

COMBINING ABILITY ASSOCIATED WITH S_1 RECURRENT SELECTION IN TWO MAIZE SYNTHETICS¹

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ABSTRACT - S_1 -progeny recurrent selection has proved effective improving the performance *per se* and the general combining ability (GCA) of maize (*Zea mays* L.) synthetic populations. Two maize synthetics, EZS1, a flint-type of Spanish origin, and EZS2, a dent population of North American origin, were produced at Zaragoza, Spain, and subjected to two cycles of S_1 recurrent selection for increased grain yield and reduced lodging and grain moisture. Our objectives were i) to assess the effect of S_1 recurrent selection on the heterotic behaviour of these synthetics, and ii) to evaluate the changes in combining ability after selection using as testers the populations themselves and three diverse inbred lines. The entries from a diallel mating design of the three cycles (0, 1, and 2) of the two populations were tested in five environments. Testcrosses involving the three selection cycles of both synthetics and three diverse inbred testers were evaluated in three environments. Selection in both synthetics resulted in more productive populations, with less lodging, and no important negative responses in other agronomic traits. Improvements were less evident in the crosses of the populations, with significant GCA change only in EZS2 for lodging. Gains due to selection for grain yield in both synthetics and for lodging in EZS2 were significant, but the gains were not consistent across testers. Selection was effective in improving the populations *per se*, and the best testcrosses were not significantly different from the hybrid checks used for comparison.

KEY WORDS: Maize; S_1 Recurrent Selection; Combining Ability; Heterotic Pattern.

INTRODUCTION

Recurrent selection based on S_1 -progenies has been proposed to improve the performance *per se*

and the general combining ability (GCA) of maize (*Zea mays* L.) synthetic populations (GENTER, 1973; GENTER and EBERHART, 1974). MORENO-GONZALEZ and CUBERO (1993) summarized the results of 19 selection experiments based on the evaluation of selfed families (S_1 or S_2). The average grain yield gains per cycle of selection were 3.56% for the populations *per se*, and 1.80% for the populations testcrosses.

The purpose of the maize project at the Aula Dei Experimental Station, Zaragoza (Spain) is to develop synthetic populations based on previous knowledge of the heterotic behaviour of their components. Production of synthetics EZS1 (made by intercrossing of traditional Spanish populations) and EZS2 (comprised of a mixture of North American populations), was initiated in 1982. Preliminary results showed that the cross of EZS1 and EZS2 was promising, and might lead to the development of superior hybrids (ALVAREZ *et al.*, 1993). As the initial productivity levels of both synthetics were low, they were improved separately with two cycles of a S_1 -progeny recurrent selection scheme to increase their potential to derive good inbred lines with superior combining ability.

Cycles 0, 1, and 2 of EZS1 and EZS2 were later evaluated in a series of trials to assess the responses to selection of several agronomic traits in the populations *per se* (GARAY *et al.*, 1996). Least square regression analysis techniques (SMITH, 1983), and diversity analysis (MOLL and HANSON, 1984) confirmed that both populations showed increased grain yield, mostly associated with additive genetic effects. But the success of a recurrent selection program in maize should be assessed not only in the populations *per se*, but also in the populations' crosses with materials which eventually will become, or will generate, complementary parents of future hybrids. Thus, EZS1 and EZS2 were re-evaluated to confirm their potential as a good heterotic pattern, and to determine the impact of selection on their combining ability. Therefore, the objectives of this

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study were i) to assess the effect of S_1 recurrent selection on the heterotic behaviour of two maize synthetics, and ii) to evaluate the changes in combining ability that occurred after selection with the populations themselves and three diverse inbred lines as testers.

