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Alterations in heterosis of maize populations derived from single-cross hybrids after reciprocal recurrent selection

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ABSTRACT - *One hundred and sixty-nine interpopulational half sib progenies were obtained from maize populations derived from the commercial single-cross hybrids AG9012 (1) and C333 (2) to investigate the efficiency of reciprocal recurrent selection (RRS). Fifteen progenies with highest hulled ear yield were obtained. Two recombination trials were sown with remnant* S_1 *seeds, and the improved* CI_1 *and* CI_2 *populations were simultaneously obtained with their hybrid combination. Yield trials were set up in three sites to assess the efficiency of the RRS. The* F_1 *from single-cross hybrid AG9012 and C333, the double-cross (*$F_{1(1)}$ *x* $F_{1(2)}$*) hybrids, the* $C0_1$ *and* $C0_2$ *populations, the interpopulational hybrid (*$C0_1$ *x* $C0_2$*), the* CI_1 *and* CI_2 *improved populations, and their hybrid (*CI_1 *x* CI_2*) were compared. A 5.7% progress was obtained in one cycle of RRS for ear yield, mainly attributed to increased heterosis. The yield of the improved hybrid was superior to the* F_1 *from single-cross hybrids AG9012 and C333, demonstrating the potential of the referred hybrid combination.*

Key words: quantitative genetics, maize, reciprocal recurrent selection, heterosis.

INTRODUCTION

The achievement of the first maize hybrid was doubtlessly one of the main gifts society received from science, as it did not only give rise to yield increases of this *Gramineae* but also led to intense applications of the heterosis phenomena in other species. Estimates claim that over 65% of the areas planted with maize crop worldwide now grow hybrid cultivars, resulting in a rise of approximately 55 million tons of grain compared to the sowing of varieties (Duvick 1999).

The productive potential of the maize hybrid is a function of the *per se* performance of the parent lines and the heterosis among them. According to studies carried out in the US which compared the performance of lines in different decades, increasing heterosis was observed over the years. However, it remained relatively stable in proportion to hybrid means, at around 70% (Lamkey and Smith 1987, Duvick 1999). A similar value has been observed in Brazil for the contribution of loci in heterozygosis (Lima et al. 2000, Souza Sobrinho et al. 2001).

One of the most efficient ways to achieve amplified heterosis is by means of interpopulational improvement. A number of studies have successfully worked with this strategy. According to Hallauer (1999), the mean gain of four US programs of reciprocal recurrent selection (RRS) which lasted several decades, have shown that heterosis, in relation to the parent population means, rose from 8.9% in cycle 0 to 42.5% in the last selective cycle. In other words, there was a 3.7 fold increase of the mean value observed in the original cycles, providing a realized gain from selection of 5.2% in grain productivity at every selective cycle.

Generally, the populations used in most RRS programs are populations with a so-called broad genetic basis, i.e., composites, varieties, and/or synthetics. We know, however, that in many situations, simple commercial hybrids crosses, especially from different companies, present great heterosis (Souza Sobrinho et al. 2001). It is rather questionable though, whether this heterosis could be improved by RRS. A study conducted in the US applied recurrent selection to simple

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hybrid-derived populations, where the real gain from selection in the performance of the interpopulational hybrid derived from the latter was estimated. It was verified that in the average of the originated hybrids, the grain yield gain was 5.3% after five RRS cycles (Coors 1999). In Brazil, specifically, there are ongoing RRS programs. However, there have been no reports on real gain in heterosis by means of RRS and, much less yet, reports on the use of populations derived from simple hybrids. This study was realized to obtain information on this aspect with the aim of evaluating the efficiency of RRS at increasing the heterosis of two populations derived from simple commercial hybrids.

MATERIAL AND METHODS

This study was carried out in two stages: in the first, interpopulational half-sib progenies were obtained and evaluated; in the second, improved populations were obtained, the interpopulational hybrid generated from among them, and its performance compared with the unimproved hybrid.

