$. The analysis of variance combined over locations is based on the model $\overline{Y}_{ixk} = m + t_i + r_{x:i} + p_k + (tp)_{ik} + (rp)_{xk:i} + \bar{e}_i$, which includes three additional effects: p_k is the fixed effect of location; k = 1,2; $(tp)_{ik}$ is the interaction of the fixed effects treatment x location; and $(rp)_{xk::i}$ is the interaction reciprocal effect x location within the i^th treatment. In the combined model, $E(\bar{e}^{\,2}_i) = \frac{1}{r}\sigma^2$ is under the assumption of homogeneity of the variance error in the two locations; thus, the variance error in the combined analysis is pooled over locations. The significance of effects in the model was searched out by the Snedecor´s *F* test.

For the estimation of heterosis and the effects of combining ability, another symbology was used: Y_{ii} and Y_{jj} to represent the means (over replications) of the parental populations of groups I and II, respectively; and Y_{ij} to represent the mean (over replications and reciprocal crosses) of the hybrid combination i x j; each cross is represented by the mean of the two reciprocal crosses. Therefore, the heterosis effect was calculated by the contrast $h_{ij} = Y_{ij} - {}^1/2\,(Y_{ii} + Y_{jj})$ with variance $V(h_{ij}) = \underline{\sigma}^2$, where $\underline{\sigma}^2$ is the error variance adjusted to the treatment means over replications. Average heterosis was obtained by $\bar{h} = \overline{Y}_H - \frac{1}{2}(\overline{Y}_I + \overline{Y}_{II})$, with variance $V(\bar{h}) = \frac{2+I+J}{4IJ}\underline{\sigma}^2$; in the given formula, $\overline{Y}_H, \overline{Y}_I$, and $\overline{Y}_{II}$ stand for the mean of all hybrid crosses, and means of groups I and II, respectively.

The mating scheme used in the present study allows the estimation of the effects known as general combining ability (GCA) and specific combining ability (SCA), by analogy to method 4 of Griffing (1956), as shown by Geraldi and Miranda Filho 1988. However, this scheme is represented essentially by factorial model when the parent varieties are not included. Thus, the factorial model $Y_{ij} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \bar{e}_{ij}$, represented by the general mean of all crosses (m), by the effects of the factors A and B (a_i and b_j), by the interaction AxB (effect $(ab)_{ij}$), and by the error term ($\bar{e}_{ij}$) is adapted to $Y_{ij} = \mu + g_i + g_j + s_{ij} + \bar{e}_{ij}$, where g_i and g_j are the GCA effects of parents in each group, and s_{ij} is the specific combining ability. In this model, the estimates are obtained by $\hat{g}_i = \overline{Y}_i - \overline{Y}$, $\hat{g}_j = \overline{Y}_j - \overline{Y}$ e $\hat{S}_{ij} = Y_{ij} - \overline{Y}_{i.} - \overline{Y}_{.j} + \overline{Y}_{..}$; such procedure has already been indicated by Vencovsky and Barriga (1992) in the analysis of testcrosses (lines x testers). Estimates of s_{ij} were not used since they are dissipated in the predicted means.

As already mentioned, the final purpose of the present work is to identify local and adapted populations to be used as base for the incorporation of the exotic population. Recombination of population crosses (intergroup) leads to a new population (composite) that will have 50% of the exotic population in each case. Thus, the base populations can be identified by predicting the mean of the possible composites by using one or more base populations for incorporation. The following general formula was used for prediction (Hallauer and Miranda Filho 1988):

$$\varphi_{co} = {}^1/2\,(m_0 + m_v) + {}^1/2\ \bar{h}_0 + \frac{n-1}{4n}\,\bar{h}_v$$

where n is the number of local varieties (populations) used as base for incorporation, with a total proportion of 50% or $\frac{1}{2n}$ for each variety; m_0 is the mean of the exotic population that will be incorporated; m_V is the mean of the base populations used for incorporation; $\bar{h}_0$ is the average heterosis of all crosses between the exotic population (NAP) and the local populations (HG); $\bar{h}_v$ is the average heterosis of all crosses between the local populations. The option in the present project was to use only one local population for incorporation, with mean symbolized by m_p; then, n = 1, $\bar{h}_v$ does not exist, and the prediction formula reduces to $\varphi_{co} = {}^1/2\,(m_0 + m_p) + {}^1/2\ \bar{h}_{0P}$, that is the formula given by Mather and Jinks (1982) to predict the mean of the F_2 generation in the cross between two parents.