MATERIALS AND METHODS

Development of synthetic populations

The synthetic populations were created at the Aula Dei Experimental Station, Zaragoza, Spain. Synthetic EZS1 was formed in the Aula Dei Experimental Station, by intercrossing four old Spanish open-pollinated cultivars of diverse geographic origins and agronomic characteristics: 'Amarillo de Utrera', 'Hembrilla', both described by SÁNCHEZ-MONGE (1962), 'Fino', and 'Hembrilla/Queixaler'. EZS2 was derived from crosses between the populations AS-3(HT)C3 (PETERSON *et al.*, 1976), BS3 (HALLAUER *et al.*, 1974), BS17, and BS1(HS)C1 (RUSSELL, 1979). EZS2 includes a wide diversity of North American germplasm improved for grain yield, combining ability, and resistance to European Corn Borer (*Ostrinia nubilalis* Hübner). Crosses to form the synthetics were made in 1982 and 1983. The synthetics were later intermated twice, and labeled as cycle 0, or original, populations.

Selection procedures

The C0 populations were subjected to two cycles of intrapopulation S_1 recurrent selection between 1986 and 1991. In each cycle, a rank summation index for each progeny was calculated as the sum of the ranks for grain yield (adjusted to 140 g kg⁻¹ moisture) and lodging percentage. The 10 progenies with lowest index values, and grain moisture below the median, were selected. The original 100 progenies were pre-selected from about 750 selfed plants per population for plant health, ear size and shape, and seed weight. Remnant S_1 seed of the 10 selected families was used for recombination.

Genetic Materials Evaluated

Progress obtained following selection was evaluated in two sets of trials. One trial included the entries from a diallel mating design among the six populations, and the other included testcrosses of the populations to three inbred testers.

The six populations (cycles 0, 1, and 2 of EZS1 and EZS2, respectively) were selfed, and intercrossed in a greenhouse in 1991 and 1992, following a diallel mating design (without reciprocals). The following 27 entries were evaluated: six populations *per se*, six populations selfed (populations coming from one generation of selfing in a population *per se*), and 15 crosses among the six populations *per se*. Each cross and selfing was based on 50 ears.

Testcrosses of the six populations to three inbred lines (B73, Mo17, and EZ8) were made in 1992. B73 and Mo17 are widely used testers, representative of two distinct North American heterotic groups (Reid Yellow Dent, and Lancaster Sure Crop). EZ8 is an advanced flint-type local breeding line, whose origins can be traced back to Argentina. For each testcross, 40 plants per population were sampled and utilized as females. The 40 ears were bulked, taking equal amounts of seed from each ear.

Evaluation trials. Population diallel

The 27 entries of the population diallel were tested for two years (1992 and 1993) at Montañana and Peñaflores and at Villamayor

or in 1993, all in the province of Zaragoza. The trials were flood irrigated throughout the growing seasons. The 1992 trials received 7 irrigations (about 80 mm each), and the 1993 trials received 10 irrigations at Peñaflores and Montañana, and 11 at Villamayor, to supplement the low natural rainfall (230 mm and 190 mm during the growing seasons in 1992 and 1993, respectively). Cultural operations, fertilization, and pest and weed control, followed local practice. All trials were machine-planted, in mid-June (1992) and mid-May (1993), with a stand density of 66 000 plants ha⁻¹. Each plot included two 5-m rows spaced 0.75 m apart. The plots were harvested manually in mid-November in both years.

Data were recorded for plant height, measured as the distance from the ground to insertion of flag leaf; ear leaf area, measured for 10 competitive plants per plot; days to anthesis; grain yield, adjusted to 140 g kg⁻¹ grain moisture; grain moisture at harvest; and lodging, estimated as the percentage of plants showing either root or stalk lodging.

Experimental design was a 6x6 triple lattice. Nine additional entries were included to complete the lattice. Because the combining ability analyses considered only the six populations *per se* and the 15 crosses among them (a total of 21 entries), the analyses of variance were done assuming a randomized complete block design, which is consistent with the lattice layout. Environments were considered random effects, and entries were considered fixed effects. Replication within environments mean squares were used as denominators in tests of significance for environments. The appropriate entry-by-environment mean squares were used in tests of significance for differences among entries (i.e., testcrosses-by-environment for testcrosses; checks-by-environments for checks, and so on). Entry-by-environment mean squares were tested against the appropriate residual effects.