Two populations were used in Hardy-Weinberg equilibrium, spawned by the commercial single-cross hybrids AG9012 (1) and C333 (2). Of each population, 169 plants were self-pollinated. A part of these self-pollinated seeds of each plant were stored and the rest used to achieve progenies of interpopulational half-siblings (MI inter). Two isolated fields were used to obtain these progenies. On the first one, the male line consisted of cycle zero seeds of population 1 ($C0_1$) and the female lines, which were evidently detasseled, were made up by the 169 inbred S_1 progenies of population 2. The inverse was used to establish the second field, that is, the female lines consisted of S_1 progenies of population 1 and the male lines of $C0_2$ seeds.

The progenies obtained this way were evaluated in two experiments, one for each population used as female. These experiments were conducted on the experimental area of the Department of Biology of the Federal University of Lavras, in the South of the State of Minas Gerais. A simple lattice design 13 x 13 with plots made up of one 3 m row was used. In both experiments, the weight of hulled ears, which was corrected to a standard moisture of 13% and an ideal stand of 15 plants per plot, through the utilization of covariance (Vencovsky and Barriga 1992). In both experiments, the 15 top yield progenies were selected. Two isolated fields (A and B) were sown with remnant S_1 seeds, aiming at a recombination of the populations and, simultaneously, the achievement of the improved hybrid combination. These recombination fields were sown in May 2000, on the experimental area of the Centro de Pesquisa Agroflorestal de Roraima (CPAP-EMBRAPA).

A mixture of 100 S_1 seeds of each progeny was used for recombination. Part of the seed mixture of population 1 employed as female on the field (A) was detasseled at the moment of flowering. The rest of the seeds of this same population were used as male line on the other field (B). The opposite happened with population 2 seeds, that is, on field (A) the seeds of this population were sown as male line and on field (B) as female lines. At harvest time, the male lines, harvested on both isolated fields, brought forth the improved populations CI_1 and CI_2. The female lines of the two lots were harvested and mixed, generating the interpopulational hybrid CI_1 x CI_2. The hybrid of the original populations $C0_1$ x $C0_2$ was also obtained through manual crosses of at least 100 plants of both populations. Double hybrid $F_{1(1)}$ x $F_{1(2)}$ was obtained likewise, however with a smaller number of crosses.

Thereafter, the nine treatments $F_{1(1)}$, $F_{1(2)}$, $F_{1(1)}$ x $F_{1(2)}$, $C0_1$, $C0_2$, $C0_1$ x $C0_2$, CI_1, CI_2, and CI_1 x CI_2 were evaluated in 2000/01, at three sites in the South of the State of Minas Gerais: in Lavras, Ijaci, and Lambari. It is worth mentioning that eight treatments were evaluated in the experiments conducted in Ijaci and Lambari, since hybrid C333 was not included. The experiments were arranged in a randomized block design with nine replications, with plots of two five meter rows. The traits plant height and prolificacy were evaluated, besides the hulled ear yield. In the beginning, individual variance analyses were carried out considering fixed mean and treatment effects. Subsequently, joint variance analyses of the sites were realized for all traits. Yield data were also corrected to the ideal stand and to 13% moisture (Vencovsky and Barriga 1992).

Heterosis, in relation to the mid parent (h) for hulled ear yield, was estimated by mean data, based on the following estimators:

$$h\left(F_{1(1)} \text{ x } F_{1(2)}\right) = (F_{1(1)} \text{ x } F_{1(2)}) - \left(\frac{F_{1(1)} + F_{1(2)}}{2}\right)$$

$$h(C0_1 \text{ x } C0_2) = (C0_1 \text{ x } C0_2) - \left(\frac{C0_1 + C0_2}{2}\right)$$

$$h(CI_1 \text{ x } CI_2) = (CI_1 \text{ x } CI_2) - \left(\frac{CI_1 + CI_2}{2}\right)$$

RESULTS AND DISCUSSION

A variance analysis summary of the experiment with interpopulational half-sib progenies of both populations is presented in Table 1. A similar experimental precision, assessed by the variation coefficient (VC%),was observed in both experiments: 24.92% and 22.18%, for populations 1 and 2, respectively. Consequently, the experimental precision was rated intermediate, as these estimates are close to others found in literature for maize trial (Scapim et al. 1995, Ribeiro 1998, Gonçalves et al. 1999). This precision allowed the identification of significant differences among progenies, suggesting, as expected, the existence of variability, which is confirmed by the frequency distributions presented in Figure 1. Mean progeny yield varied from 1.60 to 3.57 kg plot^{-1}, in other words, approximately 78.0% of population 1 mean, and from 1.50 to 3.49 kg plot^{-1} equivalent to 80.0% of population 2 mean.