RESULTS AND DISCUSSION

The analysis of grain yield data was carried out with the estimation of effects of combining ability, mid-parent heterosis and prediction of means for yield of newly synthesized composites of size k=2, resulting from individual crosses (NAP x HG). The reason to use only GY in the prediction formulas is because the correlation coefficients between the heterosis of both traits were 0.975 and 0.985 in L1 and L2.

Analysis of variance

The experiments in both locations, following the complete randomized block design (**CRB**), showed heterogeneity among blocks for all yield traits (tests not shown), thus indicating the efficiency of the CRB design to control the variance error. The analyses of variance are shown in Table 1. The total variance of treatments was significant (*F* test, $P < 0.01$) for traits in both locations. Significance within groups (I and II) was found for EY and SW ($P < 0.01$) and GY ($P < 0.05$) and L1, but only for Group-II ($P < 0.01$), for all traits in L2. The total variance among hybrids (Hybrids^{T} ≡ crosses + reciprocals), as well as the variance of hybrids (Hybrids^{C} ≡ sum of reciprocal crosses) was significant ($P < 0.01$) for all traits in both locations. The pooled variance between reciprocal crosses within hybrids was significant for GY and EY in both locations, but SW showed no significance in both locations. The comparison of means representing the three groups showed significance for all traits in both locations. In fact, the observed means were in the sequence $m_{II} < m_{I} < m_{H}$ for GY and EY; and $m_{II} < m_{H} < m_{I}$ for SW in both locations. The contrast $\kappa = m_{I} – m_{II}$, represented by the source of variation [GI *vs*. GII], was significant ($m_{II} < m_{I}$) for GY and EY in both locations. For SW, the difference (58 unities in both locations) was small ($m_{II} < m_{I}$) and non-significant. The higher yielding potential of the exotic populations over the local populations was evident. In such comparisons, two points deserve considerations: Initially, it should be acceptable the hypothesis that, because their own condition of being exotics in higher or lower degrees, the populations of Group-I should exhibit a lower yield potential than those of Group-II, which were developed from commercial hybrids in the Southwest region of the state of Goiás. However, the populations labeled from 1 to 4 (subgroup IA) in Group-I were originated from a strong selection pressure of individual ears (phenotypic selection) in the recombination blocks that resulted in the formation of populations labeled from 5 to 9 (subgroup IB) in Group-I; this selection surely resulted in an expressive increase in the yield potential of subgroup IA. On the other hand, population of the subgroup IB, selected for specific disease resistance, undergwent two cycles of recurrent selection with half-sib families, with an expressive gain from selection as indicated by the magnitude of additive genetic variance (σ^2_A, g plant^{-1}) of the five composites. In the first cycle (Anhembi, SP), the estimates were 241.46 for NAP-HT; 481.93 for NAP-PP; 426.24 for NAP-PZ; 684.85 for NAP-PM; and 651.41 for NAP-CS; the corresponding estimates of the coefficient of heritability for family means were 0.403, 0.430, 0.476, 0.580 and 0.563. In the second cycle, in off-season ("safrinha" in Jataí, GO) the estimates of σ^2_A were larger than in the first cycle, or, 887.6, 1413.0, 763.8, 1298.4 and 732.9. Even considering the distinct traits shown above, the subgroup IA with yield means of 5839 and 4916 kg ha^{-1} in L1 and L2 were higher than subgroup IB (means of 5427 e 4442 kg ha^{-1}) in 7.6% and 10.8%, respectively.