General (GCA), and specific (SCA) combining abilities were estimated using the linear model for Analysis III of GARDNER and EBERHART (1966), for the 15 crosses of the population diallel. This model is:

$$Y_{ij} = \mu_c + g_i + g_j + s_{ij}$$

where the mean of each cross (Y_{ij}) is decomposed into the mean of all crosses (μ_c), the GCA effects of the parents (g_i and g_j), and the SCA of the specific cross (s_{ij}). Because the parents also were included in the trial, the 'variety effects' (μ_i) were calculated, as in GARDNER and EBERHART (1966). This effect is written as:

$$Y_i = \mu_v + v_i$$

where μ_v is the mean of all parental populations, and v_i represent the deviations of each population from the overall mean, μ_v .

Least significant differences (LSD) for g_i effects were calculated as:

$$LSD_{g_i} = t_{0.05, n} \sqrt{(2 \cdot EMS / rek)^{1/2}}$$

where EMS was the GCA-by-environment mean squares, r was the number of replications, e was the number of environments, k was the number of crosses involved in the calculation of GCA for each population-cycle combination, and $t_{0.05, 20}$ was the tabulated t value for $P=0.05$ and $n=(p-1)(e-1)$ degrees of freedom, where p was the number of population-cycle combinations. Least significant differences for v_i effects were calculated as

$$LSD_{v_i} = t_{0.05, 20} \sqrt{(2 \cdot EMS / 1p)^{1/2}}$$

where EMS was the population-by-environment mean squares, r was the number of replications, p was the number of population-cycle combinations (6), and $t_{0.05, 20}$ was the tabulated t value for $P=0.05$ and $(p-1)(e-1)$ degrees of freedom.

TABLE 1 - Estimates of variety effects (v_i) and general combining ability effects (g_i) for six traits in six maize populations (cycles of selection 0, 1, and 2 of synthetics EZS1 and EZS2), evaluated in five environments.

Trait	Effect	EZS1			EZS2			LSD*
		C0	C1	C2	C0	C1	C2	
Grain yield, kg ha ⁻¹	g_i	-36.3	-56.0	121.7	-44.6	-141.0	156.3	384.2
	v_i	-424.3	-151.4	139.5	-669.1	129.6	975.6	783.2
Lodging, %	g_i	4.6	2.2	2.8	-2.0	-1.1	-6.5	4.6
	v_i	4.8	6.9	7.8	1.2	-7.2	-13.4	6.9
Grain moisture, %	g_i	-1.0	-0.2	-0.2	0.0	0.3	1.1	1.6
	v_i	-0.9	-0.9	0.2	-1.5	2.1	1.0	2.8
Plant height, cm	g_i	-4.3	-3.5	-2.0	0.4	3.8	5.5	5.0
	v_i	-6.3	-13.8	-8.9	2.9	14.2	11.9	17.7
Ear leaf area, cm ²	g_i	-6.1	-17.9	-10.9	8.1	11.5	15.3	12.8
	v_i	-0.8	-42.0	-44.2	14.7	34.5	37.8	35.9
Days to anthesis, days	g_i	-1.7	-1.3	-0.9	1.0	1.6	1.3	0.7
	v_i	-2.6	-3.2	-1.7	2.3	2.5	2.7	1.3

* Least significant difference between cycles of selection (between and within populations) at the 0.05 probability level.

Realized responses to selection were compared with the expected responses to selection calculated as

$$\Delta G = b^2 * D$$

where ΔG is the expected response to selection, b^2 is the heritability, and D is the selection differential (i.e., the difference between the selected progenies and the population mean) for a particular trait, calculated from the selection trials carried out in 1987 and 1990.

Evaluation trials. Testcrosses

The testcrosses of the six populations to B73, Mo17, and EZ8 (18 testcrosses) were evaluated only in 1993, in the same three environments as the population diallel, following a randomized complete block design with three replications. Two F₁ hybrid checks were included: B73 x Mo17, a well-known American dent cross, and EZ18 x EZ8, a productive Spanish flint experimental hybrid. Cultural operations, irrigation schedule, plot size, characters measured, and analyses of variance were the same as for the population diallel trials.