The estimates of interpopulational genetic variance were similar to those reported by Raposo (2002) who evaluated another sample of the same size, made up by hybrid progenies

Table 1. Summary of variance analyses for hulled ears weight (kg plot^{-1}), originated from the progenies of interpopulational half-siblings stemming from populations 1 and 2; estimates of phenotypic variance ($\hat{\sigma}^2_F$), genetic variance ($\hat{\sigma}^2_G$), and heritability($\hat{h}^2_m$)

Sources	df	Mean Squares	
		Population 1	Population 2
Replication	1	0.919	4.005
Treatments	168	0.436**	0.435**
Error	168 (144)[a]	0.366	0.289
Lattice (%)		5.33	0
Mean		2.49	2.49
VC (%)		24.92	22.18
$\hat{\sigma}^2_F$ x 10^4		2180.00	2174.00
$\hat{\sigma}^2_G$ x 10^4		350.00	729.00
$\hat{h}^2_m$ (%)		16.05	33.53
LL (%)[b]		-14.91	9.05
UL (%)[c]		38.91	50.95

[a] In brackets, degrees of freedom of the trial in which population 1 was used as female; [b] lower and [c] upper limit of heritability.

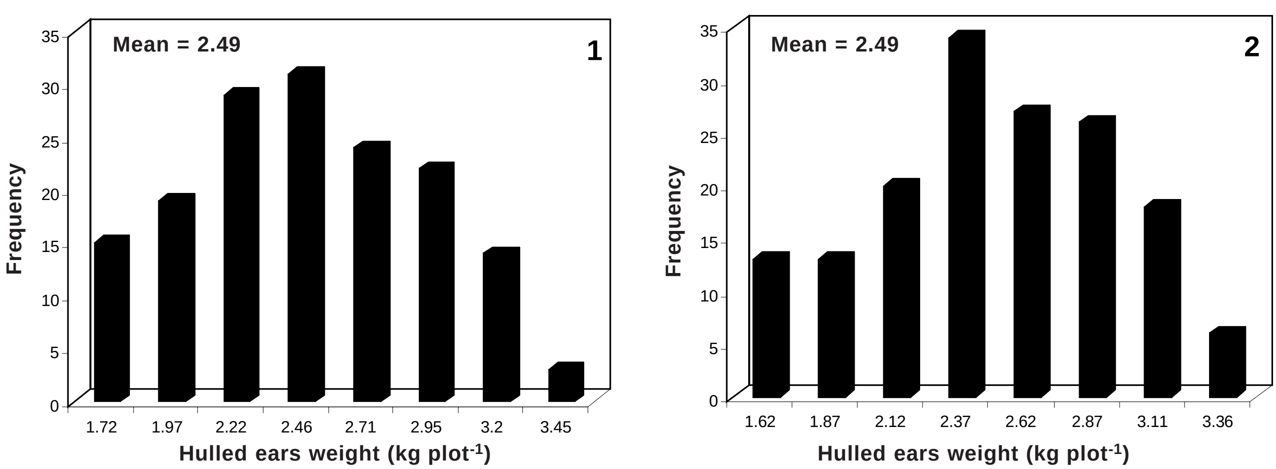

Figure 1. Frequency distribution for the hulled ears weight (kg plot^{-1}) in trials of interpopulational half-sib progenies of populations 1 and 2.

of these same populations. The h^2_m estimates are comparable to findings described in literature for interpopulational half-sib progenies (Lamkey and Hallauer 1987, Takeda 1997). Once more, populations derived from simple hybrids are confirmed as favorable for selection since they offer an elevated mean and sufficient genetic variability to acquire additional selection gain.