Another point to be considered is that the populations (HG) in Group-II were chosen because they were developed from commercial hybrids with desirable pattern of yield and agronomic traits (plant architecture, resistance to stresses, lodging resistance, ear and kernel types, etc.), which would contribute for the enhancement of the genetic pattern of the

Table 1. Mean squares (MS) in the analysis of variance for yield traits in two groups of populations and their crosses with reciprocals in two locations

		Jataí (GO)			Rio Verde (GO)		
Source	df	GY	EY	SW	GY	EY	SW
Treatments	122	49.049‡	64.872‡	22.240‡	47.572‡	71.145‡	46.581‡
Group I (GI)	8	17.220†	24.148‡	81.461‡	16.746	27.066	22.625
Group II (GII)	5	19.864†	29.192‡	20.890‡	32.280‡	50.767‡	89.867‡
Hybrids^{T}	107	15.695‡	21.844‡	17.448‡	23.776‡	35.460‡	41.919‡
Hybrids^{C}	53	20.271‡	30.675‡	28.590‡	28.352‡	41.527‡	55.489‡
Hybrids^{R}	54	11.204‡	13.176†	6.5116	19.286‡	29.505‡	28.600
Groups	2	2033.8‡	2619.0‡	45.123‡	1482.2‡	2207.5‡	283.61‡
GI *vs*. GII	1	539.03‡	648.11‡	0.0232	25.327	15.285	108.90
(GI+GII) *vs*.GH	1	3528.5‡	4589.9‡	90.222‡	2939.0‡	4399.8‡	458.33‡
Error	366	6.7295	9.0002	5.7661	11.116	15.649	28.341
CV (%)		7.9	7.7	1.9	11.4	11.0	6.9
Means		6558	7751	796	5859	7170	794

^{T} refers to the whole set of combinations (9x6 =54 hybrids + 54 reciprocal crosses); ^{C} represents the 54 combinations by the total of their reciprocal crosses; ^{R}: variation between reciprocal crosses for each combination. GI, GII, GH: populations is groups I and II, and hybrids, respectively. †,‡: significant F test at $P < 0.05$ and $P < 0.01$, respectively]. GY: grain yield (t ha^{-1}), EY: ear yield (t ha^{-1}), SW: specific weight (g L^{-1})

exotic materials. However, the yield level of such hybrids decreases expressively after recombination to generate the F_2 population. The decrease is directly related to the expression of heterosis in the F_1 hybrid so that the highest losses in yield occur in the more heterotic crosses. The decrease in yield also depends on the level of dominance controlling the trait, which is very expressive in grain yield and affects heterosis directly. For traits with low dominance, the decrease in the mean is little expressive after recombination of the F_1 hybrid (Hallauer and Miranda Filho 1988, Miranda Filho 1999). The decrease in yield also depends on the type of hybrid considered. For instance, single crosses and double crosses, that are very common hybrids in the market, will represent synthetics of size k=2 and k=4 after recombination; the predicted means of such synthetics are given by the general formula $j_s = m_0 + \frac{k-1}{k}\,\bar{h}$, which is a variation of the Wright´s formula for the prediction of synthetics; therefore, the loss in mean is $(1-\frac{k-1}{k})\bar{h} = \frac{1}{k}\bar{h}$, and in the case of single cross and double cross, the loss will be ½ and ¼ of the average heterosis expressed in the F_1 hybrids. Thus, it is reasonable to suppose that the HG hybrids have revealed expressive heterosis in the F_1 generation, decreasing sensibly the mean yield after recombination. Summarizing the above considerations, grain yield for Group-I (5610 kg ha^{-1}) was

Table 2. Observed means of grain yield in two groups (I and II) of parental populations and their crosses (H) with reciprocals. Two locations (L1: Jataí, GO; L2: Rio Verde, GO)