The analysis of variance for grain yield (averaged across three environments) was extended according to the additive-main and multiplicative-interaction analysis (AMMI), as in Zobel *et al.* (1988). The table of residuals after accounting for 'Population' and 'Tester' main effects, i.e., the 'Tester by Population', or SCA, effects, was analyzed by principal components. All calculations were done with SAS (1989) statistical package.

RESULTS AND DISCUSSION

Population Diallel Evaluation

The combined analyses of variance (not shown) across five environments for the population diallel evaluation (populations selfed omitted from this analyses) showed that the mean squares for entries were significant ($P \leq 0.05$) for all traits except for grain moisture, and that genotype-by-environment interac-

tion was highly significant ($P \leq 0.01$), except for lodging. The mean squares due to populations vs. crosses, which is a measure of average heterosis in our experiment, was significant only for lodging, suggesting the presence of nonadditive genetic effects for lodging. The lack of significance of SCA, however, did not support this conclusion. The partition of the sums of squares among crosses between GCA and SCA for lodging showed that 85% of the sums of squares could be attributed to GCA, indicating the greater importance of additive effects in the control of the expression of lodging in these synthetics.

The analysis for grain yield revealed highly significant variation among populations *per se*, but the differences among crosses, GCA, and SCA were not significant. The lack of nonadditive effects affecting this trait was also suggested by the nonsignificant difference between populations *per se* and crosses.

Both GCA and SCA effects were significant for plant height, ear leaf area, and days to anthesis, suggesting that the variation among crosses was due to both additive and dominant gene effects. This finding agrees with a previous study (GARAY *et al.*, 1996) who found additive and dominant gene effects in the control of these three traits in the original populations.

Both EZS1 and EZS2 showed favorable trends of g_i change with cycles of selection for grain yield and lodging (Table 1). These trends, however, were not significant except for a significant change in lodging g_i from cycle 0 to cycle 2, in EZS2. EZS2 also showed an undesirable shift in g_i for plant height. EZS1 showed a significant change in g_i only for days to an-

TABLE 2 - Specific combining abilities (SCA) for grain yield (- above diagonal) and lodging (below diagonal), for a diallel of six maize populations (cycles of selection 0, 1, and 2 of synthetics EZS1 and EZS2).

Population	EZS1C0	EZS1C1	EZS1C2	EZS2C0	EZS2C1	EZS2C2
EZS1C0	-	-332	-344	-151	569*	259
EZS1C1	-1.7	-	-238	237	147	186
EZS1C2	-1.0	0.0	-	444*	5	143
EZS2C0	2.1	-1.8	0.1	-	-327	-204
EZS2C1	-0.1	4.8**	2.1	-0.3	-	-384
EZS2C2	0.7	-1.2	3.1	-0.1	-2.3	-

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

thesis. Most differences among g_i effects were in the comparison of EZS1 vs. EZS2 populations, which in many cases showed opposite g_i signs. This was a consequence of the large differences among synthetics for these traits, and of the method of calculation of g_i effects, as $\sum g_i$ must be equal to 0. All comparisons between both synthetics were significant for ear leaf area and days to anthesis GCA, and most for lodging and plant height GCA. EZS2 contributed to the better lodging and larger leaf area to the crosses, whereas EZS1 was a source of earliness and reduced plant height. Thus, EZS1 and EZS2 were generally complementary for these traits.

Individual estimates of GCA (g_i) and variety effects (v_i) for all traits mostly followed similar trends between populations, and within populations across cycles of selection (Table 2). The two exceptions were lodging and plant height in EZS1, but the changes were not significant. For most traits, especially grain yield, the changes in g_i were small compared with those in v_i .

The differences between cycles of selection for v_i and g_i are realised responses to selection for the populations *per se*. These values, however, are not comparable with the expected responses to selection that might be calculated for the selection trials, as these were done on selfed (S_1) families. The appropriate comparison must involve the sets of S_1 progenies tested in the selection trials and the selfed populations included in the population diallel trials. As the productivity levels varied among years, the comparison was made on a percentage basis. The realised responses to selection for grain yield were 30 and 32% of the expected values for EZS1 and EZS2, respectively (average of the two cycles). The realised responses to selection for lodging were 0 and 21% of the expected values for EZS1 and EZS2. These low values might be caused

partly because the expected responses to selection were calculated with heritabilities derived from single environment trials. Thus, genotype-by-environment (GxE) variances could not be calculated. If GxE variances were large in our conditions, heritabilities could be overestimated. This explanation is supported by the fact that GxE variance for grain yield in the population diallel evaluation trials was 44% larger than the genotypic variance. For lodging, however, GxE variance in the same set of trials was almost negligible compared with genotypic variance (not shown).