In a next step, the expected gain with selection was obtained for the interpopulational hybrid. Two procedures were used for this purpose: the selection differential (***ds***) and the intensity of standardized selection (***i***). The percentile estimates, obtained by these different proceedings, were alike, validating that the hulled ear productivity of the hybrid ancestors presented a good adjustment to normal distribution. In a comparison, the mean estimated gain of 16.3% in this situation and the one established by Raposo (2002) were equal. This expresses, once more, the potential these populations have for an RRS program (Table 2).

In order to assess the realized selection gain, as mentioned before, the three hybrid combinations were synthesized: the double hybrid derived from cross $F_{1(1)}$ x $F_{1(2)}$ of the interpopulational hybrid of cycle zero, $C0_1$ x $C0_2$, and the improved hybrid CI_1 x CI_2, generated by the intercrossing of the best progenies, identified in the previous stage. These hybrid combinations, together with their parents, were compared in trials carried out at three sites. A summary of variance analyses of the joint trials for the different traits is presented in Table 3. The remarkably low variation coefficients (VC%) showed the good experimental precision (Scapim et al. 1995, Palomino 1998, Gonçalves et al. 1999, Souza Sobrinho et al. 2002).

Test F pointed out significant differences between the treatments (P = 0.01) for all traits. However, no significant differences were detected for the source of sites x treatments interaction, indicating the random behavior of populations and their hybrids at the evaluated sites (Table 3). The established mean productivity of 9.4 t ha^{-1} can be considered high, varying from 7.6 t ha^{-1}, in population CI_1, to 11.2 t ha^{-1} in the interpopulational hybrid of the same cycle CI_1 x CI_2 (Table 4). We emphasize that the treatments with lowest productivity were, as expected in advance, the populations in balance which, theoretically, present a 50% reduction in heterosis compared to the respective hybrids in generation F_1. In a comparison of, for instance, the performance of commercial hybrids in generation F_1 and of the original cycle in generation S_0 in Lavras, the mean reduction was slightly above 20%, a similar value to the one obtained by Souza Sobrinho et al. (2001).

Important aspect of this study was an evaluation of changes in the performance of cycle zero hybrid compared to cycle one hybrid (CI), in other words, a comparison of CI_1 x CI_2, whose yield mean of the three sites was 5.7% above that obtained with hybrid $C0_1$ x $C0_2$. Considering only the result of Lavras, where the selection had been carried out, this increase was 4.4%, indicating that in spite of the expressive interaction progenies x sites in maize trial, the interaction, in this case, had a small effect on the result of selective progress (Arias 1995, Takeda 1997). Moreover, the fact that interaction of populations x sites was not significant in this study confirms this observation (Table 3).

Few reports in literature describe RRS programs which make use of populations derived from two hybrids, as in the case of our study. One of the only reports found was proposed by Coors (1999). This author states that five RRS cycles have already been completed at the University of Wisconsin for the improvement of two double hybrids W577 and W03545. The direct response to RRS with W577 was 6.2% per cycle and 4.5% with W03545, that is, a similar genetic gains to the one observed in the present study. Realized gain results in RRS programs with other population types are more frequent, mainly in the USA. An investigation carried out by Coors (1999) presented the mean gain of 14 RRS programs, with over four complete selection cycles, where the gain per cycle was 4.6%.

The response in heterosis to reciprocal recurrent selection is exhibited in Table 4. When the estimates of $h_{(C01 \times C02)}$ and $h_{(CI1 \times CI2)}$ were compared, the latter was 41.9% above the parent population means and superior to $h_{(C01 \times C02)}$ with 32.3%. It is adequate to emphasize that the greatest heterosis reported in these cases for generation F_1, is ascribed to the reference population. This can be explained by the fact that, in this last case, the parents are F_1 generations of the two simple hybrids, in contrast to observations in the other situation, where the

Table 2. Estimates of the expected gain (***Gs***) for the productivity in hulled ears of the interpopulational hybrid (kg $plot^{-1}$), obtained by the selection differential (***ds***) and also selection intensity 8.8% (***i*** = 1.811)