	Grain yield			Grain yield			Grain yield			Grain yield	
Pop	**L1**	**L2**	**Pop**	**L1**	**L2**	**Pop**	**L1**	**L2**	**Pop**	**L1**	**L2**
1	6513	5344	1’x2	6876	6169	6’x4	6563	5790	5’x7	6710	6219
2	5716	4701	2x2’	6779	6041	5x1’	6179	5502	7x6’	6714	6069
3	5704	5128	2’x2	6707	5772	1’x5	6353	5932	6’x7	6239	6169
4	5424	4493	2x3’	7082	6078	5x2’	6658	5438	8x1’	6964	6338
5	4935	3965	3’x2	6593	6530	2’x5	6519	5733	1’x8	7026	5961
6	5623	4543	2x4’	6435	5367	5x3’	5674	5799	8x2’	7024	6586
7	5668	4322	4’x2	7024	6022	3’x5	5896	4657	2’x8	7359	6289
8	5473	4615	2x5’	6976	7083	5x4’	6565	5036	8x3’	6562	6599
9	5437	4768	5’x2	7338	6433	4’x5	6047	5615	3’x8	7531	5578
m_I	5610	4653	2x6’	6027	6469	5x5’	7013	6956	8x4’	6504	6103
m_{Ia}	6513	4577	6’x2	6353	5928	5’x5	6167	5642	4’x8	7265	7965
m_{Ib}	4935	4563	3x1’	6561	6056	5x6’	6373	5849	8x5’	7113	5929
1’	4160	4284	1’x3	7179	6021	6’x5	6258	6201	5’x8	7034	5803
2’	4914	4663	3x2’	6648	5687	6x1’	7349	6052	8x6’	6576	6241
3’	4371	5155	2’x3	6950	6196	1’x6	6466	5878	6’x8	6625	6038
4’	4896	4257	3x3’	6906	6173	6x2’	6915	5549	9x1’	6564	6298
5’	4199	4531	3’x3	6407	5560	2’x6	7122	5561	1’x9	7166	6406
6’	3779	3438	3x4’	7520	6487	6x3’	6797	6528	9x2’	6504	6077
m_{II}	4387	4388	4’x3	7227	5756	3’x6	6686	5298	2’x9	6765	5929
m_{IIa}	4914	5155	3x5’	7017	7324	6x4’	6955	6354	9x3’	6695	5623
m_{IIb}	3779	3438	5’x3	7293	6884	4’x6	6840	5484	3’x9	6590	5640
1x1’	6739	5962	3x6’	6395	6297	6x5’	6880	6578	9x4’	7496	6602
1’x1	6868	6256	6’x3	6654	6102	5’x6	7180	6363	4’x9	6957	5236
1x2’	7086	6005	4x1’	6802	6520	6x6’	6478	6366	9x5’	7345	6169
2’x1	7065	6416	1’x4	6064	6278	6’x6	6330	5897	5’x9	6760	6018
1x3’	6820	5708	4x2’	6680	5747	7x1’	6203	5524	9x6’	6134	5847
3’x1	6106	5918	2’x4	6774	6281	1’x7	6944	6184	6’x9	6835	4834
1x4’	7381	5311	4x3’	6439	5445	7x2’	6597	6013			
4’x1	6925	5632	3’x4	6626	6262	2’x7	6798	5313	m_H	6758	6041
1x5’	6562	6788	4x4’	6660	6181	7x3’	5976	5700	m_{Ha}	7642	7965
5’x1	7406	5884	4’x4	7642	5973	3’x7	6674	6172	m_{Hb}	5674	4657
1x6’	6808	6913	4x5’	6871	6083	7x4’	6784	6481	m_T	6558	5859
6’x1	6518	6734	5’x4	7230	6132	4’x7	7298	5885	m_C	8571	8051
2x1’	7235	5986	4x6’	6188	5734	7x5’	6783	5943	m_T%	76.5	72.8

m_I, m_{II}, m_H: group means and their maximum (a) and minimum (b) values; m_T, m_C and m_T%: overall mean, check mean and m_T in percent of m_C. Pop (parental populations) - Group I: 1(NAP-FA), 2 (NAP-FL), 3 (NAP-FB), 4 (NAP-DB), 5 (NAP-HT), 6 (NAP-PP), 7 (NAP-PZ), 8 (NAP-PM), and 9 (NAP-CS); Group II: 1’(HG-34), 2’(HG–39), 3’(HG–41), 4’(HG–49), 5’(HG–71), and 6’(HG–78).