Significant changes in SCA were not expected because selection for the two populations was conducted independently, as in STANGLAND *et al.* (1983). The SCA effects were not significant for grain yield and lodging (Table 2), but three individual SCA estimates were significantly different from 0 (Table 2). For grain yield, two significant SCA estimates included EZS1C0 x EZS2C1 and EZS2C0 x EZS2C2. This might be interpreted as selection imposing divergence in each synthetic from the original populations of the other synthetic. But selection must have acted on the same favourable dominant genes in both synthetics, because the SCAs in crosses of populations in the same cycle of selection were not significantly different from 0. Convergence may have occurred in these synthetics after selection GARAY *et al.* (1996).

Testcrosses Evaluation

Testcrosses were evaluated to define the heterotic response of the synthetics, and to determine any possible shifts in heterotic behavior due to the selection process. The differences among testcrosses were significant for all six traits as determined by the analyses of variance (not shown). There were significant differences in both testers and populations, and a significant interaction between testers and populations for all traits but lodging. Lodging presented the most consistent response across testers, because there were no significant differences for testers or for testers by populations. For lodging, the significance of the populations effect was due only to differences among synthetics (EZS1 and EZS2), and not due to differences between cycles of selection.

The means for the most relevant testcrosses and checks are presented in Table 3. Overall, the crosses to B73 had the fewest days to anthesis and the lower grain moisture; the crosses to Mo17 had the largest leaf area and were more productive than the other testcrosses (significantly so when compared to EZ8); the crosses to EZ8 were the shortest, less productive, and had greatest grain moisture. The averages of testcross-

TABLE 3 - Average performance of six traits for the testcrosses of six maize populations (cycles of selection 0, 1, and 2 of maize synthetics EZS1 and EZS2) and three inbred testers, and two hybrid checks, evaluated in three environments.

Population	Grain yield	Lodging	Grain moisture	Plant height	Ear leaf area	Days to anthesis
	kg ha ⁻¹	%	%	cm	cm ²	days
	Tester B73					
EZS1C0	4241	22	31	166	478	72
EZS1C1	7181	36	33	187	495	74
EZS1C2	7166	25	33	186	507	75
EZS2C0	5178	28	31	180	488	77
EZS2C1	6084	22	32	186	525	78
EZS2C2	5653	17	31	191	525	79
Tester average	5917	25	32	183	503	76
	Tester EZ8					
EZS1C0	4727	29	33	170	479	74
EZS1C1	4915	35	32	172	509	75
EZS1C2	4248	34	35	175	493	75
EZS2C0	5761	20	35	191	580	77
EZS2C1	6174	21	36	186	560	78
EZS2C2	6268	27	36	192	574	79
Tester average	5349	28	34	181	533	77
	Tester Mo17					
EZS1C0	6073	32	33	182	572	75
EZS1C1	5495	26	34	176	513	74
EZS1C2	7188	30	35	185	565	76
EZS2C0	5601	25	34	182	537	78
EZS2C1	6455	29	34	190	539	78
EZS2C2	6648	25	33	187	564	79
Tester average	6244	28	34	184	548	77
	Checks					
B73 x Mo17	6981	22	30	188	549	77
EZ18 x EZ8	7142	30	39	197	622	81
LSD* (0.05)	883	9	2	7	37	1

* LSD among individual testcrosses and checks.

es with both synthetics were not significantly different for grain yield (5682 kg ha⁻¹ for EZS1, and 5936 kg ha⁻¹ for EZS2); this difference was largely due to the low yield of the testcrosses between EZS1 and EZ8. This difference was expected because EZS1 and EZ8 might be genetically more similar than the other materials studied. The best testcrosses for grain yield always included an improved version of either EZS1 or EZS2. For EZS2, the grain yields of cycle 0 testcrosses were always lower than at least one of the improved cycles. This improvement matched the gain of the population *per se*. For EZS1, however, the response to selection varied between testers (Tables 1 and 3). Response to selection was larger than the gain in the population *per se* for the crosses with B73, similar to it for Mo17 crosses, and negligible for EZ8 crosses.