Progenies HS inter	Selection differential				Selection intensity		
	X_0[a]	X_s[b]	$\hat{h}^2_m$ (%)	Gs	$\hat{\sigma}^2_A$ * x 10^4	$\hat{\sigma}^2_F$ * x 10^4	Gs
AG9012	2.49	3.31	16.05	0.131	1400.0	2180.0	0.135
C333	2.49	3.29	33.53	0.268	2916.0	2174.0	0.283
				0.399 (16.0%)			0.418 (16.7%)

[a] Progenies mean in the original population; [b] Selected progenies mean; * Interpopulational additive and phenotypic variances in the reference population.

Table 3. Summary of the joint variance analyses for the weight of hulled ears (kg $plot^{-1}$); prolificacy and plant height (meters), in three sites

Sources	df	Weight of hulled ears		Prolificacy		Plant height	
		Mean Squares	Prob.	Mean Squares	Prob.	Mean Squares	Prob.
Sites (S)	1(2)[1]	55.737	0.000	0.432	0.000	0.486	0.000
Treatments (T)	7	51.786	0.000	0.027	0.002	0.315	0.000
S x T	14	0.180	0.995	0.009	0.352	0.009	0.630
Error	112 (168)	0.656		0.008		0.012	
Mean		8.46		1.10		2.43	
VC (%)		9.57		8.13		4.50	

[1] Values in brackets are degrees of freedom of the weight of hulled ears.

parents are an S_0 generation (C0), which present a mean reduction of 22.0%, owing to the inbreeding depression. Finally, we point out that the increase in heterosis of two populations by means of recurrent selection is in line with findings reported in literature (Coors 1999, Hallauer 1999).

It is important to mention what happened with the performance of the *per se* population in the RRS. Taking the mean of the three sites into consideration, in the case of the population originated by hybrid C333, productivity was practically equal among the original population C0 and after one improvement cycle CI. In the case of AG9012, however, although no significant difference was detected, a slight tendency of productivity reduction in the *per se* population was observed after the selection. According to Souza Júnior (1993), most RRS programs are in line with observations of improvement *per se* in one of the populations and yield reduction in the other.

The most interesting aspect of a program of this kind, that is, programs which involve populations originated from simple commercial hybrids, is to verify whether improved populations produce hybrids with a comparable performance to generation F_1 of the simple parent hybrids. In this specific case, it was observed that the interpopulational CI hybrid, in the mean of the three locations, surpassed the simple hybrid AG9012 significantly by approximately 7.2%. However, when the comparison was carried out in Lavras, where all treatments were evaluated, the superiority observed in relation to the simple hybrid C333 was 6.5%.

Finally, the alteration in ear productivity with RRS did not comprise an increase in plant height, which would be undesirable (Table 5). Significant differences were only found between the parent populations, while those derived from C333 were the highest, regardless of the selection cycle.

Table 4. Means of hulled ear yield (kg plot^{-1}) and the average midparent heterosis (h), obtained in an evaluation of maize hybrids at three sites

Treatments[1]	Hulled ears weight			
	Lavras	Ijaci	Lambari	Mean
$F_{1(1)}$	10.372 A[2]	8.833 B	9.147 A	9.451 B
$F_{1(2)}$	10.424 A	-	-	-
$F_{1(1)}$ x $F_{1(2)}$	10.842 A	8.875 B	9.617 A	9.778 B
$h_{(F_{1(1)} \times F_{1(2)})}$	0.44 (4.23%)	-	-	-
$C0_1$	8.018 B	6.219 D	6.945 B	7.061 D
$C0_2$	8.166 B	6.874 C	7.195 B	7.412 C
$C0_1$ x $C0_2$	10.632 A	8.591 B	9.521 A	9.581 B
$h_{(C0_1 \times C0_2)}$	2.54 (31.38%)	2.04 (31.16%)	2.45 (34.65%)	2.34 (32.33%)
CI_1	7.878 B	6.000 D	6.774 B	6.884 D
CI_2	8.288 B	6.607 C	7.312 B	7.402 C
CI_1 x CI_2	11.102 A	9.403 A	9.887 A	10.131 A
$h_{(CI_1 \times CI_2)}$	3.02 (37.36%)	3.10 (49.17%)	2.84 (40.32%)	2.99 (41.86%)

[1] F_1 - Single-cross hybrid; C0 = F_1 self-pollinated; CI – first improvement cycle; 1 (AG9012) and 2 (C333). [2] In the same column, means followed by the same letter did not differ at the Scott and Knott test (P ≤ 0.1).