27.9% higher than for Group-II (4387 kg ha^{-1}) in L1. In L2, grain yields were 4653 and 4388 kg ha^{-1}, respectively, with a superiority of 6.0% for Group-I. The results presented in this context emphasize the importance of experimental results to establish the correct direction for the synthesis of new populations.

The contrast $ƙ = m_H - ½ (m_I + m_{II})$, represented by the source of variation identified by [(GI+GII) *vs*.GH], was significant ($P < 0.01$) for all traits in both locations. The contrast is a direct measure of the average heterosis of all crosses and has the same meaning of the average heterosis defined in the model of Gardner and Eberhart (1966) for diallel crosses. Estimates of the average heterosis for grain yield (Table 3) were 1758, 1520, and 1640 kg ha^{-1} in locations L1, L2, and combined over locations, respectively; in percentage of the mid-parent, the average heterosis represent 35.2, 33.6 and 34.5%, respectively.

The combined analysis of variance over locations showed significance ($P < 0.01$) for the components of the treatment effect in the three traits (GY, PY, SW), except for Hybrids^R (reciprocal effects: significant at $P < 0.05$ in SW) and GI *vs*. GII (non significant in SW). The interaction Treatments x Locations was significant ($P < 0.01$) for the three traits; and also for their components, except for the variation within groups (I and II), and for the contrast ƙ related to the average heterosis. The interaction Treatments x Locations for GY is particularly important since it indicates that the prediction procedure to select the best base population for incorporation of exotic germplasm in each case must be based on results of the two locations, increasing the opportunity of a better adaptation of the new populations to varying environments.

Table 3. Mid-parent heterosis GY (grain yield, kg ha^{-1}) in crosses between two groups of parental populations. Jataí (GO), Rio Verde (GO) and combined over locations