The tester that discriminated best among synthetics

for grain yield was EZ8. EZ8 also gave the lowest yields, which agrees with the view of RAWLINGS and THOMPSON (1962) that the best tester would have the lowest frequency of favorable alleles. Within cycles of selection in each synthetic, however, EZ8 testcrosses had the less variation, compared with B73 or Mo17. Thus, EZ8 was able to discriminate consistently among synthetics, but selection had a weak impact on the genes involved in combining ability with EZ8.

EZS2 testcrosses were significantly better than those of EZS1 for lodging (23.9% and 29.4%, respectively), in agreement with the behaviour of the populations *per se* (v_i in Table 2). The improvement produced by selection in EZS2 *per se* (Table 2), however, was only evident in the testcrosses to B73, and not with the other two testers.

Nearly all trends in the testcrosses means for the

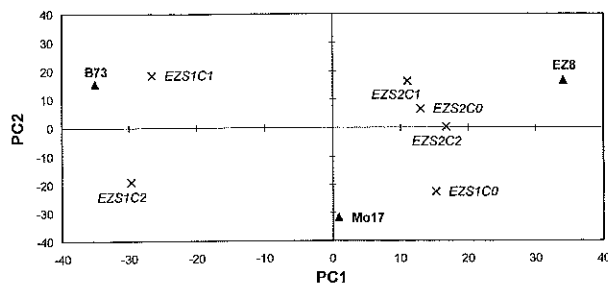


FIGURE 1 - Principal components biplot of the SCAs from the testcross trials of six maize populations (cycles of selection 0, 1, and 2 of maize synthetics EZS1 and EZS2) and three inbred testers (details in the text).

other traits followed the same trend observed in the populations *per se* (in the diallel trials, Table 1). For plant height, EZS2 testcrosses were significantly taller than EZS1 crosses, but the differences between the synthetics were smaller than among the populations *per se*, except in EZ8 testcrosses. The unexpected selection-induced reduction in ear leaf area observed in EZS1 (Table 2) was not evident either in their testcrosses (Table 3) or in the population diallel. Therefore, this reduction must have been caused by non-additive gene effects, which were not evident in the crosses to materials other than EZS1.

The best testcrosses involved advanced cycles of selection of the two synthetics, and had grain yields and lodging percentages which did not differ significantly from the hybrid checks (Table 3). B73 x Mo17 and EZ18 x EZ8 are representative of the production potential in the area. We conclude that the two synthetics have an acceptable agronomic performance, and can be the source of productive new lines, which was the objective when selection was initiated.

We used an AMMI analysis to describe the relationships among testers and populations based on grain yield. This analysis has generally been used to reveal trends in genotype-by-environment interaction. In this case we considered the testers as 'genetic environments' for our synthetics. We did the analysis on mean grain yields for the 18 testcrosses. In a first step, main effects ('tester' and 'population', i.e., GCAs) were calculated and removed. In a second step, we ran a principal component (PC) analysis on the residuals after removing the main effects (i.e., SCAs). The PC scores for all entries were scaled to allow direct calculation of SCAs through a linear function of the products of the population PC scores by the testers PC scores (Fig. 1). The lengths of the plot axes are proportional to the percentage of variation explained by the respec-

tive principal component. Two PCs explained all the variance in the table of residuals, or SCAs. The three testers were placed at distant ends of the plot, as could be expected from previous knowledge of their heterotic responses. The first component explained 71% of the SCA variance, and resulted from the contrast of the testcrosses to B73 and EZ8. The second PC was a contrast between the testcrosses to Mo17 and the other two testers, and explained the remaining 29% of SCA variance. The populations appeared scattered between the testers, closer to the testers with which they had larger positive SCA effect, and further from those with which they had larger negative SCA effect.