Table 5. Prolificacy and mean plant height (m), obtained by the evaluation of maize hybrids at three sites

Treatments[1]	Prolificacy			Plant height		
	Lavras	Ijaci	Mean	Lavras	Ijaci	Mean
$F_{1(1)}$	1.06 B[2]	1.03 B	1.04 B	2.51 B	2.41 A	2.46 B
$F_{1(2)}$	1.28 A	-	-	2.65 A	-	-
$F_{1(1)}$ x $F_{1(2)}$	1.17 A	1.06 A	1.11 A	2.68 A	2.50 A	2.59 A
$C0_1$	1.18 A	1.03 B	1.10 A	2.30 C	2.27 B	2.28 D
$C0_2$	1.18 A	1.06 A	1.12 A	2.46 B	2.31 B	2.38 C
$C0_1$ x $C0_2$	1.16 A	1.07 A	1.11 A	2.62 A	2.48 A	2.55 A
CI_1	1.10 B	1.01 B	1.05 B	2.27 C	2.22 B	2.24 D
CI_2	1.25 A	1.05 A	1.15 A	2.46 B	2.30 B	2.38 C
CI_1 x CI_2	1.11 B	1.03 B	1.07 B	2.64 A	2.52 A	2.58 A

[1] F_1 - Single-cross hybrid; C0 = F_1 self-pollinated; CI - one improvement cycle; 1 (AG9012) and 2 (C333). [2] in the same column, means followed by same letters did not differ at the Scott and Knott test (P ≤ 0.1).

The highest yield population CI_1 x CI_2 was not the one with the greatest prolificacy, in contrast to some situations cited in literature, where the correlation between ear productivity and prolificacy is positive (Paterniani 1978).

CONCLUSIONS

For hulled ear production, the real gain of a single cycle of reciprocal recurrent selection was 5.7%. This selection gain can be ascribed in the first place to increased heterosis, since the performance of both populations *per se* was similar, when taking the C0 and CI populations into consideration. The improved hybrid performance outstripped generation F_1 of the simple hybrids AG9012 and C333, demonstrating the potential of the referred hybrid combination.

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Alterações na heterose após a seleção recorrente recíproca em populações derivadas de híbridos simples de milho

RESUMO - *Para verificar a eficiência da seleção recorrente recíproca (SRR) em populações originárias dos híbridos simples comerciais AG9012 (1) e C333 (2) foram obtidas, inicialmente, 169 progênies de meios-irmãos interpopulacionais. As 15 melhores progênies em produção de espigas despalhadas foram identificadas. Utilizando-se sementes* S_1 *remanescentes, semearam-se dois campos de recombinação, sendo simultaneamente obtidas as populações melhoradas* CI_1 *e* CI_2 *e a combinação híbrida entre elas. Os experimentos para avaliar a eficiência da SRR foram instalados em três locais. Foram comparados o* F_1 *dos híbridos simples AG9012 e C333, o híbrido duplo* $F_{1(1)}$ x $F_{1(2)}$ *entre eles, as populações* $C0_1$ *e* $C0_2$*, o híbrido interpopulacional (*$C0_1$ x $C0_2$*), as populações melhoradas* CI_1 *e* CI_2 *e a sua combinação híbrida (*CI_1 x CI_2*). O progresso com um ciclo de SRR foi de 5,7% para a produção de espigas e deveu-se, principalmente, ao incremento na heterose. O desempenho do híbrido melhorado superou a geração* F_1 *dos híbridos simples AG9012 e C333, evidenciando o potencial da referida combinação híbrida.*

Palavras-chave: genética quantitativa, milho, seleção recorrente recíproca, heterose.

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