	HG–34	HG–39	HG–41	HG–49	HG–71	HG–78
Jataí, GO	Average heterosis $\bar{h} = 1758$, $h_{max} = 2238$, $h_{min} = 1021$ kg ha^{-1}; $\bar{h}\% = 35.2$					
NAP–FA	1467 [27.5]	1362 [23.8]	1021[18.8]	1449 [25.4]	1628 [30.4]	1517 [29.5]
NAP–FL	2118 [42.9]	1428 [26.9]	1794 [35.6]	1424 [26.8]	2200 [44.4]	1442 [30.4]
NAP–FB	1938 [39.3]	1490 [28.1]	1619 [32.1]	2074 [39.1]	2204 [44.5]	1783 [37.6]
NAP–DB	1641 [34.2]	1558 [30.1]	1635 [33.4]	1991 [38.6]	2238 [46.5]	1774 [38.5]
NAP–HT	1719 [37.8]	1664 [33.8]	1133 [24.3]	1391 [28.3]	2023 [44.3]	1959 [45.0]
NAP–PP	2016 [41.2]	1750 [33.2]	1745 [34.9]	1638 [31.1]	2119 [43.1]	1703 [36.2]
NAP–PZ	1659 [33.8]	1406 [26.6]	1305 [26.0]	1759 [33.3]	1812 [36.7]	1753 [37.1]
NAP–PM	2178 [45.2]	1998 [38.5]	2125 [43.2]	1700 [32.8]	2237 [46.3]	1974 [42.7]
NAP–CS	2067 [43.1]	1459 [28.2]	1739 [35.5]	2060 [39.9]	2235 [46.4]	1876 [40.7]
Rio Verde, GO	Average heterosis $\bar{h} = 1520$, $h_{max} = 2598$, $h_{min} = 564$ kg ha^{-1}; $\bar{h}\% = 33.6$					
NAP–FA	1295 [26.9]	1208 [24.1]	564 [10.7]	671 [14.0]	1399 [28.3]	2435[55.4]
NAP–FL	1585 [35.3]	1224 [26.1]	1376[27.9]	1215 [27.1]	2142 [46.4]	2128 [52.3]
NAP–FB	1332 [28.3]	1046 [21.4]	725 [14.1]	1429 [30.5]	2275 [47.1]	1917 [44.7]
NAP–DB	2011 [45.8]	1436 [31.4]	1030 [21.3]	1702 [38.9]	1595 [35.4]	1797 [45.3]
NAP–HT	1592 [38.6]	1271 [29.5]	668 [14.7]	1214 [29.5]	2051 [48.3]	2323 [62.8]
NAP–PP	1551 [35.2]	952 [20.7]	1064[21.9]	1519 [34.5]	1934 [42.6]	2141 [53.7]
NAP–PZ	1551 [36.1]	1170 [26.1]	1198 [25.3]	1894 [44.1]	1654 [37.4]	2239 [57.7]
NAP–PM	1700 [38.2]	1799 [38.8]	1203 [24.6]	2598 [58.6]	1293 [28.3]	2113 [52.5]
NAP–CS	1826 [40.4]	1288 [27.3]	670 [13.5]	1407 [31.2]	1444 [31.1]	1238 [30.2]
Combined:	Average heterosis $\bar{h} = 1640$, $h_{max} = 2239$, $h_{min} = 792$ kg ha^{-1}; $\bar{h}\% = 34.5$					
NAP–FA	1381 [-0.3]	1285 [24.0]	792 [14.8]	1060 [19.7]	1514 [29.4]	1975 [42.4]
NAP–FL	1851 [39.1]	1326 [26.5]	1585 [31.7]	1319 [27.0]	2171 [45.4]	1785 [41.3]
NAP–FB	1635 [33.8]	1268 [24.7]	1172 [23.1]	1751 [34.8]	2239 [45.8]	1850 [41.2]
NAP–DB	1826 [40.0]	1497 [30.8]	1333 [27.4]	1846 [38.7]	1917 [40.9]	1785 [41.9]
NAP–HT	1655 [38.2]	1468 [31.6]	900 [19.5]	1303 [28.9]	2037 [46.3]	2141 [53.9]
NAP–PP	1784 [38.2]	1351 [26.9]	1405 [28.4]	1579 [32.8]	2026 [42.9]	1922 [44.9]
NAP–PZ	1605 [34.9]	1288 [26.3]	1251 [25.6]	1826 [38.7]	1733 [37.1]	1996 [47.4]
NAP–PM	1939 [41.7]	1898 [38.6]	1664 [33.9]	2149 [45.7]	1765 [37.3]	2043 [47.6]
NAP–CS	1947 [41.7]	1373 [27.7]	1204 [24.5]	1733 [35.5]	1839 [38.7]	1557 [35.4]

Within brackets: heterosis in percentage of mid-parent; $\bar{h}$ - mid-parent heterosis; $\bar{h}\%$ - heterosis in percent of mid-parent.

Observed means

The means of grain yield over four replications are shown in Table 2 for two locations (Jataí-GO; Rio Verde – GO). GY is the most important trait for the present discussion, since EY is correlated with GY, and SW was used only as complementary information. The best population in Group-I was NAP-FA in both locations (6513 and 5344 kg ha^{-1}, respectively). In Group-II, the best populations were HG-39 (4914 kg ha^{-1}) in L1, and HG-41 (5155 kg ha^{-1}) in L2. Among the hybrid crosses, the highest yielding was HG-49 x NAP-DB (7642 kg ha^{-1}) in L1, and HG-49 x NAP-PM (7965 kg ha^{-1}) in L2. Results shown in Table 2 were used to calculate the heterosis for each hybrid cross, which were the base to predict the mean yield of the newly formed populations.