EZS2 populations and the tester EZ8 had similar sign loads on the first PC, as might be expected from the crossing of improved flint and dent germplasms. EZS1 populations, however, were always further from EZ8, which may also be expected, both being flint materials. The large distance from B73 to the EZS2 populations might be explained because some of the populations originally crossed to form EZS2 belong to the Reid Yellow Dent heterotic group, as did B73. The heterotic behavior of EZS1 was affected by the selection process. Selection in EZS1 had no impact on the performance of the testcrosses to EZ8, suggesting that the alleles responsible for the improvement in EZS1 were masked by the alleles of the tester.

This plot, shown in Fig. 1, does not include information on crosses between EZS1 and EZS2. Thus, the potential SCA between these populations can only be estimated indirectly through the behavior of their testcrosses to the inbred testers. The three EZS2 populations were clustered very close to each other, meaning that the selection process caused no appreciable shift in their heterotic response to the testers used. EZS1 populations appeared more dispersed; EZS1C0 was differentiated from EZS2 populations only by a sizable negative load in the second principal component. But the two improved cycles of EZS1 were located opposite to EZS2 populations. The farther apart the populations appear in the plot, the more distinct their heterotic behavior.

The results of the testcrosses, however, did not agree completely with the population diallel trials. The crossing of populations distant in Fig. 1, such as EZS1 cycles 1 and 2 to any EZS2 version, would likely produce large and positive SCA effects. Nevertheless, this was not observed in the diallel evaluation (Table 1), except for EZS1C2 x EZS2C0. The crosses among EZS2 populations showed negative, though nonsignificant SCAs in the diallel evaluation (Table 2), which agrees with their close clustering in Fig. 1. For EZS1, the SCAs

for the crosses within this synthetic were also small. So far, these results agreed with the expectation of genetic closeness among populations belonging to the same synthetic. However, EZS1 populations were separated in Fig. 1, indicating distinct heterotic behavior. Regarding the crosses between EZS1 and EZS2, the loss of heterosis which occurred as selection advanced (GARAY *et al.*, 1996) was not evident from Fig. 1, as the two improved cycles of EZS1 were separated from EZS2 populations. The explanation for this mismatch might be that the set of genes determining the behaviour of the populations in the testcrosses, and thus their distribution on the PC plot, and the set of genes affected by selection do not overlap completely.

SUMMARY

Two cycles of S_1 -progeny recurrent selection in the synthetics EZS1 and EZS2 resulted in more productive populations, with less lodging in EZS2, and no important negative responses in other agronomic traits. These improvements caused positive changes in the GCA of EZS2 for lodging, but not for grain yield. Cycle 0 of both synthetics had significantly lower grain yield in the testcrosses, as well as the lowest v_i and g_i effects in the population diallel trials, compared with cycles 1 and 2. Lodging improvement realized in EZS2 was partially transmitted to the crosses. The best testcrosses of advanced cycles of selection were not significantly different from the hybrid checks used for comparison. SCA between EZS1 and EZS2, however, was low and not affected by selection.

Future work with EZS1 and EZS2 could be formulated along the following lines. One would be to start a testcross-selection scheme based on the best combinations of testers and populations arising from the testcross trials, following an approach similar to those suggested by HORNER *et al.* (1973) and WALEJKO and RUSSELL (1977). The more promising pairs found were EZS1C2 with either B73 or Mo17, and EZS2C2 with EZ8. Alternatively, other more modern testers belonging to the same heterotic groups might be used. Another approach would be to start reciprocal recurrent selection (COMSTOCK *et al.*, 1949) with the latest cycles of EZS1 and EZS2. Though the selection has likely produced a convergence phenomenon, which was evident in the population diallel trials, the testcrosses evaluation revealed different heterotic behavior for both synthetics in our conditions. It seems possible to capitalize on these remaining differences using a reciprocal recurrent selection scheme, to recover the heterotic pattern initially present between EZS1 and EZS2.

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