The exploitation of heterosis in crosses among populations offer a great amount of information, mainly for the identification of heterotic groups or specific heterotic pairs, and for the synthesis of new populalions, particularly when exotic germplasm is involved (Hallauer and Miranda Filho 1988, Miranda Filho and Chaves 1991). The estimates of mid-parent heterosis for the 54 crosses between two groups of parental populations are shown in Table 3 for the two locations (L1 and L2) and for the combined analysis. The average heterosis ($\bar{h}$) were 1758 kg ha^{-1}, 1520 kg ha^{-1} and 1640 kg ha^{-1}, respectively; such values are equivalent to 35.2 %, 33.6% and 34.5% of the mid-parents. Hallauer and Miranda Filho (1988) reported estimates of mid-parent heterosis for yield in 1394 hybrid combinations, varying from 4.2% to 72.0%, with average of 19.5%. High heterosis estimates were reported by Paterniani and Lonnquist (1963), varying from -11.0% to 101.0% in crosses among 12 Brazilian races of maize, and by Werle et al. (2014), varying from 40.5 to 386.4%, noting that L6 x L10 was considered a promising hybrid because it associated grain yield. High heterosis were also reported by Castro et al. (1968), Paterniani (1980), Crossa et al. (1990) and Ribeiro (2012), with means of 24.8, 39.0, 18.6 and 102,6% respectively. Lower estimates of heterosis for yield were reported by Miranda Filho and Vencovsky (1984), Gorgulho and Miranda Filho (2001), Morello et al. (2001), Silva and Miranda Filho (2003), with averages of 7.4, 9.2, 3.75 and 23.5, 16.7% (two sets), respectively. In the present work, the highest heterosis were for crosses NAP-DB x HG-71 (2238 kg ha^{-1} or 46.5%) in L1, NAP-HT x HG-78 (2323 kg ha^{-1} or 62.8%), NAP-PM x HG-49 (2598 kg ha^{-1} or 58.6%) in L2 and NAP-HT x HG-78 (2141 kg ha^{-1}or 53.9%) in the combined analysis. Donà et al. (2011) studying F_2 populations of commercial hybrids found high values of heterosis, and reported that populations derived from F_2 generations of simple hybrids present a more narrow genetic base, which results in high expression of heterosis when combined.

The heterotic pattern in the present study was considered relatively high, as compared to most of the reports. In general, high heterosis are found in crosses between low yielding population of restricted genetic base so that pairs of populations can exhibit enough genetic divergence for the expression of heterosis in crosses. The effect of inbreeding, which occurs in old races multiplied for long time under small effective population size, also affects the heterosis in crosses (Miranda Filho 1999). Many studies on heterosis for yield have shown that low heterosis are found in crosses between large base populations such as composites, open-pollinated varieties and synthetics, whose most of their genes are in frequencies around ½ , which naturally decreases the chance of high genetic divergence. Miranda Filho (1999) also hypothesized that in crosses between populations as described above, the expected heterosis will rarely be above 20%, most probably in the range up to 10% of the mid-parents; heterosis beyond these limits indicates some abnormality caused by narrow genetic base, small population size followed by inbreeding, or lower yielding caused by the origin of the parental populations (indigenous races, farmer landraces, exotics, etc.).

A two-way table for GY was organized with hybrid crosses (means of reciprocal crosses) for the estimation of general combinng ability, g_i and g_j, for parent populations of groups I and II. The highest estimates for g_i were 208 and 244 kg ha^{-1} (NAP-PM in both locations); and for g_j were 224 and 305 kg ha^{-1} (HG-71 in both locations). It must be noted that the general combing ability effects is also related to the choice of parents for the synthesis of new population, as shown by Miranda Filho and Chaves (1991). In fact, the local populations HG–71 and HG–49 showed the highest estimates of $g_{j,}$ and participated in most of the selected composites.

The predicted means (m_j) for grain yield in composites of size k = 2 (i.e., NAP x HG) were calculated for each location ($j^{\underline{1}}$, $j^{\underline{2}}$) and for the combined analysis ($j^{\underline{12}}$). For reasons already mentioned, the selection of composites was based only in $j^{\underline{12}}$, by identifying one HG population to be used as base for the incorporation of each NAP population. In this sense, the following composites were chosen: $\varphi_{12'}$, $\varphi_{25'}$, $\varphi_{35'}$, $\varphi_{44'}$, $\varphi_{55'}$, $\varphi_{65'}$, $\varphi_{74'}$, $\varphi_{84'}$, $\varphi_{94'}$. The mean of the whole set of composites (54) was 5579 kg ha^{-1}, varying from 5057 kg ha^{-1} to 6010 kg ha^{-1}, which are equivalent to 67.1%, 60.8% and 72.3% of the hybrid check mean.

The expected yield gains, as compared to the original NAP populations, were 1%, 13%, 11%, 15%, 22%, 13%, 14%, 17% and 12%, respectively. Note that the first four NAP populations (Group IA) showed the lower expected gains after incorporation. The corresponding expected means for grain yield (kg ha^{-1}) after incorporation are 6001, 5872, 6010, 5691, 5426, 5737, 5699, 5885 and 5706; which are equivalent to 72.2, 70.7, 72.3, 68.5, 65.3, 69.0, 68.6, 70.8 and 68.7 of the check mean. If the new composites are submitted to two cycles or recurrent selection with expected gain of 10% per cycle, the expected population means would be more than 83% of the hybrid check (m_C), on the average; two composites ($\varphi_{12'}$ and $\varphi_{35'}$) would reach near 87% of m_C. Even considering a lower (5%) expected gain per cycle, the expected means would reach 76.5% of m_C, on the average; the two best composites would reach near 80%. From the exposed above, one can conclude that the semiexotic populations show an acceptable level of yield to be used as base populations in recurrent selection programs. At this point, no information is available in relation to the actual genetic variability of important traits, neither on the expression of agronomic traits at the population level. However, an important fact is that the exotic populations, previously selected for important leaf diseases, have now a chance to be really used in applied maize breeding programs.

Finally, despite the choice to use only one local population (HG) as base for incorporation, there is a possibility of using more than one HG in special cases; there are instances where the inclusion of two HG´s would reduce the composite mean in less than 5% with the advantage to increase the expected variability in the newly formed population. The great amount of information available from this project allowed us to accept that the used methodology was considered feasible and efficient, so that the strategy can be recommended for programs aiming at the incorporation of exotic germplasm (or other sources) into adapted local populations.

Heterose e capacidade de combinação entre dois grupos de populações de milho de polinização aberta

Resumo – *A rápida expansão do milho no Brasil indica claramente a necessidade de explorar novas fontes de germoplasma. Assim, o uso mais amplo de germoplasma local e a introdução de germoplasma exótico parecem uma estratégia recomendável para atingir níveis mais elevados de produtividade e adaptabilidade. O objetivo deste trabalho foi gerar informação sobre o potencial de dois grupos de populações (NAP – exótico; HG – local) e seu potencial heterótico em combinações híbridas para a síntese de novas populações. Populações e híbridos foram avaliados em blocos casualizados com três repetições em dois locais e três caracteres de produção foram estudados (GY – produção de grãos, EY – produção de espigas, SW – peso específico). A estratégia básica foi a seleção de uma população HG como base para incorporação de cada população exótica. O ganho esperado na produção das melhores combinações variou de 1 a 22%. A heterose média para peso de grãos foi de 34,5%.*

Palavras-chave: *Germoplasma exótico, síntese de populações, incorporação, predição.*

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